

Soil seed bank characteristics in Cameroonian rainforests and implications for post-logging forest recovery

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ABSTRACT

The soil seed bank is considered as an important component for resilience of climatic vegetation. Whereas several related studies have been conducted in Asian, American and some African tropical forests, no investigation has ever been conducted in Central African rainforests, especially in logged forests where the soil seed bank could contribute to regeneration of timber of trees species. We studied the soil seed bank characteristics in relation to the standing vegetation in three Cameroonian forest zones with different disturbance regimes. There was no significant difference between sites in terms of density of the seed bank; the average mean density was 87.6 seeds m⁻². But dissimilarities of the floristic compositions between sites were quite high. Overall, seeds came from 43 species including three commercial tree species. Whereas the seedlings emerging from soil samples mostly came from weedy and short-lived pioneer species, climax species predominated in the extant vegetation, leading to a very weak similarity between soil seed flora and the surrounding vegetation: Sorensen's index ranged from 3.5 to 7.6%. Canopy openness could significantly affect the species richness of soil seed stocks but not the seed density. These results show that the soil seed bank contribution to the resilience of mature tropical forests is low. In particular, very few timber tree species could benefit from soil seed stocks for their regeneration. Therefore, the development of enrichment techniques including use of the soil seed bank as a source of tree regeneration in such a context would be irrelevant.

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1. Introduction

Since Symington (1933) found a large quantity of seeds in Malaysian forest soil and as seed rain seems to account for only a small proportion of forest regeneration in disturbed zones (Putz and Appanah, 1987; Lawton and Putz, 1988), the importance of seed banks in vegetation dynamics is receiving increasing attention. Seed banks are a significant source of regeneration (Hosogi and Kameyama, 2006) and have been included in several restoration projects (Lemauiel et al., 2005; Williams et al., 2008) or weed control programs (Marks and Nwachuku, 2006).

A soil seed bank is defined as the number or store of viable seeds buried in the soil at a given time, representing a record of the recent vegetation of an area (Martins and Engel, 2007). Accord-

ing to Swaine and Whitmore (1988), seeds in the soil are of two kinds: (a) transient or ephemeral seeds, from species with very brief viability in forest soils (either they germinate quickly when water is available, or they die); (b) persistent seeds of species which have an extended viability in soil, and are commonly associated with the phenomenon of dormancy. However, various authors have emphasized the continuity between these two groups of species. Regarding tropical regions, Garwood (1989) defined three more soil seed bank strategies as intermediates to the two categories mentioned earlier.

Studies tend to show that persistent and pseudo-persistent seeds of weedy and short-lived pioneer species are the most commonly observed (Hopkins and Graham, 1983; Garwood, 1989; Dalling et al., 1998). Schmidt (2007) reported that many trees of humid tropical forests are animal-dispersed and rarely have post-dispersal seed dormancy; their seeds are adapted to rapid germination, even in shaded environments. Thus, seed banks in tropical forests, even in primary forests may be composed almost entirely of pioneers (*sensu* Swaine and Whitmore, 1988). In fact, several studies from tropical America (e.g., Ten Hoopen and Kapelle,

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2006; Dalling and Brown, 2009), Asia (e.g., Chandrashekara and Ramakrishnan, 1993; Metcalfe and Turner, 1998; Howlett and Davidson, 2003) and some parts of Africa (e.g., Keay, 1960; Hall and Swaine, 1980; De Villiers et al., 2003; Kassahun et al., 2009) have confirmed that the soil seed bank could be an important mechanism for the regeneration of only pioneer and secondary forest species (see also Garwood, 1989; Jankowska-Błaszczuk and Grubb, 2006).

Concerning the role of environmental patterns on seed bank characteristics, the effect of canopy disturbance on seed stocks in tropical forest soils has also been studied, but no clear trend can be seen. For instance, whereas Lindner (2009) found no relationship between canopy openness and seed bank characteristics, Perera (2005) revealed an influence of canopy openness on the species richness of the forest soil.

In the Congo Basin rainforests, many surveys of regeneration have been performed (Hall et al., 2003; Kouadio, 2009), but these studies have not been able to disentangle the relative contributions of seed rain and seed bank. In particular, in regard to logged African tropical forests, addressing the role of soil seed bank is relevant as it could be an interesting tool in forest management. Nowadays, national regulations for logging concessions in Central Africa recommend implementation of enrichment techniques with a significant cost (Doucet et al., 2009). Thus, beyond its contribution to the natural maintenance of biodiversity, a soil containing numerous seeds of timber trees could be implicated in forest enrichment in a number of ways. For example, as soil in logging gaps is generally compacted, repeated stirring of the soil could favor the emergence of commercial seedlings. Similarly, the transportation of seed-rich topsoil from an intact forest zone to nearby degraded lands could contribute to accelerate development of the appropriate vegetation (Skoglund, 1992). As most timber tree species are light-demanders (Doucet, 2003), their regeneration rates could be considerably improved with such techniques.

Up to now, no prior studies have documented soil seed bank characteristics and their possible relevance in Central African rainforests. Here, we investigated the potential of soil seed stocks in a Cameroonian forest concession, in relation with the main pattern of disturbance in this context: forest gaps made by cutting activities. We aimed to respond to the following questions:

- (1) What are the dominant life-forms in seed banks of Central African rainforests, and hence, what stages in forest succession could benefit from forest soil for their regeneration?
- (2) In order to promote regeneration of timber tree species through the potential of the soil seed bank, can forest soils be an important source of seedlings for these commercial species?
- (3) How are the seed bank characteristics affected by canopy disturbance patterns?

