Litterfall, litter standing crops and nutrient dynamics as influenced by selective logging in tropical rainforest of Ebom, Southwest Cameroon

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Litterfall, litter standing crops, nutrient dynamics and their turnover were studied in Ebom tropical rainforest of Cameroon six years after selective logging practices. Two sample sites, one in the logging part of the forest (disturbed site) and the other in the part of forest not affected by selective logging (undisturbed site) were used for the study. After two years of field experiment, the mean annual of litterfall varied from 1.95 to 10.93 t.ha⁻¹.y⁻¹ in undisturbed site, and from 1.49 to 9.07 t.ha⁻¹.y⁻¹ in logging site respectively for wood litter and the total litterfall. The greatest significant of total litterfall were recorded in long dry season in the two sites. The litter standing crops varied from 0.96 for wood to 2.09 t.ha⁻¹ for leaf litter in the undisturbed site and from 0.49 for rest litter to 1.58 t.ha⁻¹ for leaf litter in the logging site. The turnover (K₁) of litter varied from 0.89 to 3.57 for wood in the logging site and from 0.49 to 2.99 for leaf litter in the undisturbed site. Overall, the nutrient amounts in litter fractions are higher in the undisturbed site than in the logging site, except that of Na. The logging impact, six years after logging, was negligible on the litterfall, but results in much faster release of Mg and Na which were low in the Ebom forest soil. It would take more than six years for the logging effects to cancel out.

Key words: Litterfall, litter standing crops, litter turnover, logging, nutrient dynamics, tropical rainforest, Cameroon.

INTRODUCTION

In South Cameroon, the degradation of tropical forests, mainly due to shifting cultivation and logging (van Gemerden, 2004) is currently one of the major problems for the forest management (Jonkers and Foahom, 2003). Impacts on the reduction of biodiversity, soil depletion and loss of productivity are undeniable (Jonkers and Foahom, 2003). To remedy this, Tropenbos Cameroon Programme (TCP) developed a strategy for the sustainable...
management of these forest ecosystems. According to TCP, one of the alternatives that can lead to the sustainable exploitation of these tropical forests without compromising their existence is to take into account, in forest management, the interests of riparian populations (Jonkers and Foahom, 2003) and the functional aspects of these forests, as litterfall, litter standing crops and nutrient contents.

Litter is a major source of organic matter and nutrients in forest ecosystems (Vitousek and Sanford, 1986; Devi and Singh, 2017). The litterfall contributes to the assessment of net primary production and is also the major pathway for the return of dead organic matter and nutrients from aerial vegetation to forest soil (Vitousek and Sanford, 1986). In the forest ecosystem, litterfall reduce bulk density, increase water holding and the cation exchange capacity of the soil (Seta et al., 2018). In addition, litter on the forest floor plays a significant role in determining the moisture status, runoff pattern and release of nutrients accumulated in the aerial parts of the vegetation (Parsons et al., 2014). The litterfall influences also its decomposition, growth of vegetation and soil fertility through the feedback mechanisms (Brouwer, 1996). Under a fertile soil forest, leaf renewal, litterfall and its decomposition are rapid because of a low energy investment for the synthesis of secondary metabolites. On the other hand, regarding infertile soil, leaf turnover, litterfall and its decomposition are low due to a high investment in metabolites (Berendse, 1994).

However, the litterfall production pattern is directly affected by climate, seasonality, tree species composition, stand structure, soil fertility, elevation and latitude (Vitousek and Sanford, 1986; Parsons et al., 2014; Becker et al., 2015; Das and Mondal, 2016; Devi and Singh, 2017; Seta et al., 2018). Qiu et al. (1998) observed that abiotic factors such as rainfall, temperature and light play an important role in litterfall, flushing among dominant canopy species in the forest. Other workers reported that seasonal patterns of litterfall show unimodal, bimodal or irregular modes, and the litter peaks might occur in several months of the year (Sundarapandian and Swamy, 1999; Zhang et al., 2014). Consequently, this phenomenon may affect the dynamics of ecosystem carbon and nutrient cycling (Das and Ramakrishnan, 1985).

Other variables that affect litterfall pattern and litter nutrients dynamics in the tropical rainforests are disturbances (van Dam, 2001). Natural or artificial gaps resulting from logging are considered as a disturbance, which alter the environmental conditions, such as temperature, availability of light, nutrients and moisture to plants (Denslow et al., 1998; Burivalova et al., 2016). These changes affect the flora and fauna composition, influence carbon emissions (Harris et al., 2012), the plant litter decomposition process (Brouwer, 1996; Van Dam, 2001; Ibrahima et al., 2016) and litterfall dynamics (Chandrasheker and Ramakrishnan, 1994; van Dam, 2001).

Despite many studies were conducted in tropical rainforests of Cameroon, little information exists on litterfall and nutrient dynamic (Songwe et al., 1988; Chuyong et al., 2000; Ibrahima et al., 2002), but no study has been carried out to understand the effects of logging activities on litterfall. The purpose of this study was to determine the impact of selective logging on litterfall components (total and fractions), nutrient dynamics and their turnover in the Ebom tropical rainforest of southwestern Cameroon.

MATERIALS AND METHODS

Study sites

The experiment was conducted in Ebom Forest, within the Tropenbos Cameroon Programme (TCP) research area, which is located in the western portion of the Atlantic Bioregion of Cameroon, lying within the Congo-Guinea refugia. The experimental sites are located at 3°05′N and 10°41′E, with elevation of ~440 m. The bedrock is composed of Precambrian metamorphic as well as old volcanic rocks (Franqueville, 1973). The soil is very clayey (35-70%) and strongly acidic (van Gemerden and Hazeu, 1999). The climate is humid tropical with four seasons: a long dry season (from mid-November to mid-March) and a short one (mid-May to mid-August), as well as a short rainy season (mid-March to mid-May) and a long rainy season (mid-August to mid-November). Mean annual rainfall is about 2100 mm and mean annual temperature is 22.9°C (van Gemerden and Hazeu, 1999). Relevant characteristics of these sites like location, rainfall data and soil physico-chemical characteristics are presented in our previous studies (Ibrahima et al., 2002, 2016). Vegetation consists of evergreen forest rich in Caesalpinioideae (Letouzy, 1985), characterised by tall trees that reach heights of about 60 m, with four strata and one closed canopy (Bibani and Jonkers, 2001). Tree density was about 521 trees per hectare, basal area of about 29.84 m² ha⁻¹ and diameter classes ranged from 9.39 to 150 cm, with a mean of 21.34 cm (Ibrahima et al., 2002). At some places in the forest Bantou people practice shifting agriculture with short fallows (Nounamou and Yemefack, 2001), while Banyeli Pygmy live from gathering and hunting. Many non-timber forest products like bushmeat, honey, mushrooms, fruits, leaves, seeds and roots are harvested (van Dijk, 1999).

