
SOIL SEED BANKS IN TWO TROPICAL FOREST TYPES: ON THE RELEVANCE OF SAMPLING DEEP SOIL LAYERS

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<https://doi.org/10.35410/IJAEB.2020.5593>

ABSTRACT

The soil seed banks play a crucial role in the resilience of forests to disturbance. Sampling strategies are generally limited to the first 10 or 15 centimetres of the soil while deeper layers could conceal specific taxa. This study evaluates the variability of the seed bank as a function of depth or type of soil in two rainforests in the Congo. At each study site, 30 samples were taken per soil layer (litter, 0-5 cm, 5-10 cm and 10-20 cm). The diversity and abundance of the seeds were estimated after they were brought to germination. Two means of estimating the species richness and the rarefaction curves were used in order to estimate the diversity of the flora in each layer of soil. The results showed great variability between types of forest. They also highlighted greater diversity and higher abundance in the first 10 centimetres of soil. However, the proportions were nonetheless not negligible between 10 and 20 cm, and 21 % of plant species were encountered exclusively in this layer. The latter may therefore have a fundamental role in the resilience of forests to anthropogenic disturbances, including logging. Complementary studies are indispensable in order to better understand this role as well as the factors which have an effect on the temporal and spatial variability of the soil seed bank.

Keywords: soil seed bank; rarefaction curve; species richness; forest resilience; rainforests.

1. INTRODUCTION

The soil seed bank, which designates the stock of viable seeds present in the soil (Roberts, 1981; Garwood, 1989), has an important role in the maintenance of the ecological diversity of natural ecosystems (Livingstone and Alessio, 1968; Thompson and Grime, 1979; Brown and Venable, 1986; Houle and Phillips, 1988). Seeds buried in the soil may be brought back to the surface either by movements of roots or by organisms living in the soil or by anthropogenic disturbances (Vasquez-Yanes and Orozco-Segovia, 1993). For example, logging activities disturb the top soil by creating roads and skidding timber (Kleinschrot et al., 2015). The subsequent resilience of the forest will depend on the abundance of seeds and their germination rates in the different disturbed layers (Fayolle et al., 2014). Despite a growing number of studies on this subject, the sampling protocols are very variable from one study to another. Typically, a characterisation of the soil seed bank of a region necessitates samples from a soil of known dimensions, which are then placed in optimal conditions for germination. The vast majority of studies touching on this

subject carry out unitary sampling which is on a small scale and focus on the first centimetres of soil (Shen et al., 2014).

However, the procedures of sampling soil in order to study the seed bank are far from being unanimously accepted. For example, even though most of these studies take samples corresponding to a total surface area of less than 1 m² (e.g. Moles et al., 1999; Hosogi et al., 2006; Dainou et al., 2011), Shen et al. (2014) recently demonstrated that it is necessary to collect almost four times as much in order to estimate the floristic richness of the emperate forest soil seed bank. Similarly, most studies concentrate sampling on the first 5 to 10 centimetres of the soil (Pakeman & Small, 2005; Hosogi et al., 2006; Martins & Engel, 2007; Dainou et al., 2011). However, taking into account the deeper layers may be necessary given that (i) numerous studies have demonstrated that the viability of seeds seems to grow with depth, some taxa display life durations close to a century; (ii) the abundance of certain species increases with depth they belong to the species of the first stages of plant succession, species which may no longer be represented in the surrounding environment (Warr et al., 1993 ; Grandin and Rydin, 1998; Csontos and Tamas, 2003).

Finally, the nature of the substrate may play a crucial role in the soil seed bank. It may not only influence the abundance of seed banks, independently of the densities of population of the forest stand (Warr et al., 1993), but also promote the emergence of the buried seeds. In particular, sandy soils, which are more mobile than heavy clay soils, tend to have more frequent emergences (Zhang and Maun, 1994; Leicht-Young et al., 2009).