2. Materials and methods

2.1. Study sites

The study was conducted in a Cameroonian forest concession of 118,052 ha located at the west of the Dja Reserve and logged by the company Pallisco (Fig. 1). The concession has a mean elevation of about 650 m and extends between 3°01'–3°25'N and 14°05'–14°31'E in a mostly a semi-deciduous forest zone (Kouadio and Doucet, 2009). Rainfall is distributed in two rainy periods (from March to June, and from August to December) alternating with two dry seasons. The mean annual rainfall and temperature are respectively about 1550 mm and 24 °C (DMNC, 2009). Humidity is high throughout the year. The concession zone is a low fairly flat plateau

laid on a substratum of schists, gneisses and quartzite (Laclavère, 1979).

Three sites of late secondary forest with various logging histories were selected for the present study. The first stand of 8.25 ha, located in a protected forest area, *PF*, was never been exploited. The second site covered 4.80 ha and was located in a recently logged forest, *RLF*, where the most recent logging was performed two years ago. The third site was a 9-year-old logged forest, *OLF*, and covered 7.80 ha. Distances from one site to another varied from 10 to 20 km. These sites were fairly similar in species composition (Cerisier, 2009).

2.2. Soil sampling and seedling emergence test

Within each forest site, two or three transects were established with respect to the size of the site. The total length of transects was 300, 705 and 555 m for *RLF*, *OLF* and *PF*, respectively. Soil samples were collected every 15 m along the transects providing 21, 49 and 40 samples for *RLF*, *OLF* and *PF*, respectively. Each soil sample was a mixture obtained from three quadrats of 10 cm × 10 cm and 5 cm in depth established at the top of a 1 m-sided equilateral triangle. Large items of litter were removed before soil sampling. Thus, a total area of 3.3 m² and a total volume of 165,000 cm³ of soil were sampled. Since Mbarga et al. (1999) noted that November to March is the period of the lowest level of fruiting in South-Cameroonian rainforests, the samples were collected in February to limit seed rain inclusions.

Quantitative and qualitative composition of the seed banks was investigated using the seedling emergence method. Samples were sieved before the experiment began, in order to detect large and viable diaspores. The seedling emergence experiment was performed in a greenhouse at Gembloux Agro-Bio Tech (University of Liege), under average temperature and humidity of 25 °C and 60.5%, respectively. Each soil sample was spread to 1 cm depth onto a substrate of sterilized sandy loam in a tray. The containers were watered as required, at least once a day. They were also redistributed randomly inside the greenhouse each week. The seeds found during sieving were also put to germination in the same greenhouse. Each emergent seedling was removed and repotted for further growth until large enough for identification. The seedling emergence experiment was ended after 16 weeks, as all germination events occurred during the first 12 weeks.

2.3. Characterization of habitats

Canopy openness was estimated within each site, assuming that this parameter could affect soil seed bank characteristics. Canopy cover was estimated 1 m above the ground using a spherical densiometer. Densiometer measures were performed by the same person at each soil sampling point and under similar weather conditions. The spherical densiometer is known to be a good compromise between speed and accuracy as far as measurement of canopy cover is concerned (Korhonen et al., 2006). Moreover, this instrument is well adapted to estimate canopy closure which is defined as the fraction of non-visible sky within a certain angle of view whereas canopy cover is the fraction of ground area covered by crowns (Paletto and Tosi, 2009).

The extant vegetation of tree species with diameter at breast height (dbh) >10 cm was also surveyed up to 50 m each side of the transects on which soil sampling was performed. This inventory was performed to (a) verify the similarity in the woody flora between sites, and (b) compare its characteristics to those of the soil seed bank. In total, 3, 5.5 and 7.1 ha were surveyed in *RLF*, *OLF* and *PLF*, respectively.

