Scientific Research Publishing

Open Journal of Forestry, 2023, 13, 294-314
https://www.scirp.org/journal/ojf
ISSN Online: 2163-0437
ISSN Print: 2163-0429

Soil Seed Bank Characteristics in Congolese Rainforests and Implications for Post-Logging Plots Reforestation

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How to cite this paper: Douh, C., Mabengo, B. C., de Dieu Nzila, J., Malonga, L. M., Nsongola, G., Loumeto, J. J., Mankessi, F., Ndzaï, S. F., & Koubouana, F. (2023). Soil Seed Bank Characteristics in Congolese Rainforests and Implications for Post-Logging Plots Reforestation. *Open Journal of Forestry, 13,* 294-314.
https://doi.org/10.4236/ojf.2023.133018

Received: February 24, 2023
Accepted: July 2, 2023
Published: July 5, 2023

Abstract

The soil seed bank is considered as an important mechanism for the natural regeneration, resilience and conservation of the forests after disturbances. This study evaluates the characteristics of the soil seed bank in two post-logging plots of Loundoungou-Toukoulaka Forest Management Unit: one plot exploited in 2008 and another exploited in 2021. In each study plot, 40 samples were collected per soil layer (0 - 5 cm, 5 - 10 cm, 10 - 15 cm, 15 - 20 cm and 20 - 25 cm depth). The species diversity and abundance of the soil seed bank were estimated after soil samples were brought to germination. The results demonstrated that 347 seedlings belonging to 37 species in the plot exploited in 2008 and 418 seedlings belonging to 27 species in that exploited in 2021 germinated during 20 weeks of monitoring. The total densities of the seedlings identified were respectively 1446 seedlings/m^2 and 1742 seedlings/m^2. The plot exploited in 2021 presented a higher proportion of herbaceous species (93.78%) compared to that exploited in 2008 (82.71%). Two pioneer species were recorded in the plot exploited in 2008. These are *Macaranga barteri* (0.29%) in the 0 - 5 cm layer and *Musanga cecropioides* (2.31%) up to 20 cm deep. On the other hand, in the plot exploited in 2021, *Macaranga spinosa* (0.96%) in the 0 - 5 cm layer and *M. cecropioides* (0.96%) up to 20 cm deep were identified. In the plot exploited in 2008, the 20 - 25 cm layer demonstrated important proportions in woody species (9%), these are in particular

Rubiaceae sp.4 and *Nauclea diderrichii.* While that exploited in 2021, presented 19% of woody species, namely the species of Rubiaceae sp.4, Rubiaceae sp.5 and *N. diderrichii*, greatly exceeding the proportions obtained in the 15 - 20 cm layer of the two plots. Nonetheless, *N. diderrichii* was the only commercial species recorded with densities of 108 seedlings/m^2 and 4 seedlings/m^2, respectively in the plot exploited in 2008 and that exploited in 2021. Commercial tree species are poorly represented in the soil seed bank. Consequently, the study suggests that to improve the natural regeneration of the commercial species, silvicultural interventions based on planting techniques in the exploited plots should be more effective in order to sustainably manage these production forests.

Keywords

Soil Seed Bank, Natural Regeneration, Logging, Commercial Tree Species, Central African Rainforests

1. Introduction

Tropical forests are currently subject to diverse disturbances such as fires, illegal logging, slash-and-burn agriculture, with impacts on their natural regeneration potential (Krauss et al., 2010; Nunez-Cruz et al., 2018). These disturbances can over time entrain the alteration of ecosystem functions (Silvério et al., 2019). Nowadays, the restoration of disturbed ecosystems is a major challenge (Doucet et al., 2009; Krauss et al., 2010; Adjalla et al., 2022).

Soil seed bank could be a natural solution for biodiversity conservation of the disturbed ecosystems (Garwood, 1989; Bakker et al., 1996). It is considered as an important mechanism of the natural regeneration of ecosystems in the process of ecological successions of the tropical forests (Martins & Engel, 2007; Plue et al., 2010; Douh et al., 2018a). The soil seed bank generally includes all viable seeds buried in the soil, the litter and humus (Garwood, 1989; Walck et al., 2005; Douh et al., 2014; Douh et al., 2018a). These viable seeds, buried in the soil, play an important role in the conservation and restoration of the plant communities and, are an indicator of the forests resilience after disturbance (Thompson et al., 1997; Martins & Engel, 2007).

Thus, the soil seed bank is a negligible compartment of the dynamics of disturbed forest stands (Warr et al., 1993), but remains very little studied in Central African rainforests (Douh et al., 2014). The taking into account of the soil seed bank is therefore necessary in order to define relatively effective conservation, management and/or restoration strategies (Garwood, 1989; Zebaze et al., 2021).

Previous studies (Daïnou et al., 2011; Douh et al., 2014; Douh et al., 2018a; Zebaze et al., 2021; Adjalla et al., 2022) demonstrated that the soil seed bank is mainly contained in the first 20 centimeters of soil depth with relatively low spe-

cies densities and diversities in the deeper layers. Nonetheless, some works carried out in Cameroon and Republic of Congo on the soil seed bank are limited respectively in the first 5 and 20 centimeters of soil (Daïnou et al., 2011; Zebaze et al., 2021; Douh et al., 2018a). To our knowledge, no study has been leaded in Central African forests up to 25 cm soil depth in the post-logging forest plots. Consequently, the germination pace, composition and density of the seeds stored in 25 cm soil layers are still unknown.

In so far as it is relatively difficult to predict the natural regeneration potential and the resilience of the forests currently exploited in forests Central Africa and more particularly in Republic of Congo, this study proposes to evaluate the natural regeneration potential through the soil seed bank of the post-logging plots. Knowledge of these information will allow to understand the dynamics of floristic potential over time after logging. The aim of this study consists to assess the potential of natural regeneration through the soil seed bank in the post-logging plots. Three following hypotheses are formulated: 1) the depth of soil sample collection significantly influences the germination potential of the soil seed bank of each plot studied; 2) the floristic composition and the density of the soil seed bank varies in terms of seniority of the logged plots and the soil layers and, 3) the biological diversity of the soil seed bank varies considerably between plots and soil layers.

