Litter production in an Atlantic beech (Fagus sylvatic L.) time sequence

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Original article

Litter production in an Atlantic beech (*Fagus sylvatica* L.) time sequence

Myriam Lebret[a,*], Claude Nys[b] and Françoise Forgeard[a]

[a] Laboratoire d'Écologie Végétale, UMR 6553, Complexe Scientifique de Beaulieu, Université de Rennes 1, 35042 Rennes Cedex, France
[b] Équipe Cycle Biogéochimique, Inra – Centre de Nancy, 54280 Champenoux, France

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Abstract – Litterfall is the first phase of the biogeochemical cycle and returns nutrients to the soil. This paper demonstrates the quantitative distribution of the different components throughout the year in four stands of a beech time sequence. Litterfall increases as the forest evolves and as basal area increases: from 2.1 t/ha/an in the thicket to 4.7 t/ha/an in the mature high forest. Leaves represent 90% of the total litterfall in the young stand and 70% in the oldest stand. The proportion of leaves decreases during forest rotation. Most of the categories are related to the age and basal area, because of the architecture and maturity of the trees. Other factors could explain litterfall dynamics, e.g. human management or animals. Climate is a preponderant factor for the litterfall production and plays a role in the species phenology. The litterfall dynamics during the time sequence, and the observed shifts in phenology give rise to different pedogenetic processes.

litter production / beech / time sequence / dry matter

Résumé – Production de litière dans une chronoséquence d'une hêtraie (*Fagus sylvatica*) atlantique. Les retombées de litière sont à la base des cycles biogéochimiques et assurent le retour au sol des nutriments. Cet article présente la répartition quantitative, par compartiment, au cours de deux ans de suivi et dans quatre peuplements de hêtre d'une chronoséquence. Les retombées totales de litière augmentent avec l'âge de la parcelle et la surface terrière : de 2,1 t/ha/an dans le fourré à 4,7 t/ha/an dans la vieille futaie. Les feuilles représentent 90 % des retombées totales dans le jeune peuplement et 70 % dans la parcelle âgée. La proportion de feuilles diminue au cours de la chronoséquence. La plupart des catégories sont reliées à l'âge et à la surface terrière, par l'intermédiaire de l'architecture et de la maturité du peuplement. D'autres facteurs peuvent expliquer la dynamique des retombées: la sylviculture, les animaux. Le climat est un facteur prépondérant dans la production de litière et a un rôle également sur la phénologie des espèces. La dynamique des retombées de litière au cours de la chronoséquence ainsi que les décalages phénologiques observés sont à la base de processus pédogénétiques différents.

hêtre / retour litière / chronoséquence / matière sèche

* Correspondence and reprints
Tel. 33 02 99 28 61 52; e-mail: myriam.lebret@univ-rennes1.fr

1. INTRODUCTION

Many studies of litterfall have been made in different forest ecosystems throughout the world since the first synthesis by Bray and Gorham [7] in 1964. On a global scale, litterfall increases with latitude and the richer the soil, the greater the litter production [26]. The quality and quantity of litterfall is related to primary production [9]. Litterfall constitutes an important phase of the biogeochemical cycle which includes organic matter and nutrients [35].

At present several research teams are trying to model biogeochemical processes, for example the carbon cycle [36] or nutrient cycling in several forest ecosystems [22]. Data on litterfall are required to establish the input-output budgets, but they are often incomplete. In fact interest has concentrated essentially on the fall of chlorophyll-rich parts (leaves and needles), which are the essential components of the litter whatever the ecosystem. The other components, present in smaller quantities may also be important, as they may be the source of the variability in the chemical composition of the litter. This is an essential factor in soil biological activity [25]. In the global change theory, the first phase of the biogeochemical cycle is relevant, because climatic disturbance in the short and long term could influence the pattern of litterfall production [33]. Work carried out has mainly concentrated on comparing temperate species with tropical species [44], broadleaved ecosystems with coniferous ecosystems [2, 32, 33], with different deciduous tree species [30], or with different production classes [6]. Few studies have measured the changes in litterfall during a forest rotation on the same site. However, Gloaguen and Touffet [17] have studied the subject in Villecartier (Brittany), and Ranger et al. [34] in some Beaujolais forests under Douglas fir (*Pseudotsuga menziesii*). Hughes and Fahey [21] also studied litterfall dynamics during forest development in a forest in the North of the United States. In France, even-aged beech forest is a forest management system used in many productive forests; this system allows the examination of litter production in a time-sequence and to carry out synchronised research on one site to simulate the life of a stand during the forest rotation.

The present study is part of a multi-disciplinary programme working on beech ecosystem function. The forest chosen is an Atlantic beech forest where the time-sequence includes ages varying from 10 to nearly 150 years old.

Botanical composition and stand structure are known to evolve during a forest rotation: is there also a modification in litter production in terms of quantity and quality? The aim of our study is to quantify these two parameters relative to the age of the stand, and to study the factors affecting litterfall production. Other aspects of litterfall will be defined: the inter-annual and seasonal variability, the phenological differences between plots, the level of spatial variation of different components, and of the plots examined. The qualitative aspect will be studied using the mineral concentrations of the different categories and will be the subject of a second paper.

2. MATERIALS AND METHODS

2.1. Site characteristics

The site is a 1660 ha beech stand in the Fougères forest in the north-east of Ille-et-Vilaine (Brittany, France, grid reference: 48°20’ N, 1°10’ E), situated at an elevation of 115–191 m above sea level. This forest is dominantly beech (*Fagus sylvatica* L.) 75%, with pedunculate oak (*Quercus robur* L.) and sessile oak (*Quercus petraea* (Mattuschka) Liebl.) 15%, and conifers 8%. The understorey consists essentially of holly (*Ilex aquifolium* L.). Fougères forest is in the *Vaccinio-Quercetum sessiliflora* group [10].