In Central Africa, studies dealing with the soil seed bank are extremely rare (Dainou et al., 2011), and have never concentrated on the variability of the seed bank as a function of depth or the type of soil. This paper concentrates on these questions, considering the environmental context of two tropical rainforests, developing on two different substrates in the north of the Republic of Congo. More specifically, it studies the characteristics of the soil seed bank at depths rarely studied, between 10 and 20 cm. The hypotheses orienting the study are: (1) the characteristics of the soil seed bank vary significantly depending on the depth and the substrate; (2) deep layers conceal a not inconsiderable seed bank; (3) the specific species of deep layers are characteristic of pioneer taxa.

2. MATERIALS AND METHODS

2.1. Study sites

The study was carried out in two rainforests in the north of the Republic of Congo. The first site, within the forest management unit attributed to CIB/OLAM, is close to Loundoungou Forests (FL). The second site, within the forest management unit of Mokabi-Dzanga, is close to Mokabi Forests (FM). FL and FM extend respectively between 02°18' – 02°22'N and 17°31' – 17°34'E then 03°01' — 03°37'N and 16°30' — 17°22'E (Figure 1). The two areas are relatively flat with average altitudes between 430 m and 530 m. They display a bimodal distribution of seasonal precipitation. The average annual rainfalls and the average temperatures are 1729 mm and 25°C for FL, and 1670 mm and 24°C for FM (Bégué, 1967). The two sites differ with respect to the composition of their flora and substrate: the Loundoungou forests are semi-deciduous, and are located on clay soils developing on alluvial deposits in the Cuvette of the Congo. The Mokabi

forests are transitional forests between the semi-deciduous and evergreen types, established on sandy soils on the sandstones of Carnot.

In terms of chemical fertility, the soils of FM are relatively poorer than those of FL (Boulvert, 1996; Verelst, 2009; Fayolle et al., 2012; Freycon, 2014). The Loundoungou forests shelter numerous species typical of old secondary forests such as *Erythrophleum suaveolens*, *Triplochiton scleroxylon* and *Terminalia superba*. Those Mokabi forests have a composition which is typical of more mature forests, with species such as *Prioria oxyphylla*, *Staudtia kamerunensis*, *Polyalthia suaveolens*, *Manilkara mabokeensis*, *Autranella congolensis* (Fayolle et al., 2012 ; Gond et al., 2013).

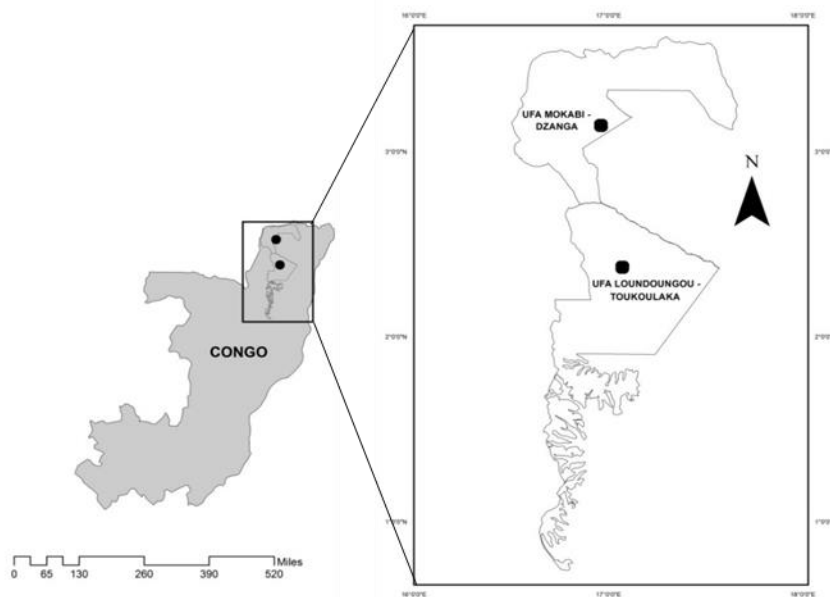


Figure 1. Location of the two study sites in the forest management units of Mokabi (FM) and Loundoungou (FL).

