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ARTICLE



Effects of microclimate on bolete species richness and biomass in a Northern Benin woodland

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Abstract

Studies examining the role of abiotic variables on fructification sequences of ectomycorrhizal symbionts (boletes), the extent and direction of these effects are quite rare in Africa. In the current study, we assessed the effects of microclimate on the distribution and productivity of boletes in Benin. Nine permanent plots of 2500 m² each split into 25 subplots of 100 m² were installed in three different vegetation types. The first vegetation type is dominated by *Isoberlinia doka*, the second by *Isoberlinia tomentosa* and the third by *Uapaca togoensis*. Abiotic variables, including soil temperature, air temperature, air relative humidity and soil moisture, were recorded every 30 min from June to October. Each plot was surveyed twice a week during the mushroom season over 3 years (2015, 2016 and 2017) to record the abundance and the fresh biomass. The effects of microclimate on boletes productivity were evaluated using generalised linear mixed models in R. Boletes give the largest natural production in July and the lowest in October. Only soil moisture has a significant negative influence on the abundance (p > 0.05). The fruiting periods of boletes are known according to the variability of the microclimatic parameters and the vegetation.

KEYWORDS

Benin, Boletes, fresh biomass, microclimate, vegetation

Résumé

Les études examinant le rôle des variables abiotiques sur les séquences de fructification des symbiotes ectomycorhiziens (bolets), l'étendue et la direction de ces effets sont assez rares en Afrique. Dans la présente étude, nous avons évalué les effets du microclimat sur la distribution et la productivité des bolets au Bénin. Neuf placeaux permanents de 2 500 m² chacune divisées en 25 placettes de 100 m² ont été installées dans trois types de groupéments végétaux différents. Le premier type de végétation était dominer par *Isoberlinia doka*, le second par *Isoberlinia tomentosa* et le troisième par *Uapaca togoensis*. Les variables abiotiques, notamment la température du sol et la température de l'air, l'humidité relative de l'air et la teneur en eau du sol, ont été enregistrées toutes les 30 minutes de Juin à Octobre. Chaque placeau a été prospecté deux fois par semaine pendant la saison des champignons sur trois ans (2015, 2016 et 2017) pour enregistrer la présence/absence et la biomasse fraîche des

bolets. Les effets du microclimat sur la productivité des bolets ont été évalués à l'aide des modèles mixtes linéaires généralisés dans R. Les bolets donnent la plus grande production naturelle en juillet et la plus faible en octobre. Seule l'humidité du sol a une influence négative significative sur l'abondance des bolets (p > 0,05). Les périodes de fructification des bolets sont connues en fonction de la variabilité des paramètres microclimatiques et de la végétation.

1 | INTRODUCTION

Fungi play an important role in the regeneration of natural forest ecosystems in tropical Africa (Diédhiou et al., 2005). In addition, they promote the survival of seedlings in many forest ecosystems (Diédhiou et al., 2004; McGuire, 2007; Nara, 2006; Onguene & Kuyper, 2002). In West Africa, ectomycorrhizal (EcM) fungi are found in the Guineo-Sudanian to Sudanian forests (White, 1983) dominated by Fabaceae, Phyllanthaceae and Dipterocarpaceae (Bâ et al., 2012). Among EcM fungi, boletes are widespread and play an important role in the ecosystems of African tropical forests. Beyond their ecological importance, local communities depend on certain boletes species for food (Guissou et al., 2005). This dependency is perceptible through the common use of some boletes such as Phlebopus sudanicus (Har. & Pat.) Heinem. was source of proteins (Guissou et al., 2005, 2008), substituting animal proteins in a context where bush meat is scarce and expensive (De Kesel et al., 2002; Guissou et al., 2005).

