

Shift in the Spatio-Temporal Natural Fruiting of Boletes in West African Woodlands: the Key Role of the Soil Moisture

Akotchayé Sylvestre Badou (✉ sbadou@gmail.com)

Research Unit Tropical Mycology and Plants Soils Fungi Interactions <https://orcid.org/0000-0001-5024-1863>

Roel D. Houdanon

Research Unit in Tropical Mycology and Plants-Soils-Fungi (MyTIPS)

Kassim I. Tchan

Research Unit in Tropical Mycology and Plants-Soils-Fungi (MyTIPS)

D.M.T. Apollon Hègbè

Research Unit Tropical Mycology and Plants-Soils-Fungi Interactions (MyTIPS)

Nourou Soulemame Yorou

Research Unit Tropical Mycology and Plants-Soils-Fungi (MyTIPS)

Research

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Abstract

Background: The ectomycorrhizal fungi display strong fluctuations during the mycological season. However, how abiotic parameters affect the fruiting sequences of ectomycorrhizal fungi and also the direction and extent of this effect are not yet tapped adequately. The present study seeks to assess the microclimate effect on the natural production of boletes. Nine permanent plots of 2500 m² (50m x 50m) split into 25 subplots of 100 m² (10m x 10m) were installed in three different vegetation dominated respectively by *Isoberlinia doka*, *Isoberlinia tomentosa* and *Uapaca togoensis*. Microclimatic parameters were recorded each 30 minutes throughout by mean of a Micro Station Data Logger - H21-002 the mycological seasons. Each plot was surveyed twice a week (from May to October) over three years (2015, 2016 and 2017) to record the presence/absence of fruit bodies and fresh biomass of boletes. To evaluate the effect of time and microclimate variables on natural production, we used mixed effects and generalized linear models using R version 3.5.3.

Results: In total, during the three years (2015, 2016 and 2017), we recorded 14 species of boletes. Species richness does not change over time ($P > 0.05$). In addition, fresh biomass varies within years and vegetation ($P < 0.05$). The combination of year and month of collection has a significant effect on the number of fruit bodies ($P < 0.05$). Only the soil moisture has a significant positive influence on the species richness of boletes ($P > 0.05$).

Conclusions: When the soil moisture decreases by four units, the number of fruit bodies of ectomycorrhizal fungi is significantly reduced by one unit. Therefore, above 0.25 m³ / m³ and below 0.05 m³ / m³ there is a decrease in the number of fruit bodies.

Introduction

Fungi play an important role in the regeneration of natural forest ecosystems in tropical Africa (Diedhiou et al. 2010). In West Africa, ectomycorrhizal (EcM) fungi in general, and particularly the Boletes, are mainly found in the Guineo-Sudanian to Sudanian forests (White 1983) dominated by Fabaceae, Phyllantaceae and Dipterocarpaceae (Bâ et al. 2012; Felten *et al.* 2012). Boletes are excellent symbionts known to play an important role in restoring the ecosystems of African tropical forests. In addition, several authors (Parladé et al. 2017) emphasize that local populations depend on certain boletes for food during the shortage period which coincides with the rainy season. Likewise, in West Africa, this dependence is perceptible through the common use of some boletes such as *Phlebopus sudanicus* as source of proteins (Guissou et al. 2005, 2008), replacing animal proteins in a context where bush meat is scarce and expensive (Yorou et al. 2002a, b; Guissou et al. 2005; Boni & Yorou 2015; Fadeyi et al. 2017).

In natural habitats, boletes communities are influenced by various microclimatic parameters such as precipitation, temperature, humidity (Gévry 2010; Gillet et al. 2010), which directly affect their abundance, species richness and spatial distribution. Knowledge of intra and inter seasonal variations in the fruiting of boletes in relation to microclimatic parameters is of high importance in order to provide effective

sustainable management measures (Kauserud et al. 2008, 2010, 2012). It allows a better understanding of factors governing the fructification of fungi, for instance by precisely documenting the response of certain species according to the vegetation, the harvest period (for example the number of months, the harvest year, etc.) and the variability of the microclimatic parameters (Selosse et al. 2001; Pilz & Molina 2002). This understanding would be helpful in proposing effective measures for the sustainable management of wild edible mushrooms and to ensure a better understanding of the natural production over time and space.

Soil temperature, air temperature and precipitation are among the main microclimatic factors that govern the large-scale distribution and variation of the species richness of EcM fungi (Thuiller et al. 2005; Menéndez *et al.* 2006; Grytnes et al. 2014). As a result, the microclimate seems to play a predominant role in the origin of local ecological processes which in turn lead to perceptible changes (Andrew et al. 2016). However, it is difficult to know how these ecological processes work on a small scale in the face of microclimatic parameters (Randin et al. 2009; Engler *et al.* 2011). To date, most studies on the spatiotemporal variation of the natural production of EcM fungi have been done only on the whole community of EcM fungi and less informative at the group or species level (Vogt *et al.* 1992; Ammirati *et al.* 1994).

In the present study, we are attempting to describing the spatio-temporal variation of the natural production (species richness and fresh biomass) of boletes according to the variability of microclimate characteristics. For this to be achieved, we used a cumulative dataset of three years (2015, 2016 and 2017) to observe whether the variability of the microclimatic parameters affects the spatio-temporal variation of the Boletes community.

Materials And Methods

Study area

The study was carried out in the “Ouémé Supérieur” forest reserve, located in northern Benin (Fig.1). This forest reserve is dominated by EcM fungi (Boni & Yorou 2015, Fadeyi *et al.* 2019). The climate of this area is tropical type characterized by a rainy season from May to October (Gnanglè *et al.* 2011) that strongly contrasts with a dry season from November to April. The vegetation is dominated by species such as *Isobertia doka* Craib & Stapf, *Isobertia tomentosa* (Harms) Craib & Stapf, *Uapaca togoensis* Pax, etc.) (Houdanon *et al.* 2019).

Plots establishment

Nine permanent plots of 50 mx 50 m were installed in three different types of vegetation, with three plots per site (Angaradebou, Gando and Sonnonmon), for long-term monitoring of EcM fungi. Each plot was subdivided into 25 quadrats of 10m x 10m. The geographic coordinate of each plot and acronym is recorded at the center of the plot by mean of the Garmin 60 GPS device and can be consulted in supplementary file 1 (Table.1; Table.2).

Mycological surveys, specimens sampling and processing

Plots were surveyed twice a week during the overall mycological seasons that range from June to October each year (2015, 2016 and 2017). The collection technique consisted of scanning the plots by a parallel strip of 2 m wide to avoid omissions (Yorou *et al.* 2001). During the surveys, fruit bodies of any boletes were harvested and sorted per plot. Once back at the field laboratory, the species were identified using field guides (De Kesel *et al.* 2002, 2017, Eyi-Ndong *et al.* 2011) but also through the use of a catalogue of over 1500 colored pictures of fungi compiled since 2000. Taxa identification were confirmed through microscopic examination by mean of a Leica DM 2700 M. The fruit bodies were counted by species and by plot for each sampling week. The fresh biomass of each species is recorded using a 0.01 g electronic scale type Sagitta. After recording the fresh biomass, representative fruit bodies of each species is dried using a field dryer (De Kesel 2001). The dried specimens are then tagged and stored in plastic bags (Minigrip) and deposited at UNIPAR (Thiers *et al.* 2020), the Mycological Herbarium of the University of Parakou, Benin.

Recording microclimatic data

A HOBO H21-002 Micro Station Data Logger (Onset Company) has been installed in the middle of each plots (at subplot 13) to record the following data: the soil temperature, air temperature, air relative humidity and soil moisture. The Micro Station Data Logger - H21-002 was installed to record these data every 30 minutes during the mycological seasons from June to October over three years (2015, 2016 and 2017).

Statistical analysis

Natural production (fresh biomass, number of fruit bodies) and species richness was considered as dependent variable. The microclimate parameters (soil temperature, air temperature, air relative humidity and soil moisture) were considered as independent variables. For each microclimatic variable recorded in our study, we considered the weekly maximum, mean and minimum values. The boletes community was assessed through the weekly estimation of fresh biomass, number of fruit bodies and species richness. The fresh biomass was log-transformed to make this variable normal. Mixed-effect models (LMEM) with the R package (Pinheiro *et al.* 2018) have been 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 number of fruit bodies and the fresh biomass using the Spearman rank correlation rho test. A generalized mixed effect linear model (GLMM) with the negative binomial family was used to assess the impact of microclimatic variables on the number of fruit bodies and the fresh biomass whilst a GLMM with the Poisson family were 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 has been chosen on the basis of the Akaike Information Criterion (AIC), the smallest value corresponds to the best model. In addition, we calculated fitted means only for the significant terms of the best model. 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 analysis were

implemented with the emmeans package (Lenth 2018). To test the variability of the microclimate parameters according to the vegetation, we considered weekly mean for the microclimate variables (air temperature, soil temperature, soil moisture and air relative humidity). An analysis of the time series was applied to verify their temporal variation. All analyses was performed in statistical software R version 3.6.0 (R Core Team 2019).

