Rapport Année pleine de recherche 1/2
2010/2011

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Time trends in forest litterfall production and relationships with environmental changes: An exploratory approach on data collected from 1995 to 2007 in the RENECOFOR monitoring network

Stage effectué à l'Office National des Forêts
Sous la direction de **Manuel NICOLAS**
Du 1er septembre 2010 au 31 janvier 2011

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Abstract

Litterfall dynamics is a key parameter for forest monitoring as litterfall is both an indicator of forest health and a major flux in biogeochemical cycles. In France, litterfall mass has been continuously monitored since 1995 on the RENECOFOR network, that is made of 102 permanent plots covering the main productive tree species (Common/Sessile oak, Beech, Douglas fir, Silver fir, Maritime pine, Scots pine, Norway spruce, Corsican pine and European Larch). The aim of this study was to explore this unusual dataset in order to calculate (i) mid-term trends in annual litterfall masses and (ii) relationships with annual defoliation, stand basal area, disturbances (loggings and windthrows) and meteorological factors (Temperatures, Precipitations, Evapotranspiration). Over the 1995-2007 period no general trends in litterfall production can be found: both positive and negative correlations are significant depending on tree species and plot. Few significant relationships are detected with defoliation. On the other hand strong relationships are found between leaf litterfall and stand basal area for heliophilic tree species. Moreover stand disturbances (logging and windthrows) are negatively related to interannual litterfall changes, with significant linear regressions for some tree species. Finally, significant multiple regressions are calculated with meteorological parameters considered up to two years before leaf litterfall: R^2 can reach 0.53 for Maritime pine whereas Scots pine and Silver fir show no significant results.

Remerciements

Je tiens particulièrement à remercier **Jean-François DHÔTE** pour m'avoir accueilli au sein du département R&D et de m'avoir ainsi permis de découvrir le fonctionnement d'une agence telle qu'est l'Office Nationale des Forêts.

Je remercie également **Manuel NICOLAS, Luc CROISE** ainsi que **Marc LANIER** pour toutes les connaissances qu'ils ont partagées et les conseils éclairés qu'ils m'ont apportés au quotidien lors des analyses et de la rédaction de ce rapport. Leur disponibilité, leur patience ainsi que leur rigueur scientifique ont été d'une aide précieuse. Je vous suis extrêmement reconnaissant de m'avoir permis de m'investir totalement dans ce projet et de m'avoir soutenu dans mes démarches, ainsi que pour la confiance et l'autonomie que vous m'avez accordée durant ce stage tout en gardant un œil avisé sur mon travail.

Je remercie aussi chaleureusement **Erwin ULRICH** sans qui je n'aurais jamais trouvé ce stage ainsi que **Sébastien CECCINI** pour avoir contribué à l'évolution positive de ce projet grâce à des aides et des conseils très précieux.

Encore un grand merci à toute l'équipe pour leur dévouement et leur contribution qui ont rendu ce séjour réellement très agréable.

Contents

Abbreviations

CHP: Common Oak
CHS: Sessile Oak
CPS: Common and Sessile Oak
CH: Oak (all species together)
DOU: Douglas-fir
EPC: Spruce
ETP: Turc Evapotranspiration
G: Stand basal area
HET: Beech
LF: litterfall
MEL: European Larch
P: Precipitations
PL: Corsican Pine
PM: Maritime Pine
PS: Scot Pine
RENECOFOR: Réseau National de suivi à long terme des ECOsystèmes FORestiers
SP: Silver Fir

Introduction

Litterfall production is a key parameter in forest monitoring as it reflects stand vitality and also because it is a major flux in biogeochemical cycles (Bray et Gorham 1964; Vogt et al. 1986; Figure 1).

Forest ecosystems are characterized by their ability to grow without nutrient input even on the poorest soils. And this ability depends on the efficiency of the internal nutrient turnover. The most part of the nutrients taken up annually by the trees can be transferred back to the soil and mainly through litterfall as it was observed for example in Douglas fir plantations (Ranger et al. 2003).