The climate in Brittany is oceanic and characterised by an unstable weather system with an abundant, evenly distributed annual precipitation of 900 mm, and a moderate temperature range (12.9 °C). The warmest month (August) has a mean temperature of 17.8 °C and the minimum temperature of 4.9 °C is in January. The mean annual temperature is 11 °C (French Meteorology Data, means of 1951–1980). *Table I* shows the climatic conditions during the two years of the experiments. Data came from the meteorological station present in the forest.

The soil is an Alocrisol luvisol according to the FAO/UNESCO soil system with fragic characteristics [20] (a weakly leached acid brown soil, weakly hydromorphic at depth [40]).

The parent material of the forest is derived from the Vire type granite or Brioverian slates at the edge of the forest. The time sequence plots are situated on the Vire type granite.

The forest is managed as a regular high forest, and it is divided into even-aged stands [5]. Four plots representing the time sequence were chosen in areas with identical

Table I. Climatic conditions during the two years of the study.

Month	Monthly mean of air temperature (°C)	Monthly mean of air humidity (%)	Monthly total of precipitations (mm)	Monthly total of solar radiation (J/cm²)	Monthly mean of maximum wind velocity (m/s)
March 97	9.2	83.1	16.8	27 871	6.4
April 97	9.9	64.8	33.8	77 726	7.0
May 97	13.2	73.6	81.8	55 410	8.4
June 97	14.5	81.6	216.0	97 940	7.4
July 97	16.9	78.7	16.6	59 257	5.3
Aug. 97	19.9	81.8	76.0	46 002	5.2
Sept. 97	16.0	74.3	84.8	86 546	5.0
Oct. 97	11.8	82.9	82.0	22 234	6.7
Nov. 97	8.8	92.6	169.8	32 762	7.8
Dec. 97	5.6	95.9	142.4	6 368	8.1
Jan. 98	4.6	89.3	117.6	10 466	9.4
Feb. 98	6.1	83.8	139.0	23 014	6.0
March 98	7.9	79.5	47.2	22 130	6.9
April 98	7.9	87.1	234.0	51 808	8.7
May 98	14.5	72.2	30.2	54 999	6.2
June 98	14.8	79.1	141.8	105 209	7.3
July 98	15.2	83.3	72.6	43 952	6.3
Aug. 98	16.8	75.5	26.2	55 010	4.8
Sept. 98	15.0	82.8	186.2	83 660	6.8
Oct. 98	11.1	92.4	150.4	14 771	7.5
Nov. 98	5.6	87.5	231.6	26 871	6.3
Dec. 98	5.4	94.0	144.6	5 578	7.5
Jan. 99	6.2	91.9	108.8	7 887	8.3
Feb. 99	5.0	83.9	217.2	20 719	6.4

site characteristics (forestry, soil, tree provenance) so as to carry out a synchronised study, i.e. to be able to compare spatial changes with temporal changes. The plots are close to each other (no more than 2 km between them).

The plots are represented by enclosures of 4000 to 6000 m^2, which are managed in the same way as the rest of the forest plot.

The four sites identified at the beginning of this study in 1996 are a 10-year-old thicket stage stand, a 27-year-old sapling stage stand, an 83-year-old young high forest stand, and a 147 year old mature high forest stand. The plot characteristics are given in *table II*.

2.2. Litter sampling

The four plots are equipped with evenly distributed litterfall collectors. In the youngest plot it was impossible to use collectors due to the very high tree density, so 41 plastic trays 30 cm × 47 cm, 15 cm deep were placed on the ground. In the other three plots collectors of 0.5 m^2, placed at a height of 50 cm above the ground were used. 16 collectors were used in the sapling and young high forest plots, and 24 in the mature forest due to the lower tree density.

The litter was collected every month and the samples were dried at 65 °C to a constant weight (> 48hrs). The

Table II. Characteristics of studied plots.

Age in 1997 (yrs)	Name	Mean height (m)	Mean diameter (cm)	Density (ha^{-1})	% beech	Basal Area (m^2)
10	Thicket	2.5	1.5	16815	= 80%	2.9
27	Sapling	11.2	6.2	4281	> 80%	15.3
83	Young high forest	27.3	29.7	304	> 95%	21.1
147	Old high forest	31.6	45.4	208	> 95%	33.7

data given here includes the litter from 1st April 1997 to 1st March 1999, and includes two vegetation cycles. The results are corrected to 30 days per month as recommended by Alley et al. [1].

2.3. Component categories

The dry samples were sorted into about thirty different categories. Material of animal origin (whole animals, feathers, wing cases, droppings) were not included. For the data analysis the different litter components were grouped into three main categories:

– the first category included the vegetative parts divided in four different components: beech leaves, oak leaves, wood, including dead wood and bark falling from the trees, and green wood broken by the wind. Wood was mainly beech, but sometimes oak. Bud scales which fell at bud burst were also included in this category;
– the second category, the reproductive parts, mainly consisted of male beech flowers, oak catkins, beech mast and their husks, acorns and their cups, blackberries and sweet chestnuts;
– the last category included mosses and lichens, these were epiphytic species on the tree trunks. The most dominant moss species was *Hypnum cupressiforme var. filiformis*. The most common lichen species were from the *Parmelia genus*. The herbaceous plants also fell into this category, and consisted mainly of ivy leaves (*Hedera helix*) in the older forests and bracken (*Pteridium aquilinum*) and brambles (*Rubus fruticosus*) in the thicket stage.