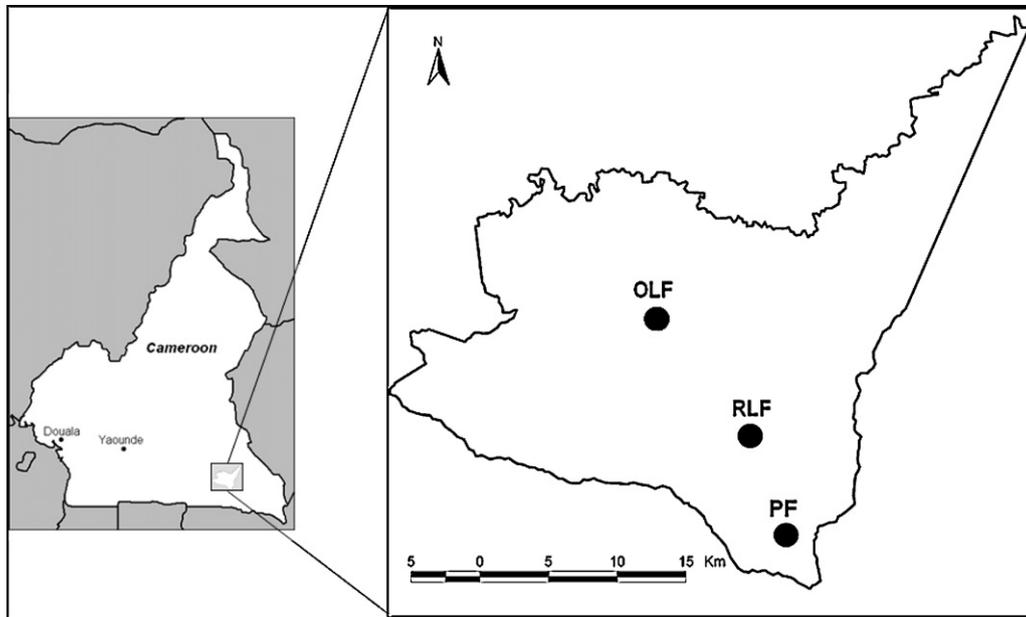


Fig. 1. Study sites in a Cameroonian logging concession. OLF: 9-year-old logged forest; RLF: recently logged forest; PF: protected forest area.

2.4. Data analyses

Hawthorne (1995) defined six regeneration guilds for tropical forest trees which were used here to categorize seeds in terms of light-requirements. The dispersal syndromes of the observed species were also mentioned as this information can help to understand the relationship between the soil flora and the surrounding vegetation. The existence of a significant correlation between species richness and density of seeds in the soil was investigated using Pearson's correlation coefficient. The following parameters were used to describe abundance of seeds: 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) and the relative frequency RF (%), proportion of samples containing the given species) (Butler and Chazdon, 1998; Martins and Engel, 2007). To infer the α -diversity of the seed bank, two kinds of ecological indicators were computed using EstimateS 8.2.0 (Colwell, 2006): (i) observed species richness, S_{obs} , and (ii) estimates of total species richness, S_{chao2} and S_{ice} , following Chao (1984, 2005) and Lee and Chao (1994). These estimates are defined as follows:

$$S_{chao2} = S_{obs} + \left(\frac{Q_1^2}{2Q_2} \right)$$

$$S_{ice} = S_{freq} + \left(\frac{S_{infr}}{C_{ice}} \right) + \left(\frac{Q_1}{C_{ice}} \right) + \gamma_{ice}^2$$

where Q_1 is the number of species occurring in exactly one sample (unique), Q_2 is the number of species occurring in exactly two samples (duplicates), S_{freq} is the number of frequent species, that is, those found in more than 10 quadrats, S_{infr} is the number of infrequent species (found in 10 or fewer quadrats), C_{ice} is the sample incidence coverage estimator (Lee and Chao, 1994), and γ_{ice}^2 is the estimated coefficient of variation of the infrequent species. The assumption of these estimators is that the real species richness of a site is as higher as the number of rare and infrequent species increases. S_{chao2} and S_{ice} are among the least-biased species richness estimators; the former adapted to small numbers of samples (Colwell and Coddington, 1994; Chazdon et al., 1998; Walther and Moore, 2005).

The effect of age of disturbance oldness on the canopy openness was first tested with a Kruskal–Wallis analysis of variance (as the assumption of equal variances was not met even after variable transformation) followed by a Mann–Whitney U -Test where necessary. A test of homogeneity of slopes regression in ANCOVA was then performed to determine if differences existed between soil flora characteristics of sites with regards to canopy openness. Sites were treated as random effects and canopy openness as a covariate. To examine whether seeds of trees in the forest soil depends on the surrounding tree vegetation, the Sorensen's similarity index C_S was used at site level.

Similarity in the soil flora between sites was also determined by Sorensen's index. To compare abundance between sites, a one-way analysis of variance (ANOVA) was performed after a log transformation. However, as differences in the structure of the seed bank could be related to both species composition and abundance, data were ordinated by Principal Component Analysis (PCA) based on a covariance matrix and using STATISTICA 6.0 (StatSoft France, 2004).

3. Results

3.1. Seed bank characteristics

Throughout the experiment, a total of 289 seedlings was recorded from 3.3 m^2 of forest soil providing an average of 87.6 seeds m^{-2} . All seedlings emerged within the first 12 weeks. Seeds of 43 species germinated, including 17 herbaceous species (39.5%), 11 liana species (25.6%) and 15 shrub and tree species (34.9%), including three timber tree species: *Ceiba pentandra* (L.) Gaertn., *Erythrophleum suaveolens* (Guill. & Perr.) Brenan and *Terminalia superba* Engl. & Diels. Only one taxon, *Strombosia pustulata* Oliv. can be considered as a climax species. Zoochory was the most prevalent dispersal syndrome in the soil flora: 58.1% of the seedlings come exclusively from animal-dispersed seeds whereas only 9.3% of the seeds in the soil are dispersed by wind and 7.0% by autochory. The rest of the represented plant species (25.6%) combine autochory and zoochory (Table 1).

There was a significant correlation between seed density and species richness of the soil flora in RLF (Pearson's $R=0.89$ and

Table 1
Composition of soil seed banks in three forest zones. Dispersal syndromes: Au = autochory, An = anemochory, Z = zoochory. AD = absolute density, RD = relative density and RF = relative frequency. Regarding species temperament, the following guilds were used (Hawthorne, 1995; J-L. Doucet, pers. comm.): SB = shade-bearer, P = pioneer and NPLD = non-pioneer light-demander. Underlined taxa are those specific to the considered site. The taxa are ordered according to their importance in terms of absolute density (AD).