Annual litterfall mass is an also indicator of stand productivity. It usually represents more than a half of total aboveground production and reflects also the crown condition (Bray et Gorham 1964; Miller et Rechel 1999; J Bille-Hansen et K Hansen 2001). According to literature, annual litterfall mass in temperate regions varies from 2000 to 8000 $Kg.ha^{-1}.y^{-1}$ depending on the dominant tree species and the forest localization (Bray et Gorham 1964; Vogt et al. 1986).

Forest production depends on the status of the soil, meteorological and environmental conditions which are highly influenced by human activities. In France, almost all forests are managed. There is substantial literature reporting influent factors on litterfall. Litterfall is influenced by tree species (Cuevas et Lugo 1998), stand density and basal area (Hennessey et al. 1992; Turnbull et Madden 1983), defoliation (J Bille-Hansen et K Hansen 2001), precipitation, temperature and evapotranspiration (B. Berg et Meentemeyer 2001) and also forest management (Aber et al. 1979). However few studies deal with the influence of stand disturbances caused by loggings and windthrows or simply exclude them from considered data (Aber et al. 1979; Liu et al. 2004). And the literature is scarce about the litterfall production dynamics and trends over time.

On the other hand intensive forest monitoring has been implemented in all Europe since the 1980's and coordinated by an International Co-operative Programme (ICP Forests) under the UNECE Convention on Long-range Transboundary Air Pollution. This intensive forest monitoring includes litterfall measurements and it aims at detecting long-term changes in forest ecosystems and at understanding the reasons for these changes. However the litterfall data from forest monitoring are not fully exploited. They were used is some studies but only at the scale of few countries like Denmark and Finland and only on short-term periods (J Bille-Hansen et K Hansen 2001; Lebret, Nys, et Forgeard 2001; Saarsalmi et al. 2007).

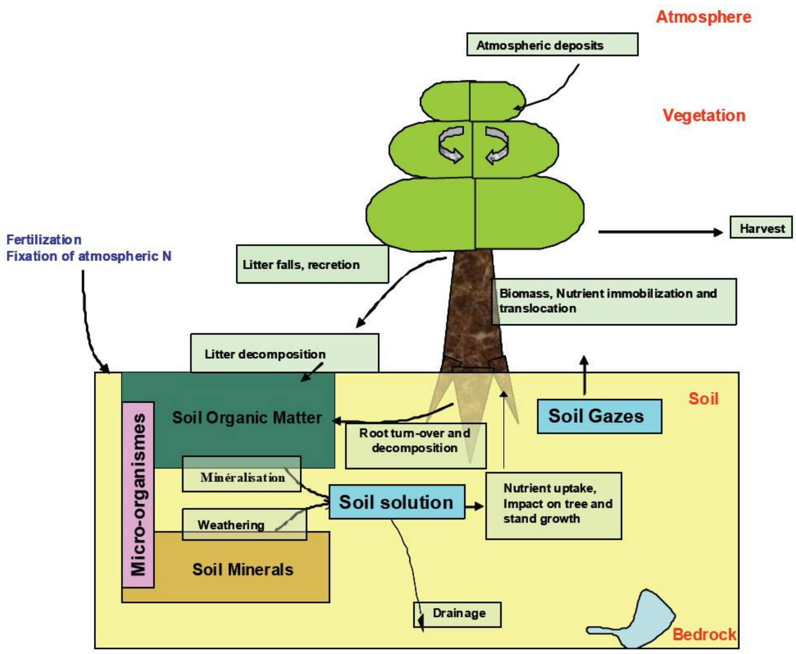

Figure 1: *Biogeochimical cycles in forest ecosystems. Nutrient circulation and immobilization in the soil and in vegetation (F-ORE-T 2011)*

This work is part of the French National Network for the long-term monitoring of Forest Ecosystems (RENECOFOR, Annex 1) that is part of the international ICP Forests monitoring network. In a previous study on RENECOFOR data, (Pasquet 2002) explored the relationships between the mean annual litterfall mass and plot variables like geographical context, soil chemistry, stand main characteristics and mean climate.

Our study focuses on litterfall production dynamics by using the data collected for 13 years from 1995 to 2007 on the 102 RENECOFOR plots. The first objective is to detect trends in annual litterfall masses at the scale of each plot. Then we will separately explore the relationships between litterfall production and the following parameters:

- annual defoliation,
- stand basal area dynamics including human and windthrow disturbances,
- annual and summer meteorological data (temperatures, precipitation and evapotranspiration).