Table.1: Geo-location of the different plots

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

Table. 2: List of boletes collected from 2015 to 2017

Vouchers	Species name	Sequence access numbers				References
		atp6	tef1	rpb2	LSU	
BADOU 258	<i>Boletus sp1</i>	-	-	-	-	
BADOU 248	<i>Boletus sp2</i>	-	-	-	-	-
KIT 0295	<i>Boletus acidulus</i> nom. prov.		-	-	MK908838	This study
LAG- 0101	<i>Boletus pseudolosii</i> nom. Prov.	-	-	-	MK908839	This study
HLA- 0100	<i>Gyrodon sp A1</i>		-	-	MK908837	This study
HLA- 0036	<i>Gyroporus virido-odorata</i> nom. prov.	-	-	-	-	-
HLA- 0043	<i>Phlebopus sudanicus</i>	-				
HLA- 0026	<i>Phylloporus tubipedes</i>	-				
FOG0504	<i>Porphyrellus sp</i>	-				
SAB0629	<i>Pulveroboletus sokponianus</i>	MH983001	MH983002	MH983003	-	Badou <i>et al.</i> 2018
BADOU- 0009	<i>Tylopilus sp</i>	-				
HLA- 0100	<i>Xerocomus luteovelutipes</i> nom prov.		-	-	-	-
LAG 0101	<i>Xerocomus sp</i>		-	-	-	-
HDR 0029	<i>Xerocomus sp1</i>	-	-	-	-	-
LAG- 0141	<i>Xerocomus subspinulosus</i>		-	-	-	-

Results

Species richness of boletes recorded in the Ouémé Supérieur forest reserves

The highest species richness (14) is obtained in 2016 while in 2015 and 2017 the lowest species richness (2) was recorded (2) (Fig. 2). The vegetation dominated by *I. tomentosa* is the most productive in species richness (14) and the least productive is the vegetation dominated by *I. doka* (Fig.2).

Descriptive analysis of the spatio-temporal variation in the fresh biomass and number of fruit bodies

A total of 105 kg / ha of fresh biomass and 7000 of boletes fruit bodies were recorded from 2015 to 2017 (Fig.3a, Fig.3b). The largest fresh biomass (70 kg / ha) (*U. togoensis*) was obtained in 2016 while the lowest fresh biomass (10 kg / ha) (*I. tomentosa*) in 2017 (Fig. 3a). The large number of fruit bodies (5000 fruit bodies / ha) while the lowest number of fruit bodies (1500 fruit bodies / ha) was recorded respectively in 2016 and 2017 (Fig.3b).

Effect of the year, the month and the vegetation on the fresh biomass, number of fruit bodies and species richness

The individual effect of the number of months and the year had a significant positive influence on the spatio-temporal variation of the fresh biomass ($P < 0.05$, Table 3). However, the vegetation has no significant influence on the fresh biomass ($P < 0.05$, Table 3). However, the combination of the year and the month has an influence on the number of fruit bodies ($P < 0.05$, Table 3). On the other hand, the species richness remains fixed whatever the years ($P > 0.05$, Table 3).

Table.3. Analysis of variance on the models testing the effects of the year, month and the vegetation on the fresh biomass and the number of fruit bodies.

	Fresh biomass		Number of fruit bodies		Species richness	
	F	Prob	Chisq	Prob	Chisq	Prob
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

F.: Fisher statistic, Prob.: Probability value. Chisq. : Chi-square statistic. Asterisks represent the significance level for each term of the model: *** significant at 0.1%; ** significant at 1 %; * significant at 5 %; ns not significant.

Intra-annual variation in the number of fruit bodies and fresh biomass

We obtained the largest fresh biomass in July (2016) (Fig. 4a; Fig. 5b). However, the lowest is obtained in October (2017) (Fig. 4a; Fig. 5c). The highest number of fruit bodies (8000 fruit bodies / ha) in July

(2016) (Fig. 4b; Fig. 6b). However, the lowest number (500 fruit bodies / ha) is obtained in October (2015) (Fig. 4b; Fig. 6a). Then, we observe a variation of the fresh biomass and the number of fruit bodies from one year to another (inter-annual variation) (Fig. 4a, b; Fig. 5a, b, c and Fig. 6a, b, c).

Spatial and temporal variability of microclimate parameters

The highest weekly mean air temperature and weekly mean soil temperature were recorded at the end of the season and at the start of the season, respectively (30 ° C; 29 ° C) and the lowest in July respectively and September (24.5 ° C; 25 ° C) (Fig. 7). However, the highest mean soil moisture and mean relative air humidity are obtained (0.30 m³ / m³; 100%) respectively in mid-season while the lowest respectively (0.1 m³ / m³; 75%) are recorded at the start of the season (Fig. 7, Fig. 8 and Fig. 9).

Influence of microclimatic parameters on the natural production of the boletes

Air temperature and soil temperature have no significant effect on fresh biomass and species richness (P > 0.05, Table 4). Only soil moisture significantly influences the number of boletes fruit bodies (P < 0.5, Table 4). We noticed a negative relationship between soil moisture and the number of fruit bodies (P < 0.05, Table 4, Figure 13). When the soil moisture decreases by four units, the number of fruit bodies of boletes decreases, which leads to a negative correlation (Coef. = -0.04) between soil moisture and the number of fruit bodies. Then, above 0.25 m³ / m³ and below 0.05 m³ / m³ there is a decrease in the number of fruit bodies. Thus, the interval of soil moisture at which fruiting of boletes is possible is (0.05 m³ / m³; 0.25 m³ / m³). Hence, the appearance or not of the fruit bodies of boletes is conditioned by the soil moisture.

Table.4. Summary of the linear models testing the relationship between climatic variables the number of fruit bodies, the fresh biomass and the species richness

		Number of fruit bodies		Fresh biomass		Species richness	
Factors	Terms	Coef.	Prob.	Coef.	Prob.	Coef.	Prob.
	Intercept	2.38	< 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

Coef. : Regression coefficient, Prob.: Probability value. "-": term not present in the final model.

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

Discussion

The patterns of spatio-temporal variation within natural production (fresh biomass, number of fruit bodies and species richness) of boletes as a function of the microclimate in tropical regions are still poorly understood. This can be explained by the fact that EcM fungi in general spend most of their time hidden under the ground or in other substrates. However, as large- and small-scale ecological phenomena vary due to demographic changes, the macroclimate (large scale) and the microclimate (small scale) can have an effect on local dynamic processes to cause long term changes in the behavior of boletes. Climatic variables such as air temperature, soil temperature and annual precipitation are known to be major determinants of large and small-scale models such as the spatial distribution of fungal species and the gradients in terms of diversity and the periods of appearance (fruiting) (Woodward 1987, Pearson & Dawson 2003, Araújo *et al.* 2005, Thuiller *et al.* 2005, Menéndez *et al.* 2006). Thus, small-scale processes influence the responsiveness of fungi species in general to climate-induced changes, often in complex ways (Sato *et al.* 2012; Grytnes *et al.* 2014; Ágreda *et al.* 2015; Andrew *et al.* 2016).

It is often difficult to understand ecological processes at fine scales due to the buffering of climatic effects by local processes (Randin *et al.* 2009; Engler *et al.* 2011; Lenoir *et al.* 2013). Although the importance of using molecular approaches for recording the presence of EcM fungi in the soil is getting more attention now (Lindahl *et al.* 2013), the harvesting of fruiting bodies' remains a useful tool for studying spatiotemporal variation, both on a large and fine scale (Samson & Fortin 1986; Wollan *et al.* 2008; Büntgen *et al.* 2012, 2013, 2015).