In natural habitats, like other fungi, bolete communities are influenced by microclimatic parameters such as precipitation, temperature and moisture (Gévry, 2010), which directly affects their production, species richness and spatial distribution. The microclimate plays a key role in ecological processes which in turn lead to perceptible changes (Andrew et al., 2016). Karavani et al. (2018) demonstrated that higher temperatures decrease the yield of EcM fungi, at the start of the fruiting season, but also tend to increase towards the end. Interestingly, in most cases, maximum and minimum temperatures affect yield more than average temperatures (Hernández-Rodríguez et al., 2015). Likewise, soil moisture, an indirect consequence of the intensity of precipitation, is a significant predictor of fructification of fungi (Karavani et al., 2018; Ogaya & Peñuelas, 2005). Soil temperature, air temperature and precipitation are among the main microclimatic variables that govern the largescale distribution and variation of the species richness of boletes (Pinna et al., 2010; Yang et al., 2012). However, it has been shown that even at the micro-habitat level, an influence of microclimatic variables on ecological processes is perceptible (Boddy et al., 2014; Stefansson et al., 2013).

To date, most studies on mushroom productivity of EcM fungi have focussed on the whole EcM community and not at the group or species level (Houdanon et al., 2020; Matsuoka et al., 2016; Milenge Kamalebo et al., 2019; Vogt et al., 1981; Wästerlund & Ingelög, 1980). Although the importance of using molecular approaches for studying the global diversity of EcM fungi is getting more attention now (Lindahl et al., 2013), the studies based on fungi fruiting bodies, including boletes, remain a useful way for studying their spatio-temporal variation, both on a large and fine scale (Büntgen et al., 2012, 2013, 2015; Samson & Fortin, 1986; Wollan et al., 2008).

Studying the influence of microclimate parameters on bolete communities provides a better understanding of the factors governing their fructification. The harvest period (the number of months, the year of harvest etc.) could be thereby assessed (Pilz & Molina, 2002; Selosse et al., 2001). This understanding would be helpful in proposing straightforward steps towards sustainable management of wild edible mushrooms (Kauserud et al., 2008, 2010, 2012).

In the present study, we used a cumulative data set of 3 years (2015, 2016 and 2017) to appreciate the effect of microclimate variables on the spatial distribution and the natural production (species richness and fresh biomass) of boletes.

2 | MATERIALS AND METHODS

2.1 | Study area

The study was carried out in the Ouémé Supérieur forest reserve, located in northern Benin (Figure 1). It is located between latitudes 9°11' and 9°47'N and longitudes 1°58' and 2°28'E and covers an area of 177,406 ha (Figure 1). The climate is a dry tropical one (Peel et al., 2007) characterised by a long rainy season (from April to October) and a long dry season (from November to mid-April) (Gnanglè et al., 2011). The dry season is defined as the period when the rainfall is less than half of the Potential Evapotranspiration (ETP) (Milly & Dunne, 2016). The rainy season or active period of vegetation is the period when the rainfall is greater than half of the ETP. Also, the optimal period of vegetation, that is the period when the rainfall is greater than the ETP (Milly & Dunne, 2016), goes from mid-May to mid-October. In addition, the hottest time of the year (38°C) is between March and April while the coldest period is between June and August with a mean temperature of 27°C. The mean monthly relative humidity is 62% (Gnanglè et al., 2011). The forest is dominated by species such as Isoberlinia doka Craib & Stapf.,

FIGURE 1 Vegetation map of the Ouémé Supérieur Forest Reserve



1	2	3	4	5
10	9	8	7	6
11	12	13	14	15
20	19	18	17	16
21	22	23	24	25

FIGURE 2 Device for collecting boletes in the field (50 m \times 50 m plot subdivided into 25 10 m \times 10 m subplots)

Isoberlinia tomentosa (Harms) Craib & Stapf. and Uapaca togoensis Pax. (Adomou et al., 2011; Houdanon et al., 2019).

2.2 | Study design

2.2.1 | Plots establishment

Nine permanent plots of 50 m \times 50 m (2500 m²) (Figure 2) were established to monitor EcM fungi communities in three different woodland types, with three plots per vegetation type (Yorou et al., 2001). Next, an acronym was assigned to each plot as identification code. The coordinates of each plot were recorded using a Garmin 60 GPS receiver (Table 1).