These relationships will be studied at the scale of several plots grouped by main tree species or by distinction between broadleaves and coniferous tree species.

Material and methods

Sites characteristics

Litterfall data was collected from 102 plots located in public forests and is stratified according to the major commercial tree species in metropolitan France (Figure 2).

Those plots are part of the national long-term monitoring network of forest ecosystem in France (RENECOFOR, which is part of the ICP Forest Level II program). The RENECOFOR program provides, among other things, several sanitary data as litterfall, growth, defoliation and bud flushing date. It thus gives a unique opportunity to detect possible long-term changes in the functioning of a wide variety of forest ecosystems and to look for some reasons for the changes. Eleven main tree species are distinguished among the 102 plots (number of plots in parentheses): Common Oak (*Quercus robur; 9*), Sessile Oak (*Quercus petraea; 19*), Douglas fir (*Pseudotzuga menziesii; 6*), Norway Spruce (*Picea abie; 11*), European Beech (*Fagus sylvatica; 20*), European Larch (*Larix deciduas; 1*), Corsican Pine (*Pinus nigra; 2*), maritime Pine (*Pinus pinaster; 7*), Scots pine (*Pinus sylvestris; 14*) and Silver fir (*Abies alba; 11*).

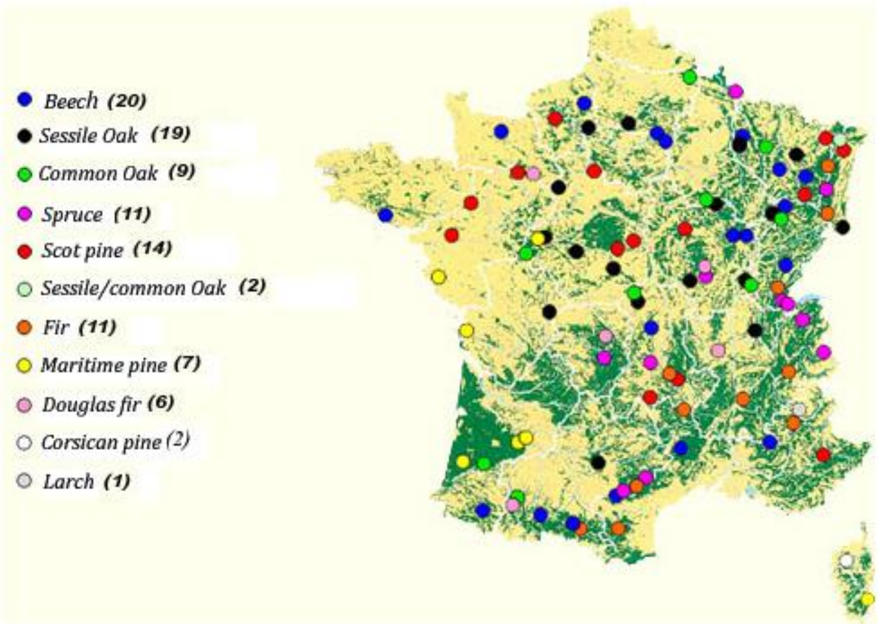

Figure 2: *Distribution of the 102 RENECOFOR plots throughout France by dominant tree species. Forested areas are represented in green on the map. Each circle represents a plot; the color represents the dominant tree species of the plot. Number of plots for each species is between parentheses.*

Litter sampling

Litterfall was collected seasonally from 1995 to 2007 on all RENECOFOR plots. 10 collectors were distributed in the 0.5ha central part of each plot (Figure3). Litter collectors were 0.5m² square traps treated against U.V. and designed with a water drainage system. Two kinds of sifter (2x2mm for needles and 4x4mm for leaves) were disposed at the bottom of the trap to retain litter. Traps were spaced of 12 m minimum from each other depending of the topography and distributed on 3 lines throughout the central plot. Collection dates were not fixed and could be postponed because of weather or logging. In this case, collects could be grouped or notified as missing. Depending on the plots, 3 to 5 samplings were performed per year.