2.4. Statistical analyses

The collections during the two years, and the different plots were compared, using an ANOVA (variance analysis) with the Tukey test [44]. The analysis of one or several factors was carried out using Unistat 5.0 to observe any interactions between plot age and year of collection. When the data distribution was not normal, a non-parametric test was used: the Kruskal-Wallis test. Correlations between stand age, basal area and quantities of litterfall were carried out using Pearson's correlation coefficient. Data variability was estimated by calculating the coefficient of variation, which is a useful parameter for estimating heterogeneity in a data series, as it represents the dispersion of values around the mean [18].

3. RESULTS

3.1. Annual return of litter to the soil

Table III summarises the results of both the total litterfall and the litterfall from different categories and components.

The most abundant litterfall ($F = 93.23$, $p < 0.0001$) was sampled in the 147 year old forest stand with a mean litter production during the two years of 4.7 t/ha/yr (*table III*). The youngest, 10-year-old thicket stand had the lowest litter production: 2.1 t/ha/yr. The 27-year-old sapling stage, and the 83-year-old young high forest were intermediate and were not significantly different: 3.8 and 3.9 t/ha/yr respectively. Therefore total litterfall increased during the forest rotation.

The monthly litterfall data (*figure 1*) showed that in general the four plots had the same seasonal evolution. The thicket stage had the lowest returns except for December 1998 and January 1999. There were two annual peaks: one major peak in the autumn in October/November and a much smaller peak in the spring.

The largest falls occurred in October for the high forest stands (young and mature). The peak was in November for the sapling stage. For the thicket stage there was no difference between the two months in the first year,

Table III. Mean fluxes of the total and different litter components for 1997 and 1998 at each plot of the time sequence (kg/ha ± standard error).

Plot	Year	Total (t/ha)	Vegetative parts				Reproductive parts		Various	
			Beech leaves	Oak leaves	Dead wood	Bud scales	Fruit and fruit husks	Flowers	Mosses and lichens	Herbaceous species
Thicket	1997	1.82 ± 0.10	979 ± 57.5	250.2 ± 58.6	143.9 ± 34.7	72.6 ± 4.6	6.6 ± 2.1	3.7 ± 0.6	2.3 ± 0.4	378.8 ± 75.5
10 yr	1998	2.45 ± 0.13	1343.3 ± 89.8	322.0 ± 68.7	67.5 ± 7.3	89.1 ± 5.6	3.0 ± 1.0	0.2 ± 0.1	0.4 ± 0.2	604.8 ± 100
	Mean	2.12 ± 0.09	1150.2 ± 66.0	290.1 ± 62.6	106.1 ± 17.3	79.8 ± 4.3	4.8 ± 1.2	1.9 ± 0.3	1.3 ± 0.2	489.9 ± 76.2
Sapling	1997	3.71 ± 0.17	2641.7 ± 144.4	172.4 ± 50.9	640.2 ± 61.1	206.5 ± 13.8	14.0 ± 7.4	0.4 ± 0.3	0.9 ± 0.3	3.1 ± 1.6
27 yr	1998	4.02 ± 0.17	2941.9 ± 108.4	175.9 ± 55.6	625.0 ± 152.6	231.9 ± 8.5	3.9 ± 3.5	0.4 ± 0.4	0.44 ± 0.2	2.3 ± 1.0
	Mean	3.86 ± 0.15	2791.8 ± 115.6	174.1 ± 51.0	632.6 ± 94.4	219.2 ± 10.3	8.9 ± 3.9	0.4 ± 0.3	0.7 ± 0.1	2.7 ± 1.2
Young	1997	3.82 ± 0.10	2670.8 ± 77.6	68.2 ± 16.2	493.2 ± 44.5	311.7 ± 10.2	175.0 ± 28.4	22.3 ± 2.4	70.0 ± 7.9	1.6± 0.9
high forest	1998	4.01 ± 0.11	3022.8 ± 84.6	52.4 ± 12.2	483.6 ± 79.0	352.2 ± 10.9	21.5 ± 7.4	6.8 ± 1.3	59.7 ± 11.5	0.6 ± 0.3
83 yr	Mean	3.92 ± 0.09	2846.8 ± 73.0	60.3 ± 13.8	488.4 ± 51.9	331.9 ± 9.6	98.2 ± 16.9	14.5 ± 1.4	64.9 ± 9.4	1.1 ± 0.5
Old high	1997	4.70 ± 0.17	2933.8 ± 42.4	38.4 ± 14.1	765.9 ± 133.5	384.4 ± 13.1	308.1 ± 36.6	51.8 ± 5.2	229.0 ± 8.9	3.5 ± 1.3
forest	1998	4.72 ± 0.35	3340.0 ± 115.9	26.4 ± 13.2	763.4 ± 288.9	424.3 ± 10.7	19.0 ± 6.5	4.4 ± 0.9	114.0 ± 14.2	1.7 ± 0.8
147 yr	Mean	4.71 ± 0.18	3136.9 ± 52.2	32.4 ± 11.3	764.7 ± 147.1	404.4 ± 6.7	163.6 ± 19.2	28.1 ± 2.6	171.5 ± 9.2	2.6 ± 0.9

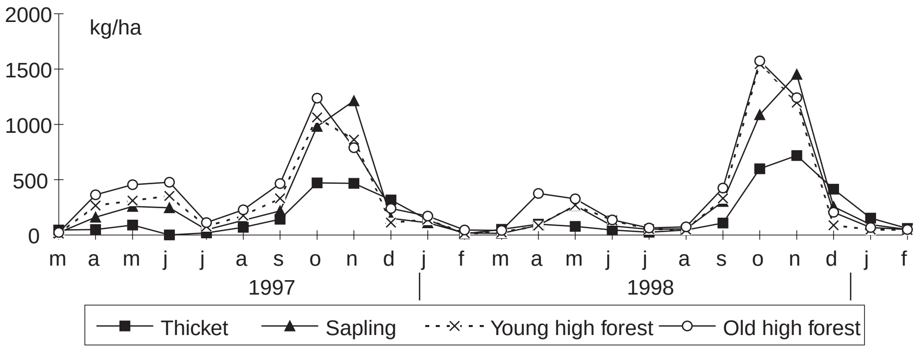

Figure 1. Monthly litterfall production monitored for two years in the 4 plots of the time sequence.