2. Material and Methods

2.1. Study Sites and Soil Sampling

The study was carried out in the moist tropical forests in the north of the Republic of Congo and more particularly within the forest management unit of Loundoungou, granted to the company Olam/Agri. Geographical coordinates of forest management unit of Loundoungou are: 02˚18' - 02˚22'N and 17˚31' - 17˚34'E (**Figure 1**). The area is relatively flat with average altitudes between 430 m and 530 m. It displays a bimodal distribution of seasonal precipitation. The average annual rainfall and the average temperature are respectively 1729 mm and 25˚C (Bégué, 1967). The forest management unit of Loundoungou is a semi-deciduous forest, installed on clay soils of the Congolese Cuvette (Gond et al., 2013; Freycon, 2014; Fayolle et al., 2014). It has been frequently disturbed in the past by traditional human activities (agricultural activities, hunting, etc.) (Oslisly et al., 2013; Morin-Rivat et al., 2014). It is composed of numerous light-demanding tree species such as: *Erythrophleum suaveolens* (Guill. & Perr.) Brenan, *Celtis* spp., *Terminalia superba* Engl. & Diels, *Petersianthus macrocarpus* (P. Beauv.) Liben and *Triplochiton scleroxylon* K. Schum. Some places of the undergrowth are invaded by lianas and giant herbaceous belonging to the Marantaceae and Zingiberaceae families (Gillet, 2013; Gond et al., 2013).

The soil samples were collected within two plots of 250,000 m^2 (one plot exploited in 2008 and another in 2021, named P08 and P21, respectively) in September 2021 at the end of the great dry season and the beginning of the short

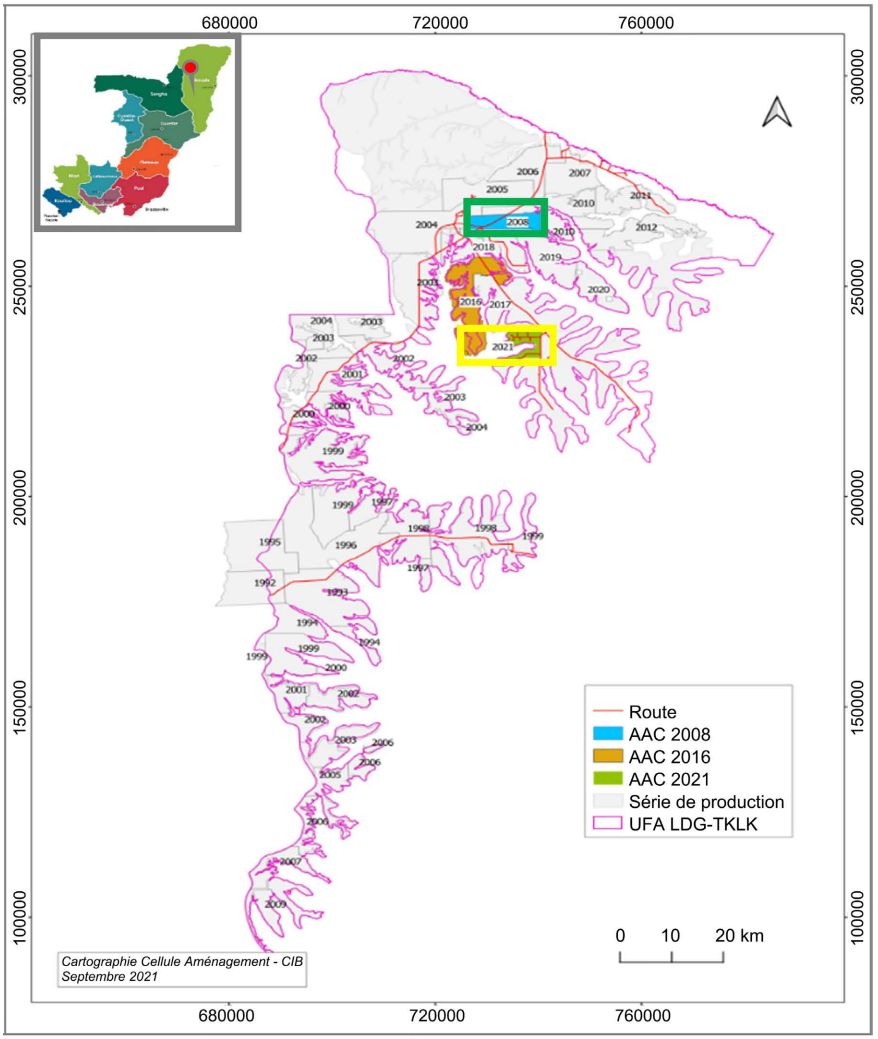

Figure 1. Location of the study site in the Loundoungou forest management unit, Olam/Agri Company (framed in yellow = plot exploited in 2021, "**P21**" and framed in green = plot exploited in 2008, "**P08**").

rainy season. Within each plot of 250,000 m^2, soil samples were collected in two plots of 20 m × 20 m, installed at the triangular end of each plot. Inward of the plots of 20 m × 20 m, each plot has been divided in four sub-plots of 10 m x 10 m, i.e. a unit area of 100 m^2 inside which soil samples were collected.

The soil has been collected using a parallelepipedic box in wood measuring 10 cm long × 10 cm wide × 5 cm deep. Sixteen collection points for all four plots were established in the center of each sub-plot, i.e. eighty composite samples for all soil layers combined.

Five superimposed soil layers were collected per point: 0 - 5 cm, 5 - 10 cm, 10 - 15 cm, 15 - 20 cm and 20 - 25 cm. Each sample was composite, that is to say from of mixture of three unit taking realized on the summits of an equilateral triangle of 1 m side, i.e. a volume per layer and per point of 1500 cm^3 (Perera, 2005; Daïnou et al., 2011; Douh et al., 2018a). The three unit taking from each sampling point were putting in a plastic bag, which contained information: type

of the plot and sub-plots, number of collection point and the level of taking of the soil layer corresponding either to the plot exploited in 2008 (P08) and/or plot exploited in 2021 (P21). A total volume of 240,000 cm^3 has been obtained for the two plots (P08 and P21), i.e. 2 × 120,000 cm^3 per plot, over a total sampling area of 0.48 ha (2 × 0.24 ha per plot).

Two weeks after collecting the soil samples, they were dispatched to Brazzaville and more precisely to the departmental nursery of SNR (Service National de Reboisement) for germination tests.

2.2. Estimation of Viable Seeds

The number of viable seeds in the soil was estimated by the germination method (Simpson et al., 1989; Sousa et al., 2017; Douh et al., 2018a). The soil samples were sieved with a 2 mm mesh size item in order to eliminate crude pieces of plants and coarse mineral elements (e.g. leaves, pieces of wood and stones). A total of two blank trays (containing only sterilized substrate) per plot have been used to verify eventual contamination of the forest soil samples; no germination was noted from the blank samples at the end of the observation period. In fact, the germination was carried out in a nursery at the SNR (Service National de Reboisement) site in Brazzaville in a nonforest zone in order to prevent contamination of the samples by seeds of the surrounding vegetation.