Two one-ha-plots (100 m × 100 m) in the experimental area in the catchments of Bibo’s Minwo near Ebom were selected: one in an undisturbed and the other in a disturbed part of the forests. The undisturbed forest, at 15 km away in the north of Ebom, is characterized by the absence of recent natural or human disturbance. The vegetation consists of evergreen forest rich in Caesalpinioideae (Letouzy, 1985), as presented before. The other plot was selected in the logging site with small gaps. The forest has been logged in recent years with the exception of the mountainous parts, by national and international companies, principally the Dutch Company, Wijma - Douala SARL (GWZ) (van Gemerden and Hazeu, 1999). The selective logging rate was low; averaging 10 m³ ha⁻¹, say 0.7 tree ha⁻¹ the last exploitation (van Gemerden and Hazeu, 1995). Only trees with diameter at breast height (DBH) > 30 cm and straight boles of at least 6 m were felled. Damages caused by this felling and extraction of the logs from the stand affected less than 8% of the forest area (Fines et al., 2001; Jonkers and van Leersum, 2000). The vegetation of this site is dominated by heliophilous (pioneer) species, particularly Musanga (Musanga cecropoides R. Brown ex. Tedlie). Tree density, the basal area and the mean DBH are respectively 417 trees per hectare, 28.48 m² ha⁻¹.
Litter collection

Small litterfall (including leaf, twigs and small branches (<2.5 cm), flowers, fruits, etc.) in each site was collected in twenty 1 m x 1 m litter traps, 1 m high above the ground. The litter traps were made of wooden frame material with a mesh size of 0.5 mm and randomly distributed in 1-ha plot. The mesh size was sufficient to allow free drainage while retaining the finer litter fragments. Litter was collected fortnightly, excepted in the large rainy season where litter was collected at weekly. Because of technical difficulties (access to plots, disturbance of litter traps by animals, etc.), experiment was only carried out two years in undisturbed site, from August 1999 to July 2001, and one and half year (from February 2000 to July 2001) in logging site. The litter samples were taken to the laboratory in polythene bags and oven-dried at 60°C to constant mass. The samples of each month were bulked and categorized into leaf (L), wood (including twigs, small-wood fraction, small branches (<2.5 cm in diameter) and bark fragments (W)), and all remaining material so called rest (R) including reproductive parts, flowers, fruits, pods, mouses, lichens, and all other unknown material. Dry mass of each component was determined by drying to a constant mass at 60°C and the mean monthly value for each site was worked out on a unit area basis (t ha⁻¹).

Coarse litterfall, comprising large wood or branches with bark, was estimated for about one year, from June 2000 to July 2001. The samples were collected every six months in five subplots of 20 m x 20 m, located near 1-ha plot of each site. The subplots were cleaned initially. The samples were transported to laboratory in polythene bags and processed, in accordance with the procedures given above for the small litterfall.

Litter standing crops of forest floor (or litter layer on the soil surface) was estimated in undisturbed and logging sites for one year. Five litter samples were collected every three months from each site, using a 0.25 m² (0.5 m x 0.5 m) quadrat frame placed randomly near 1-ha plot, transported to laboratory in polythene bags and processed, in accordance with the procedures given above for the small litterfall.

Chemical analysis

One monthly small litterfall fraction (leaf, wood, rest), and five coarse litterfall samples and five litter standing crops samples resulting from the sample bulking were taken to chemical analysis. Powder samples obtained after grinding all samples through a Micro Hammer Mill Cilatti grinder equipped with a 1 mm link filter were analyzed. The samples were firstly mineralized by passing the powder through a furnace at 550°C for 40 mn. The ashes were re-collected with a diluted HNO₃ solution for nutrient analyzing. Calcium and Magnesium were determined through EDTA titrimetric method (Association Française de Normalisation (AFNOR), 1982), while Potassium, Sodium and Phosphorous were determined according to standard methods (Rodier, 1978). The nitrogen analysis was done by the Kjeldhal method and its titration by sulphuric acid at 0.01 N (Devani et al., 1989).

Statistical analysis

Before performing any statistical analysis, all variables were tested for normality. The comparison of litter mass and their nutrients among litter fractions, and among seasons was carried out by using ANOVA, followed by Scheffe's test at 5% if ANOVA was significant. A Student provided a test of significance of litter mass and their nutrients between undisturbed and logging sites. Turnover rates (Kₜ) of the forest floor litter or its nutrients were calculated by calculating the ratio between litterfall or its nutrients and litter standing crops or its nutrients for similar fractions. These tests were conducted through SX software (statistic, version 4.0. Analytical software, 1992).

RESULTS

Litter

Litterfall and their changes in time

Average mean annual litterfall (1999-2001), its interannual variation and the contribution rate of the different fractions of litterfall in undisturbed and logging sites were presented in Table 1. Contribution of leaf fraction was higher than that of other litter fractions, more than 55% to the total litterfall in both sites, while contribution of coarse litterfall was lower than that of the total litterfall in both sites; it was of 11% in undisturbed site and 17% in logging one. Greater mean annual of the total litterfall was recorded in undisturbed site (12.29 t.ha⁻¹.year⁻¹) compared to logging site (10.90 t.ha⁻¹.year⁻¹). The mean annual of litterfall and its fraction were higher in the undisturbed site (6.24, 1.95, 2.79 and 10.93 t.ha⁻¹.year⁻¹) than in the logging site (5.64, 1.49, 1.94 and 9.07 t.ha⁻¹.year⁻¹) respectively for leaf, woods, rest fraction and the total small litterfall, while coarse litterfall was higher in the logging site (1.83 t.ha⁻¹.year⁻¹) compared to the undisturbed site (1.36 t.ha⁻¹.year⁻¹). The two sites differed significantly from one another only by their rest fraction, the total small litterfall and the annual mean of total litterfall (small + coarse).