but the litterfall was higher in November for the second year. In 1997, the spring peak occurred between April and June, while in 1998 this peak was mainly centred around May. An unexpected peak was noticeable in April 1998 for the mature high forest. For all plots, the production was highest in 1998, but the difference declined with the age of the plot. The difference between the two years was only significant for the thicket stage ($F = 14.8$, $p = 0.0002$): 1.82 t/ha in 1997 compared with 2.45 t/ha in 1998, an increase in litter production of 35%.

3.2. The different categories

3.2.1. Vegetative parts

Beech leaves (*figure 2*) formed the major part of the litter, 60–70% of the fall of both the high forests and the sapling stage, and a little more than 50% for the thicket stage. During the two years of observation, the lowest falls were observed in the thicket stage whereas the mature high forest was the most productive in terms of

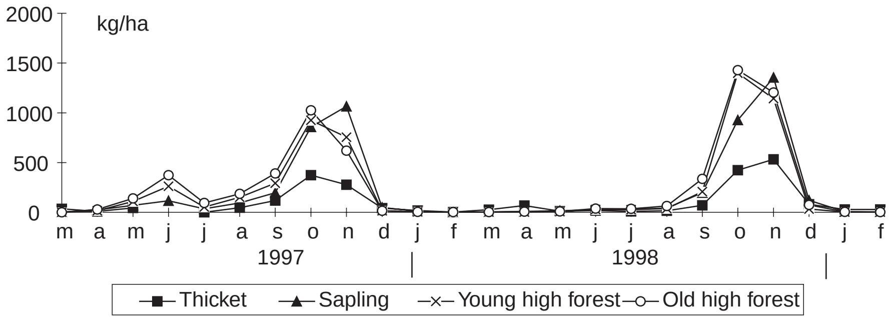

Figure 2. Monthly beech leaf litter production monitored for two years in the 4 plots of the time sequence.

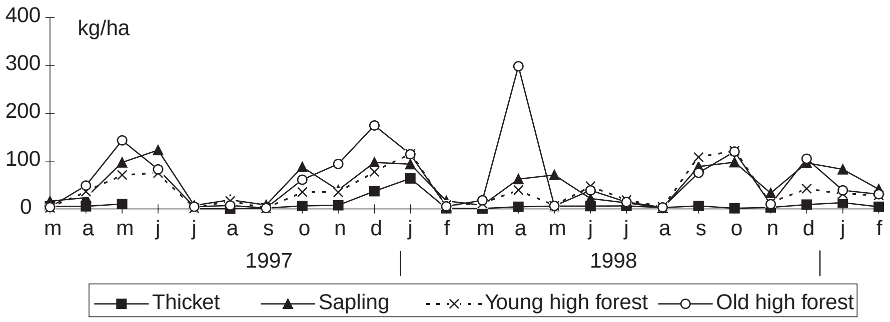

Figure 3. Monthly dead wood litter production monitored for two years in the 4 plots of the time sequence.

beech leaves. The other two plots were intermediate and were not significantly different (F = 190.76, $p < 0.0001$). The great majority of beech leaves fell in October/November (80 to 90%) with a special case in 1997 when there were considerable falls in June due to an insect attack. Especially in 1998, beech leaves fell earlier in the high forest (in October) than in the young thicket or sapling plots (in November). This was especially obvious in 1998.

Litterfall production increased in 1998 from 0.98 t/ha to 1.34 t/ha, a 37% increase for the thicket, (about 12% for the other stands), however the difference between the two years was not significant for the sapling plot (F = 2.95, $p = 0.0963$).

Total fall of oak and beech leaves was relevant because the percentage of oak leaves was high in the young plots (14% in the thicket); it was negligible in the older plots due to the thinning carried out by the foresters to eliminate this species. The combined total showed that the percentage of leaves in the litter declined during the time sequence. So from 89% of leaves in the thicket stage litter, the percentage decreased progressively to 69% in the mature high forest.

Examination of the litterfall throughout the seasons showed that the oak leaves fall mainly in November.

The amount of fallen wood was largest in the sapling stage and the mature forest plots where it reached more than 15%. Wood represented 12 to 13% of total litterfall in the young high forest and 8 to 9% in the thicket stage. These proportions represented considerable quantities: from 760 kg/ha/yr in the mature forest to 490 kg/ha/yr in the young high forest. The thicket was the only plot which was significantly different from the others (F = 26.44, $p < 0.0001$) with 106 kg/ha/yr. The amount of fallen wood was not really seasonal (*figure 3*) and was not consistent from year to year. Similarly the four plots did not show the same fluctuations with time. However there was a highly significant positive correlation between the number of days per month with a wind speed greater than 50 km/h and the monthly wood fall. The highest correlation was obtained in the mature forest (r = 0.86, $p < 0.0001$). The sapling, the young and mature high forest values were not significantly different from year to year (and are relatively similar). There was twice as much fallen wood in the thicket in 1997, but it was not significantly different. Exceptionally high falls observed in the total fall (in April 1998 for the mature forest) were due to greater wood falls in these plots (in one collector in the plot, to be precise).