The shadehouse's relative light intensity was about 30% - 40% of full sunlight. Each soil sample was spread out over a sterilized (by heat) sand substrate in a way that the average depth of the sample should not exceed 1 cm (Hall & Swaine, 1980; Douh et al., 2018a). Watering was almost daily. The monitoring of germination was performed twice a week (every 3 - 4 days). When their development stage allowed it, the seedlings were removed and transplanted individually in polyethylene bags in order to favour their growth and identification. As all the germinations took place over the course of the first 17 weeks, the experiment was stopped after 20 weeks (i.e. 5 months of experimentation). Voucher specimens were collected and species were identified by botanists (Gilbert Nsongola, Isaac Dzombo). We followed the taxonomy of the Geneva Herbaria Catalogue (http://www.ville-ge.ch/musinfo/bd/cjb/chg).

2.3. Data Analysis

To assess the effect of soil samples collection depth on seeds germination, the Generalized Linear Model (GLM) in terms of the explanatory variable "soil collection depth", followed by a classification according to Student-Newman-Keurls (SNK) between the average number of germinated seeds per soil layer within the two plots (P08 and P21) were realized using SPSS version 22.0 software (Nelder & Wedderburn, 1972). To identify the characteristics of the species observed in the soil seed bank, we classified species in terms of light-requirements and dispersal syndrome. We used the regeneration guilds of tropical forest tree species defined by Hawthorne (1995) and the dispersal syndromes of seed defined by

Armesto & Rozzi (1989) and Howe & Smallwood (1982). The herbaceous species, the liana species and the undetermined species were not taken into account. The following parameters were used to describe the abundance of seeds of two plots (P08 and P21): the absolute density *AD* (seeds/m^2), the relative density *RD* (%, number of seeds of a given species/the total number of seeds for all species), the relative frequency RF (%, proportion of samples containing the given species) and the species Importance Value Index (*IVI*) computed as the sum of *RD* and *RF* (Mueller-Dombois & Ellenberg, 1974; Borges & Engel, 1993; Butler & Chazdon, 1998; Martins & Engel, 2007; Daïnou et al., 2011). To identify the indicator species of each plot based on seedlings from the soil bank, we computed the "Indicator value index" (INDVAL), using the labdsv package implemented in the R environment (Roberts, 2012). Significance was set at $p < 0.05$. This index described by Dufrêne & Legendre (1997) is defined as follows:

$$\begin{aligned} \text{INDVAL} &= A_{ij} \times B_{ij} \times 100 \\ A_{ij} &= N_{individuals\ ij} \big/ N_{individuals\ i} \\ B_{ij} &= N_{sites\ ij} \big/ N_{sites\ j} \end{aligned} \quad (1)$$

INDVAL = the Indicator Value of species in site group *j*.

A_{ij}, is a measure of specificity (based on the abundance of species *i*);

$N_{individuals\ ij}$, is the mean number of individuals of species *i* in the sites of group *j*;

$N_{individuals\ i}$, is the number of individuals of species *i* in all groups;

B_{ij}, is a measure of fidelity (based on incidence of species *i*);

$N_{sites\ ij}$, is the number of sites in the group *j* where species *i* is present;

$N_{sites\ j}$, is the total number of sites in that group. Here, there were two groups constituted by the two plots, P08 and P21. The undetermined species were excluded from the computation.

In terms of species diversity, we first computed the observed species richness, *Sobs*. But as *Sobs* is very dependent on the sampling effort and is considered as an unreliable indicator of the total species richness (Walther et al., 2005), we also computed estimated species richness using two of the most recommended estimators: the bias-corrected Chao2, *Schao2* (based on incidence) and Jackknife1, *Sjack1* (based on abundance) (Walther & Morand, 1998; Walther & Martin, 2001; Chiarucci et al., 2003; Dove & Cribb, 2006), using the program EstimateS 9.1.0 (Colwell, 2013). Finally, the specificity of layers in terms of species found exclusively in each layer was determined by comparing these "exclusive" species with the total number of species found in the layers (%*Sexcl*).

Rarefaction curves were derived from the observed and estimated species richness to evaluate the representativeness of our sampling effort. Finally, within both plots, viable seeds density per soil layer was computed cumulating the data of each point per soil layer. The differences of mean seed densities between the two plots have been tested using a parametric Student's T test at the 5% threshold, the normality of the data having been verified by the Shapiro-Wilks and

Kolmogorov-Smirnov tests (Nelder & Wedderburn, 1972; McCullagh & Nelder, 1993).

Nevertheless, to compare the floristic composition of soil seed bank between the two plots (P08 and P21), we performed a nonmetric multidimensional scaling (NMDS) based on seed abundance data (8 collection points per plot). NMDS, applied with the R package MASS (Ripley et al., 2017), makes no assumptions about the data (Faith et al., 1987), and is considered among suitable methods for graphical representation of floristic ordination (Clarke, 1993; Glèlè Kakaï et al., 2016). The undetermined species were not taken into account in the ordination. The samples that did not provide any germination were also excluded from the analysis. Shannon's (H') and Pielou's Equitability (E) indices were respectively used to evaluate the specific diversity and the equitable distribution of individuals from the soil seed bank between the two plots and the soil layers (Cordonnier et al., 2012; Djego et al., 2012). In addition, to study the variations of diversity indices between different soil layers, we used the nonparametric Kruskall-Wallis test with post-hoc pairwise multiple comparisons between the means for a probability value of p-value < 0.05.

3. Results

3.1. Influence of Soil Sampling Depth on the Seeds Germination

Table 1 demonstrates that the explanatory variable "soil sampling depth" had a very highly significant effect (p-value = 0.000) on the germination of the soil layers of the plot exploited in 2008 (P08). On the other side, it did not have a significant effect (p-value = 0.085) on the germination of the soil layers of the plot exploited in 2021 (P21) (Table 1).

Nevertheless, in the P08, two classes of average germinations per sample were identified on the basis of the classification SNK (Student-Newman-Keuls) (Table 2).

The first class, composed of the 15 - 20 cm, 10 - 15 cm and 20 - 25 cm layers, displays relatively low average germinations per sample (Table 2). The second class, composed of the 0 - 5 cm layer, stood out others soil layers by a strong average of germinations per sample (Table 2).

Table 1. Generalized Linear Model (GLM) on the germination of the soil seed bank of two exploited plots (P08 and P21). SCE: sum of the squares of the deviations; ddl: degrees of freedom; CM: mean square; F: Fisher-Snedecor statistic; p-value: critical value.

Plot exploited in 2008 (P08)						Plot exploited in 2021 (P21)					
Source	SCE	ddl	CM	F	p-value	Source	SCE	ddl	CM	F	p-value
Corrected model	800.15	4	200.04	7.844	0.000	Corrected model	337.6	4	84.4	2.241	0.085
Constant	3010.23	1	3010.23	118.03	0.000	Constant	4389.03	1	4389.03	116.52	0.000
Depth	800.15	4	200.04	7.84	0.000	Depth	337.6	4	84.4	2.241	0.085
Error	892.63	35	25.5			Error	1318.38	35	37.67		
Total	4703	40				Total	6045	40			

Table 2. Classification of the germination means of each soil sample in the two plots (P08 and P21). Values followed by different letters are statistically different according to the Student's T test at the 5% risk threshold, and those followed by the same letter are not statistically different at the 5% risk threshold.