2.2. Sampling strategy and seedling emergence test

The soil samples were taken in January 2015, during the transition between the long dry season and the short rainy season. On each of the two sites, the soil samples were collected in a plot of 4 km² (2 x 2 km) monitored by the DynAfFor project (Picard and Gourlet-Fleury, 2008). Within each plot, five parallel trails of 2 km length each were used for the implantation of sampling points. Six collection points at intervals of 300 m were set up on each trail, making a total of 30 collection points per site (Figure 2). Four layers of soil were sampled for each point: litter, 0-5 cm, 5-10 cm and 10-20 cm. Each sample was a composite one, in other words a mix of three unitary samples carried out at the points of an equilateral triangle of 1 m side length (Perera, 2005; Daïnou et al., 2011). Each sample covered a surface area of 100 cm² (10 x 10 cm). The surface area sampled per plot was consequently 0.9 m². The depth of the samples was 5 cm for the 0-5 cm and 5-10 cm layers. It was 10 cm for the 10-20 cm layer. The number of viable seeds in the soil was estimated by the method of germination (van der Valk & Davis, 1978). The

samples were sieved before the beginning of the experiment, in order to eliminate crude plant and mineral matter (e.g. leaves or pieces of wood).

The germination was carried out in a greenhouse at the semi-industrial nursery of the SNR (National Reforestation Service) in Brazzaville, in a non-forest zone in order to limit the risk of contamination of the samples by the surrounding vegetation. The relative luminous intensity was about 30-40% of full light. Each soil sample was spread out over a layer of sand-substrate mixture with a thickness of approximately 1 cm (Hall & Swaine, 1980; Dalling et al., 1994). The substrate was previously decontaminated of any seed by heating (Hall & Swaine, 1980). Watering was almost daily, and checking of the germinations was biweekly. When their development stage allowed it, the seedlings were removed and planted individually in polyethylene bags in order to favour their growth and identification. As all of the germinations took place over the course of the next 12 weeks, the experience finished at the end of 16 weeks.

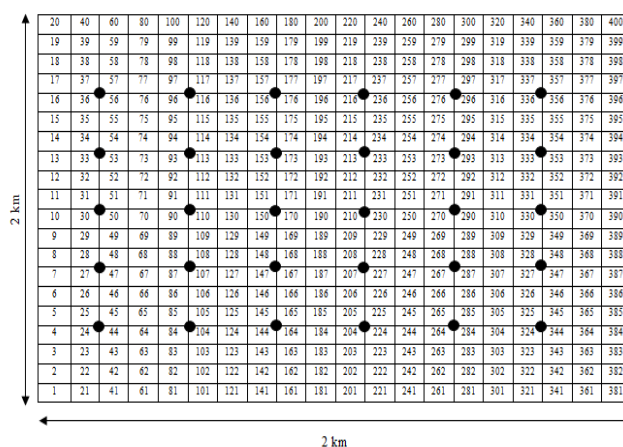


Figure 2. Sample design of the soil seed bank on a plot of 400 ha. Symbols: black circle = point of collection of soil samples; square with number = 1ha.

2.3. Data analysis

We computed the species richness observed (Walther et al., 2005), but for comparison we used the estimators Chao2 (and its “bias-corrected” version, both being based on incidence) and Jackknife1 (based on abundance) $n S_{obs}$ being very dependent on the sampling effort (Poulin, 1998; Walther and Morand, 1998; Walther and Martin, 2001; Chiarucci et al., 2003; Dove and Cribb, 2006). The program EstimateS 9.1.0 (Colwell, 2013) was used in order to generate both the observed species richness S_{obs} and the estimated richnesses, S_{chao2} (bias-corrected Chao2) and S_{jack1} . These two types of richness were illustrated by rarefaction curves. Finally, the density of viable seeds per layer was calculated by accumulating the data of each point per level of soil. A redundancy analysis RDA was carried out for each site on the basis of the Hellinger distances between samples (Rao, 1995; Legendre and Gallagher, 2001). The samples not having provided any germination were excluded from the analysis. The RDA was carried out with the program *R* and the *Vegan* package. The indices of Sorensen and Morisita-Horn were used in order to evaluate the similarity of the soil seed bank between the layers of the same site. Compared with