Taxa	Family	Guild	Dispersal mode	AD (n/m ²)	RD (%)	RF (%)
Recently logged forest (RLF)						
Weedy species (5 species)						
<i>Digitaria horizontalis</i> Willd.	Poaceae	P	Au	12.7	28.5	33,3
<i>Piper</i> sp.	Piperaceae	P	Z	9.5	21.3	23,8
<i>Palisota hirsuta</i> (Thunb.) K. Schum.	Commelinaceae	P	Z	4.8	10.8	14,3
<i>Ageratum conyzoides</i> L.	Asteraceae	P	An	1.6	3.6	4,8
<i>Euphorbia hirta</i> L.	Euphorbiaceae	P	Au/Z	1.6	3.6	4,8
Lianas (4 species)						
<i>Ficus thonningii</i> Blume	Moraceae	P	Z	4.8	10.8	14,3
<i>Ficus calyptрата</i> Thonn. ex Vahl	Moraceae	P	Z	1.6	3.6	4,8
<i>Ficus</i> sp.	Moraceae	P	Z	1.6	3.6	4,8
<i>Ficus craterostoma</i> Warb. ex Mildbr. & Burret	Moraceae	P	Z	1.6	3.6	4,8
Trees (3 species)						
<i>Erythrophleum suaveolens</i> (Guill. & Perr.) Brenan	Caesalpiniaceae	P	Au/Z	1.6	3.6	4,8
<i>Musanga cecropioides</i> R. Br.	Moraceae	P	Z	1.6	3.6	4,8
<i>Tetrorchidium didymostemon</i> (Baill.) Pax & K. Hoffm.	Euphorbiaceae	P	Au/Z	1.6	3.6	4,8
Total for RLF: 12 species, with 25% of specific taxa				41.3	100.0	
9-year-old logged forest (OLF)						
Weedy species (12 species)						
<i>Piper</i> sp.	Piperaceae	P	Z	71.4	61.4	55,1
<i>Palisota hirsuta</i> (Thunb.) K. Schum.	Commelinaceae	P	Z	6.8	5.8	16,3
<i>Palisota ambigua</i> (P. Beauv.) C.B. Clarke	Commelinaceae	P	Z	4.1	3.5	8,2
<i>Costus lucanusianus</i> J. Braun & K. Schum.	Zingiberaceae	P	Au/Z	4.1	3.5	8,2
<i>Bertiera bicarpellata</i> (K. Schum.) N. Hallé	Rubiaceae	P	Z	3.4	2.9	4,1
<i>Chromolaena odorata</i> (L.) R.M. King & H. Rob.	Asteraceae	P	An	2.7	2.3	6,1
<i>Echinochloa colona</i> (L.) Link	Poaceae	P	Au	1.4	1.2	4,1
<i>Digitaria horizontalis</i> Willd.	Poaceae	P	Au	1.4	1.2	4,1
<i>Commelina diffusa</i> Burm.f.	Commelinaceae	P	Au/Z	0.7	0.6	2,0
<i>Datura</i> sp.	Solanaceae	P	Au/Z	0.7	0.6	2,0
<i>Haumania liebrechtsiana</i> (De Wild. & T. Durand) J. Léonard	Marantaceae	P	Z	0.7	0.6	2,0
<i>Phyllanthus amarus</i> Schumacher & Thonn.	Euphorbiaceae	P	Z	0.7	0.6	2,0
Lianas (4 species)						
<i>Urera cameroonensis</i> Wedd.	Urticaceae	P	Au/Z	2.0	1.8	4,1
<i>Cissus</i> sp.	Vitaceae	P	Z	0.7	0.6	2,0
<i>Ficus elasticoides</i> De Wild.	Moraceae	P	Z	0.7	0.6	2,0
<i>Phyllanthus muellerianus</i> (Kuntze) Exell	Euphorbiaceae	P	Z	0.7	0.6	2,0
Trees and shrubs (8 species)						
<i>Musanga cecropioides</i> R. Br.	Moraceae	P	Z	3.4	2.9	8,2
<i>Trema orientalis</i> (L.) Blume	Ulmaceae	P	Z	3.4	2.9	8,2
<i>Terminalia superba</i> Engl. & Diels	Combretaceae	P	An	2.7	2.3	8,2
<i>Citrus</i> sp.	Rutaceae	P	Z	1.4	1.2	4,1
<i>Strombosia pustulata</i> Oliv.	Oleaceae	SB	Z	1.4	1.2	4,1
<i>Macaranga barteri</i> Müll.Arg.	Euphorbiaceae	P	Au/Z	0.7	0.6	2,0
<i>Margaritaria discoidea</i> (Baill.) G.L. Webster	Euphorbiaceae	P	Au/Z	0.7	0.6	2,0
<i>Xylopia aethiopica</i> (Dunal) A.Rich.	Annonaceae	P	Z	0.7	0.6	2,0
Total for OLF: 24 species, with 50% of specific taxa				116.3	100.0	
Protected forest (PF)						
Weedy species (10 species)						
<i>Palisota hirsuta</i> (Thunb.) K. Schum.	Commelinaceae	P	Z	5.8	7.6	12,5
<i>Melastomataceae</i>	Melastomataceae	–	–	2.5	3.3	5
<i>Piper</i> sp.	Piperaceae	P	Z	2.5	3.3	7,5
<i>Palisota ambigua</i> (P. Beauv.) C.B. Clarke	Commelinaceae	P	Z	1.7	2.2	5
<i>Costus lucanusianus</i> J. Braun & K. Schum.	Zingiberaceae	P	Au/Z	1.7	2.2	5
<i>Ageratum conyzoides</i> L.	Asteraceae	P	An	0.8	1.1	2,5
<i>Commelinaceae</i>	Commelinaceae	–	–	0.8	1.1	2,5
<i>Euphorbia hirta</i> L.	Euphorbiaceae	P	Au/Z	0.8	1.1	2,5
<i>Impatiens</i> sp.	Balsaminaceae	–	–	0.8	1.1	2,5
<i>Bertiera bicarpellata</i> (K. Schum.) N. Hallé	Rubiaceae	P	Z	0.8	1.1	2,5
Lianas (7 species)						
<i>Ficus thonningii</i> Blume	Moraceae	P	Z	10.0	13.0	7,5
<i>Ficus elasticoides</i> De Wild.	Moraceae	P	Z	9.2	12.0	17,5
<i>Ficus wildemaniana</i> Warb.	Moraceae	P	Z	7.5	9.8	12,5
<i>Ficus calyptрата</i> Thonn. ex Vahl	Moraceae	P	Z	5.8	7.6	5
<i>Cissus dinklagei</i> Gilg & M. Brandt	Vitaceae	P	Z	0.8	1.1	2,5
<i>Ficus barteri</i> Sprague	Moraceae	P	Z	0.8	1.1	2,5
<i>Phyllanthus muellerianus</i> (Kuntze) Exell	Euphorbiaceae	P	Z	0.8	1.1	2,5
Trees (9 species)						
<i>Margaritaria discoidea</i> (Baill.) G.L. Webster	Euphorbiaceae	P	Au/Z	13.3	17.4	10
<i>Zanthoxylum leprieurii</i> Guill. & Perr.	Rutaceae	P	Z	2.5	3.3	7,5
<i>Macaranga monandra</i> Müll.Arg.	Euphorbiaceae	P	Au/Z	0.8	1.1	2,5
<i>Tabernaemontana crassa</i> Benth.	Apocynaceae	SB	Z	1.7	2.2	5