Plot exploited in 2008 (P08)		Plot exploited in 2021 (P21)	
Soil layers (cm)	SNK (Average germinations/sample)	Soil layers (cm)	SNK (Average germinations/sample)
15 - 20	3.25 ± 3.69a	15 - 20	7.00 ± 6.32a
10 - 15	6.38 ± 4.72a	10 - 15	8.50 ± 4.14a
20 - 25	8.38 ± 5.71a	20 - 25	9.00 ± 3.69a
5 - 10	8.63 ± 4.60a	5 - 10	13.75 ± 6.07a
0 - 5	16.75 ± 6.16b	0 - 5	14.13 ± 8.98a

However, in the plot exploited in 2021, the classification SNK (Student-Newman-Keuls), demonstrates that there are no significant differences between the average germinations per sample on the soil layers (Table 2).

3.2. Floristic Composition and Density of the Soil Seed Bank

We recorded 347 seedlings in the plot exploited in 2008 (P08) and 418 seedlings in the plot exploited in 2021 (P21), with respective average densities of 1446 seeds/m^2 and 1742 seeds/m^2 (Table 3). There were no significant differences between the mean densities of the two plots (T test; F = 2.385; *p*-value = 0.128). In the P08, the seedlings belonged to 37 species whose 25 herbaceous species (82.71%), 11 trees and shrubs species (17%) and 1 liana species (0.29%). The tree and shrub species identified were *Nauclea diderrichii* (De Wild. & T. Durand) Merr. (108 seeds/m^2), *Musanga cecropioides* R. Br. (33 seeds/m^2), *Macaranga barteri* Müll.-Arg. (4 seeds/m^2), *Phyllanthus muellerianus* (Kuntze) Exell (4 seeds/m^2), *Phyllanthus* sp. (4 seeds/m^2) and *Psychotria* sp. (4 seeds/m^2) (Table 3). The most abundant herbaceous species were *Oldenlandia corymbosa* L. (425 seeds/m^2) and *Erigeron sumatrensis* Retz (275 seeds/m^2) (Table 3). However, in P21, seedlings belonged to 27 species whose 18 herbaceous species (93.78%) and 9 trees and shrubs species (6.22%). Tree and shrub species identified were *M. cecropioides* (17 seeds/m^2), *Macaranga spinosa* Müll.-Arg. (17 seeds/m^2), *Nauclea diderrichii* (4 seeds/m^2) and *Ricinodendron heudelotii* (Baill.) Pierre ex Heckel (4 seeds/m^2). The most abundant herbaceous species were *Oldenlandia corymbosa* (688 seeds/m^2) and *Erigeron sumatrensis* (608 seeds/m^2) (Table 3). Regarding indicator species, P08 displayed a single indicator species, *N. diderrichii* (IndVal = 0.843%; *p*-value = 0.004), whereas P21 displayed two indicator species: *E. sumatrensis* (IndVal = 0.689%; *p*-value = 0.041) and *O. corymbosa* (Indval = 0.618%; *p*-value = 0.032) (Table 3). The observed specific richness (*Sobs*) of P08 is estimated to 37 species, whereas the specific richness estimators *Sjack1* and *Schao2* estimate 39 and 40 species respectively (Figure 2). However, that of P21 is estimated to 27 species, whereas the *Sjack1* and *Schao2* estimators display 31 and 29 species respectively (Figure 2). In all cases, the *Sobs* curve does not truly approach the asymptote, but increases gradually with the increase

Table 3. Composition and characteristics of the soil seed banks in the two plots, Plot exploited in 2008 (P08) and Plot exploited in 2021 (P21). Dispersal syndromes: Au = autochory, Z = zoochory. *AD* = absolute density, *RD* = relative density, *RF* = relative frequency, *IVI* = species Importance Value Index. Temperament: P = pioneer and NPLD = non-pioneer light-demander. INDVAL = indicator value index and its *p*-value.

Taxa	Family	*Dispersal mode*	*Guild*	*DA* (n/m^2)	*DR* (%)	*FR* (%)	*IVI*	*IndVal* (%)	*p*-value
Plot exploited in 2008									
Tree and shrub species (11 species)									
Macaranga barteri Müll.-Arg.	Euphorbiaceae	Au/Z	P	4.2	0.3	2.5	2.8	0.13	Ns
Musanga cecropioides R. Br.	Urticaceae	Z	P	33.3	2.3	20	22.3	0.5	Ns
Nauclea diderrichii (De Wild. & T. Durand) Merr.	Rubiaceae	Z	P	108.3	7.5	65	72.5	0.84	0.004
Phyllanthus muellerianus (Kuntze) Exell	Phyllanthaceae	Au	NPLD	4.2	0.3	2.5	2.8	0.13	Ns
Phyllanthus sp.	Phyllanthaceae	-	-	4.2	0.3	2.5	2.8	0.13	Ns
Psychotria sp.	Rubiaceae	Z	P	4.2	0.3	2.5	2.8	0.13	Ns
Euphorbiaceae sp.	Euphorbiaceae	-	-	4.2	0.3	2.5	2.8	0.13	Ns
Rubiaceae sp.1	Rubiaceae	-	-	25	1.7	15	16.7	0.32	Ns
Rubiaceae sp.4	Rubiaceae	-	-	50	3.5	30	33.5	0.34	Ns
Rubiaceae sp.5	Rubiaceae	-	-	4.2	0.3	2.5	2.8	0.04	Ns
Rubiaceae sp.6	Rubiaceae	-	-	4.2	0.3	2.5	2.8	0.13	Ns
Herbaceous species (25 species)									
Ageratum conyzoides L.	Asteraceae			62.5	4.3	37.5	41.8	0.39	Ns
Asystasia gangetica (L.)T. Anders	Acanthaceae			4.2	0.3	2.5	2.8	0.13	Ns
Axonopus compressus (Sw.) P. Beauv.	Poaceae			4.2	0.3	2.5	2.8	0.13	Ns
Chromolaena odorata (L.) R. M. King & H. Rob.	Asteraceae			4.2	0.3	2.5	2.8	0.042	Ns
Crassocephalum crepidioides (Benth.) S. Moor.	Asteraceae			8.3	0.6	5	5.6	0.25	Ns
Davallia denticulata (Burm. f.) Mett. ex Kuhn	Davalliaceae			4.2	0.3	2.5	2.8	0.031	Ns
Digitaria horizontalis Willd.	Poaceae			16.7	1.2	10	11.2	0.38	Ns
Emilia sonchifolia (L.) DC.	Asteraceae			4.2	0.3	2.5	2.8	0.06	Ns
Erigeron sumatrensis Retz.	Asteraceae			275	19	165	184	0.31	Ns
Euphorbia hirta L.	Euphorbiaceae			75	5.2	45	50.2	0.5	Ns
Linderniaceae sp.1	Linderniaceae			4.2	0.3	2.5	2.8	0.042	Ns
Linderniaceae sp.2	Linderniaceae			4.2	0.3	2.5	2.8	0.13	Ns
Mitracarpus hirtus (L.) DC.	Rubiaceae			41.7	2.9	25	27.9	0.47	Ns
Mollugo verticillata Linn.	Molluginaceae			50	3.5	30	33.5	0.43	Ns
Neurotheca loeselioides (Spruce ex Progel) Baill.	Gentianaceae			8.3	0.6	5	5.6	0.13	Ns