2.2.2 | Mycological surveys, specimens sampling and processing

Plots were surveyed twice a week from June to October, and over 3 years (2015, 2016 and 2017). Sampling consisted of visiting carefully the plots in strips 2 m wide to avoid any omission of bolete specimens (Mueller & Lys, 2004; Yorou et al., 2001). During the surveys, fruiting bodies of any observed boletes were collected and sorted per plot. Once back at the field laboratory, the specimens were classified into different morphotypes using field guides (Bessette et al., 2000; De Kesel et al., 2002, 2017; Eyi Ndong et al., 2011) (see Table 2) but also through the use of a field guide of over 1500 coloured pictures of fungi compiled since 2000. Taxa identification were confirmed through microscopic examination using a Leica DM 2700 M (Badou et al., 2018). The fruiting bodies were counted per species and per plot for each sampling week. The fresh biomass of each species was recorded using a 0.01 g electronic scale type Sagitta. After recording the fresh biomass, representative fruiting body of each bolete species was dried using a field dryer (De Kesel et al., 2017). The dried specimens were then tagged and stored in plastic bags (Minigrip)

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TABLE 1 Geo-location of the different plots

Sites	Tree species	Plots (Acronym)	Geographic coordinates
	Isoberlinia doka	V1P1 = Plot <i>I. doka</i> Angaradebou	N09°45″16.4″ E002°08′26.3″
Angaradebou	Isoberlinia tomentosa	V2P1 = Plot I. tomentosa Angaradebou	N 09°45'24.4" E 002°18'24.3"
	Uapaca togoensis	V3P1 = Plot <i>U. togoensis</i> Angaradebou	N 09°46'50.0" E 002°12'58.7"
	Isoberlinia doka	V1P2 = Plot <i>I. doka</i> Gando	N09°45'16.7" E002°08'31.0"
Gando	Isoberlinia tomentosa	V2P2 = Plot I. tomentosa Gando	N 09°45'51.2" E 002°18'39.1'
	Uapaca togoensis	V3P2 = Plot <i>U. togoensis</i> Gando	N 09°46'.09.5" E 002°18'39.1"
	Isoberlinia doka	V1P3 = Plot <i>I. doka</i> Sonnonmon	N 09°45'15.7" E 002°08'08.3"
Sonnonmon	Isoberlinia tomentosa	V2P3 = Plot I. tomentosa Sonnonmon	N 09°45'15.7" E 002°08'08.3"
	Uapaca togoensis	V3P3 = Plot <i>U. togoensis</i> Sonnonmon	N 09°46'49.6" E 002°14'48.9"

TABLE 2 List of bolete collected from 2015 to 2017

		Sequence access numbers				
Vouchers	Species name	atp6	tef1	rpb2	LSU	References
BADOU-258	Boletus sp.1	-	-	-	-	
BADOU-248	Boletus sp.2	-	-	-	-	-
KIT-0295	Boletus sp.3		-	-	MK908838	This study
LAG-0101	Boletus sp.2	-	-	-	MK908839	This study
HLA-0100	Gyrodon sp. A1		-	-	MK908837	This study
HLA-0036	Gyroporus sp.	-	-	-	-	-
HLA-0043	Phlebopus sudanicus	-				
HLA-0026	Phylloporus sp.	-				
FOG0504	Porphyrellus sp.	-				
SAB-0629	Pulveroboletus sokponianus	MH983001	MH983002	MH983003	-	Badou et al. (2018)
BADOU-0009	Tylopilus sp.	-				
HLA-0100	Xerocomus sp.		-	-	-	-
LAG-0101	Xerocomus sp.1	-	-	-	-	-
HDR-0029	Xerocomus sp.2	-	-	-	-	-
LAG-0141	Xerocomus subspinulosus	-	-	-	-	-

Note: '-' means NA.

and deposited at the Mycological Herbarium of the University of Parakou (UNIPAR) (Thiers, 2019).

