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Original article

Dynamics of litterfall in a chronosequence of Douglas-fir (*Pseudotsuga menziesii* Franco) stands in the Beaujolais mounts (France)

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Abstract – Litterfall is a major component of the carbon and nutrient cycles in forest ecosystems. Results of the present study are from a chronosequence of Douglas-fir stands monitored continuously for seven years. Aboveground litterfall was measured every three months, sorted by components, and analysed for major nutrients. Results make it possible to characterize the dynamics of organic matter and nutrient returns to the forest floor during stand development. Simple extrapolation was used to estimate the total return in litter, cumulated over a 70-year-rotation length. Already published data were collected in order to try to identify simple relationships capable of predicting the litterfall return from structural stand characteristics. These models failed to be predictive, due on the one hand to insufficient data, and, on the other hand, to data not always perfectly comparable. Litterfall is a quantitative ecological measurement necessary to validate the models of ecosystem function.

Douglas-fir / litterfall / nutrient cycling / chronosequence / litter traps

Résumé – Dynamique des retombées de litière dans une chronoséquence de Douglas *(Pseudotsuga menziesii* Franco*)* située dans les Monts du Beaujolais (France). Les retombées de litières représentent un paramètre écologique fonctionnel important des écosystèmes forestiers, apportant des informations-clés sur le cycle du carbone et des éléments nutritifs. Les résultats présentés dans cette étude proviennent d'une chronoséquence de trois peuplements de Douglas situés dans les Monts du Beaujolais, étudiée pendant sept années. La litière a été collectée tous les trimestres, séparée en compartiments et analysée pour son contenu en éléments nutritifs. Les résultats permettent d'analyser en détail la dynamique des restitutions de carbone et d'éléments nutritifs au cours du développement du peuplement. Une extrapolation simple permet de calculer les retombées cumulées pour la révolution forestière complète. Une analyse bibliographique a permis de sélectionner une vingtaine de peuplements de Douglas pour lesquels les restitutions de litière ont été mesurées. L'objectif était de mettre en évidence des relations statistiques simples permettant d'estimer les restitutions de litière à partir de données de structure des peuplements, existant plus couramment dans la littérature. L'analyse des données montre que ces modèles généraux ne peuvent pas encore être élaborés, d'une part faute de données suffisamment nombreuses, et d'autre part faute de données parfaitement comparables. Les mesures écologiques quantitatives telles que les retombées de litière, doivent être poursuivies de façon à pouvoir valider des modèles de fonctionnement d'écosystèmes.

Douglas / retombées de litière / cycle des éléments / chronoséquence / pièges à litière

1. INTRODUCTION

In all forest types, the aboveground litterfall represents a major component of the carbon and nutrient cycles. It is one of the most efficient processes supporting the different soil functions over the long term i.e. agronomic, ecological and environmental.

Agronomic function. Litterfall provides the soil with soil organic matter which has numerous well known interests, e.g. substrate for organisms, efficient cement for soil aggregates, reservoir of nutrients [10]. It also provides the topsoil with large amounts of nutrients which were previously taken up from the whole available soil pool [27]. It is a natural process acting against soil acidification. In strongly acidic soils, or in soils without any weatherable minerals such as a large number of tropical soils, but also temperate ones, litterfall supplies nutrient cations (Ca, Mg, K) to the upper part of the soil profile, which tend to disappear due to their low competitiveness regarding ion exchange reactions when compared to Al [18].

Ecological function. Forest soils are characterized by a high carbon content compared with cultivated soils [4]. Organic material is the most efficient substrate for microorganisms and biodiversity is far greater in forest than in cultivated soils. The quality and amount of litterfall depends on forest vegetation leading to a direct effect of forest management on soil functions [2].

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Table I. Main soil characteristics for the three Douglas-fir stands.

	20-year-old stand			40-year-old stand			60-year-old stand		
	0–12 cm	25–40 cm	60–85 cm	0–15 cm	30–45 cm	65–85 cm	0–10 cm	20–35 cm	65–85 cm
	Ap1	Bw2	Bw3	Ap1	A/Bw	Bw2	Ap1	Bw2	Bw3
pH water	4.2	4.4	4.8	4.4	4.4	4.4	4.3	4.5	4.5
Clay content (% of fine earth at 105 °C)	19.4	18.1	16	19.9	23.6	18.5	21.7	23.2	19
MO (% of fine earth at 105 °C)	8.5	4.2	1	5.7	1.6	0.4	8.2	3.1	0.33
N (% of fine earth at 105 °C)	0.4	0.2	0.08	0.27	0.09	0.03	0.37	0.15	0.02
C/N	12	11	8	12	11	8	12.8	12.1	8
Ca exh (cmolc·kg od dry matter at 105 °C)	0.78	0.34	0.68	0.35	0.13	0.11	0.61	0.18	0.17
Mgexh (cmolc·kg od dry matter at 105 °C)	0.23	0.13	0.28	0.11	0.04	0.04	0.18	0.07	0.08
Alexh (cmolc·kg od dry matter at 105 °C)	7.1	4.7	3.7	6.6	4.8	4.3	5.8	4.2	4.2
CEC (cmolc·kg od dry matter at 105 °C)	9.1	5.6	5.1	7.8	5.3	4.8	7.7	4.9	4.9
BS%	15	13	25	9	7	8	15	11	10
P2O5 available (Duchaufour and Bonneau, 1959) [11]	0.06	0.04	0.08	0.02	0.02	0.02	0.02	0.01	0.01
Al Tamm (1922) [29]	0.71	0.63	0.51	0.66	0.37	0.23	0.62	0.39	0.2
Fe DCB (Mehra and Jackson, 1960) [20]	0.94	0.94	0.88	0.97	0.91	0.8	0.93	0.9	0.65

Environmental function. The soil carbon reservoir is one of the largest carbon reservoirs on the scale of the earth and its stability has become a major factor in global climatic changes. Soil carbon and nutrient cycles naturally alleviate soil acidification and the detrimental processes associated with it, which constrains the surface waters.

On a global scale, the amount of litterfall depends on many factors, but above all on stand productivity which is primarily controlled by the climate and secondarily by the forest species. Vogt et al. (1986) [34] calculated that litterfall (data expressed in kg·ha^{-1}·yr^{-1}) ranged between 5500 and 15 300, 3300 and 8900, and 150 to 5725 respectively for tropical, temperate and boreal forests. Broadleaved species seem to be more sensitive to climate than coniferous species, but the large variability of situations makes it difficult to identify the origin of the differences. Several reviews have been written on this topic [5, 8, 21, 27, 34].

These studies provide relevant information on a global scale, but as they mix genera, species, treatments and site conditions, they may not be helpful for local ecosystem investigations.

The objectives of the study were (i) to quantify the dynamics of C and nutrient returns to soil by means of aboveground litterfall during the particular development stages of the stand, and for the whole rotation of a Douglas-fir plantation, and, (ii) to compare the results with already published data for Douglas-fir stands in order to estimate the proportion of the stand nutrient uptake from soil reserves and recycled by litterfall directly from aboveground biomass data, which is a more easily available parameter than litterfall.

2. MATERIALS AND METHODS

2.1. Location

The study site was located in the “massif forestier des Aiguillettes”, at an altitude of 750 m in “les Monts du Beaujolais”, 40 km NW of Lyon (France). Rainfall was about 1000 mm per year and mean annual temperature was 7 °C [19].

Table II. Main stand characteristics in 1992.