Table 1 (Continued)

Taxa	Family	Guild	Dispersal mode	AD (n/m ²)	RD (%)	RF (%)
<i>Celtis adolfi-friderici</i> Engl.	Ulmaceae	NPLD	Z	1.7	2.2	5
<i>Macaranga barteri</i> Müll.Arg.	Euphorbiaceae	P	Au/Z	0.8	1.1	2,5
<i>Terminalia superba</i> Engl. & Diels	Combretaceae	P	An	0.8	1.1	2,5
<i>Ceiba pentandra</i> (L.) Gaertn.	Bombacaceae	P	An	0.8	1.1	2,5
<i>Erythrophleum suaveolens</i> (Guill. & Perr.) Brenan	Caesalpiniaceae	P	Au/Z	0.8	1.1	2,5
Total for PF: 26 species, with 42% of specific taxa				76.7	100.0	

Table 2

Species richness (observed S_{obs} , predicted number of species by S_{chao2} and S_{ice}) and similarity (C_s) between soil seed banks of the three sites: *RLF* = recently logged forest, *OLF* = 9-year-old logged forest, *PF* = protected forest. SD = standard deviation.

Sites	S_{obs}	S_{chao2} (SD)	S_{ice} (SD)	C_s (%)		
				<i>RLF</i>	<i>OLF</i>	<i>PF</i>
<i>RLF</i>	12	38.7 (20.3)	28.1 (0.0)	–	22	37
<i>OLF</i>	24	32.3 (6.9)	34.3 (0.1)	–	–	40
<i>PF</i>	26	36.3 (7.8)	38.9 (0.0)	–	–	–

$p < 0.001$). Mean density in *RLF* was 41.3 seeds m⁻². Seedlings germinated from 12 species, but estimates of species richness were higher and not congruent ($S_{ice} = 28.1$ and $S_{chao2} = 38.7$ species; Table 2). Thus only 31.0–42.7% of the predicted species richness was revealed. This means that the seed bank in this zone is considerably heterogeneous from one sample to another, and rare and infrequent species are numerous. Most of the seedlings were from weedy and lianas species (Table 1; total *RD* for herbaceous and lianas = 89.2%), with a high occurrence of the taxa *Digitaria* and *Piper*. Only three tree species were found in *RLF* and they were pioneers: *E. suaveolens* (a timber tree), *Musanga cecropioides* R. Br. and *Tetrorchidium didymostemon* (Baill.) Pax & K. Hoffm.