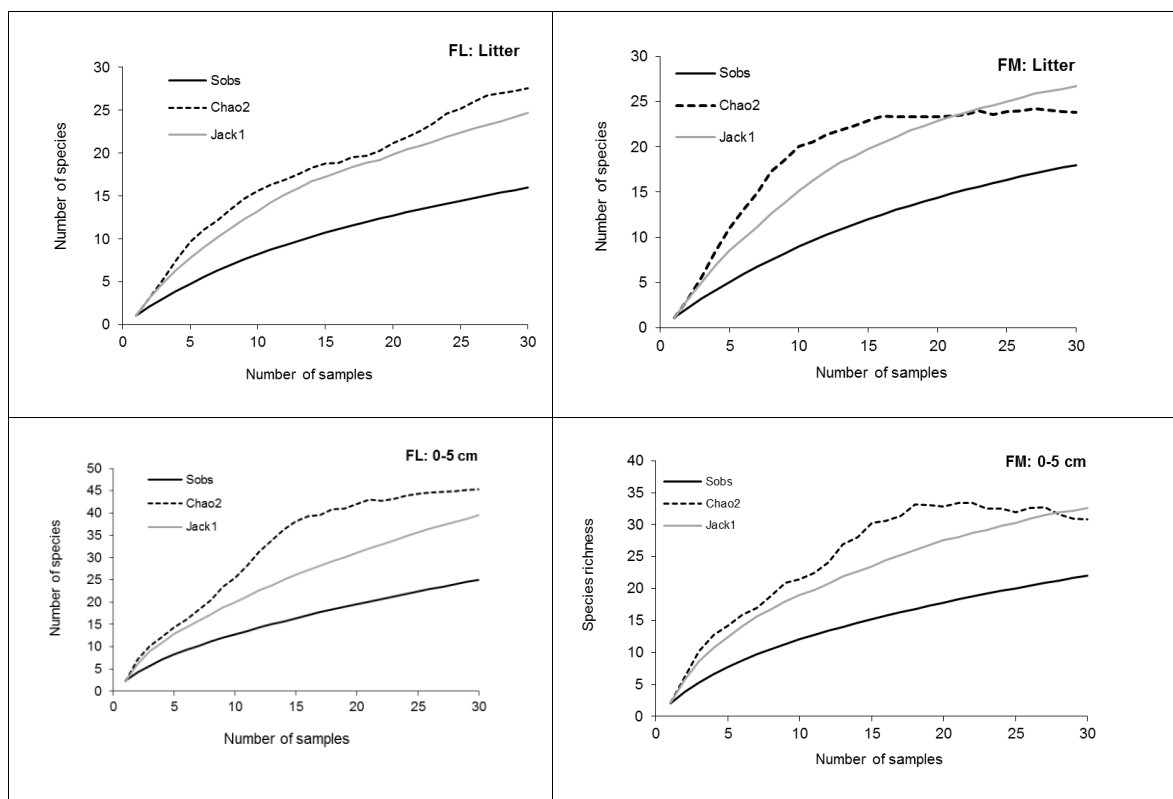
the Sorensen index, the Morisita-Horn index is more sensitive to abundant species in the communities compared (Chao et al., 2006).

Finally, the specificity of layers in terms of species found exclusively in each layer was determined by comparing these “characteristic” species with the total number of species found in the layers (% S_{char}).

3. RESULTS

3.1. Species richness and seed abundance among layers

The layers of the FL site generally display a greater richness than those of the FM site. The rarefaction curves of richness estimated by Chao2 demonstrate that the values are closer to the asymptote in the layers of FM (Figure 3).