Stand age (years)	20	40	60
Mean height (m)	14.3	28.0	36.0
Mean cbh (cm)	57	104.7	163.7
Stand basal area (m^2)	24.2	47.4	64.8
Stand density (nb of trees per ha)	922	490	312
Standing biomass (t·ha^{-1})			
– crown	34.2	38.6	65.8
– stem (bark and wood)	65.5	223.5	352
– roots (total) (1)	nd	58.3	nd

(1) Measured in 1999; at this date the standing aboveground total biomass was about the same because of a thinning operation.
Nd: not determinated.

2.2. Soil characteristics

Soils were developed on a Visean compact volcanic tuff rich in alkaline and earth alkaline elements i.e. 2% CaO and 1.9% MgO. Parent material weathering was mainly associated to dissolution processes, leading to a chemically poor residual phase [12]. The soil of the Alocrisoil [1] (i.e. Typic Dystrochrept type, [33]) was acidic (pH ranging from 4.2 to 4.5 according to the soil horizon) and desaturated (alkaline and earth alkaline cations represented between 8 and 20% of the total CEC depending on the soil horizon).

The soil organic matter content ranged between 6 and 8% with a C/N ratio between 11 and 12 in the A$_1$ horizon. The soil was coarse-textured and unevenly stony. Roots developed mainly in the top 60 cm but can reach 120 cm [19]. The main soil characteristics are listed in Table I.

2.3. Stand characteristics

A chronosequence of three stands aged 20, 40 and 60 years in 1992 were selected to study the dynamics of the ecosystem. Their main characteristics are presented in Table II [24]. Stands belong to the 1st yield class defined by Decourt (1967) [9] leading to a high mean annual production of 17 m^3·ha^{-1}·year^{-1} at age 60.

2.4. Litterfall collection

Litterfall was collected in each stand from July 1992 to August 1996 using 15 plastic containers 0.30 × 0.45 cm wide, and perforated

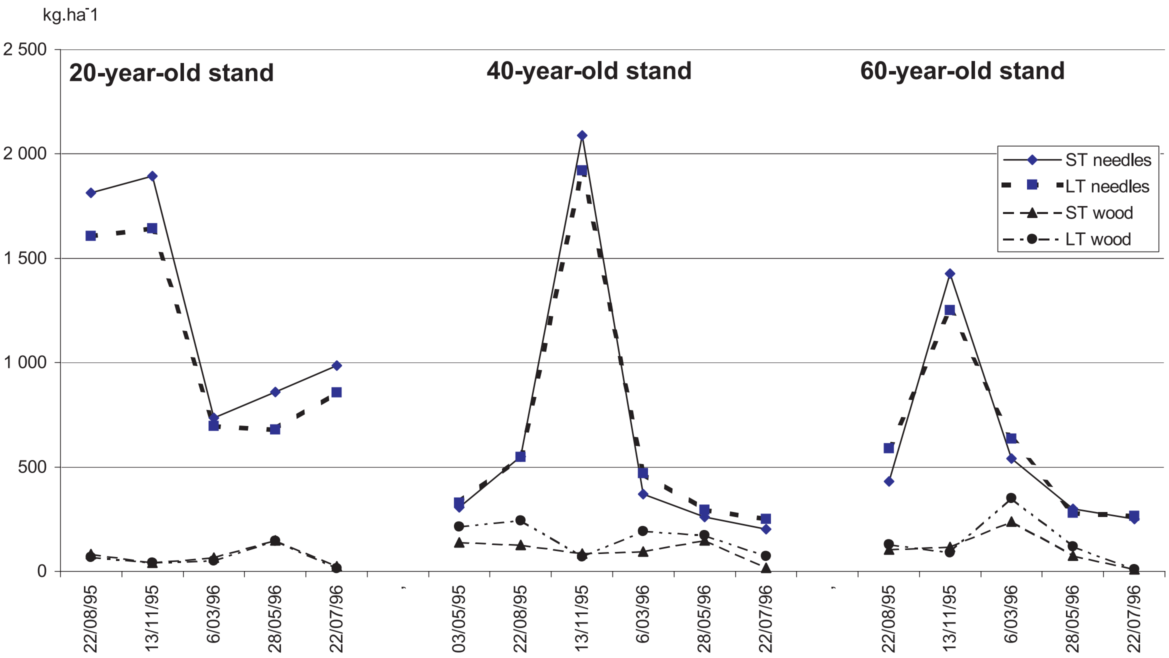


Figure 1. Comparison of two litter collectors in a 40-year-old Douglas-fir stand.

at the bottom for water drainage. They were systematically distributed in the plot along two rows (15 m between rows and 5 m between traps). The plastic containers were then replaced by larger ones, manufactured by Icare SA, 0.75 × 0.75 cm wide, in order to homogenize the data with the sites of the French Renécofor network for forest ecosystem observation [32]. Larger collectors were supposed to improve the accuracy of measurements. In fact, to test this hypothesis, the two types of collectors were used simultaneously in the three stands, for roughly 1.5 years (from spring 1995 to summer 1996). The two sets of traps were put side by side in the 40-year-old stand. Samples were collected every three months, individually for each collector at the beginning, and then together in one overall sample for the rest of the time. Samples were oven-dried to constant weight at 65 °C. They were then sorted manually into ten main components i.e. Douglas-fir brown needles (bn), Douglas-fir dead wood (dw), Douglas-fir green needles (gn), Douglas-fir living wood (lw), Douglas-fir bark (b), Douglas-fir cones (c), Douglas-fir flowers and buds (fb), leaves from other species (l) (local or brought by wind), a remaining component (fine parts impossible to identify) called miscellaneous (m).

Comparison of the two litter-traps i.e. small traps (ST) and large traps (LT), showed that there were no significant differences between the two types of traps for total litterfall, or for the different components (needles, branches and twigs). The trends were exactly the same (Fig. 1) and the mean value for one sampling was 894 kg·ha^{-1} for LT and 908 kg·ha^{-1} for ST. The agreement for needles seems relatively normal, but was more surprising for wood because the size of branches was large when compared to the collectors. This is probably due to the fact that Douglas-fir branches fell in small pieces, and not often as whole branches. This conclusion could not be extended to species with better self-pruning.

Sampling was systematically carried out every three periods of four weeks from July 92 to December 99 (except in the 60-year-old stand clear-felled in October 1998). Distribution according to seasons was made considering the maximum lapse of time belonging to a calendar season; no attempt was made to correct the discrepancy with the real calendar season. Total year was considered as the sum of four seasons.

2.5. Sample analysis

After drying to constant weight in an oven at 65 °C, the samples were finely ground and conditioned in polyethylene containers. After moisture control, samples were analysed for major nutrients (N, P, K, Ca and Mg). A mean weighed sample was analysed for each component present, in each stand at each sampling time. P, K, Ca and Mg were determined after acid digestion (H_2O_2 + $HClO_4$), by ICP spectrophotometry (Jobin Yvon Ultrase). Total N was determined by colorimetry on a Traacs microflux system, after Kjeldahl mineralisation.

2.6. Tentative generalisation using data from the literature

A literature review was made in order to collect additional data on Douglas-fir stands. Seventeen Douglas-fir sites were selected, when data on stand structure, biomass production (stem, branches and needles), and aboveground litterfall mass (needle litter and wood litter) and litterfall nutrient content were available. The additional data set concerned five sites of the French Renécofor network [32] and 12 from North American studies, both from naturally regenerated sites and from plantations [15, 16, 30, 31]. The database is presented in Annex I.