The soil in *OLF* displayed a density of 116.3 seeds m⁻² and 24 species (S_{obs} in Table 1). This richness should account for 70 or 75% of the most likely value of species richness as $S_{ice} = 34.3$ and $S_{chao2} = 32.3$ species (Table 2). Seed density and species richness were correlated (Pearson's $R = 0.39$ and $p = 0.005$). An important proportion of weedy species was also observed: 50%. More than 61% of the total density in this zone was provided by seeds of the taxon *Piper*, and weedy species accounted for 84.1% of the total number of seeds. Excluding *S. pustulata*, all trees and shrubs found in *OLF* soil were pioneers or non-pioneer light demanders.

The protected zone *PF* displayed 26 species (Table 1). This value was about of 67–72% of the predicted species richness according to S_{chao2} and S_{ice} (Table 2). Seed density was intermediate to the other sites: 76.7 seeds m⁻² (Table 1), and was significantly correlated to species richness (Pearson's $R = 0.70$ and $p < 0.001$). Although this site showed a similar number of tree species as *OLF*, several species, such as *Celtis adolfi-friderici* Engl., *C. pentandra* and *Tabernaemontana crassa* Benth. were specific to the soil of *PF*. By contrast to the other zones, *Piper* was less abundant here (*RD* = 3.26%) and appeared only in 7.5% of the samples (Table 1).

3.2. Similarity of seed banks between sites

There was no significant difference in terms of density between sites (ANOVA; $F_{2,107} = 2.44$; $p = 0.091$). Regarding floristic composition, specificity in each zone reached 25–50% of emerged species (Table 1). Similarity indices between the seed banks of the three sites were fairly low and never exceeded $C_s = 40\%$ (Table 2). The PCA ordination analysis of the seed banks from the three sites revealed no clear structure, even after removal of the most common taxon from the data set: *Piper* (Fig. 2). The two first axes explained 53.2% of the total variance and were largely determined by the taxon *Margaritaria discoidea* (Baill.) G.L. Webster, which is absent in *RLF*, and *Ficus thonningii* Blume, which was not found in the soil samples from *OLF*.

garitaria discoidea (Baill.) G.L. Webster, which is absent in *RLF*, and *Ficus thonningii* Blume, which was not found in the soil samples from *OLF*.

3.3. Influence of environmental characteristics

Forest canopy closure was significantly different between sites (Kruskal–Wallis ANOVA; $H = 10.22$, $p = 0.006$). Its value was 6% lower in the recently logged forest than in the two other sites (Fig. 3). Canopy closure could significantly affect α -diversity of the soil seed bank (ANCOVA, $F_{1,104} = 13.75$ and $p = 0.002$) whereas neither site nor interaction between site and canopy openness had a significant effect on the species richness of the forest soil (ANCOVA, $p > 0.05$). Seed density at sample level was not significantly affected by canopy closure, site or their interaction (ANCOVA, $p > 0.05$).

Floristic composition of the three forest stands did not display important differences as C_s ranged from 74% to 81% (Table 3). S_{obs} ranged from 110 to 143 species and the estimates of S_{chao2} showed that S_{obs} corresponded to 89%, 72% and 69% of the total richness of *RLF*, *OLF* and *PF* respectively. Shade-bearer and non-pioneer light-demanders are the most prevalent taxa in the woody vegetation (Table 3). Overall, the soil seed bank and the standing tree vegetation shared only 10 tree species: the light-demanding pioneer species *M. cecropioides*, *Trema orientalis* (L.) Blume, *T. superba*, *E. suaveolens*, *Tetrorchidium didymostemon*, *C. pentandra* and *Xylopia aethiopica* (Dunal) A. Rich; the shade-tolerant species *S. pustulata* and *T. crassa*, and the non-pioneer light demander *Celtis adolfi-friderici*. Therefore, the value of C_s between the standing tree vegetation and the soil seed bank in each site was very low: 3.5%, 7.6% and 6.5% in *RLF*, *OLF* and *PF* respectively.

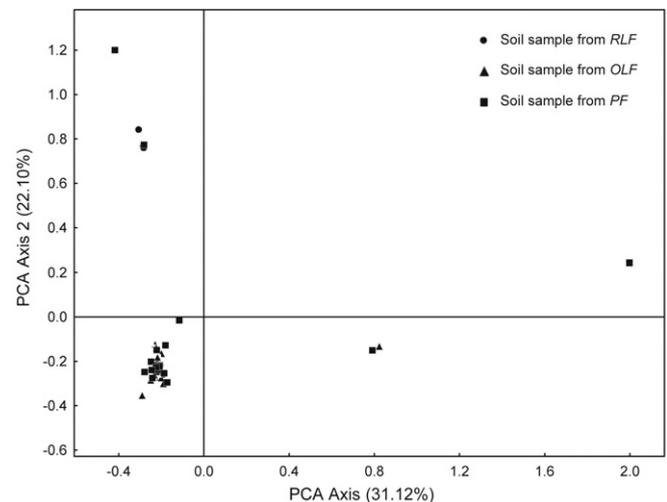


Fig. 2. Ordination diagram based on principal component analysis of seed bank abundance and species composition; the taxon *Piper* was removed from the analyzed data set since it was well distributed in all of the sites. Eigen1 = 1.97, Eigen2 = 1.40. The first axis was mainly determined by abundance of *Margaritaria discoidea* (99.8% of contribution) whereas the second axis separated samples according to *Ficus thonningii* abundance (99.4% of contribution).