2.2.3 | Microclimate data

A HOBO H21-002 Micro Station Data Logger (Onset Company) was installed in the middle of each plots (at subplot 13) to record the following data: soil temperature, air temperature, air relative humidity and soil moisture. The Micro Station Data Logger - H21-002 was calibrated to record these data every 30 min during the mushroom season.

2.3 | Statistical analysis

Fresh biomass, number of fruit bodies (abundance) and species richness of boletes were considered as the dependent variable. The microclimate variables (soil temperature, air temperature, air relative humidity and soil moisture) were considered as independent variables. For each microclimatic variable, we considered the weekly maximum, mean and minimum values. The boletes community was assessed through the weekly estimation of fresh biomass, abundance and species richness of boletes. The abundance of boletes was log-transformed to make this variable normal. Mixed-effect models (Nlme) with the R software (Pinheiro et al., 2018) were used to assess the effect of the year and the month of collection on the temporal variation of the dependent variables. We performed a correlation test between the abundance of boletes and the fresh biomass using the Spearman rank correlation test. A generalised mixed effect linear model (GLMM) with the negative binomial family was used to assess the impact of microclimatic variables on the abundance and fresh biomass of boletes while a GLMM with the Poisson family used for the species richness, with the MASS package (Venables & Ripley, 2002). The fixed terms considered are the year, the month and the vegetation, while the random term is the site. The models have been simplified, and the best model chosen was the one with the smallest AIC value. We then carried out a post hoc test to have a clear picture of the differences between the levels of the significant predictors. These two analyses were implemented using the Package 'Ismeans' (Lenth & Lenth, 2018). All analyses were performed in statistical software R version 3.6.0 (R Core Team. 2019).

3 | RESULTS

3.1 | Species richness of boletes recorded in the Ouémé Supérieur forest reserves

The highest species richness recorded was 14 species. This highest richness was obtained in 2016, while the lowest species richness was recorded in 2017 (Table 2, Figure 3). The forests dominated by *I. tomentosa* had the greatest number of species (14) and the less productive forest is dominated by *I. doka* (Figure 3).

3.2 | Descriptive analysis of the spatiotemporal variation in the fresh biomass and abundance of boletes

A total of 7000 fruit bodies weighing 105 kg/ha of fresh biomass were recorded from 2015 to 2017 (Figure 4a,b). The highest fresh biomass (70 kg/ha) was obtained in 2016 while the lowest fresh biomass (10 kg/ha) in the forest dominated by *I. tomentosa*) in 2017 (Figure 4a). The highest abundance of boletes (5000 fruit bodies/ha) and the lowest abundance (1500 fruit bodies/ha) were recorded in 2016 and 2017 respectively (Figure 4b).

3.3 | Spatio-temporal variation of the fresh biomass, abundance and species richness

There is a strong spatio-temporal variation of the fresh biomass (p < 0.05, Table 3), while the vegetation has no significant influence on the fresh biomass (p > 0.05, Table 3). The combination of the year and the month has an influence on the abundance of boletes (p < 0.05, Table 3).



FIGURE 3 Species richness according to the plots and the year (2015, 2016 and 2017)

3.4 | Intra- and inter-annual variation in the abundance and fresh biomass of boletes

The highest and lowest biomass were recorded in July 2016 and October 2017 respectively (Figure 5a).

The highest abundance of boletes (8000 fruit bodies/ha) was obtained in July (2016). The lowest abundance (500 fruit bodies/ ha) was obtained in October (2015) (Figure 5b) (intra-annual variation). Wide variation of the fresh biomass and the abundance of boletes from 1 year to another was observed (inter-annual variation) (Figure 5a,b; Figure 6).