Sample treatment

After collection, all the litter samples were separated into four compartments:leaves/needles of the dominant tree species, small branches of the dominant tree species (diameter < 2cm), fruits of the dominant tree species and rest (from secondary trees species). All compartments were air-dried at 105°C for 24 hours before weighing.

Data validation and calculation of annual litterfall masses

As the dates of seasonal collection considerably vary over time and among plots, it was decided to aggregate seasonal data at the biological year time scale which is meaningful for growth process and nutrient cycling. The beginning of the biological year was homogeneously defined as April 1st. For example 2000 denotes the 12-month period starting from 1 April 2000 to 31 March 2001. And the litterfall mass values from sampling periods overlying two subsequent biological years were split in proportion to the number of days related to each year.
The influence of fixing April 1st as starting date of the biological year was tested against the bud flushing date that has been assessed on all plots since 1997 and naturally varies over plots and years. Annual litterfall is similar with both calculation methods (Figure 4) for the four litter compartments.

In order to work on a robust dataset we defined a two step validation process (Annex 2, graph at the bottom). A collection is valid if:

- at least 8 collectors were in order on the plot

And a biological year of collection is valid if:

- less than 10% of the days of the year are missing
- no autumn day (from September 1st to December 31st) is missing

When some data were missing but criteria were respected, litterfall were gap-filled using seasonal mean values, otherwise the litterfall value for the biological year was considered as missing. Finally, litterfall production (dry mass per unit area) was calculated by dividing the litterfall masses collected by the total surface area of all the traps and then reported to one hectare.
For all the dataset (1513 records) those rules led to drop 19.6 % (296) of collections and to fill gaps for 3.1% (47) of the valid biological years.

Analyses were performed on litterfall data of the dominant tree species of each plot. Indeed, litter from other tree species was mixed in the 'rest' group.

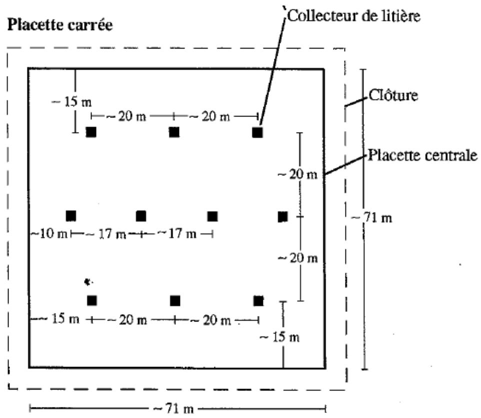

Figure 3: *Design of litterfall collectors (black squares) in the case of a square plot. Dotted line represents the fence; full line represents the central plot (0,5 ha).*

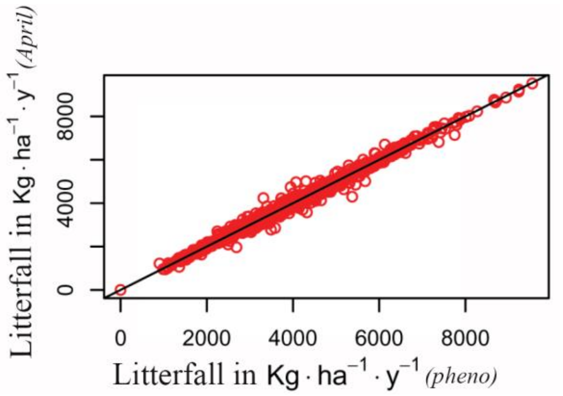

Figure 4: *comparison of two calculation methods for all the dataset. X axis represents annual litterfall calculated with bud flushing date. Y axis represents annual litterfall calculated with a fixed date (1st of April). Each red point represents a biological year collect. Slope of the linear regression is equal to 0.99 and R²=0.99.*

Litterfall trends and explanatory factors

This study has been carryed out following different stages: First, litterfall trends and relationships with defoliation data were detected on each plot ("plot scale"), on grouped plots of the same tree species ("species scale") and on broadleaves vs coniferous grouped plots ("species type scale"). Secondly, relationships with stand basal area and meteorological parameters were performed at "species scale" and "species type scale" (see parameters in Table 1).