Small litterfall varied according to seasons (Table 2). Mean seasonal of total small litterfall and leaf fraction were significantly different according to seasons in both sites, while wood fraction was significant different according to seasons only in the logging site. The greatest significant total small litterfall and leaf fraction were recorded in the long dry season (December, January and February) and the lowest were obtained in the small dry season (June, July and August) in the two sites. According to the season, the two sites were significantly different only during the small dry season and the long rainy season for the total small litterfall, during the small dry season for the leaf and woods fractions, and at least during the long rainy season for the rest fraction.

Dynamics of small litterfall and its fractions showed monthly variation during the two years of litterfall collection in the undisturbed site and the one year and half in the logging site (Figure 1). Peak of small litterfall was recorded in the end of February and that of April,
Table 1. Annual and mean annual litterfall (t.ha⁻¹.y⁻¹) in undisturbed and logging sites of tropical rainforest of Ebom, southwest Cameroon.

| Litter fractions | Undisturbed site | Logging site | t Student |
|------------------|------------------|--------------|----------|
|                  | Litter mass | %           | Litter mass | %           |          |
| Leaf 2000 – January 2001 |           |             |            |            |
| Leaf             | 6.09 (1.29) | 55          | 5.92 (1.08) | 63          | 1.24 ns |
| Wood             | 1.91 (1.38) | 17          | 1.50 (0.90) | 16          | 1.97 ns |
| Rest             | 3.04 (1.79) | 28          | 1.99 (1.03) | 21          | 2.47*    |
| Total small litterfall | 11.04 (3.08) | 100         | 9.41 (2.23) | 100         | 2.72**   |
| August 2000 - July 2001 |           |             |            |            |
| Leaf             | 5.68 (1.02) | 54          | 5.63 (1.08) | 62          | 0.11 ns |
| Wood             | 1.95 (0.86) | 17          | 1.51 (0.65) | 17          | 1.93 ns |
| Rest             | 2.95 (1.91) | 28          | 1.93 (1.06) | 21          | 2.03*    |
| Total small litterfall | 10.58 (0.65) | 100         | 9.07 (0.40) | 100         | 2.03*    |
| Leaf             | 6.24 (1.06) | 57          | 5.64 (1.00) | 62          | 1.26 ns |
| Wood             | 1.95 (1.02) | 18          | 1.49 (0.73) | 16          | 1.61 ns |
| Rest             | 2.79 (1.55) | 26          | 1.94 (1.02) | 21          | 1.68 ns |
| Total small litterfall | 10.93 (2.64) | 100         | 9.07 (1.90) | 100         | 2.05*    |
| Coarse litterfall | 1.36 (0.44) | 11          | 1.83 (0.96) | 17          | 0.88 ns |
| Total litterfall  | 12.29 (2.18) | 100         | 10.90 (1.95) | 100         | 2.31*    |

*Standard error in brackets. ns: no significant; * P < 0.05; ** P < 0.01.

Table 2. Mean seasonal small litterfall (t.ha⁻¹.season⁻¹) in undisturbed and logging sites of tropical rainforest of Ebom, southwest Cameroon.

| Season | Undisturbed site | Logging site | t Student between sites |
|--------|------------------|--------------|------------------------|
|        | Leaf | Wood | Rest | Total | Leaf | Wood | Rest | Total | Leaf | Wood | Rest | Total |
| LDS    | 2.09a | 0.49 | 0.81 | 3.39a | 2.22a | 0.38b | 0.59 | 3.19a | 1.20ns | 0.50ns | 0.60ns | 0.60ns |
| SRS    | 1.61b | 0.71 | 0.82 | 3.14a | 1.56b | 0.53a | 0.59 | 2.68a | 0.10ns | 1.10ns | 1.70ns | 1.30ns |
| SDS    | 1.12c | 0.20 | 0.45 | 1.76b | 0.73d | 0.10c | 0.33 | 1.16c | 2.80** | 2.10*  | 0.60ns | 2.80** |
| LRS    | 1.46bc | 0.51 | 0.76 | 2.73ab | 1.28c | 0.45ab | 0.53 | 2.26b | 1.10ns | 1.10ns | 2.30*  | 2.30* |
| F Fischer’s | 12.80 *** | 1.00ns | 2.00ns | 2.90* | 30.70 *** | 6.70 *** | 1.00ns | 17.90 *** |        |        |        |        |

LDS: Long dry season; SRS: short rainy season; SDS: short dry season; LRS: Long rainy season; ns: not significant; * P < 0.05; ** P < 0.01; *** P < 0.001. Different letters indicate that values are different among seasons.

particularly for the total small litterfall and leaf litterfall. The pattern of dynamics was similar in the two sites (Figure 2), excepted in July and August 2000 (short dry season) where the total small litterfall and leaf litterfall were lower in the logging site than in the undisturbed site.

Litter standing crops and turnover

Amount of small litter on the forest floor were presented in Table 3. The dry mass of small litter on the forest floor varied from 0.96 t.ha⁻¹ for wood litter to 2.09 t.ha⁻¹ for leaf litter in the undisturbed site and from 0.49 t.ha⁻¹ for rest litter to 1.58 t.ha⁻¹ for leaf litter in the logging site. The highest contribution to the total litter standing crops was recorded for leaf litter fraction in the two sites (more than 45%), while the lowest was found for wood litter fraction in undisturbed site (23%) and for the rest litter fraction in logging site (14%). The dry mass of litter standing crops was higher in the undisturbed site than in the logging one, excepted for the wood litter fraction (Table 3). But the differences between the two sites were only significant (P<0.05) for leaf litter fraction.