3.5 | Influence of microclimatic parameters on the natural production of boletes

Air and soil temperature had no significant effect on fresh biomass and species richness (p > 0.05, Table 4). A negative effect of soil moisture on the abundance of boletes (p < 0.05, Table 4) was noticed. When the soil moisture increases by four units, the abundance of boletes decreases by one unit, which leads to a negative correlation (Coef. = -0.04, Table 4). Maximal production of boletes is recorded between $0.05 \text{ m}^3/\text{m}^3$ and $0.25 \text{ m}^3/\text{m}^3$. Productivity decreases below $0.05 \text{ m}^3/\text{m}^3$ and above $0.25 \text{ m}^3/\text{m}^3$. Thus, the favourable interval of soil moisture for the optimal natural production of boletes in Ouémé Supérieur forest reserve is ' $0.05-0.25 \text{ m}^3/\text{m}^3$ '.

4 | DISCUSSION

The patterns of spatio-temporal variation within natural production of boletes as a function of the microclimate in tropical Africa are



FIGURE 4 Mean of (a) the fresh biomass (kg/ha) and (b) the abundance of boletes for each vegetation per year of study





	Fresh biomass		Abundance of boletes		Species richness		
	F	p	Chisq	p	Chisq	p	
Year	32.70	<0.0001***	0.38	0.536 ns	0.04	0.843 ns	
Month	26.58	<0.0001***	2.83	0.093 ns	2.85	0.092 ns	
Vegetation	1.28	0.279 ns	0.71	0.701 ns	3.15	0.207 ns	
Year: Month	1.95	0.163 ns	5.72	0.017*	4.8	0.305 ns	

TABLE 3 Analysis of variance on the models testing the effects of the year, month and the vegetation on the fresh biomass and the abundance of boletes

Note: F., Fisher statistic; *p*, probability value; Chisq., Chi-square statistic.

Asterisks represent the significance level for each term of the model: *** significant at 0.1%; * significant at 5%; ns not significant.



abundance of boletes and fresh biomass from 1 year to another. Letters (a and b) represent the results of multiple comparisons; the bars with the same letters do not differ significantly ($\alpha = 5\%$) and the opposite conclusion

FIGURE 5 Temporal variation of

(Abundance of boletes = Thousands of units / ha)

still poorly understood (Milenge Kamalebo et al., 2019). However, climatic variables such as air temperature, soil temperature and annual precipitation are known to govern the diversity and distribution of fungal species at various spatial scales during fructification (Kauserud et al., 2008; Pinna et al., 2010; Yang et al., 2012). On a small scale, microclimate has an influence on the yield of fungi (Ágreda et al., 2015; Andrew et al., 2016). It is often difficult to understand ecological processes at fine scales due to the variability of climatic variables even at the local level (Boddy et al., 2014; Stefansson et al., 2013).

In the Ouémé Supérieur forest reserve, there is a variation in fresh biomass and the abundance of boletes from 1 month to another (intra-annual variation) and from 1 year to another (inter-annual variation). Likewise, only the combined effect of the number of months of collection and the year of study has a significant influence on the spatio-temporal variation of the fresh biomass. We observe a high production of boletes at the beginning of the rainy season (June–July) and a low production at the end of the season (October). The same productive trends have been found by Yorou, De Kesel, Codjia, et al. (2002) and Yorou, De Kesel, Sinsin, et al. (2002). They found that the highest yields of EcM fungi are obtained at the beginning (June) and at the end (October) of the mushroom season.

The vegetation has no significant influence on the spatiotemporal variation of the fresh biomass. This neglected effect of vegetation could be explained by the fact that the forest displays FIGURE 6 A: Gyroporus sp.; B: Xerocomus subspinulosus Heinem.; C: Tylopilus sp.; D: Xerocomus sp.; E: Pulveroboletus sokponianus Badou, De Kesel, Raspé & Yorou.; F: Boletus sp.3 and H: Porphyrellus sp. Scale Barre: (A): 8 mm, (B): 8 mm, (C): 8 mm, (D): 8 mm; (E): 15 mm, (F): 15 mm and (H): 8 mm



almost similar vegetation variables (same age, floristic composition of the EcM trees and the density), and this is in line with the findings of Houdanon et al. (2019).