In the Ouémé Supérieur forest reserve, there is a variation in fresh biomass and the number of fruit bodies of boletes from one month to another (intra-annual variation) and from one year to another (inter-annual variation). Likewise, also, only the combined effect of the number of months of collection and the year of study have a significant influence on the spatiotemporal variation of the fresh biomass. This means that production changes from week to week in the same year and from year to another. In similar forest ecosystems, Yorou *et al.* (2002a, b, 2014) found the same productive trends as those observed in our study. They found that the highest yields of EcM mushrooms are obtained at the beginning and at the end of the mycological season. However, adding the vegetation has no significant influence. This neglected effect of vegetation could be explained by the fact that the forest display almost similar vegetation parameters (same age, floristic composition of the EcM tree and the density). Indeed, to cancel the effect of vegetation, we tried to choose forests with the same characteristics but nevertheless, as described by Houdanon *et al.* (2019), other environmental factors such as soil parameters could be the basis of this variation observed in the productivity of boletes.

Our study reveals that the air and soil temperature have no significant effect on the fresh biomass and the species richness. From all climatic variables studied, only the soil moisture has a significant negative effect on the number of fruit bodies.

The soil moisture is a function of the rainfall which is the trigger for the fruiting of the fruit bodies or even the appearance of the fruit bodies. Similarly, the 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). Above $0.25 \text{ m}^3 / \text{m}^3$ and below $0.05 \text{ m}^3 / \text{m}^3$ there is a decrease in the number of fruit bodies. This result is in the same way that those of Manachère (1980) which explains that excess water inhibits fruiting but stimulates the development of the mycelium. Likewise, Barroetavena *et al.* (2008) shown that if the water potential is too low, EcM fungi in general cannot obtain enough water for their fruiting. Pinna et al. (2010), also showed that the average soil moisture ($0.20 \text{ m}^3 / \text{m}^3$) promotes the fruiting of *B. aff. edulis* and *L. deterrimus* for example while in our study, the species of boletes appear between $0.05 \text{ m}^3 / \text{m}^3$ and $0.25 \text{ m}^3 / \text{m}^3$. These results could be explained by the fact that the boletes also fruit during the drought bags which settle during the rainy seasons when the other taxa return to vegetative state. Our results contradict the studies of Straatsma *et al.* (2001), where they have shown that the occurrence of fruit bodies of boletes has generally been correlated with higher temperatures and the lowest rainfall are observed at the start of the mycological season, but recent data show that fungal fruiting may correspond to climatic variables on longer time scales than previously thought (Kausrud et al. 2010). It has also been shown that drought tolerance and fruiting by EcM fungi depend on species rather than annual precipitation (Lehto & Zwiazek 2011), since the absorption of water by fungal hyphae from mycorrhizal root systems depends on fungal species (Agerer 2001). Numerous studies have already shown that boletes tolerate heat stress and are capable of fruiting under high temperatures (Lilleskov et al. 2009; Hobbie & Agerer 2010) while many other EcM taxa live in vegetative states.

Conclusion

The highest richness species (14) was obtained in 2016 while in 2015 and 2017, the lowest richness species (1.5) was recorded. The highest fresh biomass (70 kg / ha) was obtained in 2016 while the lowest (10 kg / ha) was obtained in 2017. 2016 was the most productive year with 5000 fruit bodies / ha while the lowest were recorded in 2015 and 2017 respectively (2500 fruit bodies / ha and 1500 fruit bodies / ha). The year of study and the number of months of collection had a significant influence on the spatio-temporal variation of the fresh biomass. The soil moisture has a significant negative effect on the number of fruit bodies. For this purpose, when the soil moisture decreases by four units, the number of boletes fruit bodies also decreases by one unit, which results in a negative correlation between soil moisture and the number of fruit bodies. Thus, the appearance or not of the fruit bodies is conditioned by the soil moisture.

Declarations

Ethics approval and consent to participate

All authors agree to the publication of this study.

Consent for publication

All the authors agree.

Availability of data and material

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

Competing interests 'Not applicable'

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Authors' contributions

All the authors contributed to the realization of this study.

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References

1. Adomou AC, [Sinsin B](#), Van der M, Laurentius JG (2011) Phytosociological and chorological approaches to phytogeography: a meso-scale study in Benin. *Systematics and Geography of Plants*, Volume 76, Number 2, 2006, pp. 155-178(24).
2. Altieri MA, Anderson MK, Merrick LC (1987) Peasant Agriculture and the Conservation of Crop and Wild Plant Resources. *Conservation Biology*, Vol. 1, No. 1 (May, 1987), pp. 49-58. : Wiley for Society for Conservation Biology, <http://www.jstor.org/stable/2386126>.
3. [Agerer R](#) (2001) Exploration types of ectomycorrhizae. *Mycorrhiza* volume 11, pages107–114(2001)
4. [Ágreda T](#), [Águeda B](#), [Olano JM](#), [Vicente-Serrano SM](#), [Fernández-Toirán M](#) (2015) Increased evapotranspiration demand in a Mediterranean climate might cause a decline in fungal yields under global warming. – *Global Change Biol.* 21: 3499-3510.
5. Andrew C, Heegaard E, Halvorsen R, Martinez-Peña F, Egli S, Kirk M, , Claus Bässler, BüntgenPU, Aldea J, Høiland K, Boddy L, Kauserud H (2016) Climate change impacts on fungal community and trait dynamics. – *Fungal Ecol.* 22: 17–25.
6. [Bâ AM](#), [Duponnois R](#), [Moyersoén B](#), [Diédhiou AG](#) (2012) Ectomycorrhizal symbiosis of tropical African trees. *Mycorrhiza* 22, 1–29. Doi: 10.1007/s00572-011-0415-x.

7. Badou AS, De Kesel A, Raspé O, Ryberg MK, Guelly AK, Yorou NS (2018) Two new African siblings of *Pulveroboletus ravenelii* (Boletaceae). *MycKeys* 43: 115–130.
<https://doi.org/10.3897/mycokeys.43.30776>
8. Verbeken A, Buyck B (2002) Diversity and Ecology of Tropical Ectomycorrhizal Fungi in Africa. *Tropical Mycology Volume 1, Macromycetes*. ISBN 0 85199 542 X.
9. Barroetaveña C, La Manna L, Alonso MV (2008) Variables affecting *Suillus luteus* fructification in ponderosa pine plantations of Patagonia. *Volume 256, Issue 11*, Pages 1868-1874.
<https://doi.org/10.1016/j.foreco.2008.07.029>.
10. Boni S, Yorou NS (2015) Diversité et Variabilité inter-ethniques dans la consommation de champignons sauvages de la région de N'Dali au Bénin. *Tropicultura* 33, 266–276.
11. Büntgen U, Egli S, Camarero JJ, Fischer E M, Stobbe U, Kauserud H, Tegel W, Sproll L, Stenseth N C (2012) Drought-induced decline in Mediterranean truffle harvest. – *Nat. Clim. Change* 2: 827–829.
12. Büntgen U, Egli S, Schneider L, Arx GV, Rigling A, Camarero JJ, Sangüesa-Barreda G, Fischer C R, Oliach D, Bonet JA, Colinas C, Tegel W, Ruiz Barbarin JI, Martínez-Peña F (2015) Long-term irrigation effects on Spanish holm oak growth and its black truffle symbiont. – *Agric. Ecosyst. Environ.* 202: 148–159.
13. Büntgen U, Peter M, Kauserud H, Egli S (2013) Unraveling environmental drivers of a recent increase in Swiss fungi fruiting. – *Global Change Biol.* 19: 2785–2794.
14. De Kesel A (2001) A mushroom dryer for the travelling mycologist. *Field Mycology*. *Volume 2, Issue 4*, October 2001, Pages 131-133.
15. De Kesel A, Codjia JTC, Yorou SN (2002) *Guide des champignons comestibles du Bénin*. Coco-MultiMedia. Volume/pages, 275 p.
16. Diedhiou AG, Selosse MA, Galiana A, Diabate M, Dreyfus B, Bâ AM, De Faria SM & Béna G (2010) Multi-host ectomycorrhizal fungi are predominant in a Guinean tropical rainforest and shared between canopy trees and seedlings. *Environ. Microbiol.* 12, 2219–2232.
17. Diez JM, James TY, McMunn M, Ibáñez I (2013) Predicting species-specific responses of fungi to climatic variation using historical record. *Global Change Biol.* 19: 3145–3154. Woodward, F. I. 1987. *Climate & plant distribution*. – Cambridge Univ. Press.
18. Eyi Ndong H, Degreef J, De Kesel A (2011) Champignons comestibles des forêts denses d'Afrique centrale, Taxonomie et identification. *ABC Taxa Volume 10* (2011).
19. Lilleskov EA, Bruns TD, Dawson TE, Camacho FJ (2009) Water sources and controls on water-loss rates of epigeous ectomycorrhizal fungal sporocarps during summer drought. *New Phytologist* (2009) 182: 483–494483.
20. Hobbie EA, Agerer R (2010) Nitrogen isotopes in ectomycorrhizal sporocarps correspond to belowground exploration types. *Plant Soil* (2010) 327:71–83DOI 10.1007/s11104-009-0032-z
21. Egli S, Ayer F, Peter M, Eilmann B, Rigling A (2010) Is forest mushroom productivity driven by tree growth? Results from a thinning experiment *Annals of Forest Science*, 67, 509.