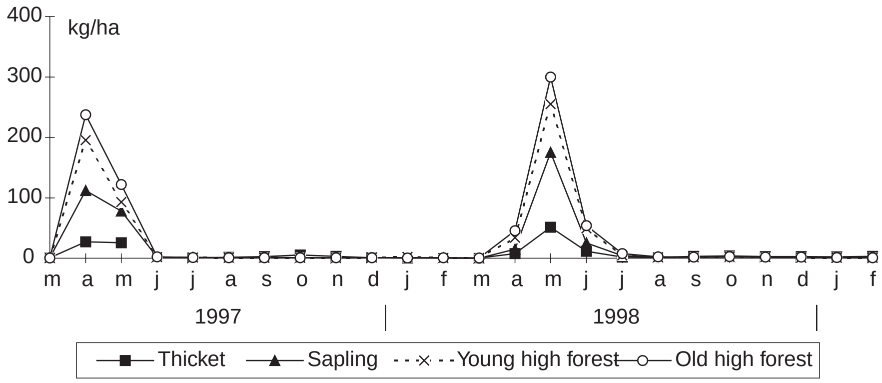

Figure 4. Monthly bud scale litter production monitored for two years in the 4 plots of the time sequence.

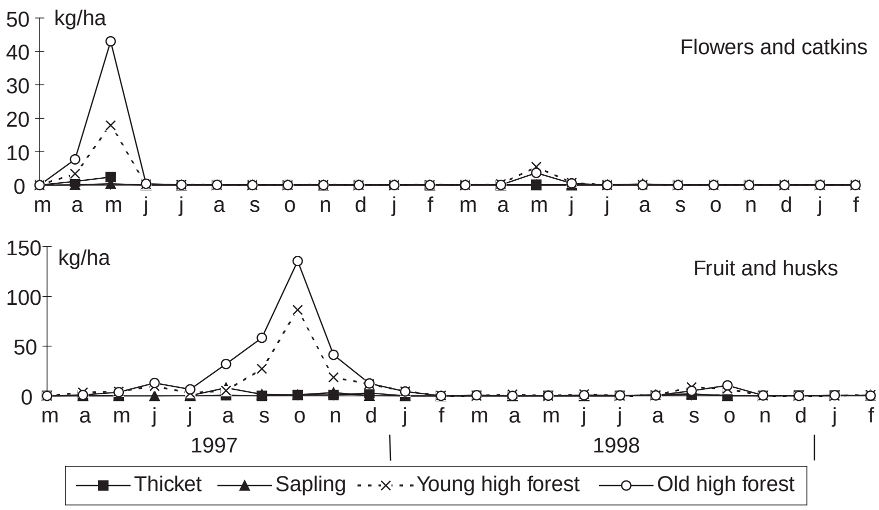

Figure 5. Monthly production of flower, catkin, fruit and fruit husks in the litter monitored for two years in the 4 plots of the time sequence.

The bud scales (*figure 4*) represented 8 to 9% in the old stands; 5 to 6% in the sapling plot and less than 4% in the thicket stage. The percentage of scales in the litter increased with the age of the stand. This proportion was stable from year to year. The four plots were significantly different from each other, in both years (F = 253.1, $p < 0.0001$ in 1997 and F = 455.9, $p < 0.0001$ in 1998).

In 1998, bud scale litterfalls were concentrated in May. In 1997, the falls peaked in April, but continued to be high in May. Production was low during the rest of the year. Falls were similar from year to year. However, the results were significantly different for the thicket stage (72.6 kg/ha in 1997 and 89 kg/ha in 1998, F = 5.3, $p = 0.024$), the young high forest (F = 7.5, $p = 0.088$) and the mature forest (F = 6.88, $p = 0.0118$).

3.2.2. Reproductive parts

Flowers and catkins (*figure 5*) were mainly present in the high forest plots (between 0.5 and 1%). In 1997, falls of male beech flowers and oak catkins were 52 kg/ha in the mature high forest and 22 kg/ha in the young high forest. The results were significantly different (F = 36.3, $p < 0.0001$). Flower and catkin production occurred in May in both years, but production was very different between 1997 and 1998.

Fruit and fruit husks only represented a small percentage of litterfall in the thicket and sapling stages (0.2%), so we have only given the data from the high forest where they consisted mainly of mast and husks. The mature high forest had falls of 310 kg/ha in 1997 and the young high forest, 175 kg/ha; the results from these two plots were significantly different at the 0.05 threshold ($F = 7.24$, $p < 0.0001$). As for the flowers, the fruit and husk falls were much higher in 1997. The maximum falls were in October (*figure 5*).

3.2.3. Other components

Mosses and lichens (*figure 6*) were mainly collected in the older plots (the high forest). The greatest quantities of mosses and lichens were collected in the mature high forest. The young high forest showed no significant difference between the two years. For the mature high forest, the falls were about twice as high in 1997: 229 kg/ha relative to 114 kg/ha in 1998. The seasonal effect was not very marked but falls were higher in winter and spring.

Herbaceous species were mainly present in the thicket stage. The sapling stage, young and mature high forest plots had about 3 kg/ha/yr of herbaceous species in their litter. For these three plots, the litter consisted mainly of ivy leaves in this category. In the thicket plot, bracken represented the highest proportion of the herbaceous category. This species was very important in the thicket stage as, after beech leaves, it was the most important category: 379 and 605 kg/ha in 1997 and 1998 respectively.

The herbaceous litterfall peak occurred in December. During the rest of the year, there was very little fall. Other herbaceous species were also found in the thicket plot: brambles, grasses, St John's Wort etc.

3.3. Variability in the fall of different components

Total within stand variability (*table IV*) established using a coefficient of variation, fluctuated depending on the age, from 10% in the young high forest to 33% in the thicket stage. There seemed to be a cyclic phenomenon, with a reduction in the variability of total litterfall at the beginning of the time sequence, then another increase at the mature high forest stage.