2.7. Statistical data processing

Elementary statistics and analysis of variance were operated using the UNISTAT statistical package (v. 5.0) in order to compare the data of the three stands of the chronosequence. Analysis of variance was used to identify the main factors of variability from the whole data set (4 annual sampling times during 7 years in the 20- and 40-year-old

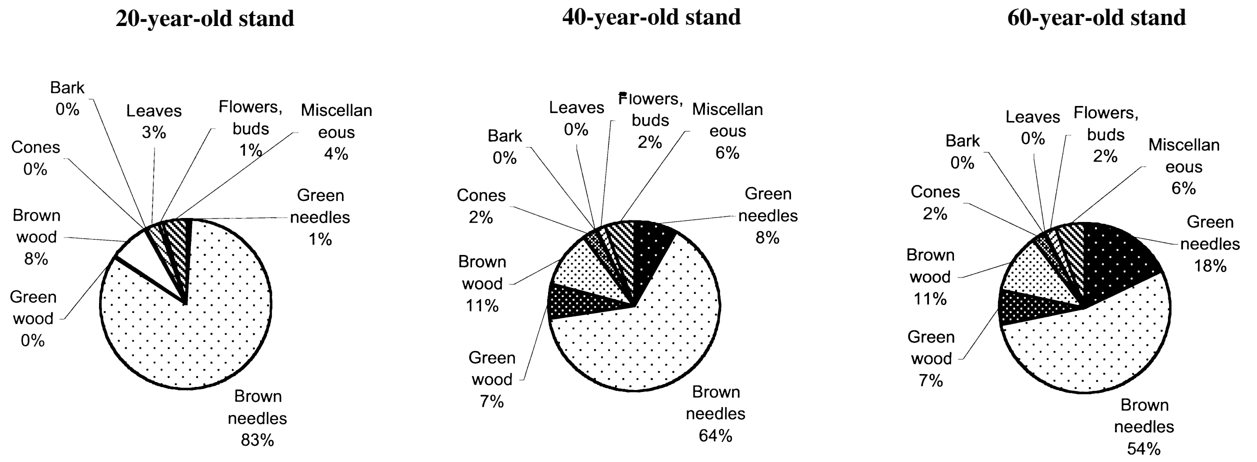


Figure 2. Pie diagram representing the distribution of the various components of litterfall in the Douglas-fir chronosequence of stands.

stands, and during 6 years in the 60-year-old stand clear-cut in Autumn 1998) i.e. stand age, season and year. As it was a non replicated experiment (i.e. not several chronosequences) the limited amount of data prevented us from testing the interaction between year effect and stand age.

3. RESULTS

3.1. Dry matter production of aboveground litterfall

Litterfall mass amounted to 3950 kg·ha^{-1}·yr^{-1} in the 20-year-old stand. It was higher than in the older stands where the production was very similar, about 3350 kg·ha^{-1}·yr^{-1} (Tab. III). Brown needles represent the largest component of the litterfall (respectively 83, 64 and 52% in the 20, 40 and 60-year old stands), dead wood was relatively constant around 10%. Another important component was the green material which increased with stand age (respectively 1, 12 and 22% in the 20-, 40- and 60-year-old stands) (Fig. 2).

The inter-annual variability was relatively high for all components. This appeared clearly in Figure 3 for total litterfall with variations reaching ± 30% of the mean value, and 150% between the minimum and the maximum values. The seasonal variability was not often significant, due to the high inter-annual variability. Significant seasonal differences appeared for brown needle fall, which occurred mainly in autumn; no seasonal trend appeared for dead wood (Fig. 4).

Stand age effect was significant for brown needles ($20 > 40 = 60$-year-old stand) but not for the dead wood. It was not significant for the total litterfall, because green needles and live wood components increased with stand age, and tended to compensate for the trend of brown needles. The mean annual trend for total litterfall production was relatively similar between the 20- and the 40-year-old stands with minimum values for the same years. The behaviour was different for the 60-year-old stand.

3.2. Nutrient concentration

The detailed results concerning the major components, i.e. brown needles and dead wood (representing between 65 and 90% of the litterfall, see previous section), and mean annual results concerning the other components are presented in Table IV.

It appeared that N, P, K and Mg were more concentrated in green needles than in brown needles; concerning wood, the dead wood was the most concentrated litter compartment in N, but it was generally the reverse for P, K and Mg. N concentration in bark was higher than in wood, but it was the reverse for P, K and Mg. Concerning Ca, old tissues were more concentrated than young ones i.e. green needles > brown needles, dead wood ≥ green wood. The relative ranking of the other components was more variable. The inter-annual variability only slightly affected the ranking between all the components.

Season had a much larger influence on needles than on wood, indicating a difference in the origin of litter: needle litter did not necessarily correspond to the oldest needles while wood litter contained old wood, strongly affected in the tree crown by internal translocation of nutrients, nutrient leaching by rainfall, physical and microbial decaying processes. Seasonal variations for needle litter were relatively constant: concentrations in the spring and the winter were higher than in the summer and the autumn for N, P and K; the reverse was observed for Ca. A lack of significant seasonal variations was observed for other elements.

The effect of stand age on nutrient concentration in major components showed a general trend of significantly higher concentrations for all elements and for all the seasons in the younger stand. This trend was confirmed for the mean annual variations (Tab. IV).

3.3. Nutrient content

The total return of nutrients per ha and year associated to litterfall amounted to 56, 33 and 32 kg for N, 3.8, 2.2 and

Table III. Litterfall biomass and nutrient content for the different components according to stand age (data in kg·ha^{-1}·yr^{-1}).