Continued

Oldenlandia corymbosa L.	Rubiaceae			425	29.4	255	284.4	0.38	Ns
Palisota sp.	Commelinaceae			4.2	0.3	2.5	2.8	0.13	Ns
Phyllanthus amarus Schum. & Thonn.	Phyllanthaceae			33.3	2.3	20	22.3	0.13	Ns
Portulaca oleracea L.	Portulacaceae			58.3	4	35	39	0.61	Ns
Richardia brasiliensis Gomes	Rubiaceae			4.2	0.3	2.5	2.8	0.13	Ns
Sauvagesia erecta L.	Ochnaceae			4.2	0.3	2.5	2.8	0.13	Ns
Stanfieldiella imperforata (C.B. Clarke) Brenan	Commelinaceae			8.3	0.6	5	5.6	0.13	Ns
Synedrella nodiflora (L.) Gaertn.	Asteraceae			4.2	0.3	2.5	2.8	0.13	Ns
Tristemma mauritianum J.F. Gmel.	Melastomataceae			16.7	1.2	10	11.2	0.25	Ns
Vandellia diffusa L.	Linderniaceae			70.8	4.9	42.5	47.4	0.48	Ns
Liana species (1 species)									
Sabicea sp.1	Rubiaceae			4.2	0.3	2.5	2.8	0.13	Ns
Total				**1445.8**	**100**				
Plot exploited in 2021									
Tree and shrub species (9 sepcies)									
Macaranga spinosa Müll.Arg.	Euphorbiaceae	Au/Z	P	16.7	1	10	11	0.38	Ns
Musanga cecropioides R. Br.	Urticaceae	Z	P	16.7	1	10	11	0.13	Ns
Nauclea diderrichii (De Wild. & T. Durand) Merr.	Rubiaceae	Z	P	4.2	0.2	2.5	2.7	0.005	Ns
Ricinodendron heudelotii (Baill.) Pierre ex Heckel	Euphorbiaceae	Au	P	4.2	0.2	2.5	2.7	0.13	Ns
Rubiaceae sp.1	Rubiaceae	-	-	4.2	0.2	2.5	2.7	0.02	Ns
Rubiaceae sp.2	Rubiaceae	-	-	4.2	0.2	2.5	2.7	0.13	Ns
Rubiaceae sp.3	Rubiaceae	-	-	8.3	0.5	5	5.5	0.13	Ns
Rubiaceae sp.4	Rubiaceae	-	-	41.7	2.4	25	27.4	0.34	Ns
Rubiaceae sp.5	Rubiaceae	-	-	8.3	0.5	5	5.5	0.08	Ns
Herbaceous species (18 species)									
Ageratum conyzoides L.	Asteraceae			37.5	2.2	22.5	24.7	0.19	Ns
Chromolaena odorata (L.) R. M. King & H. Rob.	Asteraceae			8.3	0.5	5	5.5	0.17	Ns
Davallia denticulata (Burm. f.) Mett. ex Kuhn	Davalliaceae			12.5	0.7	7.5	8.2	0.09	Ns
Emilia sonchifolia (L.) DC.	Asteraceae			4.2	0.2	2.5	2.7	0.06	Ns
Erigeron sumatrensis Retz.	Asteraceae			608.3	34.9	365	399.9	0.69	0.041
Euphorbia hirta L.	Euphorbiaceae			37.5	2.2	22.5	24.7	0.25	Ns
Linderniaceae sp.1	Linderniaceae			8.3	0.5	5	5.5	0.17	Ns
Melastomataceae sp.	Melastomataceae			8.3	0.5	5	5.5	0.25	Ns

Continued

Mitracarpus hirtus (L.) DC.	Rubiaceae	25	1.4	15	16.4	0.19	Ns
Mollugo verticillata Linn.	Molluginaceae	37.5	2.2	22.5	24.7	0.27	Ns
Neurotheca loeselioides (Spruce ex Progel) Baill.	Gentianaceae	8.3	0.5	5	5.5	0.06	Ns
Oldenlandia corymbosa L.	Rubiaceae	687.5	39.5	412.5	452	0.62	0.032
Panicum brevifolium L.	Poaceae	4.2	0.2	2.5	2.7	0.13	Ns
Phyllanthus amarus Schum. & Thonn.	Phyllanthaceae	33.3	1.9	20	21.9	0.31	Ns
Portulaca oleracea L.	Portulacaceae	37.5	2.2	22.5	24.7	0.25	Ns
Sabicea sp.2	Rubiaceae	8.3	0.5	5	5.5	0.25	Ns
Stanfieldiella imperforata (C.B. Clarke) Brenan	Commelinaceae	8.3	0.5	5	5.5	0.06	Ns
Vandellia diffusa L.	Linderniaceae	58.3	3.3	35	38.3	0.34	Ns
Total		**1741.7**	**100**				

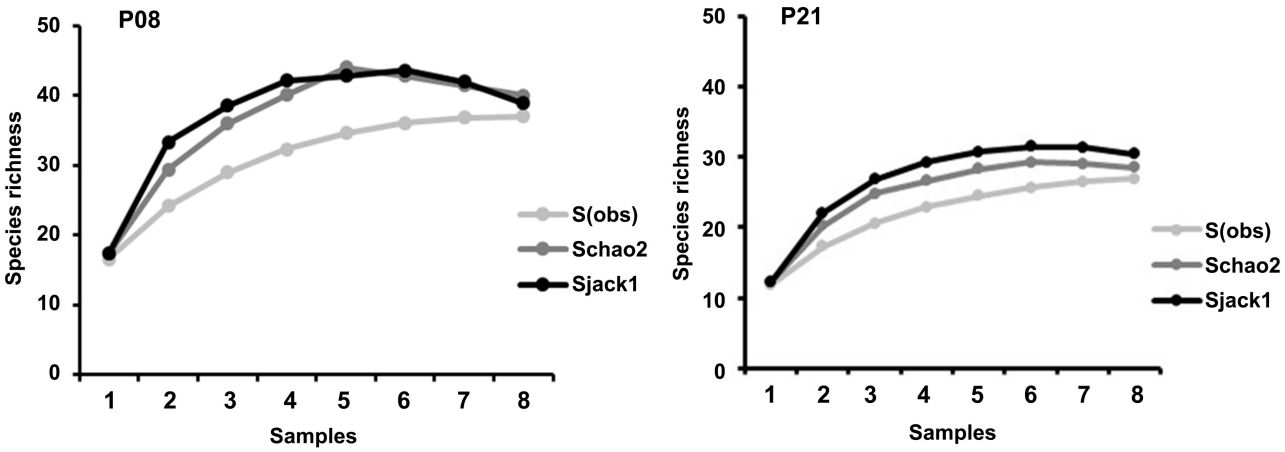

Figure 2. Rarefaction curves of the two plots (P08 = plot exploited in 2008 and P21 = plot exploited in 2021).