Values for turnover (Kₜ) of total litter and their fractions were presented in Table 4. The values for Kₜ of leaf litter fraction and total small litter was high, more than 2.5 in the two sites, while these values were lesser than 0 for wood and rest litter fraction in the same sites. The
Figure 1. Dynamics of small Litterfall (t.ha$^{-1}$) and its fractions (F, B and R) in undisturbed and logging sites of Ebom tropical rain forest, southern Cameroon, and monthly rainfall during the experiment period. Leaf litter (F), wood litter (B) and rest litter (R).
Figure 2. Comparison of dynamics of small litterfall (t.ha$^{-1}$) fractions (leaf, wood, rest and total litterfall) between undisturbed (US) and logging sites (DS) of Ebom tropical rain forest, southern Cameroon.

Table 3. Mean litter standing crops (t.ha$^{-1}$) or litter on floor in undisturbed and logging sites of tropical rainforest of Ebom, southwest Cameroon.

| Fractions | Undisturbed site | Logging site | t Student |
|-----------|-----------------|--------------|-----------|
|           | Dry mass (t/ha) | % | Dry mass (t/ha) | % |
| Leaves    | 2.09 (0.35)     | 50 | 1.58 (0.50)     | 47 | 2.60* |
| Wood      | 0.96 (0.87)     | 23 | 1.32 (0.95)     | 39 | 0.88ns |
| Rest      | 1.11 (1.01)     | 27 | 0.49 (0.23)     | 14 | 1.87ns |
| Total     | 4.16 (1.28)     | 100| 3.39 (1.24)     | 100| 1.32ns |

Turnover of litter standing crops was higher in the logging site (0.89, 2.68 and 3.57 respectively for wood, total litter and leaf litter) than in the undisturbed site (0.49, 2.63 and 2.99 respectively for the same fractions), except for the rest litter fraction which was higher in the undisturbed site (0.39) than in the logging site (0.25).  

**Nutrients**

**Litter nutrient contents**

Nutrient contents in litter varied according to litter fractions in undisturbed and logging sites (Table 5).
Table 4. Litter (kg.ha\(^{-1}\)) and nutrient (g.kg\(^{-1}\)) turnover (K\(_{L} = L/S\)) where L and S respectively litterfall and litter standing crops) in Undisturbed and logging sites of tropical rainforest of Ebom, southwestern Cameroon.

| Nutrients       | Undisturbed site | Logging site |
|-----------------|------------------|--------------|
|                 | Litter standing crops (kg/ha) | Litterfall (kg/ha) | K\(_{L}\) | Litter standing crops (kg/ha) | Litterfall (kg/ha) | K\(_{L}\) |
| Small litterfall|                  |              |         |                      |              |         |
| Leaves          | 2090             | 6240         | 2.99    | 1580                 | 5640         | 3.57    |
| Wood            | 960              | 1950         | 0.49    | 1320                 | 1490         | 0.89    |
| Rest            | 1110             | 2790         | 0.39    | 490                  | 1940         | 0.25    |
| Total           | 4160             | 10930        | 2.63    | 3390                 | 9070         | 2.68    |

| Nutrients       |          |          |         |          |          |         |
|-----------------|----------|----------|---------|----------|----------|---------|
| In leaf litter   |          |          |         |          |          |         |
| N               | 43.93    | 113.12   | 2.58    | 37.95    | 96.90    | 2.55    |
| Ca              | 1.71     | 42.14    | 24.64   | 1.91     | 20.03    | 10.49   |
| Mg              | 1.13     | 4.82     | 4.27    | 0.93     | 4.22     | 4.54    |
| K               | 1.39     | 26.82    | 19.29   | 2.48     | 12.37    | 4.99    |
| Na              | 0.05     | 0.83     | 16.60   | 0.05     | 0.67     | 13.40   |
| P               | 3.10     | 7.07     | 2.28    | 3.40     | 5.14     | 1.51    |

| In total litter |          |          |         |          |          |         |
| N               | 83.84    | 183.87   | 2.19    | 72.29    | 150.91   | 2.09    |
| Ca              | 2.44     | 73.41    | 30.09   | 3.02     | 30.45    | 10.08   |
| Mg              | 2.38     | 6.78     | 2.85    | 1.69     | 5.65     | 3.34    |
| K               | 3.49     | 41.42    | 11.87   | 4.31     | 21.96    | 5.10    |
| Na              | 0.50     | 0.61     | 1.22    | 0.10     | 1.08     | 10.80   |
| P               | 6.57     | 12.19    | 1.86    | 6.15     | 8.77     | 1.43    |

K\(_{L}\) = L/S where L and S respectively nutrient in litterfall and in litter standing crops.

Nutrient contents differed significantly between litterfall fractions, excepted K and Na in the undisturbed site, and Ca and P in logging site. In the two sites, N content was significantly lower in the wood litter fraction than in the other litterfall fractions, and that of Mg was higher in leaf litterfall than in the other litterfall fractions. Ca content was significantly the highest in wood litterfall and the lowest in coarse litterfall in the undisturbed site, that of K was significantly higher in the rest litterfall fraction than in the other litterfall fraction in the logging site. At the end, P content was significantly the highest in coarse litterfall and rest fraction, and the lowest in wood fraction in the undisturbed site.

Undisturbed and logging sites differed significantly between them according to some nutrient contents (Table 5). Mg, Na and P contents in the three fractions of small litterfall were not significantly differed between the two sites, while that of Ca in the three small litterfall fractions was significantly higher in the undisturbed site than logging site. N content differed significantly between the sites only in the wood litter fraction, that of K in leaf litterfall and that of Na in coarse litterfall.

Nutrient contents in the litter standing crops were presented in Table 5. In the two sites, N content was the highest and that of Na was the lowest in all litter fractions, except in the rest fraction where Ca content was the lowest in the undisturbed site. All the nutrient contents were generally the highest in leaf litter and the lowest in wood fraction, except N and Ca contents were present in low content in the rest fraction in the logging site. Conversely, in the undisturbed site these patterns were not clear and varied according to a given nutrient.

As for the dynamics of the nutrient content, it was variable over time and according to the nutrient considered (Figure 3). On the whole, nutrient behavior varies very slightly between the logging and undisturbed sites, except that of Na, whose concentration remains constant in 2000 and 2001 in the undisturbed site and decreases at the end of 2000 and 2001 in the logging site. Similarly, P content decreased at the end of 2000 and 2001. On the other hand, those of Ca and K increase from October 2000 onwards. Those of N and Mg remain almost constant over the two years of experience.