Compartment	Season	Dry matter			N			P			K			Ca			Mg			Mn			S			Al		
		20	40	60	20	40	60	20	40	60	20	40	60	20	40	60	20	40	60	20	40	60	20	40	60	20	40	60
Brown needles	Summer	987	462	391	13.5	5.74	4.86	1.04	0.35	0.33	2.01	0.83	0.53	9.65	3.29	2.73	1.03	0.33	0.28									
		a	b	b	a	b	b				a	b	b	a	b	b	a	b	b									
	Autumn	1010	1125	883	13.0	9.68	7.53	0.83	0.62	0.48	1.89	1.56	1.29	9.90	10.3	8.39	0.99	0.86	0.72									
		ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns									
	Spring	561	262	242	9.45	3.56	3.30	0.64	0.23	0.22	1.16	0.57	0.68	4.93	1.79	1.68	0.49	0.17	0.19									
		a	b	b	a	b	b	a	b	b	a	b	b	a	b	b	a	b	b									
	Winter	728	233	280	11.7	3.10	3.63	0.75	0.19	0.23	1.73	0.49	0.59	6.41	1.53	1.80	0.72	0.19	0.22									
		a	b	b	a	b	b	a	b	b	a	b	b	a	b	b	a	b	b									
	Total	3287	2081	1795	47.6	22.1	19.3	3.25	1.39	1.26	6.78	3.44	3.09	30.9	16.9	14.6	3.23	1.55	1.40	4.94	3.66	2.55	1.02	0.59	0.29	0.25	0.11	0.35
Brown wood	Summer	78.5	98.7	49.6	1.01	0.81	0.38	0.06	0.06	0.03	0.13	0.17	0.09	0.50	0.50	0.27	0.06	0.05	0.03									
		ns	ns	ns	ns	ns	ns				ns	ns	ns	ns	ns	ns	ns	ns	ns									
	Autumn	52.4	66.7	136	0.63	0.46	0.76	0.04	0.03	0.06	0.13	0.09	0.18	0.34	0.35	0.81	0.04	0.04	0.07									
		ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns									
	Spring	112	129	126	0.94	0.86	0.68	0.06	0.06	0.04	0.11	0.20	0.15	0.45	0.55	0.68	0.05	0.05	0.05									
		ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns									
	Winter	65.7	89.3	73.2	0.91	0.62	0.61	0.06	0.04	0.04	0.16	0.14	0.13	0.48	0.44	0.36	0.06	0.05	0.03									
		ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns									
	Total	308	383	385	3.49	2.76	2.43	0.22	0.19	0.17	0.53	0.59	0.56	1.77	1.84	2.12	0.20	0.19	0.18	0.22	0.22	0.17	0.07	0.07	0.04	0.01	0.01	0.01
Green needles		34	293	621	0.51	3.50	6.13	0.04	0.26	0.43	0.22	1.28	2.67	0.18	1.46	2.85	0.04	0.28	0.44	0.06	0.66	0.99	0.02	0.07	0.04	0.00	0.00	0.01
Green wood		8.99	245	238	0.06	1.25	1.07	0.01	0.13	0.10	0.03	0.58	0.45	0.04	0.99	0.98	0.00	0.12	0.09		0.20	0.12		0.02	0.01		0.00	0.01
Cones		10.1	75.1	77.5	0.03	0.35	0.19	0.00	0.04	0.01	0.02	0.18	0.11	0.01	0.06	0.03	0.00	0.04	0.02	0.00	0.03	0.00	0.00	0.01	0.00	0.00	0.00	0.00
Bark		4.10	5.32	9.38	0.09	0.06	0.07	0.00	0.00	0.00	0.01	0.01	0.00	0.04	0.02	0.03	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Leaves		90.1	5.76	0.00	1.53	0.08	0.00	0.10	0.00	0.00	0.30	0.02	0.00	0.97	0.03	0.00	0.16	0.01	0.00	0.18	0.01	0.00	0.05	0.00	0.00	0.00	0.00	0.00
Flowers and buds		30.2	54.1	76.2	0.17	0.23	0.53	0.01	0.03	0.04	0.05	0.08	0.09	0.07	0.13	0.21	0.02	0.03	0.04	0.01	0.03	0.00	0.01	0.02	0.00	0.00	0.00	0.00
Miscellaneous		173	194	185	2.88	2.36	2.23	0.19	0.18	0.16	0.38	0.42	0.35	1.17	0.66	0.68	0.22	0.16	0.15	0.36	0.28	0.21	0.07	0.06	0.05	0.07	0.08	0.18
Total		3946	3337	3387	56.4	32.7	32.0	3.82	2.22	2.16	8.32	6.61	7.32	35.1	22.1	21.5	3.87	2.38	2.33	5.78	5.10	4.04	1.24	0.84	0.42	0.32	0.20	0.56

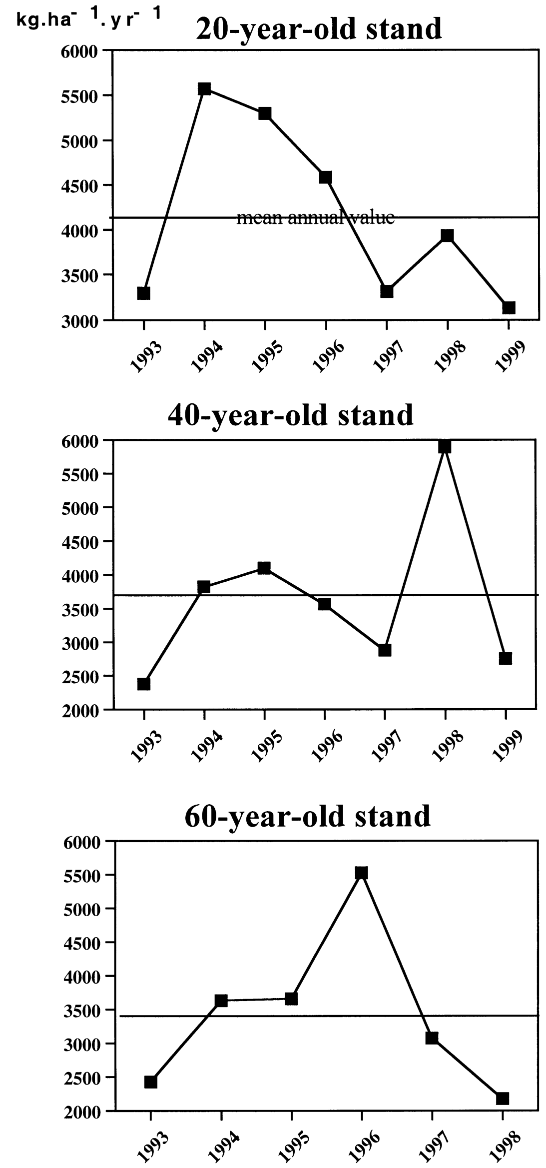
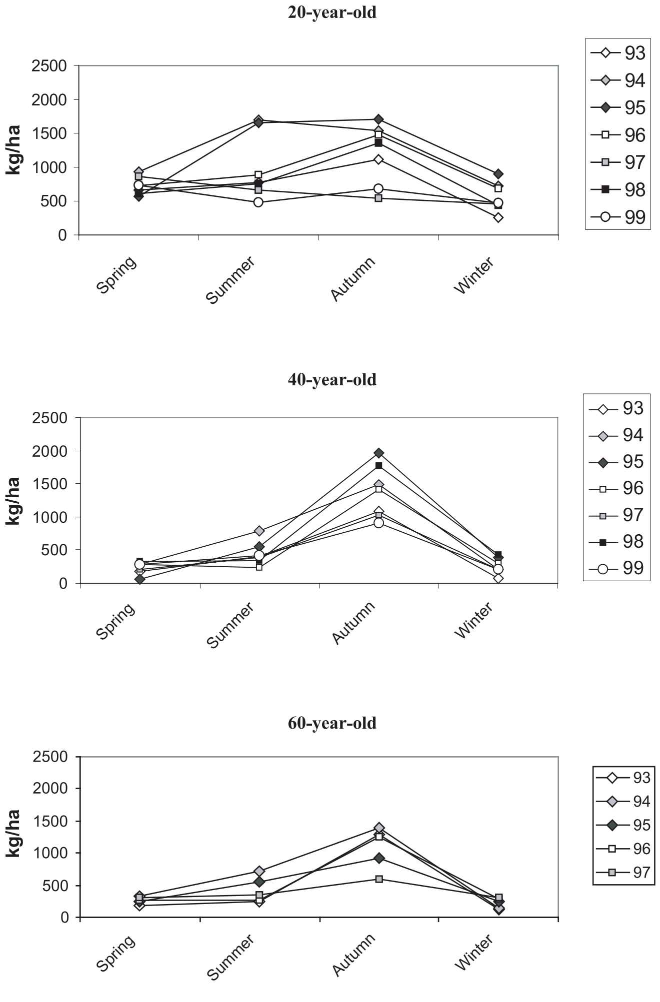


Figure 3. Inter-annual variability of total litterfall in the Douglas-fir stands.