Table 3

Some characteristics of the standing vegetation (trees with dbh ≥ 10 cm) in the three sites: RLF is a 2-year-old logged forest (or recently logged forest), OLF is a 9-year-old logged forest and PF is a protected forest. The guilds were named following Hawthorne (1995): NPLD = non-pioneer light-demander, P = pioneer, SB = shade-bearer, 'unknown' group taxa whose temperament is not well established. For other characteristics: AD = absolute density, S_{obs} = number of observed species, S_{chao2} = predicted number of species after Chao (1984, 2005). C_s is the Sorensen's similarity index.

Guilds	Guilds abundance		Additional characteristics of the standing vegetation			C_s (%)			The most prevalent taxa per site
	Percentage of species (%)	RD (%)	AD (n/ha)	S_{obs}	S_{chao2}	RLF	OLF	PF	
<i>RLF</i>									
NPLD	20.0	14.2	98.3	110	124	–	81.0	74.3	<i>Desbordesia glaucescens</i> – <i>Tabernaemontana crassa</i> – <i>Greenwayodendron suaveolens</i> – <i>Trichilia welwitschii</i> – <i>Trichilia dregeana</i> – <i>Pericopsis elata</i> – <i>Celtis adolphi-friderici</i>
P	26.4	9.6							
SB	46.3	70.5							
Unknown	7.3	5.7							
<i>OLF</i>									
NPLD	17.9	12.8	98.0	123	170	–	–	77.8	<i>Trichilia dregeana</i> – <i>Strombosia pustulata</i> – <i>Drypetes</i> sp. – <i>Diospyros</i> sp. – <i>Duboscia macrocarpa</i> – <i>Corynanthe pachyceras</i> – <i>Diospyros canaliculata</i>
P	30.1	14.7							
SB	44.7	65.3							
Unknown	7.3	7.3							
<i>PF</i>									
NPLD	23.6	18.4	135.4	143	208	–	–	–	<i>Greenwayodendron suaveolens</i> – <i>Duboscia macrocarpa</i> – <i>Pausinystalia macroceras</i> – <i>Desbordesia glaucescens</i> – <i>Hannoa klaineana</i> – <i>Anonidium mannii</i> – <i>Funtumia elastica</i>
P	24.5	7.9							
SB	46.9	70.0							
Unknown	10.5	3.7							

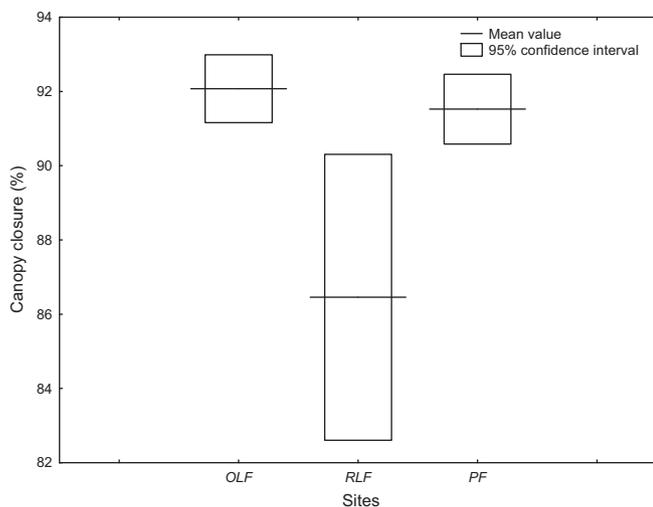


Fig. 3. Average forest canopy closure of the three study sites in a Cameroonian logging concession. OLF: 9-year-old logged forest, RLF: recently logged forest, PF: protected forest.

4. Discussion

Our data provide the first estimate of seed bank characteristics from a Central African rainforest. As we collected soil samples during the period of low tree fruiting activity and we did not include litter component in our sampling, seed rain inclusion should be negligible. However, we suspect that seeds of *T. crassa* came from seed rain as they are non-dormant (Dollet and Dubern, 1977).

4.1. Contribution of the soil seed bank in forest restoration and for the regeneration of timber trees species

By definition, the soil seed bank is supplied with dormant seeds and dormancy is commonly related to seed size (Venable and Brown, 1988). From the Neotropics, Uasuf et al. (2009) assessed seeds of several woody species and concluded that they were large

with high moisture content; indicative of adaptation to immediate germination. In the present study, herbaceous species that are typical of disturbed habitats constituted the most prevalent life-forms emerging from forest soils. Their predominance in soil seed banks can be explained by a combination of several factors. These herbaceous plants generally produce large amounts of small seeds which are less likely to be predated on or damaged by micro-organisms than large seeds of perennial tree species (Janzen, 1988). Also, small diaspores from weedy and pioneer shrub and tree species tend to germinate more slowly than larger ones (Hall and Swaine, 1980; Tweddle et al., 2003). Several studies have demonstrated that seeds of pioneer and early secondary species can survive many years in the forest soil: 2–30 years according to Hopkins and Graham (1987), Dalling et al. (1997), Floyd (1990) and Dalling and Brown (2009). In this study, shade-bearers were very rare in the soil seed banks (only *S. pustulata* is represented) although they presented a high abundance in the extant tree vegetation. Liew (1973), Hall and Swaine (1980) and Hopkins and Graham (1983) also observed that climax species account for only 12–21% of species richness in soil stocks.