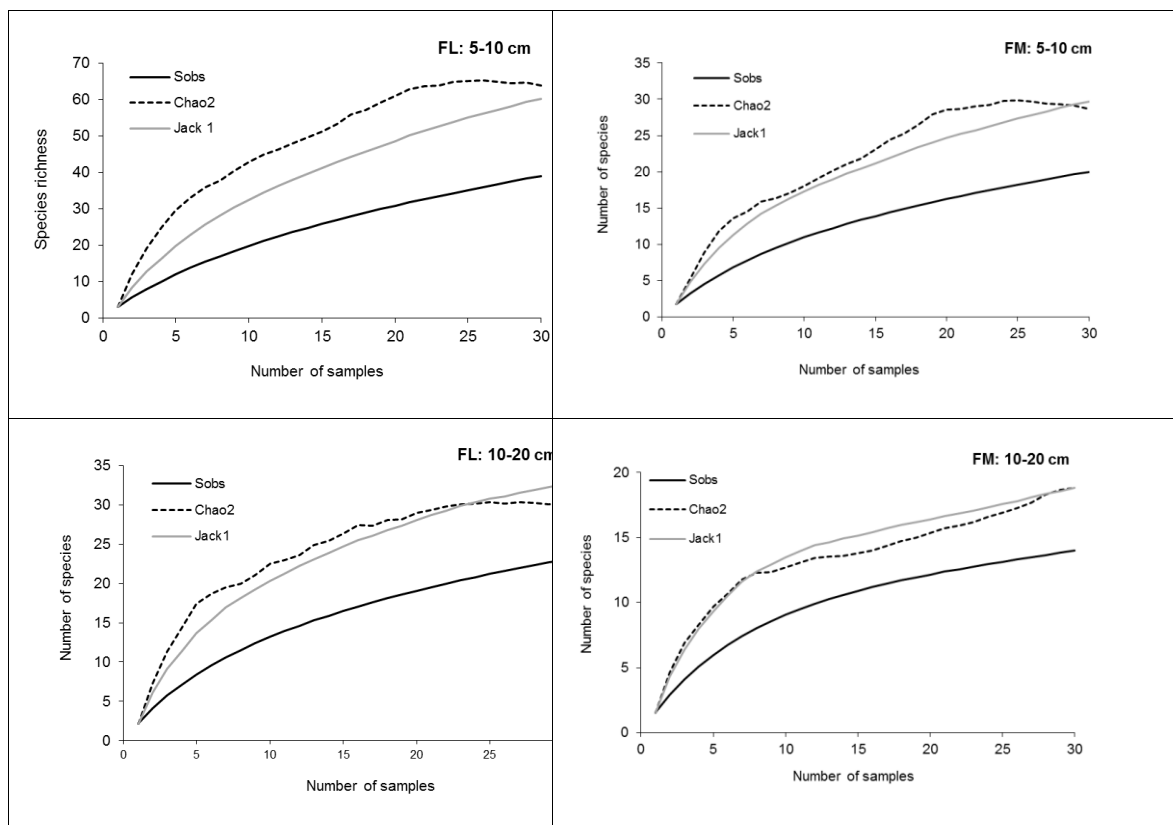


Figure 3. Rarefaction curves for each layer of the two sites studied.

Whatever the means of estimation considered, the two intermediate layers, 0-5 cm and 5-10 cm, display the highest richnesses (Table 1). At the FL site, the estimated richness in the 5-10 cm layer, approximately 60 species, is twice as high as that of the “litter” and 10-20 cm layers. At the FM site, the two intermediate layers have similar richnesses, of around 30 species. The lowest richness for FL is observed in the litter, with 25-28 species, whereas it is the 10-20 cm layer which is the least rich for FM, with 19 species.

Table 1. Specific richnesses, observed (S_{obs}) and estimated (S_{jack1} , S_{chao2}), and percentages of characteristic species ($\%S_{char}$) of the layers of soil at the two sites, FL (clay soil) and FM (sandy soil).

Layers	FL				FM			
	S_{obs}	$\%S_{char}$	S_{chao2}	S_{jack1}	S_{obs}	$\%S_{char}$	S_{chao2}	S_{jack1}
Litter	16	31.3	27.6	24.7	18	16.7	27.6	23.8
0-5 cm	25	4.0	45.3	39.5	22	27.3	30.9	32.6
5-10 cm	39	28.2	63.8	60.3	20	25.0	28.7	29.7
10-20 cm	23	21.8	30.3	32.7	14	21.4	18.8	18.8

In terms of density, the tendency observed with respect to the specific richness remains the same: the intermediate layers 0-5 cm and 5-10 cm show higher densities than those of other layers, with values between 86 and 123 seeds/m² at FL, and around 70 seeds/m² at FM (Table 2). At both sites, the proportion of seeds observed in the 10-20 cm layer represents around 25% of the seed bank of the site.