2.2 kg for P, 8.3, 6.6 and 7.3 kg for K, 35, 22 and 22 kg for Ca and 3.9, 2.4 and 2.3 kg for Mg, respectively in the 20-, 40- and 60-year-old stands. This amount was strongly related to the litterfall production, and was higher for all elements in the young stand. Brown needles represented most of the nutrients released annually to the top soil. The relative distribution of nutrients was strongly related to the biomass distribution. Some disagreement occurred for green needles, which were more concentrated than the brown ones. They accounted for 18% of the litterfall in the 60-year-old stand, but for 36% of the K. The inter-annual variability was relatively high for all components.

The seasonal variability was not often significant, compared with the high inter-annual variability. Significant seasonal differences appeared for brown needle fall, which occurred mainly in autumn.



As for dry matter, the effect of stand age was significant for the brown needle nutrient content (N, P, Ca, Mg content of 20 > 40 = 60-year-old stand) but not for the dead wood. The effect of stand age was significant for the nutrient content of total litterfall with the highest significant level of returns in the 20-year-old stand for N, P, Ca and Mg.

4. DISCUSSION

Aboveground litter production decreased with stand age, as usually observed [3]. Nevertheless, litter production measured here remained higher than the 1.5 t·ha^{-1} observed by Kestemont (1977) [17] in a 70-year-old Douglas-fir in Belgium.

The maximum total litterfall usually occurred in a forest stand during the maximum current annual production, when stand density is rather high. This may be generalized to all species, broadleaved [26] or needle leaved [28].

The inter-annual variability tended to show that the mean annual value calculated for a specific component or for the

V. Mean annual nutrient concentrations for the different components of the litterfall in the Douglas-fir chronosequence (data expressed in p100 of dry matter at 65 °C).

	N			P			K			Ca			Mg			Mn			S			Al		
Stand age/ component	20	40	60	20	40	60	20	40	60	20	40	60	20	40	60	20	40	60	20	40	60	20	40	60
Brown needles																								
Summer	1.34	1.18	1.15	0.1	0.07	0.08	0.20 a	0.18 a	0.14 b	0.97 a	0.71 b	0.70 b	0.10 a	0.07 b	0.07 b									
Autumn	1.29 a	0.91 b	0.91 b	0.08 a	0.06 b	0.06 b	0.19	0.14	0.17	0.97	0.88	0.94	0.09 a	0.07 b	0.08 ab									
Winter	1.68 a	1.38 a	1.36 a	0.11 a	0.09 b	0.09 b	0.21	0.24	0.28	0.89 a	0.66 b	0.69 b	0.09 a	0.07 b	0.08 c									
Spring	1.61 a	1.35 b	1.30 b	0.10 a	0.08 b	0.08 b	0.24	0.21	0.21	0.88 a	0.65 b	0.64 b	0.10 a	0.08 b	0.08 b									
Brown needles mean annual	1.46 a	1.18 b	1.16 b	0.1 a	0.07 b	0.08 b	0.21 ns	0.19 ns	0.2 ns	0.93 a	0.74 b	0.76 b	0.1 a	0.07 b	0.08 b	0.21 ns	0.23 ns	0.19 ns	0.07 ns	0.06 ns	0.05 ns	0.02 ns	0.01 ns	0.04 ns
Brown wood																								
Summer	1.29 a	0.82 b	0.78 b	0.08 a	0.06 b	0.05 b	0.17	0.18	0.17	0.64 a	0.51 b	0.50 b	0.07 a	0.05 b	0.05 b									
Autumn	1.34 a	0.76 b	0.64 b	0.08 a	0.05 b	0.05 b	0.25 a	0.14 b	0.14 b	0.64 a	0.49 b	0.56 ab	0.08 a	0.05 b	0.05 b									
Winter	1.41 a	0.71 b	0.57 b	0.09 a	0.05 b	0.04 b	0.16	0.17	0.13	0.65 a	0.42 b	0.54 c	0.07 a	0.04 b	0.04 b									
Spring	1.31 a	0.74 b	0.82 b	0.09 a	0.05 b	0.04 b	0.23 a	0.14 b	0.17 b	0.69 a	0.47 b	0.50 b	0.08 a	0.05 b	0.05 b									
Brown wood mean annual	1.34 a	0.76 b	0.7 b	0.08 a	0.05 b	0.05 b	0.21 a	0.16 b	0.15 b	0.65 a	0.48 b	0.53 c	0.08 a	0.05 b	0.05 b	0.11 a	0.09 b	0.08 b	0.06 ns	0.04 ns	0.04 ns	0.01 ns	0.01 ns	0.02 ns
Green needles	1.67	1.42	1.29	0.12	0.11	0.09	0.75	0.56	0.57	0.61	0.51	0.58	0.12	0.1	0.09	0.25	0.25	0.23		0.07	0.06		0.01	0.02
Green wood	0.91	0.72	0.65	0.09	0.08	0.06	0.43	0.37	0.29	0.54	0.44	0.53	0.07	0.06	0.05	0.09	0.09	0.07		0.04	0.02		0.01	0.02
Cones	0.42	0.76	0.39	0.02	0.05	0.03	0.15	0.15	0.19	0.11	0.47	0.05	0.03	0.05	0.04	0.02	0.09	0.01		0.05			0.02	
Bark	2.12	1.17	0.96	0.1	0.06	0.03	0.18	0.11	0.07	0.89	0.28	0.34	0.09	0.05	0.03	0.19	0.07	0.03						
Leaves	1.95	1.49		0.13	0.09		0.4	0.44		1.1	0.56		0.18	0.11		0.26	0.33							
Flowers and buds	1.37	0.68	0.77	0.11	0.06	0.05	0.37	0.15	0.2	0.5	0.27	0.27	0.11	0.06	0.06	0.13	0.1	0.06						
Miscellaneous	1.51	1.18	1.29	0.11	0.09	0.09	0.22	0.23	0.23	0.57	0.31	0.34	0.11	0.08	0.08	0.18	0.12	0.11						

Table V. Calculation of the dynamics of stand nutrient uptake (data expressed in kg·ha^{-1}·yr^{-1}).

Stand age		N	P	K	Ca	Mg
20 years	Immobilization	23.1	1.8	29.5	8.6	2.6
	Litterfall	56.5	3.8	8.4	35.2	3.9
	Crown leaching			28.8	0.7	1.4
	Crown uptake	12.6	0.6			
	Uptake	92.2	6.2	66.7	44.5	7.9
	Litterfall/Uptake %	61	61	13	79	49
40 years	Immobilization	9.6	0.8	9.4	4.9	0.9
	Litterfall	33	2.2	6.8	22.3	2.4
	Crown leaching			12.7	3.6	1.2
	Crown uptake	4.3	0.7			
	Uptake	46.9	3.7	28.9	30.8	4.5
	Litterfall/Uptake %	70	59	24	72	53
60 years	Immobilization	4	0.3	1.8	2.6	0.3
	Litterfall	31.9	2.2	7.3	21.5	2.3
	Crown leaching			10.2	0.9	0.8
	Crown uptake	0.2	0.8			
	Uptake	36.1	3.3	19.3	25	3.4
	Litterfall/Uptake %	88	67	38	86	68

Immobilization = calculated from biomass and nutrient tables according to Ranger et al. (1995).
Crown leaching & crown uptake: data from Ranger et al. (2002) [25].

Table VI. Cumulated litter returns for a 70-year rotation of Douglas-fir in the Beaujolais Mounts.