In the different categories, variability of the values was high in 1997 for herbaceous species, oak leaves, wood, fruit and flowers in the young plots, and was similar in 1998 for the high forest plots. Variability was low for beech leaves and bud scales.

Interactions between age/year were not observed for the total litterfall nor for the categories: beech leaves, oak leaves, bud scales, wood and herbaceous species (*table V*). Conversely fruits and fruit husks, flowers and catkins, and mosses and lichens showed a relationship between age and year, due to a large difference in the harvest between the two years.

3.4. Relationship with stand age or basal area

All the correlations were highly significant ($p < 0.0001$).

The best correlations between age in the time sequence and quantities of litterfall per category (*table VI*)

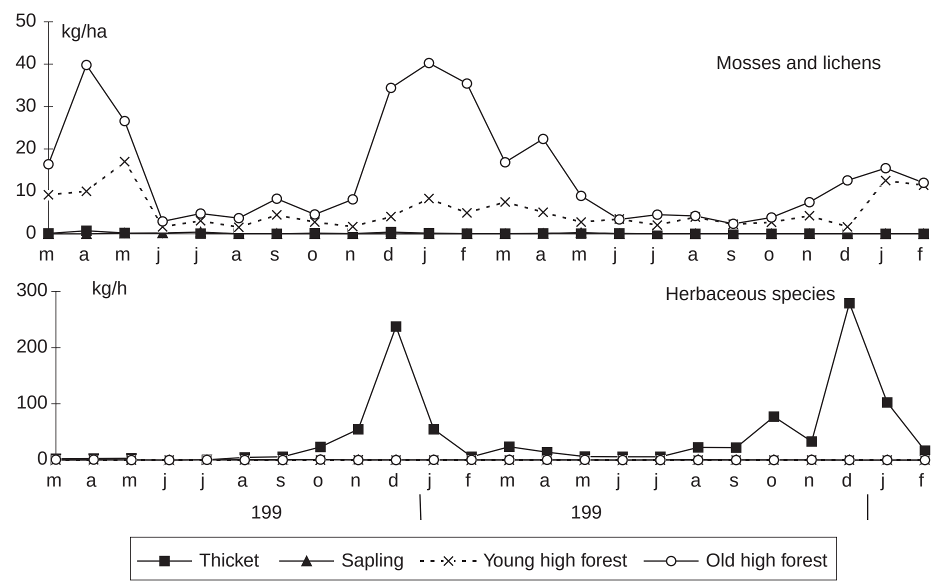

Figure 6. Monthly production of moss, lichen and herbaceous species in the litter monitored for two years in the 4 plots of the time sequence.

Table IV. Coefficient of variation of each category in each plot for the two years.

Plot	Thicket		Sapling		Young high forest		Old high forest	
Age	10 yr		27 yr		83 yr		147 yr	
Year	*1997*	*1998*	*1997*	*1998*	*1997*	*1998*	*1997*	*1998*
Total	33.1	34.1	17.5	16.2	10.3	10.4	17.4	29.1
Beech leaves	36.7	45.7	21.2	14.3	11.3	10.8	6.9	13.4
Oak leaves	146.4	140.4	114.3	122.4	91.8	89.9	176.6	192.9
Wood	150.5	67.8	36.9	94.5	34.9	63.2	83.6	146.6
Bud scales	39.5	41.0	25.9	14.3	12.7	12.0	16.4	9.7
Mosses and lichens	97.1	307.9	105.6	145.7	43.8	74.3	18.7	48.2
Fruit and husks	201.7	219.4	205.7	341.7	62.9	132.1	57.0	132.2
Flowers and catkins	104.4	326.3	266.7	351.3	41.7	72.0	48.0	76.2
Herbaceous species	124.5	107.6	191.8	171.0	225.7	184.0	179.3	178.2

Table V. Analysis of variance with two factors (F are presented). Effect of age, year and the interaction between age and year.
* indicates a significant effect ($p < 0.0001$).

Categories	Age	Year	Age * Year
Total	117.897 *	9.272 *	1.576
Beech leaves	281.156 *	34.606 *	0.100
Oak leaves	10.302 *	0.394	0.335
Wood	19.648 *	0.251	0.071
Bud scales	689.611 *	21.351 *	1.089
Fruit and husks	58.050 *	95.711 *	46.141 *
Mosses and lichens	389.186 *	55.795 *	44.707 *
Flowers and catkins	89.755 *	133.370 *	62.672 *
Herbaceous species	28.240 *	3.201	1.515

Table VI. Correlation coefficient between age or basal area of the plot and the quantity of litter production.
All correlations are highly significant ($p < 0.001$).

Categories	Age	Basal area
Total	0.77	0.84
Beech leaves	0.76	0.86
Oak leaves	–0.36	–0.38
Wood	0.48	0.48
Bud scales	0.93	0.96
Fruit and husks	0.79	0.75
Mosses and lichens	0.93	0.87
Flowers and catkins	0.85	0.79
Herbaceous species	–0.45	–0.54

were obtained for bud scales, and mosses and lichens (r = 0.93). The total litterfall, beech leaves, flowers and fruit were also significantly correlated with stand age. The correlation between fallen wood and age was significant (r = 0.48) but to a lesser extent than the other categories. Quantities of oak leaves were correlated negatively with stand age (r = –0.36) as were herbaceous species (r = –0.45).

Correlations between the basal area of each plot and the quantities of litter produced were generally better than the age factor (*table VI*). However, for fruit and husks, flowers and catkins, and mosses and lichens, the correlation remained highly significant but with lower values.