Litter nutrient amounts

The quantities of nutrients were significantly different among litter fractions at both sites (Table 6). In general, these quantities are highest in leaf litter and lowest in twigs or large litter in both sites. The nutrient amounts differed between the logging and undisturbed sites according to the nutrient considered (Table 6). Overall, the nutrient amounts in litter fractions are higher in the undisturbed site than in the logging site, except that of Na which was higher in the logging site than in the
undisturbed site. The amounts of N, Mg and Na were not significantly different between the logging and undisturbed sites, except that of Na in the coarse litter. On the other hand, that of Ca of all litter fractions was significantly higher in the undisturbed site than in the logging site, except that of the coarse litter. The amount of K in the Rest and coarse litter fractions is not significantly different (P > 0.05) between the two sites, whereas the K amount in the coarse litter of the logging site was significantly higher than that of undisturbed site.

The turnover (K1) of nutrients was presented in Table 4. In both sites, the turnover of leaf litter nutrients were generally faster than those of the total litter nutrients, except those of Ca in the undisturbed site (24.64 and 30.09 respectively for the leaf litter and total litter) and that of K in the logging site (4.99 and 5.10 respectively for the leaf litter and total litter). For the two nutrients, their turnovers in the total small litter were faster than those in the leaf litter. In the logging site, the turnover of Na and Ca were the fastest and those of N and P the weakest (Na > Ca > K > Mg > N > Ca > K > Mg > N).
Figure 3. Dynamics of nutrient contents (g kg\(^{-1}\)) of small litterfall fractions (F, W and R) in undisturbed and logging sites of Ebom tropical rain forest, southern Cameroon. Leaf litter (F), wood litter (B) and rest litter (R).
Table 6. Nutrient amounts in litter in undisturbed and logging sites of tropical rainforests of Ebom, Southwestern Cameroon.

| Nutrients | Undisturbed site | Logging site | Student's t between sites |
|-----------|------------------|--------------|---------------------------|
|           | Leaves           | Wood         | Rest          | CL    | Total    | F-values | Leaves           | Wood         | Rest          | CL    | Total    | F-values | Leaves           | Wood         | Rest          | CL    | Total    | F-values |
| Litterfall (kg.ha⁻¹.y⁻¹) |                  |              |              |      |          |          |                  |              |              |      |          |          |                  |              |              |      |          |          |
| N         | 43.93³ (7.40)    | 21.19³ (19.27) | 18.72³ (17.03) | 83.84 (0.39) | 8.09** |          | 37.95 (12.05) | 27.47 (19.78) | 6.87 (4.19) | -          | 72.29 (25.56) | 13.54*** | 1.34** ns (7.22 ns) (2.14 ns) | - | 1.03** |
| Ca        | 1.71³ (0.29)     | 0.39³ (0.36)  | 0.34³ (0.31)  | 2.45 (0.44) | 59.48*** | 1.91 (0.61) | 0.84³ (0.60) | 0.27 (0.17) | -          | 3.02 (0.94) | 27.28** | 0.91 ns (2.01 ns) (0.60 ns) | - | 1.74** |
| Mg        | 1.3³ (0.23)      | 0.3³ (0.39)   | 0.82³ (0.75)  | 2.38³ (0.80) | 4.6³ (0.30) | 0.9³ (0.39) | 0.54³ (0.39) | 0.23³ (0.14) | -          | 1.69³ (0.56) | 14.50*** | 1.78 ns (0.63 ns) (2.49 ns) | - | 2.22** |
| K         | 1.3³ (0.23)      | 1.06³ (0.97)  | 1.04³ (0.95)  | 3.49³ (1.55) | 0.5³ (0.79) | 2.48³ (0.79) | 1.14³ (0.82) | 0.7³ (0.43) | -          | 4.3³ (1.36) | 17.56*** | 4.21*** ns (0.19 ns) (1.05 ns) | - | 1.36** |
| Na        | 0.05³ (0.01)     | 0.03³ (0.02)  | 0.4³ (0.39)   | 0.5³ (0.39) | 10.10*** | 0.05³ (0.02) | 0.03³ (0.04) | 0.02³ (0.01) | -          | 0.1³ (0.03) | 10.58*** | 1.24 ns (0.62 ns) (3.35*** ns) | - | 3.22** |
| P         | 3.1³ (0.52)      | 1.5³ (1.42)   | 1.9² (1.74)   | 6.5³ (2.17) | 3.6³ (2.17) | 3.4³ (1.08) | 1.8³ (1.34) | 0.9³ (0.55) | -          | 6.1³ (2.02) | 14.69*** | 0.79 ns (0.48 ns) (1.76 ns) | - | 0.45 ns |

Fischer's values (F); Coarse litterfall (CL); ns: not significant; * P < 0.05; ** P < 0.01; *** P < 0.001. Different letters indicate that values are different among litter fractions.

P), whereas in the undisturbed site, the turnovers of Ca and K were the fastest and the turnovers of N and P the weakest in the leaf litter (Ca > K > Na > Mg > N > P). By comparing the two sites, we see that the nutrient turnovers in leaf litter and total litter of undisturbed site were superior to those of the logging site, except those of Mg of leaf litter and total litter and that of Na in total litter (Table 4). For these two nutrients, their turnovers in the logging site were superior to those in the undisturbed site.
DISCUSSION

Comparison with other tropical rainforests

Litterfall and litter standing crops

The annual average of the small litterfall and its fractions varied among tropical forests (Table 7). The results of this study ranked well among other tropical forests in general and among the highest values of rainforests developed on infertile soils (Oxisols and Ultisols) in particular. Brouwer (1996) showed that the mean (= 8.6 ± 1.2 t.ha⁻¹) small litterfall of a few South American and Southeast Asian moist tropical forests developed on infertile soils (Oxisols and Ultisols) was less than the values found in our study (10.9 ± 1.9 t.ha⁻¹). Leaf litter has generally large contribution to total litterfall than other fractions of litterfall (van Dam, 2001; Zhang et al., 2014) and its rate varies according to forest type and collecting year. Brouwer (1996) found that the contribution of leaf litter varies between 59 and 60% in Guyana Tropical rain forests, values below the average of other tropical forests (70%) and he also showed that in tropical forests developed on Spodosols / Psamments the average leaf litter was about 66%. In the Tropical Peruvian flooded, Nobel et al. (2001) reported that the proportions of small litter fractions were in the order of 60, 16 and 24%, respectively, for leaf litter, the reproductive part and the rest fraction. In this study, the contribution of leaf litter (57%), twig (18%) and rest (26%) were similar to those reported in other tropical moist forests with the same type of soils.