	DM	C	N	P	K	Ca	Mg
Litterfall cumulated for a 70-year rotation (1)(2)	255 002	148 257	3195	202	570	2107	228
Mean annual litterfall for the rotation	3643	2118	46	3	8	30	3
Nutrients available in the soil profile							
– Ol	7745	4503	88	5.6	9.9	53.3	4.3
Of + Oh	47 200	27 442	500.5	36.2	412.9	145.1	138.2
– total forest floor	54 945	31 945	588.5	41.8	422.8	198.4	142.5
– top soil with maximum roots (0.6 m)				280	360	455	79
– whole soil profile (1 m)				370	594	600	132
Apparent mean time residence (3)		15					

(1) Calculated estimating linear increment of litterfall from 0 to value observed in the 20- to 26-year-old stand, then value for 26-year-old stand was used from 15 to 30 years, value observed in the 40- to 46-year-old stand was used between 30 and 50 and finally values observed in the 60- to 66-year-old stand was used for the period 50 to 70.
(2) Litterfall from the thinned trees was added (calculation were made from inventories made by the foresters).
(3) T= F(forest floor)/L(annual litterfall) calculated only for C due to mineral pollution.

whole litterfall did not represent any simple relevant ecological parameter (see Fig. 3). As very often, the mean year was rarely found and the average value mostly resulted from years with high or low litterfall amounts. The inter-annual variability tended to decrease when the size of the component increased e.g. the maximum relative variation to the mean value was less than 50%, for brown needles, which always represented more than 55% of the total litterfall, it increased to more than 50% for dead wood representing 10% of the litterfall, and was the highest for small components (green needles, green wood, bark, cones, flowers, etc.). The proportion of litterfall coming from green needles and green wood represented 30% of the whole litter in particular years. Usually, this green litter was added to the "normal" litterfall, leading to years of exceptionally high litter production. These data confirmed that ecological studies need at least medium term observations, which also means that a lot of data from the literature resulting from short term observations are of limited interest.

Table VII. Statistical relationships between stand biomass and litterfall, between litterfall mass and its nutrient content, and between nutrients of the litterfall, for various stands evaluated by the linear correlation coefficient (all stands n = 21; plantations n = 11; french stands n = 8).

Stands concerned	Needle litter/total litterfall	Total crown biomass / needle litter	Total crown biomass /total litterfall	Crown needle biomass / needle litter
All stands	**0.82**	0	**0.64**	**0.50**
Plantations	**0.79**	0	0	0
French stands	**0.75**	0	0	0

Stands concerned	Total litterfall / N litterfall	Total litterfall / P litterfall	Needle litterfall/ N litterfall	Needle litterfall/ P litterfall
All stands	**0.55**	**0.74**	**0.82**	**0.63**
Plantations	**0.79**	**0.78**	**0.84**	**0.77**
French stands	**0.88**	**0.88**	**0.92**	**0.88**

	Nutrients in total litterfall						
Stands concerned	N/P	N/K	N/Ca	N/Mg	Ca/Mg	K/Ca	P/K
All stands	0.3	**0.42**	0.2	0.39	**0.74**	**0.68**	**0.73**
Plantations	**0.69**	0.42	0.4	**0.62**	**0.88**	**0.96**	**0.85**
French stands	**0.99**	**0.92**	**0.98**	**0.97**	**0.92**	**0.95**	**0.91**

r5% = 0.43 n = 20; r5% = 0.58 n =11; r5% = 0.66 n = 8; results in bold are significant at the 5% level.

Below-ground litter production was not measured in the present study due to extreme difficulties to do so properly.

Parameters controlling litterfall varied with each component and it is necessary to study each of them individually to characterize the whole litter production:

(i) Brown needles fell in autumn, mainly due to physiological stress, even if mechanical stress was involved.

(ii) Brown wood, and secondarily cones, fell more erratically and were more difficult to connect to physiological stress. Due to bad self-pruning, dead branches can stay on trees for years. Mechanical stress is necessary to break the most fragile parts. This was probably the reason why no difference occurred between litter traps, even for large components such as branches which in fact most often fell into small pieces.

(iii) Some components were typically seasonal like buds and flowers.

(iv) Green litter (needles and wood) typically depended on mechanical stresses. In the oldest stand of this study, and probably due to its windy situation in the countryside, "green litter" represented one third of the total litterfall as a mean. This rather large amount of matter was able to modify both amounts of carbon and nutrients, as they were considerably more concentrated in nutrients than dead material.

(v) The overall amount of litterfall was related to stand age with the maximum amount at the maximum current annual increment. Stand age also changed the relative distribution of components: dead wood, flowers and fruits, green litter increased with stand age.

Litterfall is an essential parameter for calculating stand nutrient uptake, because it is not possible to measure it directly. This has been shown from a compartment and flux model [22, 23], in which nutrient uptake of "mature" stands is defined as follows:

Uptake = immobilization + returns (litterfall and crown leaching).

Results obtained in the chronosequence of stands are presented in Table V. Litterfall represented the major part of the annual uptake of N, P, Ca and Mg (between 50 and 90% according to nutrient and stand age). As a consequence, depletion of the soil nutrient pool associated to tree nutrition was quantitatively limited to stand immobilisation when forest floor mineralisation did not limit the return of nutrients in an available form for tree uptake. The situation for K was contrasted because this element is not usually associated with organic compounds and thus may be quickly leached from the tree crown by rain. Consistently, the amount of K uptake by stands and originating from litterfall increased from 13 to 39% from the 20- to the 60-year-old stand.

The contribution of litterfall to the stand nutrient uptake increased with stand age as a result of three main factors:

(i) The amount of litterfall tended to decrease after the maximum current annual increment (MCI) and stabilized with stand age;

(ii) Current stand immobilization strongly decreased with stand age as the young stand was more or less at the MCI;

(iii) Internal translocation of nutrients increased with stand age, tending to decrease the mean annual immobilization in the ligneous compartments.

Return by litterfall is an important mechanism in the interaction between vegetation and soil: Table VI presents the data for litterfall, cumulated for the whole rotation, or as mean annual values for the rotation, and for comparison the soil reserves in the forest floor, 60 upper cm and for 1 m depth. Data confirmed the potential effect of litter returns on nutrient availability for all nutrients. The tree root system takes up elements in the whole soil profile which are later re-deposited at the soil surface [13]. Mineralisation prolongs to varying extents the time required for elements to become available again. Several authors proposed simple or more sophisticated coefficients capable of estimating the mean residence time of C and elements in the forest floor [14, 35]. These calculations presupposed that the forest floor was in a steady state, but this was not the main problem. They assumed that the nutrients associated with the organic matter, but not with the whole layer, were involved. However, even in the holorganic layers, organic matter represents only a part of the mass, depending on physical and biological parameters leading to a mixture of nutrient-bearing organic and mineral compounds. In the present study, mineral particles represented approximately half of the layer mass. Eliminating all the OM and the associated nutrients using concentrated H_2O_2 was not possible. In these conditions, it was totally erroneous to calculate any residence time for elements other than C. Even for C, this calculation was not perfect as C from fine roots colonising the organic layers can represent a non negligible amount. Only labelled material can really give the turnover of soil organic matter [36].