22. Fadeyi OG, Badou SA, Aignon HL, Codjia JEI, Moutouama JK, Yorou NS, 2017. Etudes ethnomycologiques et identification des champignons sauvages comestibles les plus consommés dans la région des Monts-Kouffe au Bénin (Afrique de l'Ouest). *Agronomie Africaine* 29 (1): 93 - 109.
23. Fadeyi OG, Assogba FM, Chabi DDCB, Yorou NS , Gbenou JD (2019) Ethnomycology, myco-chemical analyzes and antioxidant activity of eleven species of the genus *Amanita* (*Basidiomycota*, fungi) from Benin (West Africa). *Journal of Pharmacognosy and Phytochemistry*; 8(3): 335-341.
24. Gange AC, Gange EG, Sparks TH, Boddy L (2007) Rapid and recent changes in fungal fruiting patterns. – *Science* 316: 71.
25. Gnanglè CP, Glèlèkakaï R, Assogbadjo AE, Vodounnon S, Yabi JA, Sokpon N (2011) Tendances climatiques passées, modélisation, perceptions et adaptations locales au Bénin. *Climatologie*, vol. 8(2011).
26. Gévry MF (2010) *Étude des facteurs environnementaux déterminant la répartition de champignons forestiers comestibles en Gaspésie, Québec. Mémoire. Rimouski, Québec, Université du Québec à Rimouski, Département de biologie, chimie et géographie, 93 p.*
27. Gillet F, Peter M, Ayer F, Butler R, Egli S (2010) Long-term dynamics of aboveground fungal communities in a subalpine Norway spruce forest under elevated nitrogen input. *Oecologia*, 164, 499–510.
28. Guissou KML, Sankara P, Guinko S (2005) *Phlebopus sudanicus* or «la viande des Bobos», edible mushroom in Satiri (Burkina Faso), *Cryptogamie Mycologie*, 26(3):195-204.
29. Guissou KML, Lykke AM, Sankara P , Guinko S (2008) Declining Wild Mushroom Recognition and Usage in Burkina Faso. *Economic Botany* volume 62, pages530– 539.
30. Grytnes JA, Kapfer J, Jurasinski G, Birks HH, Henriksen H, Klanderud K, Odland A, Ohlson M, Wipf S, Birks HJB, 2014. Identifying the driving factors behind observed elevational range shifts on European mountains. *Global Ecol. Biogeography*. 23: 876–884.
31. Houdanon RD, Tchan IK, Laourou GA, Codjia JEI, Badou SA, Aignon LH, Boni S Yorou NS (2019) Spatial structure of ectomycorrhizal trees in wooded savannas of Guineo-soudanian Ecozone in West Africa. *Journal of Tropical Forest Science* Vol. 31, No. 1, pp. 1-11.
32. Houdanon RD, Aignon LH, Codjia JE I N, Yorou S (2019) How far soil characteristics influence species composition and structure of Ectomycorrhizal fungi in Soudano-Guinean woodlands in Bénin? *Bulletin de la Recherche Agronomique du Bénin (BRAB) Numéro 86, ISSN sur papier (on hard copy) : 1025-2355 et ISSN en ligne (on line) : 1840-7099.*
33. Kausrud H, Stige LC, Vik JO, 2010. Climate change and spring-fruited fungi. – *Proc. R. Soc. B* 277: 1169–1177.
34. Kausrud H, Heegaard E, Büntgen U (2012) Warming-induced shift in European mushroom fruiting phenology. *Proc. Natl Acad. Sci. USA* 109: 14488–14493.
35. Kausrud H, Christian Stige L, Olav Vik J, Økland RH, Høiland K, Stenseth NC (2008) Mushroom fruiting and climate change. *Proc. Natl Acad. Sci. USA* 105: 3811–3814.

36. Koné NGA, Yéo K, Konaté S, Linsenmair KE (2013) Socio-economical aspects of the exploitation of *Termitomyces* fruit bodies in central and southern Côte d' Ivoire: Raising awareness for their sustainable use. *Journal of Applied Biosciences* 70, 5580– 5590.
37. Manachère G (1980) Conditions essential for controlled fruiting of macromycetes. *Transactions of the British Mycological Society, Volume 75, Issue 2*, Pages 255-270. [https://doi.org/10.1016/S0007-1536\(80\)80088-X](https://doi.org/10.1016/S0007-1536(80)80088-X)
38. Menendez R, Gonzalez Megias A, Hill J K, Braschler B, Willis S G, Colling ham Y, Fox R, Roy D B, Thomas C D (2006) Species richness changes lag behind climate change. *Proc. R. Soc. B*, 273, 1465– 1470, doi:10.1098/rspb.2006.3484.
39. Parladé J, Martínez-Peña F, Pera J (2017) Effects of forest management and climatic variables on the mycelium dynamics and sporocarp production of the ectomycorrhizal fungus *Boletus edulis*. *Forest Ecology and Management*. 390 (2017) 73–79. <http://dx.doi.org/10.1016/j.foreco.2017.01.025>.
40. Pearson RG, Dawson T P (2003) Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? – *Global Ecol. Biogeography*. 12:361–371.
41. Pilz D, Molina R (2002) Commercial harvests of edible mushrooms from the forests of the Pacific Northwest United States: Issues, management, and monitoring for sustainability. *Forest Ecol. Manage.* 155, 3–16.
42. Pinheiro J, Bates D, DebRoy S, Sarkar D, R Core Team (2018) *Nlme: Linear and Nonlinear Mixed Effects Models*.. R package version 3.1-137. <https://CRAN.R-project.org/package=nlme>
43. Pinna S, Gévry MF, Côté M, Sirois L (2010) Factors influencing fructification phenology of edible mushrooms in a boreal mixed forest of Eastern Canada, *Forest ecology and management* 260: 294-301.
44. R Core Team (2019) *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. URL <https://www.R-project.org/>.
45. Randin CF, Engler R, Normand S, Zappa M, Zimmermann N E, Pearman P B, Vittoz P, Thuiller W, Guisan A (2009) Climate change and plant distribution: local models predict high-elevation persistence. – *Global Change Biol.* 15: 1557–1569.
46. Samson J, Fortin JA (1986) Ectomycorrhizal fungi of *Larix laricina* and the inter- specific and intra specific variation in response to temperature. *Can.J.Bot.*64, 3020–3028.
47. Sato H, Morimoto S, Hattori T (2012) A thirty-year survey reveals that ecosystem function of fungi predicts phenology of mushroom fruiting. *PLoS One* 7: e49777.
48. Selosse MA, Martin F, LeTacon F (2001) Intraspecific variation in fruiting phenology in an ectomycorrhizal *Laccaria* population under Douglas fir. *Mycol. Res.* 105, 524–531.
49. Thiers B (2019) – (continuously updated). *Index Herbarium: A global directory of public herbaria and associated staff*. New York Botanical Garden's Virtual Herbarium. <http://sweetgum.nybg.org/science/ih/>.