Table 2. Seed abundance among layers in the two studied sites (number of seeds/m²)

Layers	FL	FM
Litter	41.1 ± 4.4	38.9 ± 4.2
0-5 cm	86.7 ± 8.8	73.3 ± 7.6
5-10 cm	123.3 ± 11.5	68.9 ± 6.7
10-20 cm	78.9 ± 7.2	63.3 ± 6.3

3.2. Overall comparison of seed bank composition among layers

The comparison of the layers using an RDA on the basis of the distance of Hellinger between samples reveals overall that the characteristics of seed banks are rather similar in each layer, even though some samples stand out (Figure 4).

In both cases, no species is strongly associated with an axis (annexe 1), and it is necessary to consider the first five axes in order to obtain an explained variance of at least 20% (regular decline of eigenvalues; annexe 1). Axes 1 and 2 represented on Figure 4 explain respectively total 9.3% and 10.2% of the total variance in FL and FM.

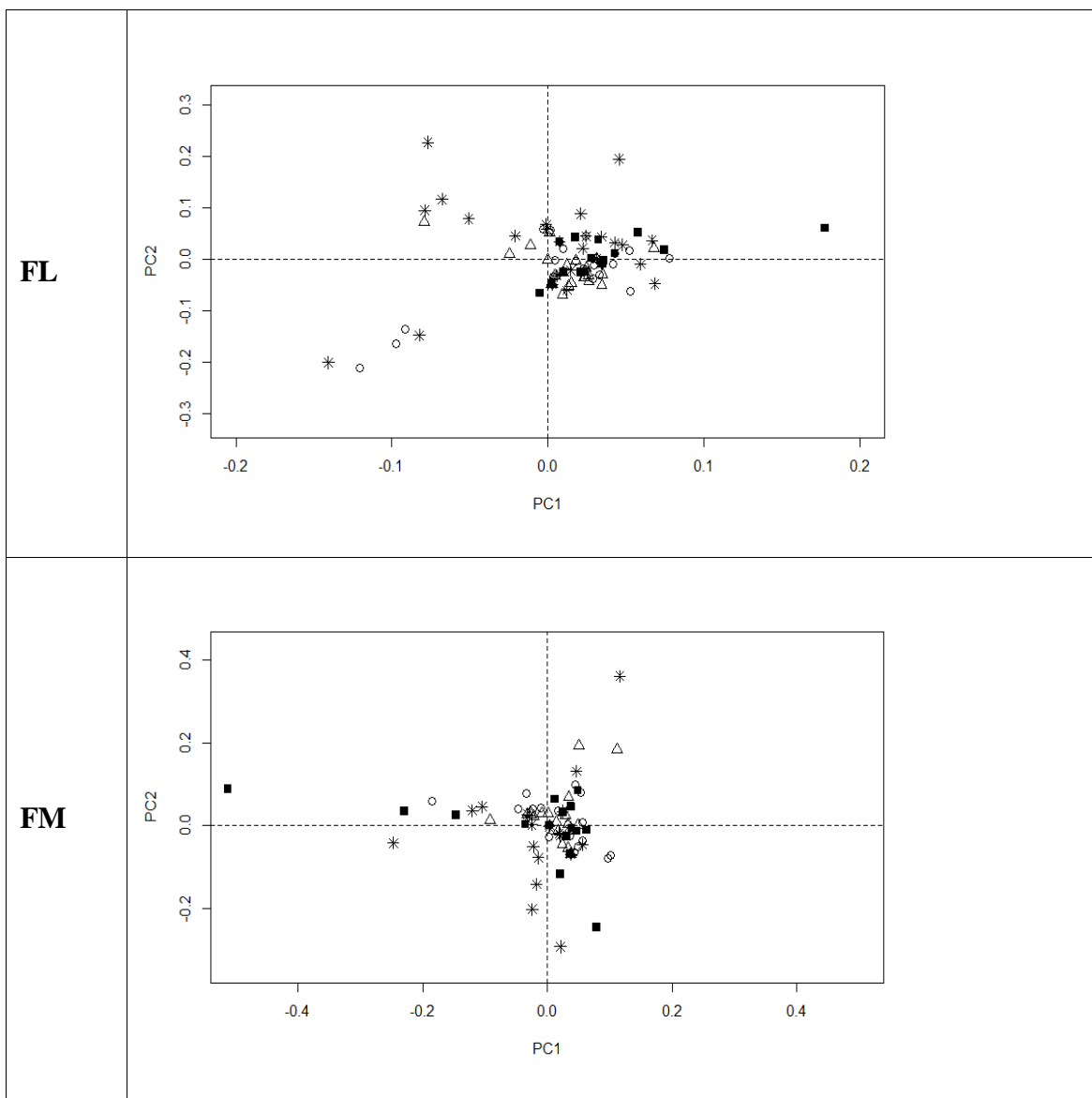


Figure 4. RDA carried out on the data of specific abundance of the layers of each site. Symbols: black square = litter; empty circle = 0-5 cm; star = 5-10 cm; triangle = 10-20 cm.

A certain specificity of the different layers is noted. In fact, apart from the 0-5 cm layer in the FL site, for which the proportion of characteristic species is virtually negligible, all of the other layers, including the deepest of each site, display rates of characteristic species which are generally higher than 20% (Table 1). The characteristic taxa for the FL site are: litter layer: 23%; 0-5 cm layer: 4%; 5-10 cm layer: 50%; 10-20 cm layer: 20%. The characteristic taxa for the FM site are: litter layer: 18%; 0-5 cm layer: 35%; 5-10 cm layer: 29%, and 10-20 cm layer: 18%.

4. DISCUSSION

The results of this study display the first tendencies showing the relevance of sampling the deeper layers of soil in rainforest of Central Africa. Even though the proportions and the species

richness are the highest between 0 and 10 cm of depth, the 10-20 cm layer is overflowing with species which are peculiar to it, as more than 21% of the species found are from this layer. Even though these observations are valid for both of the sites studied, one of the two sites are distinguished by its higher overall proportions and diversities.

4.1. Abundance and diversity per soil layer

Various mechanisms, of abiotic and biotic origin, explain the movements of seeds in the soil. Movements of roots, the subsidence of soil around the roots, the splashing effect of raindrops, the action of burrowing rodents, and the movement of earthworms and of arthropods all take part in the burying and exhumation of soil seeds (Plue & Hermy, 2012).