Litterfall is a determining process limiting soil acidification: Mineralisation releasing cations neutralises protons, while mineralisation releasing anions produces protons [6]. For forest vegetation, the balance is in favour of alkalinisation due to excess cations in the living biomass [7]. Large amounts of calcium and magnesium are released at the soil surface, counteracting the desaturation and the aluminisation of the soil exchangeable pool. In acid soils with low amounts of Ca-bearing minerals as in the present site [12], since no secondary Ca-minerals are stable, released Ca is absorbed by vegetation or temporarily fixed on the soil adsorbing complex. Ca is not competitive against Al, and tended to be leached down the soil profile. The Ca-H or Ca-Al exchange reactions in the upper soil layers are an efficient buffer for soil acidity. The constant load of Ca, K and Mg (respectively 8, 30, 3.3 and kg·ha^{-1}·yr^{-1} on average) from mineralisation strongly limited topsoil desaturation.

Belowground litter was not considered here, even if it can represent some 80% of the aboveground litterfall of Douglas-fir, according to Vogt et al. [34]. This means that the total

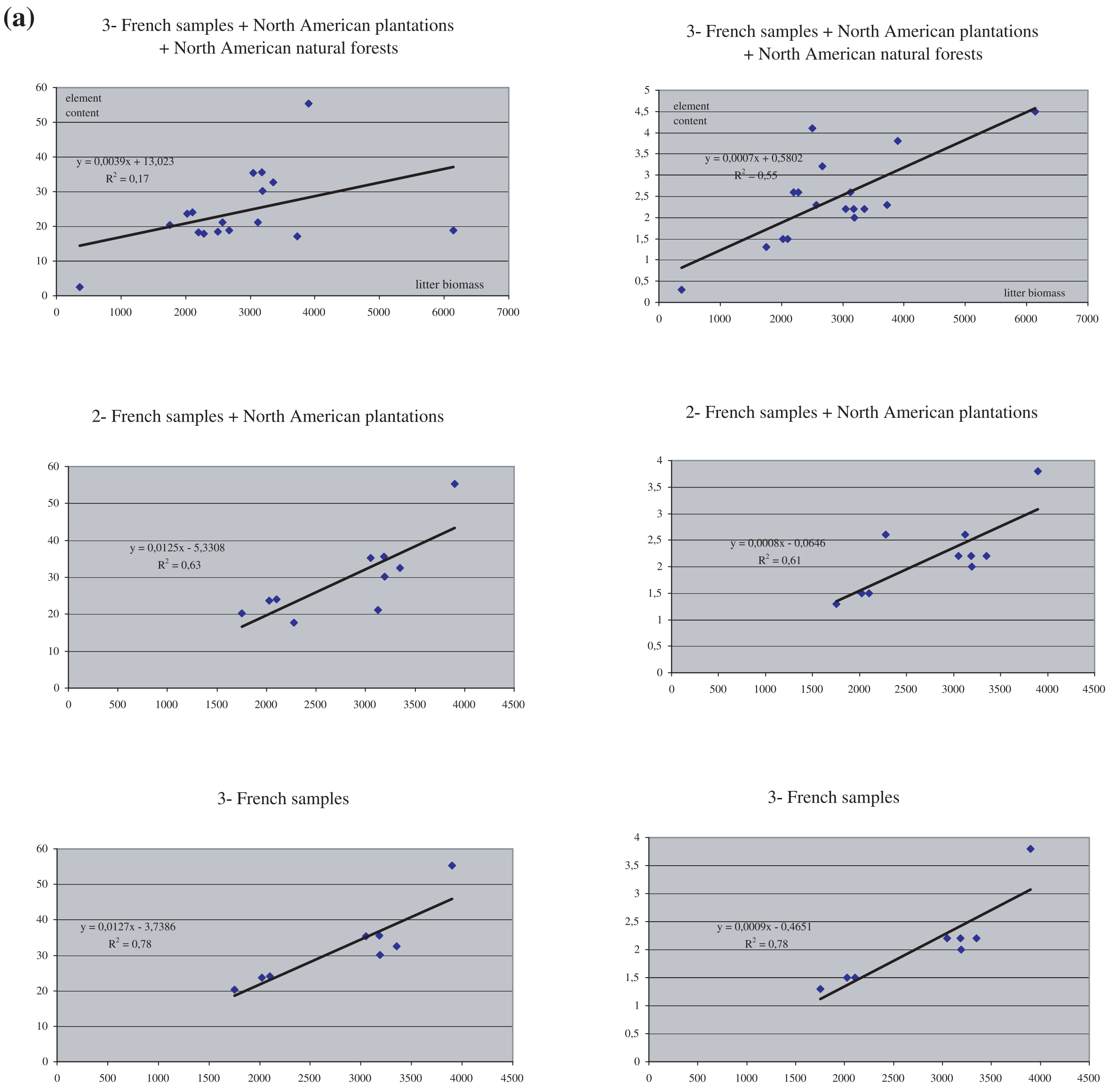


Figure 5. Relationships between litterfall biomass and its nutrient content (a), and between the different elements content in the biomass (b).