Our study revealed that the air and soil temperature have no significant effect on the natural production of boletes. This contradicts Straatsma et al. (2001), who showed that the occurrence of boletes has generally been correlated with higher temperatures and the lowest rainfall observed at the beginning of the mushroom season.

From all climatic variables studied, soil moisture has a significant negative effect on the abundance of boletes. Soil moisture is a direct deduction from the rainfall, which is known to regulate the fructification of EcM fungi in general (Pinna et al., 2010). Our results suggest that the abundance of bolete decreases when soil moisture is lower than 0.05 m³/m³ and higher than 0.25 m³/m³. These results are similar to Manachère (1980) who demonstrated that excess moisture inhibits fruiting but stimulates the development of the mycelium. In addition, Barroetaveña et al. (2008) showed that if the water potential is too low, EcM fungi in general cannot obtain enough moisture for their fructification. This proves that the soil moisture has a determining role in the fruiting of EcM fungi.

In our study, boletes fructify when soil moisture ranges between 0.05 m³/m³ and 0.25 m³/m³. These results corroborate those of Pinna et al. (2010), in which they found that the mean soil moisture (0.20 m³/m³) promotes fructification of *Boletus edulis* Bulliard. Recent data showed that fungal fructification may TABLE 4 Summary of the linear models testing the relationship between climatic variables the abundance of boletes, the fresh biomass and the species richness

		Abundance of boletes		Fresh biomass		Species richness	
Factors	Terms	Coef.	р	Coef.	р	Coef.	р
	Intercept	2.38	^a <2.00E-16***	5.77	^b 0.144 ns	2.38	0.002**
Covariates	Soil temperature	-	-	-	-	-0.06	0.192 ns
	Air temperature	-	-	-	-	0.04	0.113 ns
	Soil moisture	-0.04	0.000***	-0.09	0.338 ns	-0.14	0.015 ns

Note: Coef., Regression coefficient; *p*, probability value; '-', term not present in the final model.

Asterisks represent the significance level for each term of the model: *** significant at 0.1%; ** significant at 1%; * significant at 5%; ns not significant. ^aThe probability of factors is derived from an ANOVA (Fisher test) to test the global significance of the factor.

^bThe probability values relative to the terms are from the Student *t* test to test the significance of coefficients.

correspond to climatic variables on longer time scales than previously thought (Kauserud et al., 2010). It has also been argued that drought tolerance and fructification of EcM fungi depend on species rather than annual precipitation (Lehto & Zwiazek, 2011), since the absorption of moisture by fungal hyphae from mycorrhizal root systems depends on the fungal species (Agerer, 2001). Numerous studies have already shown that boletes tolerate heat stress and are capable of fructification under high temperatures (Hobbie & Agerer, 2010; Lilleskov et al., 2009) while many other EcM taxa live in vegetative states.

5 | CONCLUSION

We inferred that time factor (month and year) is important for the actual detection of the natural production of boletes. In addition, when soil moisture increases by four units, the abundance of boletes decreases by one, resulting in a negative correlation between soil moisture and the abundance of boletes. Our study was limited to a single environmental variable (microclimatic variable) and over a short period of 3 years of collection. This is not enough to understand with precision the influence of environmental variables on the natural production of boletes in northern Benin. Further studies taking into account the effect of edaphic variables, floristic variables and functional traits of partner trees on the natural production of boletes in woodlands over a longer period in northern Benin are needed.

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CONFLICT OF INTEREST

The authors declare that they have no competing interests.

DATA AVAILABILITY STATEMENT

Data and materials are available in the Tropical Mycology and Plant-Soil Fungi Interactions (MyTIPS) Research Unit at the University of Parakou in Benin.

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