50. Thuiller W, Lavorel S, Araújo M B, Sykes M T, Prentice I C (2005) Climate change threats to plant diversity in Europe. PNAS. 102 (23) 8245-8250; <https://doi.org/10.1073/pnas.0409902102>
51. Venables WN, Ripley B D (2002) Modern Applied Statistics with S. Fourth Edition. Springer, New York. ISBN 0-387-95457-0.
52. Villeneuve N (2000) Diversité et productivité des champignons forestiers: les apports de la recherche et de l'inventaire. (Dans Les champignons forestiers : récolte, commercialisation et conservation de la ressource). Édité par J. A. Fortin, Y. Piché. Centre de recherche en biologie forestière, *Université Laval, Québec*. Pp. 91-101.
53. Vogt KA, Edmonds RL, Grier CC (1981) Biomass and nutrient concentrations of sporocarp produced by mycorrhizal and decomposer fungi in *Abies amabilis* stands. *Oecologia* 50, 170–175.
54. Vogt KA, Edmonds R.L, Grier CC (1981) Biomass and nutrient concentrations of sporocarp produced by mycorrhizal and decomposer fungi in *Abies amabilis* stands. *Oecologia* 50, 170–175.
55. Wasterlund I, Ingelög T (1981) Fruit body production of larger fungi in some young Swedish forests with special reference to logging waste. *Forest Ecology and Management. Volume 3*, 1980, Pages 269-294.
56. White F (1983) The vegetation of Africa. *Natural Resources Research, UNESCO* 1983 Vol.20 pp.356 pp. ref.50 pp.
57. Wollan AK, Bakkestuen V, Kauserud H, Gulden G, Halvorsen R (2008) Modelling and predicting fungal distribution patterns using herbarium data. – *J. Biogeogr.* 35: 2298–2310. <https://doi.org/10.1111/j.1365-2699.2008.01965>.
58. Yorou SN, De Kesel A, Codjia JTC, Sinsin B (2002b) Biodiversité des champignons comestibles du Bénin. Proceedings of the Symposium-Workshop on Biodiversity in Benin. Abomey-Calavi (Benin) October 30th to November 18th 2002. 231-240 pp.
59. Yorou SN, De Kesel A, Sinsin B, Codjia JTC (2002a) Diversité et productivité des champignons comestibles de la forêt classée de Wari-Marou (Bénin, Afrique de l'Ouest). Proceedings of XVIth AETFAT Congress, Brussels 2000. *Systematic and Geographic of Plants* 71: 613-625.
60. Zeileis A, Kleiber C, Krämer W, Hornik K (2002) Testing and dating of structural changes in practice, Technical Report, No. 2002, 39. Universität Dortmund, Sonderforschungs bereich 475 – Komplexitäts reduktion in Multivariaten Datenstrukturen, Dortmund.

Figures

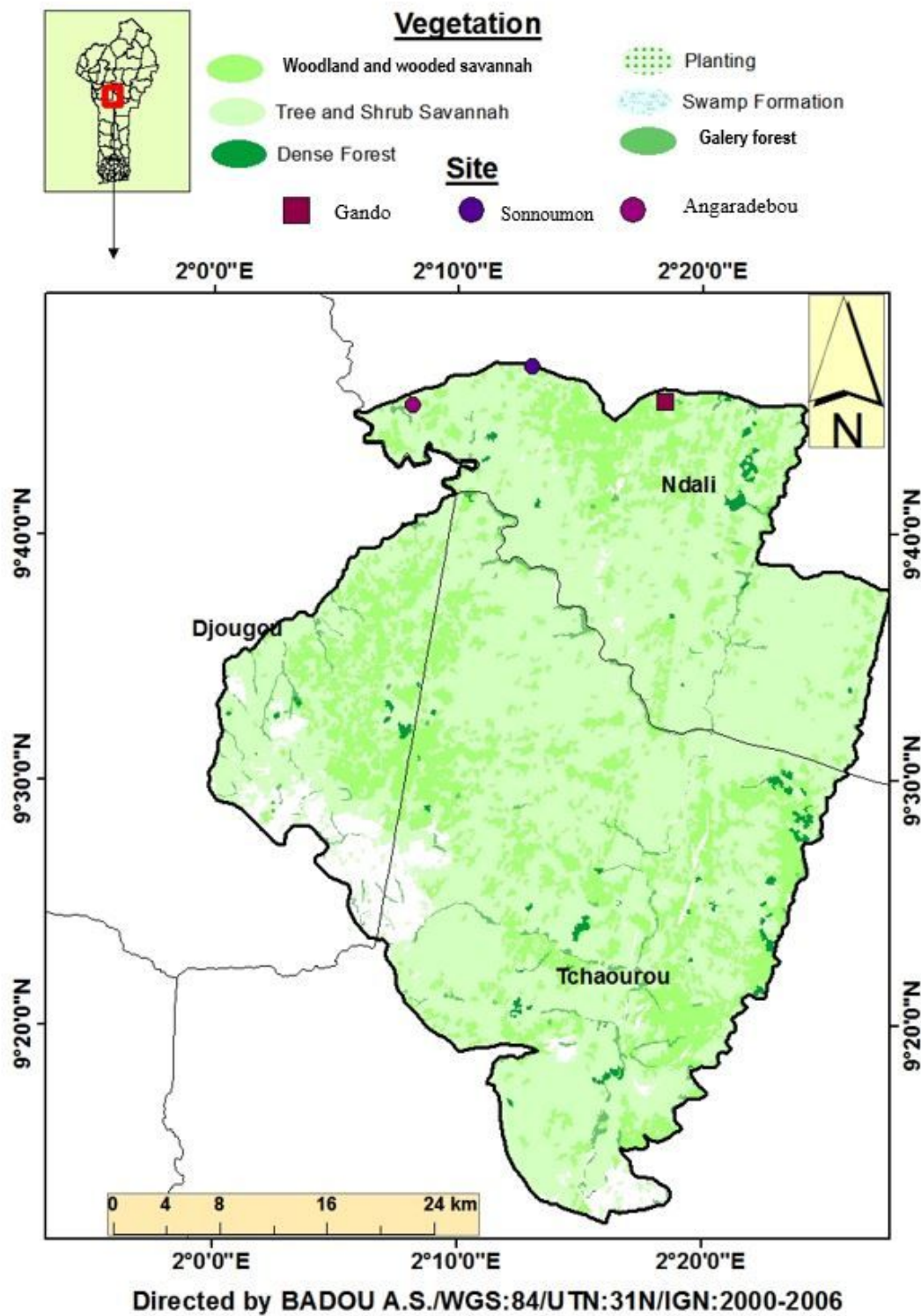
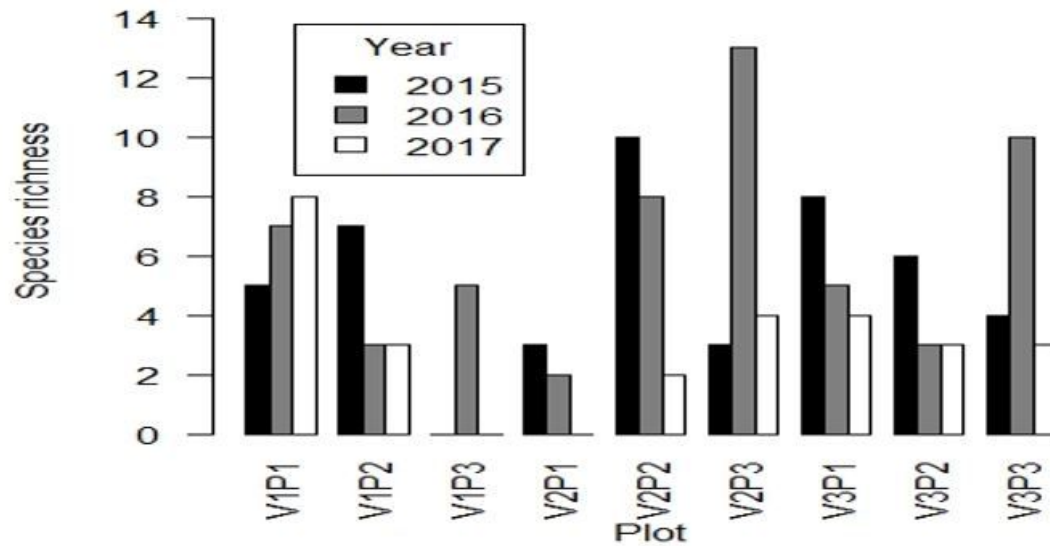