4. DISCUSSION

4.1. Annual return of litter to the soil

Values fluctuated from 1.8 t/ha/yr in the thicket stage to 4.7 t/ha/yr in the mature high forest. These values are comparable with those found by other authors in similar beech forests at equivalent ages. Thus, Aussenac et al. [3] recorded litterfall of 3.7 t/ha/yr in a sapling stage stand which was similar to the 3.85 t/ha/yr in the equivalent stand in Fougères. Many authors only record the beech leaf fall. Gloagen and Touffet [17] recorded 2.6 t/ha/yr beech leaves for the same range age, 3 t/ha/yr in the young high forest and 3.1 t/ha/yr in the mature high forest. Williams-Linera and Tolome [44] recorded leaf fall of 2.3 to 2.8 t/ha/yr in 100 to 150-year-old beech stands on acid moder soils. In Spain, Santa-Regina and Tarazona [37] estimated returns of 2.9 t/ha/yr for an adult uneven-aged beech stand.

The percentage of leaves decreased with stand age (beech and oak leaves together). Thiebaud and Vernet [39] attributed this change to the physiological state of the older trees which were more orientated towards reproduction, whereas young trees favoured vegetative growth. Alley et al. [1] estimated 64–67% of leaves in the litter, and Santa-Regina and Tarazona [37], 62%. Leaves represented 70% of the total in Mangenot and Toutain's [26] study and Pedersen and Bille-Hansen [33] confirmed values for an even-aged beech forest to be 64%; values which are all in the same range as those measured in Fougères forest.

Wood was the second most abundant constituent of litter. High amounts of fallen wood in the sapling stage could be explained by a phenomena of auto clear-cut because the density is high. In the mature forest, high amounts could be explained by ageing wood in this stand. Bud scales were the third constituent (except in the thicket stage). This category has not been studied to a great extent in the literature. They were present in large quantities and the composition of the bud scales is such that they decompose very slowly, which is why they are useful markers of successive years in the organic (Of) horizons of the soil [26].

In the fertile year (1997), fruit and fruit husks were estimated to be 300 kg/ha/yr in the mature high forest stand which corresponds with values given by Gloagen and Touffet [17] in another Atlantic beech forest. In the studied forest, Le Tacon and Oswald [24], had found falls of beech mast of 186.5 kg/ha/yr in a 140-year-old stand, and of 86.5 kg/ha/yr in a stand of the same age in the Vosges but on a less fertile soil. It is difficult to obtain mean values because of the high annual variability, so it is more relevant to compare fertile years.

The importance of the herbaceous species in the thicket stage was due to the presence of bracken (*Pteridium aquilinum*). As this species is heliophilic, it was only found in tracks, rides, young plots or clearings, and it was found in the litter in December. As the trees get older, they are gradually invaded by mosses, lichens and ivy; logically these categories were found in the older stands. The ivy leaves died and were found in the litter but did not have any particular cycle.

4.2. Factors affecting litterfall

Stand age had an effect on the quantities falling onto the ground. All categories (except herbaceous species and oak leaves) increased in quantity during the forest rotation. Biomass was higher in the old stages which were colonized with epiphytic species and had reached maturity so the trees were able to produce fruit. There is disagreement among researchers about the impact of age on litter production. So, Gloaguen and Touffet [17] and Bray and Gorham [7], consider that there is no relationship between plot age and leaf production: whatever the stand structure, the leaves tend to develop until they attain an optimum spatial cover compatible with efficient photosynthetic production [17]. Hughes and Fahey [21] and Ranger et al. [33] think that an age effect exists: as the forest gets older, the beech leaf litter continues to increase slightly. Dames et al. [12], and Ranger et al. [34], consider that litter production increases in the early stages of the time sequence and then stabilises.

For many authors, e.g. Mangenot and Toutain [26], Williams-Linera and Tolome [44] and Mehra et al. [29], the best relationship is between litterfall and the basal area in the plot concerned. This was the case for our study of total litterfall, and of leaves and bud scales; however age and basal area were highly and closely correlated.

The young plot was mainly characterised by the quantity of herbaceous plants. The position of the trays may have had some influence, but the soil vegetation cover of this plot especially, by bracken was much more widespread.

The rare oaks, had been eliminated in the older plots. So the importance of oak leaves declined throughout the time sequence. In fact, beech was favoured by the foresters in the past, as its wood was used for clog-making. However, to avoid single species management which increases risk of disease and reduces the biodiversity, the forester directed management towards mixed beech and oak stands.

4.3. Annual and seasonal variability. Litterfall phenology

During the two years examined, total litterfall was not significantly different between 1997 and 1998, except in the youngest plot, the thicket stage. The trees in this plot were growing rapidly, and at this stage the increase in biomass was visible. Beech leaf production increased from year to year, and was greater in 1998. Gloaguen and

Touffet [17] showed that leaf production was very variable from year to year and that it was increased by a wet spring (especially in April). This was the case in our study, for which 234 mm of precipitation were recorded for April 1998 (the wettest month in the two years that were studied). Some vegetation categories showed no differences between years: bud scales and wood.

The reproductive parts showed higher inter-annual variation. Beech mast had a rhythmic nature. Alley et al. [1] studied litterfall for five years and only encountered one fruiting year. In our study, fruit production was better in 1997 than in 1998. Fruit production is dependant on climatic phenomena amongst others and is thus very variable from year to year.

Climate (temperature, photoperiod, humidity) influences vegetation development, and its effects are reflected by the litterfall. Climatic conditions have an effect on the phenology of the species: on bud burst, flowering and fruiting of the trees [14].