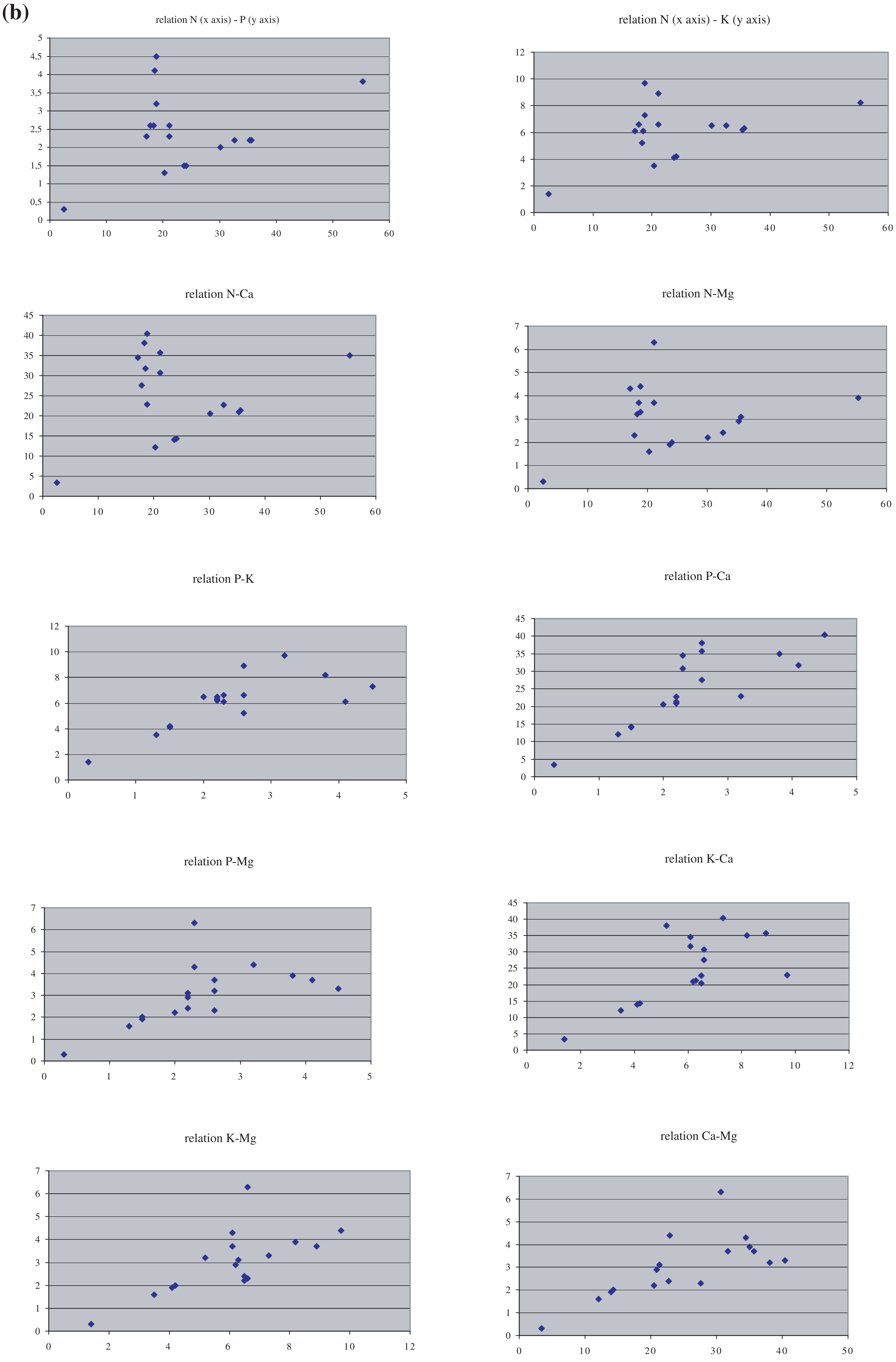


Figure 5. Continued.

returns of dry matter and nutrients from vegetation is of paramount importance for soil function and more particularly for the bioavailability of nutrients in soils.

Generalisation of relations using data from the literature: Data were grouped according to 'natural' stands or plantations. The general trends were as follows (Tab VII):

– There was a statistically significant relationship between needle litter and total litter, indicating that needles represented a constant part, indeed the main part, of litterfall in all sites (r = 0.82, n = 20).

– There was a lack of any satisfactory relationship between stand canopy biomass and partial (needles only) or total (needles + wood) litterfall. The coefficients of correlation were not significant in both individual groups ("natural" stands and plantations), but became significant by considering the whole data set. Nevertheless, the total variance could not be explained satisfactorily. This was the case for the relationship between total crown biomass and total litterfall mass (r = 0.64, n = 20), and between crown needle biomass and needle litterfall (r = 0.40, n = 20). These significant trends for the whole set of data were associated with the large variation of situations observed in the data set (from 9- to 450-year-old stands). The relatively poor relationship between crown parameters and litterfall could have various origins, such as (i) crown biomass is a cumulative parameter, which could blur needle age variation either according to stand age or to the site, or (ii) needle fall collected over relatively short periods may not give any realistic value.

– The relationships between litterfall mass and nutrients were generally significant. They indicated three main tendencies:

(i) The correlation coefficient was higher when needle fall was considered instead of total litterfall. This seemed related to the fact that brown needles represented the larger part of the total litterfall, and the variations in concentrations of this component were rather limited between sites.

(ii) Data fitting was improved when groups (natural stands and plantations) were distinguished. This could be explained by stand structure and genotypic properties, but the sample size was too limited to use this character as an explanatory variable such as stand age.

(iii) The fitting for statistical relationships between nutrients was better when N was excluded. This disagreement probably results from differences between methodologies used in the studies. This is quite surprising for such a common element. This is illustrated in Figure 5. For example, concerning the relationship between N-content and dry matter, there was a very good linearity for the "French" group, which remained correct when North American plantations were added, but which decreased when natural stands were associated (Fig. 5a). This became more obvious when the relationships between litterfall N and individual nutrients were compared to the relationships between nutrients other than N (Fig. 5b).

5. CONCLUSIONS

The chronosequence of stands, observed over the medium term, proved to be a useful tool to identify the trend of litterfall during stand development, and to quantify the dynamics of nutrient return to the forest floor. Accurate current and mean values for the rotation were provided. This study confirms that litterfall is an ecologically relevant parameter, supplying data for numerous functions characterizing an ecosystem i.e. stand nutrient uptake, soil carbon and nutrient supply from aboveground vegetation.

This research failed to find statistically significant relationships between stand characteristics and litterfall: litterfall varied with stands but variation was not related to available stand parameters from the literature, especially with stand crown biomass. More satisfactory relationships were found between litterfall and its nutrient content. Nevertheless, it seemed necessary to distinguish between plantations and natural stands which probably behaved differently.

There is growing interest in an overall model of ecosystem functioning, both for fundamental research and development purposes. Unfortunately, basic data to validate these models are insufficient. Only 20 case studies were found in the literature for identifying relationships between litterfall and stand characteristics for Douglas-fir. In addition, it appeared that measurements which were too short term in some cases, and apparent analytical heterogeneities made data difficult to compare. Harmonizing data is a prerequisite for providing general models in the future: significant duration is required and methodologies for chemical analysis need to be standardised.

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Annex I. List and characteristics of the stand used.

Type	Age	Years of observation	Stand density	Stem biomass	Aboveground biomass	Total crown biomass	Crown needles	Litter needles	Total litterfall	N	P	K	Ca	Mg	Author
Natural	450			734	802.3	68.3	14.12		6138	18.8	4.5	7.3	40.4	3.3	Grier et al., 1974
Plantation	28	5		129	166.2	37.2	14.1	2829	3049	35.3	2.2	6.2	20.9	2.9	Ulrich, 1995
Plantation	54	5		327.9	360	32.1	9.5	2516	3184	35.6	2.2	6.3	21.3	3.1	Ulrich, 1995
Plantation	36	5		165.3	194.5	29.2	9.7	1883	2104	24.1	1.5	4.2	14.3	2	Ulrich, 1995
Plantation	29	5		129.1	164.3	35.2	14.3	1600	1752	20.3	1.3	3.5	12.1	1.6	Ulrich, 1995
Plantation	26	5		127.5	159.1	31.6	12.8	1866	2025	23.7	1.5	4.1	14	1.9	Ulrich, 1995
Plantation	20	7	922	65.5	99.7	34.2	17.4	3286	3900	55.3	3.8	8.2	35	3.9	Ranger et al., 1975
Plantation	40	7	490	223.5	262.1	38.6	13.6	2082	3351	32.6	2.2	6.5	22.7	2.4	Ranger et al., 1975
Plantation	60	6	312	352	417.8	65.8	16.1	1795	3191	30.1	2	6.5	20.5	2.2	Ranger et al., 1975
Natural	9		2022	7.81	10.67	2.86	1.04	344	366	2.5	0.3	1.4	3.4	0.3	Turner and Long, 1975
Natural	22	1	2756	113.34	126.5	13.16	5	2518	2670	18.8	3.2	9.7	22.9	4.4	Turner and Long, 1975
Natural	30	1	1800	145.9	162.59	16.69	6.54	2000	2500	18.5	4.1	6.1	31.7	3.7	Turner and Long, 1975
Natural	42	1	822	177.05	196.58	19.53	8.27	1796	2573	21.1	2.3	6.6	30.7	6.3	Turner and Long, 1975
Plantation	42	1	1289	206.24	229.4	23.16	9.44	2403	3123	21.1	2.6	8.9	35.7	3.7	Turner and Long, 1975
Plantation	49	1	1067	201.19	224.55	23.36	9.39	1780	2280	17.8	2.6	6.6	27.6	2.3	Turner and Long, 1975
Natural	73	1	1889	267.33	293.52	26.19	10.75	1891	3725	17.1	2.3	6.1	34.5	4.3	Turner and Long, 1975
Natural	95	1	644	319.34	347.51	28.17	12.88	1119	2195	18.3	2.6	5.2	38.1	3.2	Turner and Long, 1975

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