Figure 1

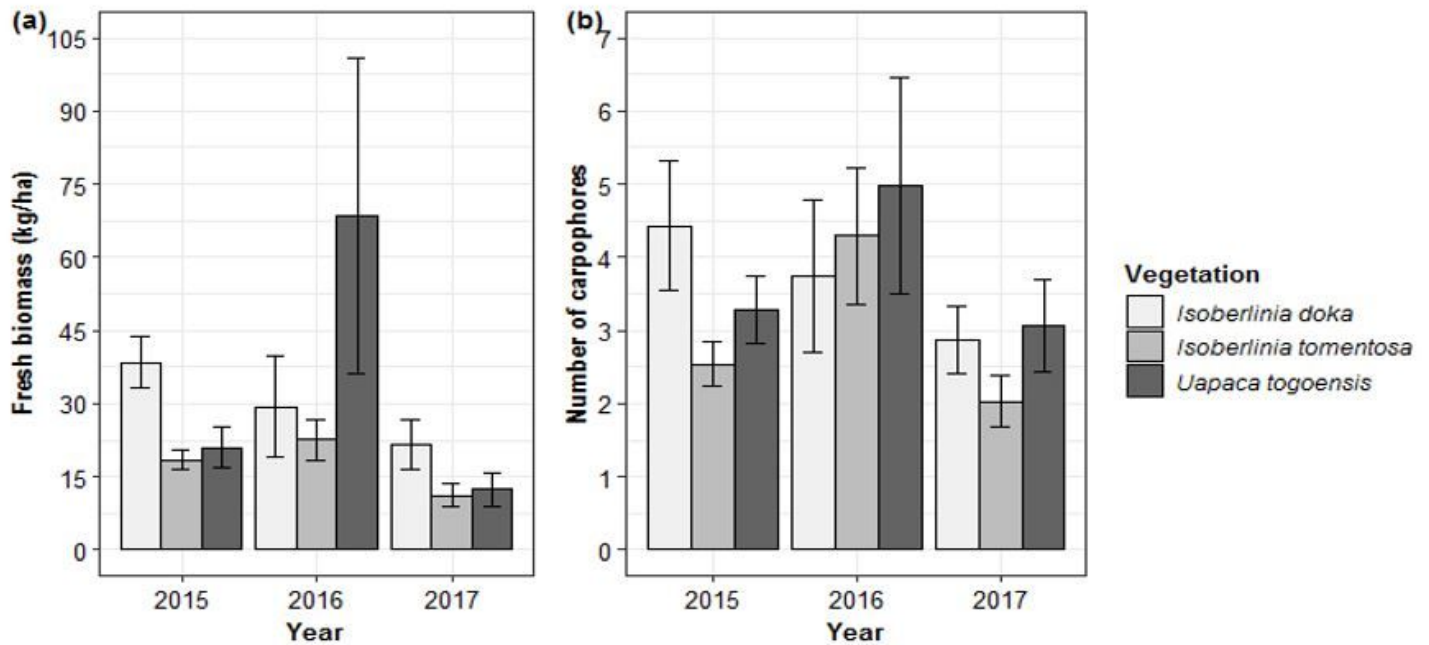
Vegetation map of the Ouémé Supérieur Forest Reserve



V1P1 = Plot *I. doka* Angaradebou
 V2P1 = Plot *I. tomentosa* Angaradebou
 V3P1 = Plot *U. togoensis* Angaradebou
 V1P2 = Plot *I. doka* Gando
 V2P2 = Plot *I. tomentosa* Gando
 V3P2 = Plot *U. togoensis* Gando
 V1P3 = Plot *I. doka* Sonnonmon
 V2P3 = Plot *I. tomentosa* Sonnonmon
 V3P3 = Plot *U. togoensis* Sonnonmon

Figure 2

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



(Fruit bodies measurement unit =
Thousands of units / ha)

Figure 3

Mean of (a) the fresh biomass (Kg/ha) and (b) the number of fruit bodies for each vegetation per year of study

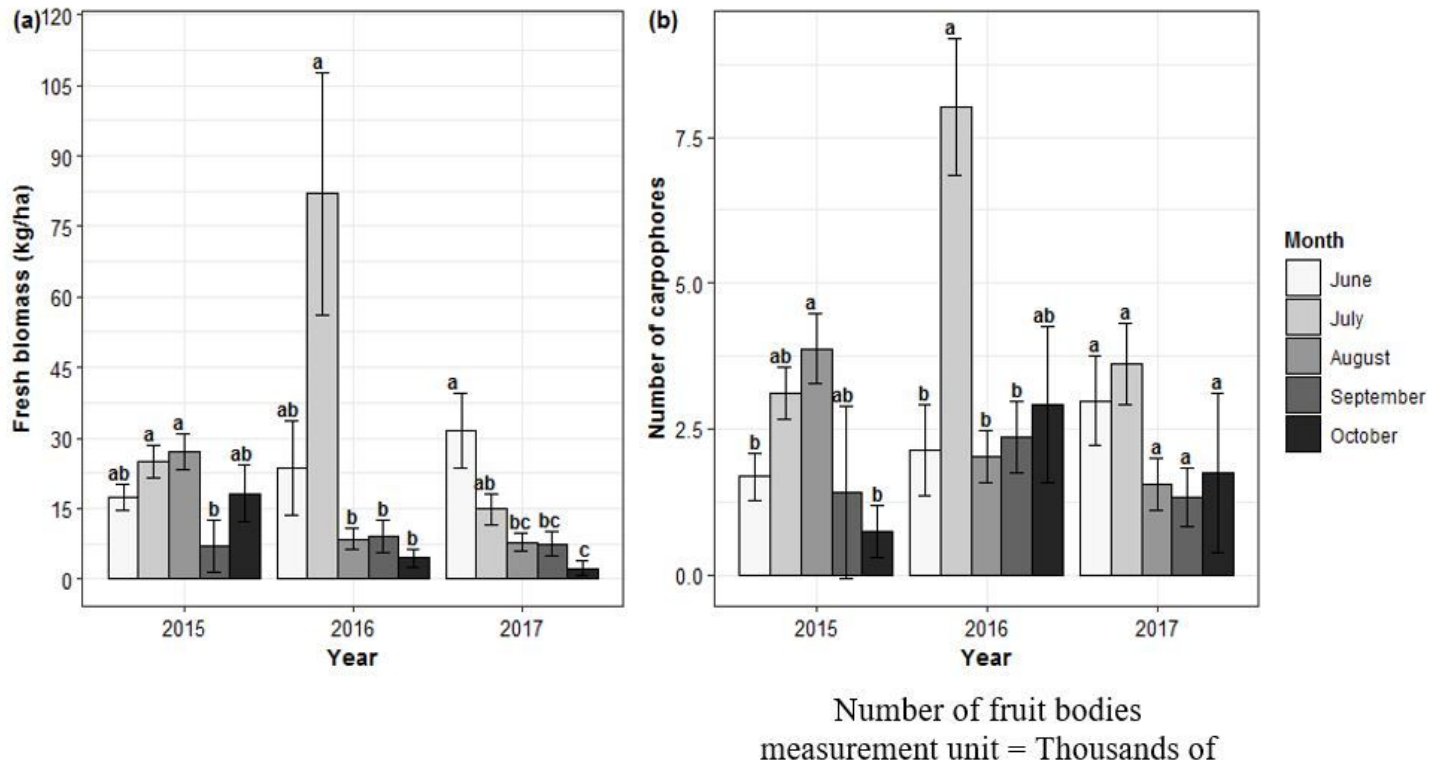


Figure 4

Temporal variation of fresh biomass from one 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 holds for different letters.