Interannual and seasonal variation of small litter fall

The average annual small litterfall in our study varied according to the year as reported by Songwe et al. (1988) in the rainforests of Bakundu, Cameroon. This variation may be related to the phenology of the vegetation, the interannual variation of climate such as wind or rainfall, etc. The ratio between the maximum and the minimum litterfall between the years in our study (ratio: 1.1), in two years, was similar to that reported by Spain (1984) in Australian rainforests (ratio: 1.1), but lower than that found by Bernhard (1970) in the tropical forests of Ivory Coast (ratio: 1.3).

The seasonality of small litterfall in tropical forests has been demonstrated in the literature (van Dam, 2001; Zhang et al., 2014). The litterfall peaks were observed in or just after the dry season (Brouwer, 1996; Celentano et al., 2011) or in or just after the rainy season (Devi and Singh, 2017). In Cameroon's rainforest in the Bakundu reserve (Songwe et al., 1988) and in most Amazonian and Guyana forests (Brouwer, 1996), the peaks of the maximum small litterfall, especially leaf litterfall, were located in the dry seasons. These two authors have shown that maximum peak of small litterfall were related to the period of water stress, with the maximum in the dry season. Other explanations have been put forward, such as climate, the conjuction of biological and mechanical phenomena, the character of the dry season (Becker et al., 2015; Rozas et al., 2015). In the present study, the monthly analysis of small litterfall clearly showed seasonality effects. The maximum of small litterfall, especially leaf litterfall, occurred during the long dry season (December - February) and the minimum in the short dry season (June-August), and was related to rainfall.

Litter nutrients

The nutrients of litterfall and litter standing crops in the Ebom rainforest in the TCP research area were compared with litterfall in other tropical forests (Table 8). The results of nutrient contents of litterfall reported in other Tropical forests were similar to those found in our study, except P was very high and Mg was much lower in our study. Nitrogen (N) and phosphorous (P) have very high amounts, whereas those of Na, Ca, especially Mg were very low compared to values found in tropical rainforests developed on the same type of soil as ours. For N, Vitousek and Sanford (1986) have shown that the availability of N was not a limiting factor in all tropical rainforests. In the TCP research area, comprising Ebom rainforest, van Gemerden and Hazeu (1999) found that N amount was high and could not be a limiting factor, at least in the first year after harvesting.

The P amount returning annually to the soil by the small litterfall was high. However, according to van Gemerden and Hazeu (1999), P available in the soil was low; Al and Fe contents were high in the soils of the TCP research area. The high acidity of the soil facilitates the absorption of P by Fe and Al to form iron and aluminum phosphate and makes available very low P amounts in the soil (Brouwer, 1996; Raaimakers et al., 1995). The cultivation practice can therefore lead to a very rapid decrease of P stock in the soil and after one year, its deficit will be significant (van Gemerden and Hazeu, 1999). The Mg content in litterfall was very low. Similarly, this nutrient contents as an exchangeable base was also low in soil solutions (van Gemerden and Hazeu, 1999). This assumes that Mg would be effectively used or undergoes very easy leaching at plant material level.

Impact of logging

On litterfall and litter standing crops

Impact of selective logging on litterfall is low in the Ebom Forest, six years after selective logging and estimated from a one-ha-plot. However, this impact is still perceptible on the annual average of total small litterfall during the low litterfall season (short dry season and long
Table 7. Small litterfall (t.ha⁻¹.y⁻¹) and litter standing crops (t.ha⁻¹) of some tropical rainforests in the world.