of number samples. Consequently, the sampling effort is relatively considerable in the two plots studied (Figure 2).

Nonetheless, the floristic composition of the soil seed bank of the two plots (P08 and P21), illustrated using the NMDS, demonstrates that there is a spatial structuring of the samples confirming that the species from the seed bank of the soil of the two plots are globally similar (Figure 3).

Concerning the specific richness at the level of the soil layers, the P08 presents a relatively high specific richness compared to the soil layers of the P21 which seems relatively constant at the level of the superficial layers compared to the deepest layers of soil (Table 4). The observed species richness values (*Sobs*) at the level 0 - 5 cm layers of P08 and P21 are respectively 29 to 14 species. Nonetheless, the *Schao2* and *Sjack1* estimators displays 36 (33 species) and 29 (15 species), respectively (Table 4). On the other side, the specific richness of the layers 20 - 25 cm is of 13 species for P08 and 16 species for P21. The *Schao2* and

Table 4. Soil seed bank characteristics for different soil layers in the two plots. *Sobs* = observed species richness; *Schao2* = specific richness estimated according to the Chao2 approach; Sjack1 = estimated species richness following Jackniffe 1 approach; %*Sexcl* = percentage of exclusive species in each soil layer; Abund. = Mean (± SD) of the number of seeds per unit area.

Soil layers (cm)	P08					P21				
	Sobs	*Sexclu* (%)	*Schao2*	*Sjack1*	*Abund.* (*seeds*/*m*²: *mean* ± *SD*)	*Sobs*	*Sexclu* (%)	*Schao2*	*Sjack1*	*Abund.* (*seeds*/*m*²: *mean* ± *SD*)
0 - 5	29	41.4	36.1	33.1	554 ± 248	14	28.6	15	15.9	467 ± 53
5 - 10	19	15.8	23.1	27.6	288 ± 127	12	8.3	13.5	14.6	233 ± 51
10 - 15	14	7.1	14.9	15.8	213 ± 95	15	20	16.1	17.2	300 ± 22
15 - 20	14	14.3	15.1	16.6	108 ± 49	11	0	12.1	12.8	283 ± 29
20 - 25	13	7.7	13.8	14.8	279 ± 125	16	18.8	16.9	18	458 ± 49

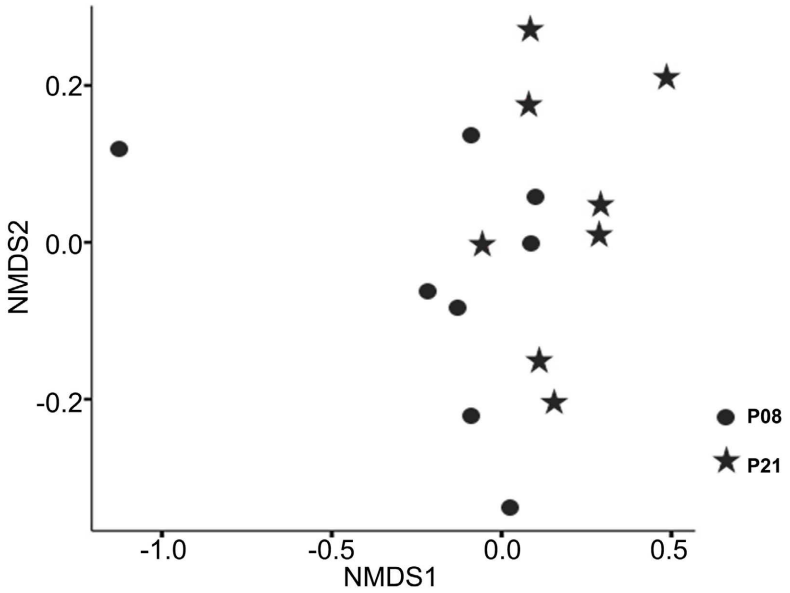

Figure 3. Two-dimensional nonmetric multidimensional scaling (NMDS) ordination of soil samples of the two studied plots types.

Sjack1 estimators respectively estimate 14 (14 species) and 17 (18 species) (Table 4).

Interesting fact, in the 20 - 25 cm layer, we record 7.7% of exclusive species for P08 and 18.8% for P21 (Table 4). The species found exclusively in the 20 - 25 cm layer of P08 was Rubiaceae sp.4. While in P21, the species found exclusively in the 20 - 25 cm layer were *Nauclea diderrichii*, Rubiaceae sp.5 and *Davallia denticulata* (Burm. f.) Mett. ex Kuhn. Otherwise, the average seed densities obtained in the 20 - 25 cm layer were 279 ± 125 seeds/m² for P08 and 458 ± 49 seeds/m² for P21, compared to the superficial layers 10 - 15 cm and 15 - 20 cm. What illustrates well the necessity to explore the deeper layers which abound in non-negligible densities of seeds in the soil (Table 4). Nonetheless, the values of the average densities seeds at the level of the soil layers of the two plots using the Student's T test revealed no significant difference ($p = 0.514$) (Table 4).

3.3. Soil Seed Bank Biological Diversity

The values of Shannon index were revealed higher and vary between 2.53 and 1.82, respectively in P08 and P21, contrary to the values of the Pielou equitability index of the two plots. Regarding the soil layers of the two plots, the Shannon index varies from 0.60 to 1.05 in P08 and from 0.42 to 0.88 in P21. However, the Pielou equitability index displays 0.72 to 1 in P08 and from 0.53 to 0.81 in P21. It appears that the soil seed bank of the two plots is less diversified. Consequently, the analysis of the variations of the indices of diversity between soil layers by the nonparametric test of Kruskall Wallis did not revealed any significant difference (p-value > 0.05) between these two indices in the plots studied (Figure 4).

4. Discussion

In this study, we demonstrated that the 20 - 25 cm soil layers contain 7.7% to 18.8% of exclusive species recorded respectively in the plot exploited in 2008 (P08) and the plot exploited in 2021 (P21).