We have shown that there was a delay of one month between bud burst in 1997 and 1998 (whatever the plots), due to the poor climatic conditions in 1998. The later appearance of the leaves did not have any effect on the time of leaf fall. Dates of foliation and defoliation were independent [4]. Leaf fall occurred in October in the old plots and in November in the young plots. There were phenologic shifts in litter production depending on the age (and structure) of the stand. The young stands were more protected because of the greater density, of trees and so the leaves remained on the trees [21]. In the youngest stand of our time sequence, the thicket stage, some of the leaves fell in March. These were the dead leaves which remained on the tree during the winter and only fell in the spring [4]. We can only compare two broad-leaved species on the phenological level: beech and oak. Oak leaves fell later. Zamoun [46] showed that oak leaf fall occurred mainly in mid-November. We have little information about bud burst of oak as the scales, due to the bud form, are much smaller than those of beech. To examine this, we need to study an oak stand. According to Becker [4], the leaf burst in beech occurs 15 days before that of oak.

Flower production occurred in May for both years but in different quantities. Flowering occurred at the same time as leafing [4]. Fruits matured in September or October when the husks open to liberate the mast. Trees reached maturity between 60 to 80 years old [4]. The young stands did not produce any fruit.

Certain events may have had an effect on the fall in other categories. Thus the production of large quantities of reproductive organs leads to a reduction in leaf production the following year [14, 17]. The energy taken by reproduction creates a deficit for the vegetative organs. In our work, this tendency was true in the mature stands, but we only had two years of harvest, and cannot state whether 1997 was really a good fruiting year for these trees. This phenomena was also observed in other forest systems. Thus in a cork oak forest, high acorn production was accompanied by a small leaf fall [9]. In this case it was not offset by one year, the phenomena was simultaneous.

Fall of wood showed no seasonal change, it was relatively anarchic but was influenced by the wind (especially the maximum wind velocity, which indicated that gusts of wind were more relevant than mean wind speed).

Mosses and lichens fell mainly in winter and spring. Their presence in the litter was due to intervention by birds, which detached the mosses and lichens whilst looking for small animals to eat during this difficult period.

In June 1997, there was a beech leaf fall in all the plots. This fall was due to an attack by a beetle: *Orchestes fagii*. This beetle lays its eggs in the principal nerve of the leaves, resulting in dehydration and premature fall [19].

4.4. Spatial variation

Total intra-population variation fluctuated from 10 to 33% as noted by Vanseveren and Herbauts [42] (14.9 to 25.2%), whereas Parmentier and Remacle [32] recorded less variable results of 13.6 to 15.5%, with a relatively homogeneous leaf fall. The categories showing the lowest variation were those which were produced in large quantities (the leaves) and with low densities (bud scales). These categories were spread uniformly on the ground due to wind dispersion. Conversely, heavy (wood, husks, cups) or rare (plants) material were very variable [35]. The different parts of the tree which return to the soil were not very variable in weight except for the wood (leaves taken separately all had similar weights). The twigs may have fallen from the trees, and similarly for pieces of branches, which are dead wood or green wood broken by the wind. The estimation of small wood fall over a small area was very difficult and variable [46]. So, it was the wood that was responsible for the variation in the values; and it was large falls of wood in one collector in particular which caused the exceptional peak. Our method was not very well adapted to the estimation of wood fall, a higher surface area for collection would be better.

When present in large quantities, in the high forest in 1997, the fruits and husks showed a variation of 57 to 68%, 49 to 68% was recorded by Parmentier and Remacle [32]. The wide heterogeneity was due to natural variability in fruiting between trees [16].

Overall, the thicket stage was the most heterogeneous plot, then overall variability declined throughout the time sequence and increased again in the mature high forest stage, the trees being more widely spaced [16].

4.5. Effect on decomposition

Litterfall was quantitatively different throughout the time sequence and each plant category had a specific chemical composition related to the physiological component, and for the same component, to the species [8]. It is unlikely that litterfall quantity would have affected the decomposition processes, but the qualitative composition is known to have an effect on micro-organism activity. For example, the beech leaves are richer in lignin than the other leaves [41, 43]. Due to their differing chemical compositions, the different categories do not decompose in the same way. In general, the herbaceous species decompose much faster than the woody species [45]. Microclimatic conditions like temperature, atmospheric humidity and shade also influence the decomposition rate [23]. The phenologic differences observed result in different decomposition conditions for the litter. Shifts in the time of litter fall result in the leaves (and another components) finding different conditions on the soil surface (microclimate, micro-organisms biomass etc.). Litter quality affects not only the rate of mass loss, but also the patterns and rates of nutrient immobilisation or release [38].

Many authors, [27, 28, 45] have carried out research on decomposition indices and it seems to be the nitrogen content and the C/N ratio that are indicators of decomposition rates, as well as the lignin content [15]. Plants modify soil processes by their litterfall, the turn-over rate and absorption by the roots [14]. Different microbial and fungal populations are involved depending on the components to be broken down [11, 13]. This demonstrates that even vegetation cover present in small quantities has some importance as it contributes different nutrients. For example, acorns contribute 55% of the annual falls of phosphorus [8].

The spatial variation observed in litterfall could have an effect on soil heterogeneity. Isolated components like twigs and beech husks create micro sites in which white fungi could develop [26].

5. CONCLUSION

Litterfall increased with the age of the stand, in relation to basal area, colonization with epiphytic species and the maturation of trees. So, as the forest ecosystem became more complex, the litter composition (in terms of categories) increased. Other factors could explain the litterfall: human management, and the contribution by animals. Climate could have an effect on litterfall quantity and the phenology of different components. The variations in litterfall observed during the time sequence also affected the pedogenetic processes.

Information about quality of returns to the soil is essential to the understanding of decomposition and humification, and the consequent effects on nutrient availability. This availability influences tree and the under-storey vegetation growth which interact closely, under the control of climatic phenomena. The second part of this work will present the qualitative and quantitative results on mineral element returns, which represent an important flux in the establishment of a fertility budget throughout the forest rotation.

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