Several studies have demonstrated that, generally, the proportion of seeds in the soil diminishes progressively with depth (for instance Kellman, 1970; Moore & Wein, 1977; Putz, 1983; Putz & Appanah, 1987; Kramer and Johnson, 1987). Perera (2005) reported that at least 70% of seeds were stored in the first four centimetres of the soil in tropical semi-deciduous forests of Sri Lanka.

Nonetheless, opinions diverge on this overall tendency: Young et al. (1987), report an almost uniform distribution in a tropical forest of Costa Rica. There are great variabilities depending on the species considered: some species are more abundant in the upper layers and others in the intermediate layers, whereas another group seems to be best represented in the deepest layers (Warr et al., 1993). The capacity to germinate *a priori* seems to be better for seed stores in the upper layers, which are made up of more recent deposits than those of deeper layers. The latter contain more seeds which have been dormant for longer (Ray et al., 1983). Rampton & Ching (1970) are of the opinion that the viability of seeds increases with their depth of burying in the soil, and that this viability may last greater than a century but there are very few studies on seed banks relating to layers reaching a depth of 20 cm.

The pioneer species of the first stages of succession display more dormant seeds than the species of later stages (Hall and Swaine, 1980; Garwood, 1989). Moreover, these pioneer species are generally seeds of smaller dimensions which are likely to escape the effect of granivorous animals, which may explain their dominance in seed banks (Venable, 1989). According to Page et al (2006), the number of unobserved species varies according to the circumstances, and it is necessary to use means of estimating the specific richness in order (1) to evaluate the reliability of the sampling, (2) to give a precise value of the species richness. Heck et al. (1975) and Karakassis (1995) nonetheless remind that studies of species richness must deal with homogenous groupings, and that the stratification of communities may be indispensable. Our study was carried out with forest stands of which an inventory had previously been made (DynAfFor project), displaying a homogeneous floristic composition over the area of sampling. The results which emerge are therefore not biased by any heterogeneity of the groupings. The proportion of richness directly revealed by the study, in comparison with that suggested by the "bias-corrected Chao2", varies between 58-65% in the first layers and 74-76% in the deep layer (10-20 cm). However, the curves of rarefaction based on the Jackknife estimator do not in fact converge towards the asymptote for any layer. According to Walther et al. (2005) and Marcon

(2016), this reflects insufficient sampling, even though a total surface area of 1.8 m² was sampled in our two sites.