Factor	units	Period
Basal Tree area (G)	m².ha^{-1}	5 years
Disturbances (Dist)	% (m².ha^{-1})	-
Late frost	days	Annual
Min Temperature (Tmin)	°C	Annual + Seasonal
Max temperature (Tmax)	°C	Annual + Seasonal
Mean temperature (Tmean)	°C	Annual + Seasonal
Precipitation (P)	mm	Annual + Seasonal
ETP Turc	mm	Annual + Seasonal
P-ETP	mm	Annual + Seasonal

Table 1*: List of explanatory factors. 'Period' represents maximum frequency between two measures. ETP=Evapotranspiration*

- Stand basal area dynamics

Circumference at breath height (1.30m) was measured every five years on all trees (circumference > 15 cm) of the central part of each plot (Figure 5; 52 trees are used for measures. 36 trees in the central plot and 16 trees outside are used for health status observations sampling) and it was repeated just before and after logging. Stand basal area ranges from 7.1 to 75.5 m².ha^{-1}. Each tree is numbered and can be followed over time. Links were performed between the stand basal area and the annual litterfall of the dominant tree species. Only years with effective circumference measurements and without stand disturbance (loggings or windthrows) were considered.

- Stand basal area disturbances

A disturbance is defined as the minimum percentage of stand basal area loss in relation to the value before disturbance. We considered both windthrows and thinning are considered together as disturbances. Thinning range goes from 0.6 to 50.9 % and windthrows from 1.8 to 68 % of the stand basal area. When plots were entirely stroke by storms, litterfall monitoring was stopped, thus no disturbance above 68 % was used for analyses. Disturbances were correlated to the difference in litterfall between the year n-1 preceding the disturbance and the year n+1 because litterfall of the biological year n was thus disturbed. When a disturbance period was not precisely defined over time (logging period covering several months) and overlapped two biological years the litterfall variation was calculated between years n-1 and n+2 for analysis. But disturbances were excluded from the analysis if the uncertainty on their date exceeds one year. No difference is visible if a fixed rule for the calculation of litterfall difference (LF_{n-1}-LF_{n+1} or LF_{n-1}-LF_{n+2}) is used.

- Defoliation

Defoliation is assessed in percentage of the crown every summer on a subset of 52 trees corresponding to the dominant species and to the overstorey of each plot (Figure 5). Mean annual defoliation is considered here. Annual defoliation range from 0% to 92% (HET 30) and widely varies between tree species. Quality assurance and control assessments performed on the network show a between-operator error around +- 10 %.

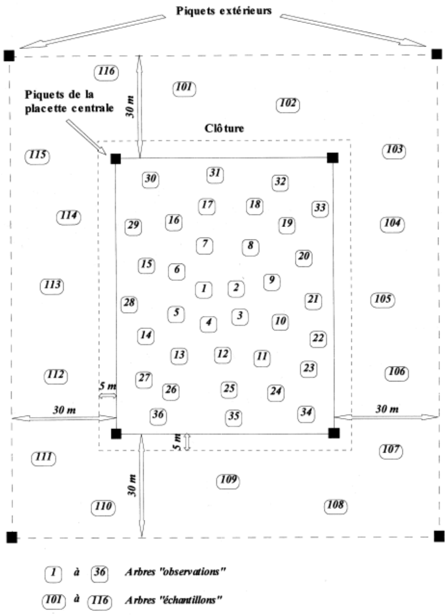

Figure 5: *52 trees are used for measures. 36 trees (1 to 36 or more) in the central plot and 16 trees (101 to 116 or more) are used for health status observations and the same 16 trees outside the central plot are used for foliar sampling.*

- Climatic factors

Relationships were explored between annual leaf litterfall and meteorological parameters (minimum *Tmin*, maximum *Tmax* and mean temperatures *Tmean*, precipitations *P*, evapotranspiration *ETP* and water deficit *P-ETP*) calculated both on yearly and summer (july to September) scale and considered up to two years before litterfall measurements (Table 1).

Annual and seasonal meteorological parameters were calculated from daily data (minimum and maximum temperatures, precipitation and global radiation) supplied by Meteo France stations selected for the most complete dataset from 1993 to 2007 and within a maximal range of 50 km from each plot. Data from one meteorological station can be used for two or three plots (Table 4) and no appropriate meteorological station was found for only 5 plots. Any year with more than 5% of missing data was excluded. Otherwise gaps in daily data were filled prior aggregation at the yearly or seasonal time step. Daily gaps were filled (i) when possible by a value modeled from some available data (linear regressions calculated between temperatures and radiation), (ii) else by a monthly mean value. Evapotranspiration was calculated from global radiation and temperature data according to Turc formula for temperate countries with the hypothesis of a humidity rate over 50% (Turc 1955; Turc 1961).