The species found exclusively in the 20 - 25 cm soil layer of P08 was Rubiaceae sp.4. While in P21, the species found exclusively in the 20 - 25 cm soil layer were *Nauclea diderrichii*, Rubiaceae sp.5 and *Davallia denticulata* (Burm. f.) Mett. ex Kuhn. This confirms well that P21 is a plot recently exploited by finding the long-lived pioneer species as *N. diderrichii* in the 25 cm deep soil layer, contrary in P08 where the species is found in the superficial layers of 0 - 5 cm, 5 - 10 cm. Also, the results clearly showed that the average seed densities obtained in the 20 - 25 cm soil layer were 279 ± 125 seeds/m^2 for P08 and 458 ± 49 seeds/m^2 for P21, compared to the superficial layers 10 - 15 cm and 15 - 20 cm.

Nonetheless, the two exploited plots (P08 and P21) installed on clay soil have substantial regeneration potential thanks to the soil seed bank. However, this potential seems higher in P21 than in P08. Pioneer taxa dominated in the soil seed bank of the two plots studied, with more pioneer species in P08 (5 woody pioneer species) than in P21 (4 woody pioneer species).

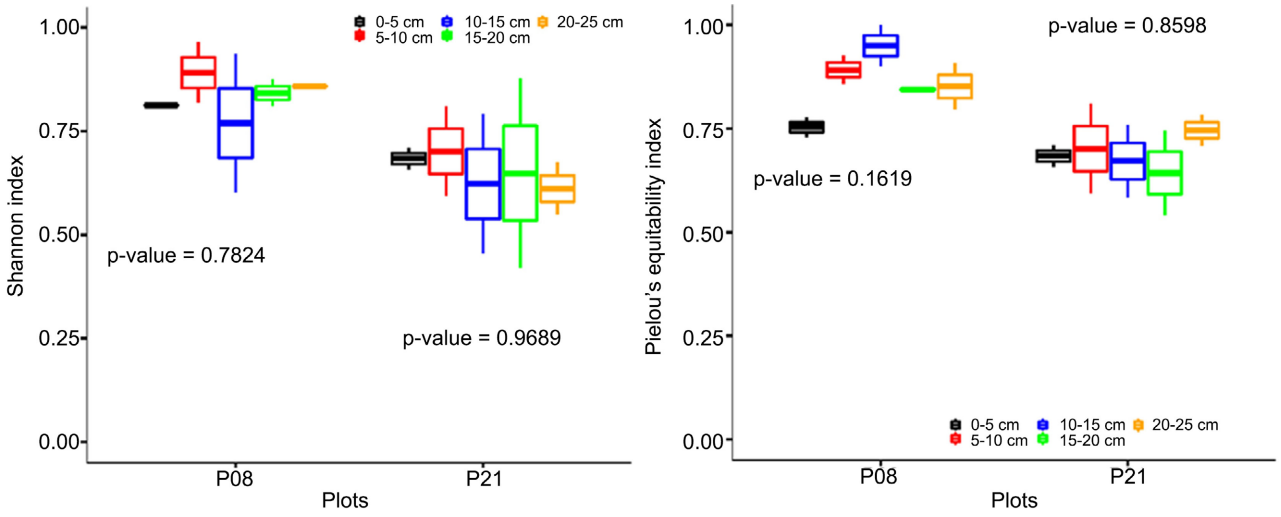

Figure 4. Variation of the diversity indices in terms of the soil layers of two plots (Plots exploited in 2008 "P08" and 2021 "P21").

Contrary to the assumption according to which seeds abundance and species richness of the soil seed bank decrease progressively with soil depth (Garwood, 1989), this study demonstrated that deeper soil layers should not neglected in the studies dealing of the soil seed bank.

4.1. Soil Seed Bank Germination Varies in Terms of the Plots and Soil Layers

Average numbers of germinated seeds per soil layer demonstrated that soil depth had a significant effect on the germination of the soil seed bank in one of the plots (P08). Indeed, in the plot exploited in 2008, the 0 - 5 cm soil layer stood out from other soil layers by a relatively high germination average per sample (p-value = 0.000). This difference could be explained by the fact that the first centimeters of soil abound more seeds, because they directly receive the seeds from the litter. Our results are similar to those obtained by Daïnou et al. (2011); Zebaze et al. (2021) in Cameroon, Douh et al. (2018a) in Congo, Adjalla et al. (2022) in Benin, who have worked in tropical forests. This observation confirms that the soil seed bank would be more abundant in the top 5 centimeters of soil than in the deeper layers (Garwood, 1989; Warr et al., 1993). While, in the plot exploited in 2021, the differences observed in terms of average germination per sample in each soil layer are not significant (p-value = 0.085).

Which demonstrates that the average germination numbers per sample between different soil layers in this plot are relatively close. Thereby, the 20 - 25 cm layer of soil demonstrated not negligible germination in the two plots studied, hence the interest to consider the latter in the next studies of the soil seed bank.

Globally, the soil seed bank of the two plots started germination from the 2nd week of observation. The average number of germination was higher in the recently disturbed plot (P21) than in that formerly disturbed (P08) with respectively 418 and 347 seedlings germinated during 20 weeks of monitoring. This difference could be explained by the fact that the plot exploited in 2021 was newly disturbed and that the stay of the seeds in the soil bank probably would have started the breaking of dormancy allowing water to reach the seed embryos (Douh et al., 2018b). In addition, germination peaks were observed during weeks 3 and 9 in each of the two plots.

Our results are different from those obtained by Daïnou et al. (2011) in Cameroon, who observed spontaneous germination of the soil samples taken with a total of 289 individuals germinated in 16 weeks and germination peaks during the 5th, 6th and 7th weeks of the experiment. Whereas Douh (2018), recorded 61 individuals germinated in 8 weeks and observed germination peaks during the 3 th and 4th weeks. Nonetheless, Zebaze et al. (2021), after a month of latency, had obtained 230 germinated individuals over a period of 20 weeks, and noticed two peaks of germination during the 12th and 13th weeks. This difference could be explained by the fact that these authors only explored the soil samples in the first 20 centimeters, and that the germination monitoring time has been relatively short compared to the present study. This sighting led us to hypothesize accord-

ing to which, more recent the disturbance, more the soil seed bank germinates spontaneously in abundance taking advantage of the opening of the canopy.

4.2. The Density and Floristic Composition of the Soil Seed Bank Varies in Terms of the Plots and Soil Layers

The density and floristic composition of the soil seed bank in tropical forests are variable.