| Location             | Rainfall (mm) | Small litterfall | Litter on floor | Source                                      |
|----------------------|---------------|------------------|-----------------|---------------------------------------------|
|                      |               | L    | B    | Re  | Total |                                 |
| Oxisols/Ultisols     |               |      |      |     |       |                                |
| Brazil               | 2600          | -    | -    | -   | 8.0   | - Dantas and Phillipson (1989)¹ |
| Brazil               | 2300          | 6.3  | -    | -   | 9.3   | 4.6 Scott et al. (1992)¹       |
| Brazil               | -             | 5.4  | -    | -   | 7.8   | 6.5 Luizão (1995)¹             |
| Brazil               | 2300          | 8.0  | -    | -   | 9.9   | - Klinge (1977)¹               |
| Brazil               | 1800          | 6.4  | -    | -   | 8.1   | - Sampaio et al. (1993)¹       |
| Brazil               | 1800          | 6.4  | -    | -   | 7.9   | - Franken et al. (1979)¹       |
| Cameroon             | 2131          | 6.2  | 1.9  | -   | 10.9  | 4.1 This study                 |
| Cameroon             | 1828-2131     | 5.5-6.5| 1.7-2.2| - | 8.6-10.9 | 3.4-4.2 Ibrahima et al. (2002) |
| Colombia             | 3100          | 6.1  | -    | -   | 7.4   | - Duivenvoorden and Lips (1995) |
| Guyana               | 2700          | 5.4  | -    | -   | 9.1   | 7.4 Brouwer (1996)             |
| French Guyana        | 3200          | 5.7  | -    | -   | 7.9   | 4.2 Puig and Delolbe (1988)¹   |
| Malaysia             | 5100          | 5.4  | -    | -   | 8.8   | - Proctor et al. (1983)¹       |
| Malaysia             | 2800          | 6.5  | -    | -   | 11.1  | - Burghouts (1993)³            |
| Surinam              | 2200          | 7.1  | -    | -   | 11.7  | -                               |
| Trinidad             | 1800          | 6.9  | -    | -   | 6.8-7 | 3.9-4.2 Comforth (1970)¹        |
| Venezuela            | 3500          | 7.6  | -    | -   | 10.3  | - Cuevas and Medina (1986)³    |
|                      |               |      |      |     |       |                                |
| Other soil types     |               |      |      |     |       |                                |
| Africa               |               |      |      |     |       |                                |
| Cameroon             | -             | -    | -    | -   | 13.5  | 10.8 Songwé et al. (1995)      |
| Cameroon             | -             | -    | -    | -   | 12.9-14.1 | - Songwé et al. (1998)   |
| Ivory coast          | 1800          | 6.3-7.1| 1.4-2.3| 0.5-1.1| 9.1-9.6 | - Bernhard (1970)²             |
| Ivory coast          | 2100          | 7.6-8.2| 1.1-2.6| 0.7-1.1| 9.3-12.4 | - Bernhard (1970)²             |
| Gabon                | 1700          | 6.5  | -    | -   | 13.3  | - Hladik (1978)²               |
| Ghana                | 1650          | 7.4  | 1.0  | 0.4 | 9.7   | - John (1973)²                 |
| Ghana                | 1650          | 7.0  | -    | -   | 10.5  | - Nye (1961)²                  |
| Nigeria              | 1321          | -    | -    | -   | 4.6-7.2| 1.8-3 Hopkins (1966)³          |
| Nigeria              | 1200          | 3.7  | -    | -   | 5.6   | - Madge (1965)²                |
| DRC (former Zaire)   | 1828          | -    | -    | -   | 12.3  | - Laudelout and Meyer (1954)²  |
| DRC (former Zaire)   | 1273-1279     | 4.5-4.7| 1.2-3.0| 1.5-0.2| 5.1-9.1 | - Malaisse et al. (1975)²     |
|                     |               |      |      |     |       |                                |
| America              |               |      |      |     |       |                                |
| Jamaica              | 2600          | 4.4-5.5| 0.2-1.5| - | 5.6-6.6| 8-12 Tanner (1981)²            |
| Guatemala            | 3747          | 6.7-7.3| 1.5-2.1| 0.4-1.0| 9.3-10.0| - Kunkel-Westphal and Kunkel (1979)² |
| Panama               | 2725          | 5.8  | 2.3  | 1.2 | 11.1  | - Haines and Foster (1977)²    |
| Peru                 | 2715          | 4.2  | 1.7  | 1.1 | 7.0   | - Nebel et al. (2001)          |
| Venezuela            | 1500          | 3.4  | 2.3  | 1.1 | 7.0   | - Steinhardt (1979)²           |
| Colombia             | 3000          | 6.8-8.6| 2.0-3.1| 0.1-0.4| 8.7-12.0| - Foster and de las Salas (1976)² |
| Colombia             | 2769          | -    | -    | -   | 10.1  | 5-17 Jenny et al. (1949)²      |
| French Guyana        | 3373          | 5.9  | 1.9  | 1.0 | 8.7   | - Puig (1980)²                 |
| Venezuela            | 3521          | 6.1  | 3.4  | -   | 9.5   | - Jordan and Escalante (1980)² |
| Brazil               | 1771          | 4.3  | 1.1  | 1.0 | 6.4   | - Franken et al. (1979)²       |
| Asia                 |               |      |      |     |       |                                |
| Indonesia            | 2800          | 4.3  | -    | -   | 5.9   | - Saharjo and Watanabe (2000)² |
| India                | 1219          | 3.9  | 1.3  | 0.3 | 5.6   | - Blasco and Tassy (1975)²     |
| India                | 2338          | 4.1-6.8| 0.7-1.6| 0.3-0.5| 5.6-8.7| 3.8-5.5 Sundarapandian and Swamy (1999)² |
Table 7. Contd.

| Location | N  | Ca | Mg | K  | P  | Source                      |
|----------|----|----|----|----|----|------------------------------|
| Malaysia | 2054 | 6.5 | 2.0 | 0.4 | 9.2 | Ogawa and Lim (1978)\(^1\)  |
| Java     | 3380 | 4.5 | 1.0 | 0.4 | 6.0 | Yamada (1976)\(^2\)         |

| Australia | | | | | | |

| Location | N  | Ca | Mg | K  | P  | Source                      |
|----------|----|----|----|----|----|------------------------------|
| Papua N. Guinea | 3985 | 6.4 | 1.1 | - | 7.6 | 6.1-7.7 | Edwards (1977)\(^2\) |
| Australia | 1626 | 4.6 | 0.9 | 0.6 | 8.1 | 6.3 | Spain (1984) |
| Australia | 3609 | 4.9 | 1.6 | 1.3 | 9.7 | 4.4 | Spain (1984) |

Sources: \(^1\)Brouwer (1996); \(^2\)Spain (1984); \(^3\)Sundarapandian & Swamy (1999). L: leaves, B: twigs and small litter fall; Re.: rest

Table 8. Nutrient contents (%) of some tropical rain forests of the World.

| Location            | N  | Ca | Mg | K  | P  | Source                      |
|---------------------|----|----|----|----|----|------------------------------|
| **Oxisols/Ultisols**|    |    |    |    |    |                              |
| Cameroon            | 1.6 | 0.7 | 0.05 | 0.4 | 0.11 | This study                  |
| Guyana              | 1.3 | 0.4 | 0.2 | 0.1 | 0.02 | Brouwer (1996)              |
| Brazil              | 1.3 | 0.7 | 0.3 | 0.5 | 0.06 | Scott et al. (1992)\(^1\)  |
| Brazil              | 1.8 | 0.4 | 0.2 | 0.2 | 0.02 | Luizão (1989)\(^1\)         |
| Brazil              | 1.5 | 0.2 | 0.1 | 0.1 | 0.03 | Luizão (1995)\(^1\)         |
| Colombia            | 1.5 | 0.2 | 0.1 | 0.2 | 0.02 | Duivengoorden and Lips (1995) |
| French Guyana       | 1.5 | 0.4 | 0.1 | 0.1 | -   | Puig and Delobelle (1988)\(^1\) |
| Malaysia            | 1.0 | 0.2 | 0.1 | 0.5 | 0.01 | Proctor et al. (1983b)\(^1\) |
| Malaysia            | 1.4 | 0.6 | 0.2 | 0.5 | 0.04 | Burghouts (1993)\(^1\)     |
| Surinam             | 1.4 | 0.6 | 0.2 | 0.3 | 0.04 |                            |
| Trinidad            | 0.8 | 0.8 | 0.2 | 0.2 | 0.03 | Corth (1970)\(^1\)         |
| Venezuela           | 1.6 | 0.2 | 0.07 | 0.2 | 0.03 | Cuevas and Medina (1988)\(^1\) |