Analysis method

To explain spatial and temporal variations in annual litterfall production, we investigated relationships between litterfall, site, stand and health/meteorological factors mentioned previously. First, descriptive statistics and trends detection for each plot were performed respectively with Kruskal-Wallis test (litterfall distribution being not Normal for 29/102 plots and at species scale for 6/8 species – *Shapiro-Wilk test with error fixed at 10%* –) (Table 2) and Spearman’s rank correlation method. Secondly, litterfall relationships with defoliation and stand basal area were analyzed with Spearman’s rank correlation method and then characterized with single linear regression. Finally, we performed Spearman’s rank correlation on meteorological data to select a set of parameters able to influence litterfall. From this selection we derived best multiple linear regression models predicting litterfall. Analyses were performed using the R software (R Development Core Team, 2003) for statistical computing (coupled with the *lmtest* package for regression analysis). Standard error is fixed at 5% for all tests.

species	p	W	n
C.oak	0,08	0,97	110
S.oak	8,00E-08	0,94	239
D.fir	0,44	0,98	66
beech	1,00E-12	0,88	244
spruce	0,47	0,989	121
M.pine	2,30E-02	0,97	81
S.pine	0,01	0,97	171
S.fir	2,50E-02	0,98	145

Table 2: *Shapiro-Wilk test on leaves litterfall data. p represents the p-value of the test and W represents the ratio of two estimated variance of the population.*
N represents the number of data used for the analysis. When p<0.05 it means that the Normality hypothesis is rejected. Results at plot scale are not shown.

Results

Annual total and leaf litterfall production is higher for broadleaves stands (Table 3), with a total litterfall of 4963.9 $kg.ha^{-1}.y^{-1}$ and a leaf litterfall of 2402.3 $kg.ha^{-1}.y^{-1}$, than for coniferous stands LF_{total}=3580.4 $kg.ha^{-1}.y^{-1}$ and LF_{leaves}=2336.5 $kg.ha^{-1}.y^{-1}$ (Kruskal-Wallis $\chi^2_{total}=278.5$; df=1; $p<10^{-3}$; $\chi^2_{leaves}=54.9$; df=1; $p<10^{-3}$). At the species scale, Maritime pine plots show the highest leaf litterfall rate and Silver fir plots the lowest. However, proportions differ between compartments. For example leaf litterfall represent 66.7% of the total litter for broadleaves plots and 49.2% for coniferous.

Litterfall trends

Only 13 of the 102 plots show a significant correlation with years for the total litterfall, 19 plots for the leaf compartment, 14 for the branches compartment, 33 for the rest compartment and 10 for the fruit compartment (Table 4). Both positive and negative trends are visible for a same species and no significant correlation is detectable for plots grouped by main tree species.