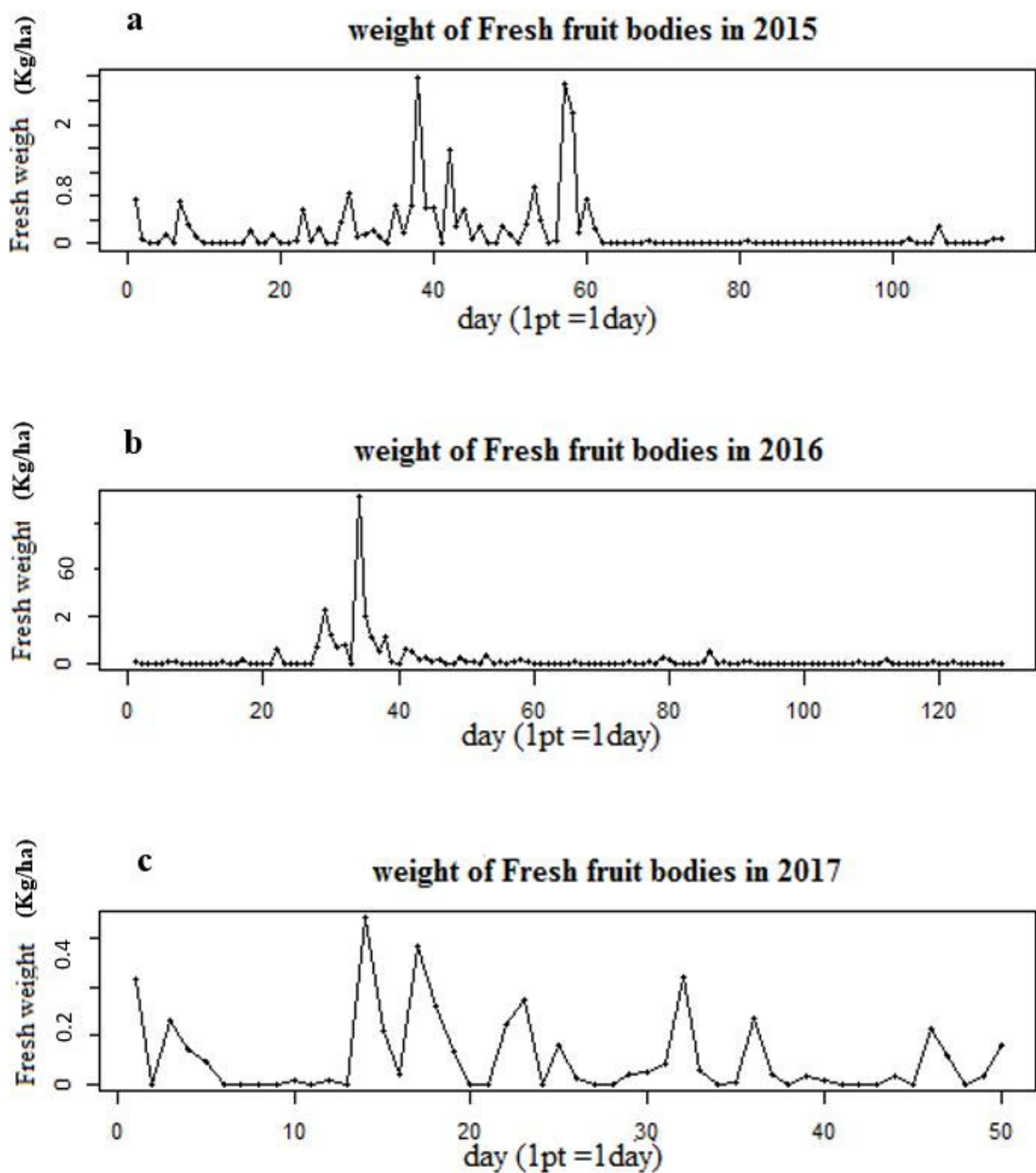


Figure 5

Temporal variation of fresh biomass of all vegetation combined in 2015, 2016 and 2017

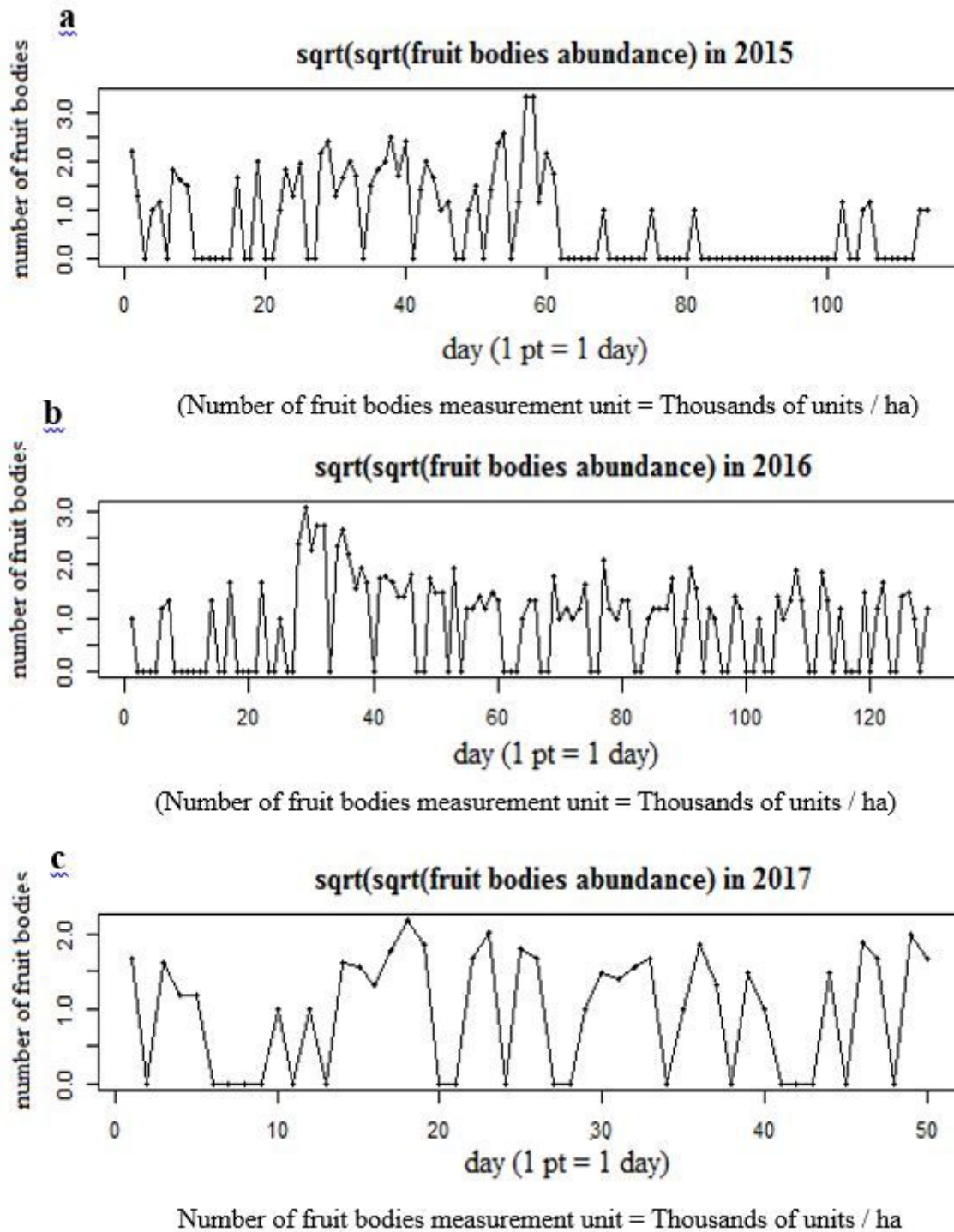


Figure 6

Temporal variation in the abundance of all vegetation combined in 2015, 2016 and 2017