The forest soil appears to not contribute largely to the regeneration of timber trees species. In our case, (i) only three timber species were represented in the forest soil, (ii) these species were at very low density (AD never exceeded 2.7 seeds m^{-2}) and (iii) they were found in less than 9% of the collected samples. In West Africa, Hall and Swaine (1980) also observed very low amounts of seeds from commercial tree species in the forest soil (from only four species out of 90). Clearly, the forest soil could not provide a good supply of diaspores of commercial trees, although some important species may be favored: *C. pentandra*, *Erythrophleum* spp. and *Terminalia* spp. Thus no efficient strategy can include the use of forest soil as far as the enrichment of degraded lands with commercial species is concerned. For such purpose, planting in logging gaps with seedlings coming from tree nursery should be more efficient (Doucet et al., 2009).

The low values of similarity indices between the seed bank and the mature vegetation provided more proof of the weak contribution of soil seed stocks to mature stands. Hall and Swaine (1980) found coefficients of similarity between forest soil and vegetation ranging from 0 to 9% (using Jaccard's coefficient). Similar

conclusions were made from other studies (Perera, 2005; Uasuf et al., 2009). Dispersal syndromes cannot explain this dissimilarity since zoochory was prevalent in both floristic components. Finally, Baskin and Baskin (2003) and Schmidt (2007) were probably right when they noted that trees of the humid tropical forests rarely have post-dispersal seed dormancy.

As shown by Russel-Smith and Setterfield (2006), the present results also suggest that seed rain may play a more important role than soil seed stocks in tree species regeneration in mature tropical rainforests. However, the role of the soil seed bank in forest recruitment is still debatable because many other studies have shown its contribution to tree regeneration. Disturbance is very important for regeneration of tropical forests, and the extent, type and the timing of disturbance may fundamentally determine the species response, regardless of seed sources (Denslow, 1980). Under this hypothesis, the local contribution of the seed bank to the standing vegetation can vary greatly between sites.

4.2. Heterogeneity in density and species composition of the soil seed bank

A large proportion of seed bank studies conducted in tropical zones confirm the spatial heterogeneity of soil seed bank characteristics (Hall and Swaine, 1980; Perera, 2005; Uasuf et al., 2009). The absence of partitioning in the PCA analysis highlights an important heterogeneity between sites as well as within sites. Variation in canopy closure can partially explain this heterogeneity (Leckie et al., 2000; Isselin-Nodédeu and Bédécarrats, 2007). Martins and Engel (2007) showed that reduced canopy closure in a forest zone can induce a slight increase in seed bank density and species richness whereas Lindner (2009) found no relationship between canopy openness and seed bank characteristics. Although we demonstrated a possible link between canopy closure and species richness, this requires further investigation.

In the present study, seed densities in the forest soil ranged from 41 to 116 seeds m^{-2} . In general, seed density tends to be lower in upland evergreen forests and wet evergreen forests than in more disturbed ones (Aubréville, 1947; Keay, 1960; Alexandre, 1978; Hall and Swaine, 1980). According to Garwood (1989), seed density in tropical forests is broadly variable and ranges from 25 to 3350 seeds m^{-2} . This huge variation might also be due to diversity in methods of seed bank characterization (Warr et al., 1993). Although our data were consistent with previous studies they may be considered as conservative since the number of emerged seedlings may have been underestimated as a result of the experimental conditions: (i) some small seeds could fail to germinate because they were too deeply covered by soil and (ii) quiescent species (which just need an environmental factor to germinate; Baskin and Baskin, 2003) should germinate within a few weeks, but this may not be the case for the dormant ones which can persist in the soil for a long time.

Regarding species richness of the soil flora, the values of S_{obs} found here lie within the range of data collected from West African forest soils: 11–43 species according to Hall and Swaine (1980) and Keay (1960). Although most related studies provide only S_{obs} , Walther and Moore (2005) confirmed that the use of any estimator is preferable to a simple species count, unless sampling has been exhaustive. When analyzing values of observed and predicted species richness, Butler and Chazdon (1998) and Garcia (1995) showed that S_{obs} generally accounts for 70–85% of the predicted species richness of tropical forest soils. Despite a significant sampling effort in RLF in relation to the size of the site, this threshold was not reached, suggesting that the recent disturbance could have influenced the species richness and the heterogeneity of the forest soil flora.

5. Conclusions

Patterns of forest soil seed bank in Cameroonian are similar to those in West African rainforests. Our results indicate an important spatial variation in soil seed bank characteristics between sites despite a pronounced similarity in standing tree vegetation in different sites. As noted in other tropical rainforest sites, the soil seed bank is dominated by weedy and short-lived pioneer species which are light-demanders and could only emerge under adequate conditions, that is, in forest gaps. Thus, the contribution that soil seed stocks make to logged forest recovery may be notable in early stages of forest succession. Accordingly, very few timber tree species can benefit from soil seed stocks for their regeneration and therefore no opportune enrichment technique should be proposed in the context of tropical humid forests. For the light-demanding commercial species, planting in logging gaps may be a more efficient way to perpetuate their populations in these ecosystems. This work is the first attempt towards characterizing soil seed banks in a Central African rainforest. Further studies are needed to investigate the role of soil seed banks in forest regeneration, regarding burial conditions, topographic position and soil properties.

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