Hall & Swaine (1980) in Ghana reported that in tropical forests the density of the soil seed bank varies from 100 to 700 seeds/m^2. Otherwise, in the Amazon rainforest of Brazil, Sousa et al. (2017) quantified 662 seeds/m^2 in the top three centimeters of soil. In the present study, the densities vary between 1446 and 1742 seeds/m^2 over the 25 cm soil depth. These results confirm the works of Garwood (1989), who pointed out that in tropical forests, the abundance of seeds varies from 25 to 3350 seeds/m^2.

Our results differ from those obtained by other authors. Indeed, Martins & Engel (2007) in Brazil, obtained a density of 800.3 seeds/m^2 in the first five centimeters of soil. However, in Cameroon, Daïnou et al. (2011) demonstrated densities of 88 to 116 seeds/m^2 in the top five centimeters of soil. Recently, Zebaze et al. (2021) demonstrate densities that vary between 1099 and 5495 seeds/m^2 in the first 20 centimeters of the forests of the Dja reserve in Cameroon. While in the Republic of Congo, the works of Douh et al. (2018a) revealed densities of 247 to 330 seeds/m^2, respectively in "*Manilkara* forest" and "*Celtis* forest".

These two previous studies concerned the first 20 centimeters of soil. These considerable variations of densities obtained could be due to the diversity of methods of characterizing of the soil seed bank, in particular the size of the soil samples collected, the samples collection season, the treatment of the samples and especially the depth of the soil sampled (Garwood, 1989; Warr et al., 1993; Adjalla et al., 2022).

Nonetheless, Garwood (1989) reminds that the density of the seed bank decreases gradually with the depth of soil. In the present study, this hypothesis concord relatively well in the plot exploited in 2008 (P08) up to 20 cm from of the soil. But, interesting fact, the 20 - 25 cm soil layer demonstrated a superior density to 10 - 15 cm and 15 - 20 cm layers. This a priori surprising observation, suggests that the density of the soil seed bank can increase and/or decrease with the depth of the soil, whatever the biotope considered. On the other side, in the recently exploited plot, it is the 0 - 5 cm layer which displayed a relatively high density, followed of the 20 - 25 cm and 10 - 15 cm layers, while the 15 - 20 and 5 - 10 cm layers demonstrated relatively lower densities. Whence the necessity to explore the 20 - 25 cm soil layer, because it abounds considerable viable seeds potential.

Furthermore, the results of the present study revealed that the plot exploited in 2021 presented a higher percentage of herbaceous species (93.78%) than that exploited in 2008 (82.71%). This could be explained by the fact that the recently

exploited forest just got disturbed and, it is the herbaceous species that naturally initiate the healing of after a recent disturbance (Hallé et al., 1978; Daïnou et al., 2011; Vargas et al., 2017). This could justify the fact that two herbaceous species (*Erigeron sumatrensis*, *IndVal* = 0.689 %; *p*-value = 0.041 and *Oldenlandia corymbosa*, *Indval* = 0.618 %; *p*-value = 0.032) are identified indicator species in this plot.

Otherwise, this predominance of the herbaceous species could be explained by the fact that 1) these plants produce a large quantity of small seeds susceptive to escape at the predation of seed-eating animals (Janzen, 1988); 2) these seeds progressively accumulate in large quantities in the soil bank (Borges & Engel, 1993; Arnolds et al., 2015; Vargas et al., 2017); and 3) they are able to retain their viability for several decades in the soil bank (Hopkins & Graham, 1987). These results confirm those obtained in most studies and testify a dominance of the proportions of herbaceous species in the vegetation expressed, i.e. 39.5% in Cameroon (Daïnou et al., 2011), 41% to 45.3% in Congo (Douh et al., 2018a).

Two pioneer species of first stage of the plant succession were recorded in the plot exploited in 2008. These include: *Musanga cecropioides* (2.31%) et *Macaranga barteri* (0.29%). While, in the plot exploited in 2021, we identified *M. cecropioides* and *Macaranga spinosa* to the identical proportions (0.96%). These species have been observed up to 20 cm from the soil in each plot and were more represented in the formerly exploited plot (P08). What suggests that this last would tend towards the process of maturity. But, these low proportions are detrimental to these exploited forests because, according to Hallé et al. (1978), Hopkins & Graham (1987), good production of the litter from pioneer species of first stage of the plant succession would be propitious to the installation of long-lived pioneer species such as *Nauclea diderrichii*, *Entandrophragma utile*, *Triplochyton scleroxylon*, *Autranella congolensis*, many prized by loggers in northern Congo.

Finally, the particularity of the present study resides in the 20 - 25 cm layer which displayed significant proportions of woody species (9%) in the plot exploited in 2008, these are Rubiaceae sp.4 and *N. diderrichii*. While that exploited in 2021, abounded in 19% of woody species, namely Rubiaceae sp.4, Rubiaceae sp.5 and *N. diderrichii*, greatly exceeding the proportions obtained in the 15 - 20 cm layer of each of the two plots. The presence of *N. diderrichii* in the 20 - 25 cm layer of each plot could be explained by the fact that the species produces a large quantity of dormant seeds and small sizes able to retain their viability in the soil bank. In addition, the presence of seeds up to this depth of soil could also be explained by the activity of the soil organisms would involve the seeds into the deep layers of soil (Beaune et al., 2013; Evrard et al., 2017). Otherwise, Plue & Hermy (2012) assign the presence of seeds in the deep layers of soil to the cracks observed at soil level, to the subsidence of soil around the roots of trees and to rainwater which could convey the seeds in their path of infiltration into the soil.

5. Conclusion

The present study consisted to assess the potential of natural regeneration through the soil seed bank in the post-logging plots. The results highlighted the role that the soil seed bank could play in the natural regeneration of logged forests. We have showed that the characteristics of the soil seed bank depend of the types of plots. We can overall remember that: 1) the soil seed bank of each type of plot was dominated by herbaceous species; 2) seed stocks were substantial up to 25 cm soil depth, and some pioneer tree species presented viable seeds in the soil; 3) seed density did not regress with soil burial depth; and 4) populations of commercial tree species are not well represented in the soil seed bank (Nasi et al., 2012; Douh et al., 2018a). Consequently, the reforestation of commercial species in the exploited plots is necessary to sustainably manage these Congolese tropical forests.

Acknowledgements

The authors thank Marien Ngouabi University (Republic of the Congo), the DynAfFor project (Dynamique des Forêts d'Afrique Centrale) leaded by CIRAD, Gembloux Agro-Bio Tech and Nature+, as well as the logging company OLAM/Agri for their financial, scientific and technical support, and for their aid with fieldwork. Finally, we would like to thank Bijoux Toumba-Paka, Christian Moussoumbou, Julienne Bonazaba, Jean-Louis Doucet, Baptiste Leborgne, Vincent Istace, Eric Forni, Mercier Mayinga, Isaac Dzombo, Ati N'gouabi and Patricia Kitsoukou for their various contributions and their advice.

Conflicts of Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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