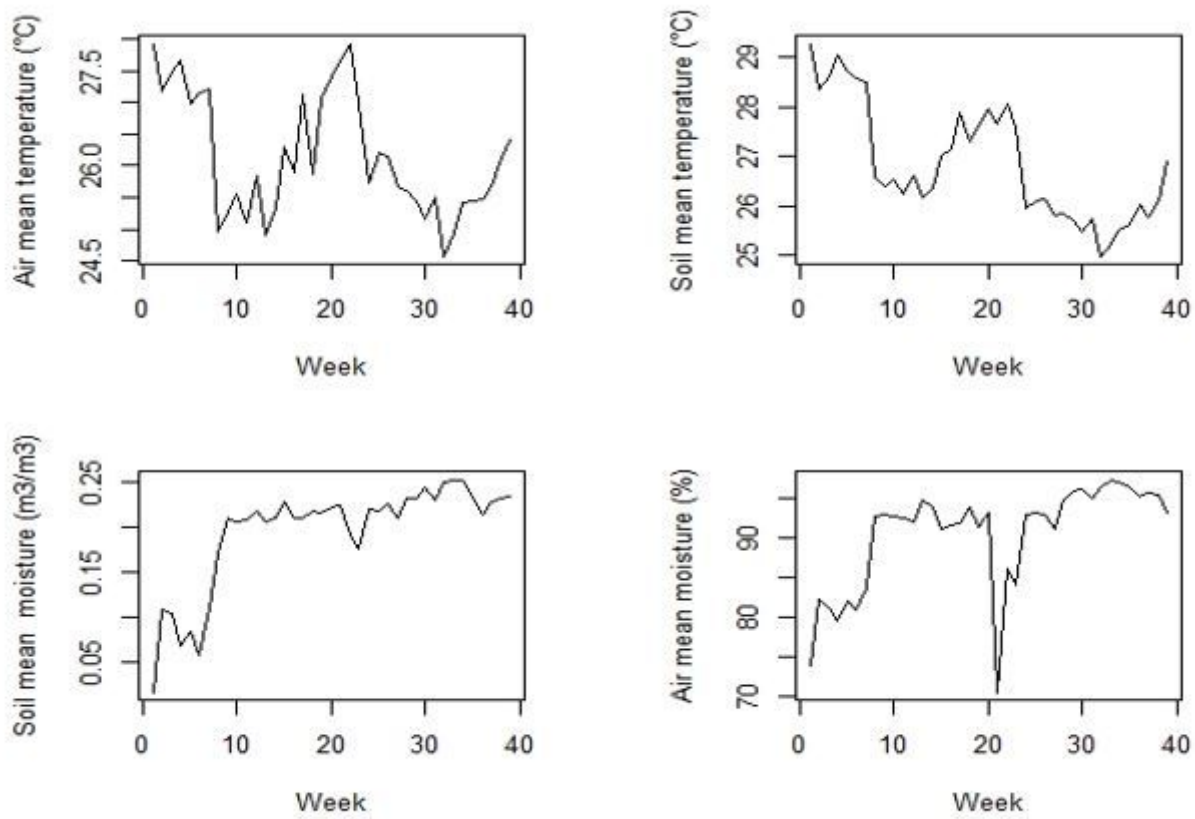


Figure 7

Temporal variation of the weekly mean of the microclimatic parameters in 2015

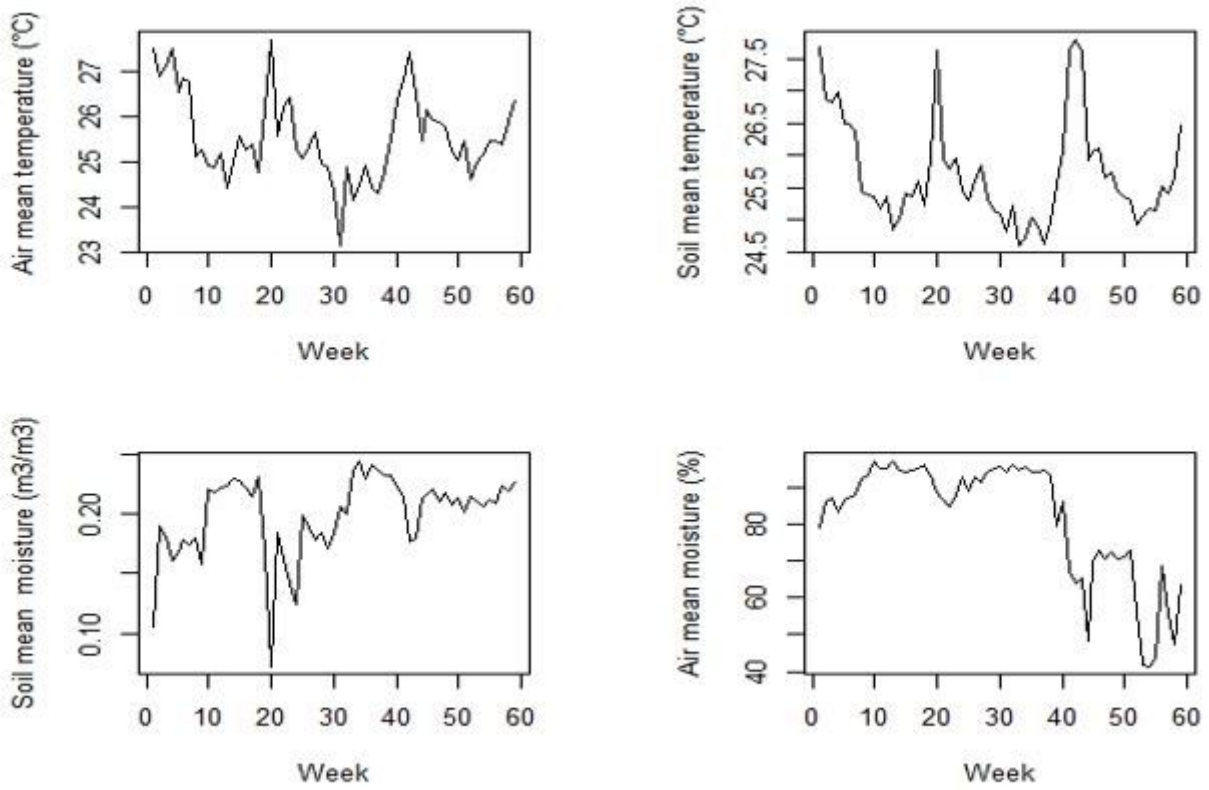


Figure 8

Temporal variation of the weekly mean of the microclimatic parameters in 2016.

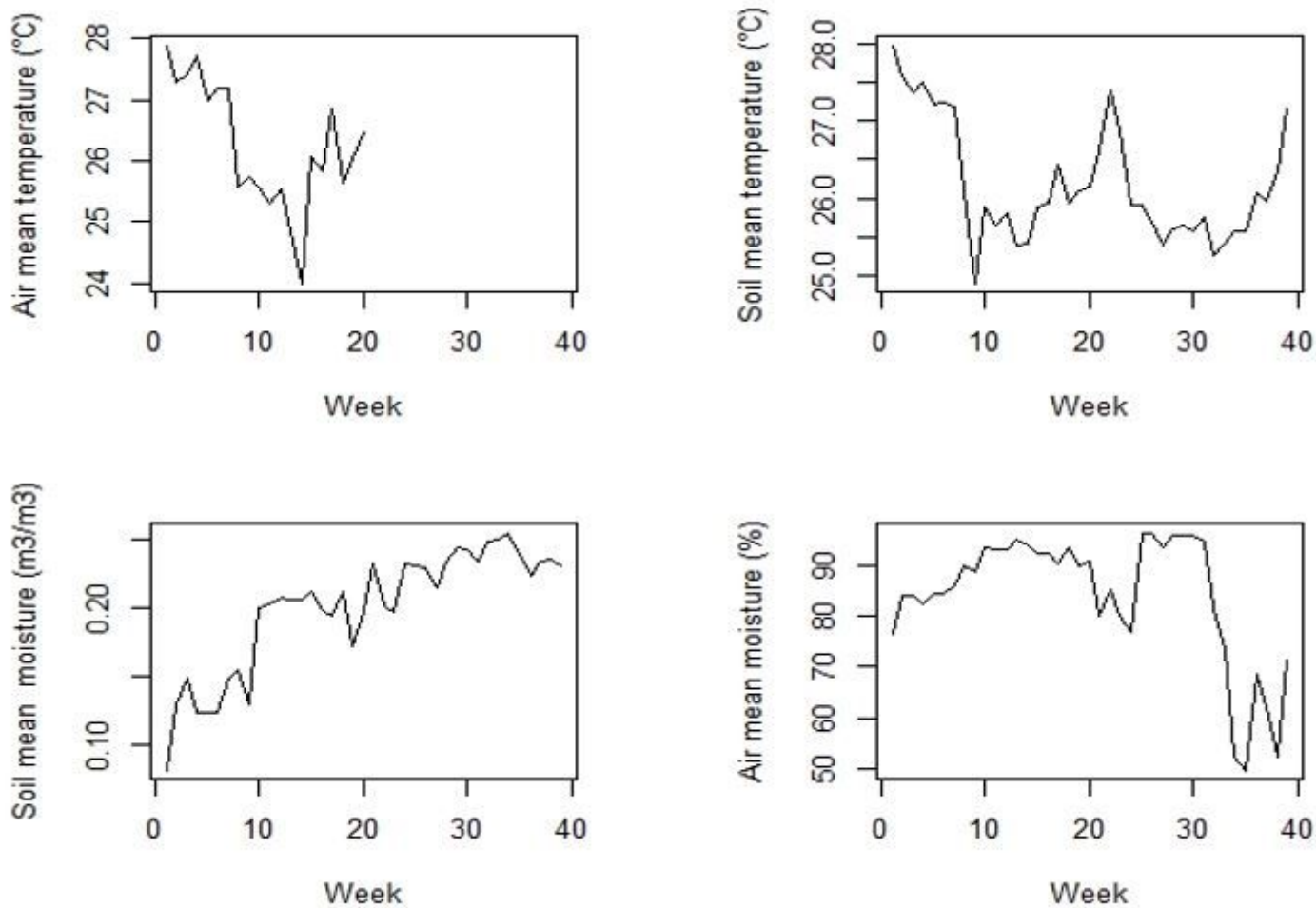


Figure 9

Temporal variation of the weekly mean of the microclimatic parameters in 2017.

Supplementary Files

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