| **Other soil types**|    |    |    |    |    |                              |

| Location  | N  | Ca | Mg | K  | P  | Source                      |
|-----------|----|----|----|----|----|------------------------------|
| Guyana    | 1.2 | 0.7 | 0.2 | 0.2 | 0.02 | Brouwer (1996)              |
| Brazil    | 1.4 | 0.8 | 0.2 | 0.3 | 0.03 | Luizão (1989)\(^1\)         |
| Brazil    | 1.1 | 0.2 | 0.1 | 0.1 | 0.06 | Luizão (1995)\(^1\)         |
| Colombia  | 1.1 | 0.7 | 0.2 | 0.3 | 0.02 | Duivengoorden and Lips (1995) |
| Malaysia  | 0.6 | 0.9 | 0.2 | 0.2 | 0.01 | Proctor et al. (1983b)\(^1\) |
| Venezuela | 0.7 | 0.8 | 0.3 | 0.2 | 0.05 | Cuevas and Medina (1986)\(^1\) |
| Sarawak   | 0.8-1.1 | 0.4-3.5 | - | 0.1-0.4 | 0.01-0.04 | Anderson et al. (1983)\(^1\) |

Average of moderate fertile soils | 1.5 | 1.3 | 0.03 | 0.3 | 0.07 | Vitousek and Sanford (1986) |
Average of infertile soils (Oxisols/Ultisols) | 1.2 | 0.3 | 0.08 | 0.2 | 0.03 | Vitousek and Sanford (1986) |
Spodosols/Psammnets | 0.7 | 0.8 | 0.1 | 0.3 | 0.03 | Vitousek and Sanford (1986) |

\(^1\) Source: Brouwer (1996).

rainy season) and on the leaf litter fraction of the litter standing crops. In both logging and undisturbed sites, the leaf litter and total litter turnover were much higher than those of the twigs and rest because the latter two were made up of material whose degradation is very slow (Swift et al., 1979). In both sites, the turnover decrease in the following order: leaf > total > twig > rest. However, these two sites differed from one another by their turnover. The logging site is characterized by a faster turnover than the undisturbed site, with the exception of the rest fraction. These results suggested, by this level of disturbance, that the biological activity was more important or intense in the logging site than the undisturbed site, and explained by effects of climate (Denslow et al., 1998). Devi and Yadava (2010) mentioned that the higher turnover rate may be due to a high
temperature and rainfall pattern in gap area, favoring microbial activities. According to Odewe and Muoghalu (2003), the significant higher litterfall in forest 14 years after the ground fire and the changes in litter fraction contributions to the total litterfall agree with assertion of Chandrasheker and Ramakrishnan (1994). They reported that litter production and nutrient cycling patterns are likely to change during succession and may be affected by gap size, intensity of disturbance and age. Denslow et al. (1998) also found the gap size not only has direct effect on light levels in turn affecting plant growth rate, but also correlated with fine litterfall ($r^2 = 0.88$, P<0.05 and n=6).

**On litter nutrients**

The nutrient amounts differed between the undisturbed and logging sites of the Ebom Forest depending on the small litterfall or small litter standing crops. But it is difficult to draw a conclusion by considering only the litterfall and litter standing crops. It would be preferable to consider the turnover rate that informs about the release of these nutrients from litter to the soil and affected by climate condition in the gap (Devi and Yadava, 2010). In the undisturbed site, the order of nutrient release varied according to the litter fractions (decreasing order): Ca > K > Mg > N > P > Na for the small leaf litter and Ca > K > Na > Mg > N > P for the total small litter. In the logging site, the pattern was the same for the total small litter and the leaf litter: Ca > Na > K > Mg > N > P. These results showed that forest logging causes the Na turnover much faster than that of K, which in the absence of disturbance was faster than that of Na. Moreover, the Mg turnover in the total small litter, in the leaf litter and that of Na in the small leaf litter were faster in a logging site than in the undisturbed site.

The soils of the Ebom forests are characterized by high acidity and a very low exchangeable K, Mg and Ca in the soil solutions (van Gemeren and Hazeu, 1999). As in the case of the small litterfall, our results showed that the forest disturbed by the logging differed from the undisturbed forest only by Ca, K and Mg, whose quantities are much higher in the undisturbed forest than in the logging forest. Six years after logging abandoning, the logging forest has not yet reached the equivalent of the undisturbed forest for these three nutrients. Moreover, these nutrients amount in the small litterfall were low. Our results showed that for a logging with an intensity of one tree per hectare, the consequences are such that it would be necessary to wait more than six years to mitigate the effects of this logging for the exchangeable bases.

**CONCLUSION**

It emerges from this study that the small litterfall and its turnover were among the highest values of the rainforests developed on infertile soils (Oxisols/Ullisols). The contribution of the leaf litter to the total litterfall was higher than that of the other fractions. The maximum small litterfall was during the long dry seasons and it is related to rainfall. This production showed interannual variation, due to the phenology of the vegetation. Among the nutrients, only Ca, K and Mg return annually to the soil in small quantities through small litterfall. The impact of logging six years after selective logging was negligible on the small litterfall, but results in much faster release of Mg and Na which were low in soil solution of the forest of Ebom. It would take more than six years for the effects of logging to cancel out. This study of litter and the effect of selective logging was useful for improving selective logging practices, and silvicultural and environmental approaches for the management of the Ebom Tropical rainforest of Cameroon.

**CONFLICT OF INTERESTS**

The authors have not declared any conflict of interests.

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