4.2. Inter-site variation

The layers of the FL display a greater richness than do those of the FM, more precisely at the two intermediate layers, 0-5 cm and 5-10 cm. The floristic composition of the FL corresponds to a semi-deciduous forest, with a more marked seasonality: the species with dormant seeds may therefore be greater in number there (Martins and Engel, 2007; Chen et al., 2013). This forest has also experienced numerous anthropogenic disturbances in the past (Oslisly et al., 2013; Morin-Rivat et al., 2014); it is therefore younger and more dominated by light-demanding species. According to Han et al (2012), the light-demanding species of the first stages of plant succession produce many more seeds than the species of mature forests and, consequently, display more dormant seeds than the species of mature forests.

However, Alvarez-Aquino et al (2005) specify that forests having been subjected to disturbances in the past conceal greater proportions of soil seed banks dominated by pioneer species. This suggests that the disturbed forests at the FL site may have a greater potential for regeneration compared to forests at the FM site, which are typical of more mature forests.

Moreover, pioneer trees adapt better to deteriorated environments, and the germination of their seeds is inherently linked with a strong light intensity created by the degree of opening of the canopy (Pearson et al., 2003).

The nature of the soil, principally its acidity and porosity, may also have an influence on the abundance of the seed bank, although these influences have mainly been studied in temperate zones and savannahs (Wilson and Witkowski, 2003; Witkowski and Garner, 2008). The few studies realised in tropical forests of Asia and America (Chen et al., 2013; dos Santos et al., 2013) tend to demonstrate that the soil seed banks were more developed in relatively rich soils, compared with relatively poor soils. The survival of the soil seed bank of tropical forests could be correlated with the quantity of nutritive reserves in the soil (Osunkoya et al., 1992; Hammond and Brown, 1995; Baraloto, 2001). The FM, based on soils characterised by a low availability of resources such as water and nutrients (Fayolle et al., 2012) could be less favourable for the conservation of seeds in comparison with the FL site, which is based on clay soils and which is characterised by high availability of resources such as water and nutrients (Fayolle et al., 2012).

5. CONCLUSION

Our results show a significant variability in the soil seed bank, on the one hand between soil layers, and on the other hand between sites. The presence of seeds only found in the 10-20 cm layer may have some notable implications, in particular with respect to the resilience of forests to anthropogenic disturbances, including logging activities. Logging is the most significant form of legal occupation of land in the Congo Basin (Nasi et al., 2012). The speed of recolonization of the roads, skidding trails and gaps depends on the soil seed bank (Kleinschrot et al., 2015). During exploitation activities, the soil may be disturbed to non-negligible depths, and so the abundance and diversity of seeds present in the soil are fundamental constituents of forest recolonization. The factors determining the spatial and temporal variation of the soil seed bank

and its development in forest stands exploited by man should therefore be studied in detail in order to gain a better understanding thereof.

Acknowledgements

The authors wish to thank Marien NGOUABI University (Republic of the Congo), the University of Liège and its faculty Gembloux Agro-Bio Tech (Belgium), the PEFOGRN-BC projects (support project for the wider programme of training in natural resources management in the Congo Basin), the associations Nature + and DynAfFor project (*Dynamique des Forêts d'Afrique Centrale*, Dynamics of Central African Forests), as well as the logging companies Mokabi-Dzanga (Groupe Rougier) and CIB/OLAM for their financial, scientific and technical support, and for their aid with fieldwork.

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Annexe 1. Positioning of the variables (species) on axes 1 and 2, and total proportion of the explained characteristic values by each axis of the RDA for the FL and FM sites. (A): FM site; (B): FL site.