species	Leaves $Kg.ha^{-1}.y^{-1}$	CV_L %	Prop. %	Branches $Kg.ha^{-1}.y^{-1}$	CV_B %	Prop. %	Fruits $Kg.ha^{-1}.y^{-1}$	CV_{Fr} %	Prop. %	Rest $Kg.ha^{-1}.y^{-1}$	CV_R %	Prop. %	Total $Kg.ha^{-1}.y^{-1}$	CV_T %	n
C.oak	2184,6	27,3	43,5	939,8	41,7	18,7	244,8	156,9	4,9	1657,1	50,1	33,0	5026,3	21,6	110
S.oak	2488,5	29,2	48,6	954,9	54,2	18,7	254,5	157,0	5,0	1420,3	52,4	27,8	5118,2	20,1	239
C&S.oak	2067,2	17,0	38,6	963,2	35,7	18,0	409,7	122,3	7,6	1921,7	19,5	35,8	5361,8	16,6	29
All oak	2246,7	8,4	43,5	952,6	9,4	18,4	303,0	21,0	5,9	1666,4	14,6	32,2	5168,7	1,9	378
D.fir	2036,7	31,8	84,5	282,5	73,0	11,7	73,0	140,6	3,0	19,1	165,2	0,8	2411,3	30,4	66
Spruce	2692,6	30,6	72,8	477,5	47,6	12,9	468,7	104,0	12,7	59,8	141,6	1,6	3698,6	30,0	121
Beech	2869,0	27,7	66,0	863,2	77,7	19,8	191,9	180,3	4,4	425,3	97,9	9,8	4349,4	32,1	244
Larch	2251,5	16,0	74,4	580,1	28,3	19,2	136,0	62,8	4,5	58,7	114,4	1,9	3026,4	14,1	13
C.pine	2447,2	24,3	51,6	922,6	61,9	19,5	734,5	74,1	15,5	636,0	84,4	13,4	4740,4	18,4	21
M.pine	3175,4	30,3	76,1	498,7	70,7	12,0	380,7	81,3	9,1	117,7	103,3	2,8	4172,4	28,0	81
S.pine	1859,5	34,6	49,6	814,4	49,7	21,7	504,5	57,7	13,5	572,0	108,3	15,3	3750,4	30,0	171
S.fir	1892,2	37,2	58,0	564,4	61,0	17,3	374,6	120,1	11,5	432,0	106,5	13,2	3263,2	33,0	145
coniferous	2336,5	20,4	49,2	591,5	36,3	16,3	381,7	58,9	10,0	270,8	98,5	7,0	3580,4	21,4	624
broadleaves	2402,3	14,9	66,7	930,3	4,9	18,8	275,2	34,1	5,5	1356,1	48,2	26,6	4963,9	8,7	622

Table 3: *Mean annual litterfall rate ($Kg.ha^{-1}.y^{-1}$), Variation Coefficient (CV, %), Litterfall proportion of each litterfall compartment (%) and number of litterfall data for each species. (n =1246)*

Species	Total	Leaves	Branches	Fruits	Rest	n
CHP	0,03	-0,13	-0,07	0,19*	0,13	110
CHS	0,16**	0	0,09	0,18**	0,14*	239
CPS	0,13	-0,58***	0,18	0,15	0,45**	29
DOU	-0,03	-0,14	0,31**	0,35***	0,08	66
EPC	0,05	-0,03	-0,02	0,25**	0,04	121
HET	-0,01	0,04	-0,04	0,07	-0,03	244
MEL	0,76***	0,65*	0,1	0,77***	0,36	13
PL	-0,26	-0,3	-0,48*	-0,03	0,41°	21
PM	-0,09	-0,17	0,08	0,02	0,28**	81
PS	-0,18*	-0,33***	-0,1	-0,23***	0,17*	171
SP	0,08	-0,07	-0,02	0,18*	0,17*	145

Table 4*: Detected time trends for groups of plots with the same dominant tree species (right) and for all plots (bottom). Plot characteristics are specified. Ho is the dominant height of dominant tree species (I). r is the Spearman correlation coefficient between litterfall and time (‘°’=$\alpha<0.1$; ‘*’= $\alpha<0.05$; ‘**’= $\alpha<0.01$; ‘***’= $\alpha<0.001$). For each plot, presence of logging events is represented by “¤” and windthrows events by “†”.*
n represents the number of data used for analysis.
CHP=common oak; CHS=sessile oak; CPS=common & sessile oak; DOU=Douglas-fir; HET=beech; MEL=Larch; PL=Corsican pine; PM=maritime pine; PS=Scot pine; SP=Silver fir

Plot	MeanAge in 94	Mean Ho (91 à93)	Basal area I	Basal area all	Weather station distance	Weather station altitude difference	Nb years	Mean litterfall in Kg.ha^{-1}.y^{-1}					Trends - Spearman Correlation Coefficient				
		(m)	m^2.ha-1		(km)	(m)		Total	Leaves	Branches	Fruits	Rest	Total	Leaves	Branches	Fruits	Rest
CHP 10¤	133,1	22,9	22,5	25,9	12,56	25	14	6105,9	2444,5	1418,2	322,8	1920,4	0,01	-0,45	-0,47°	0,20	0,72**
CHP 18¤	57,1	18,5	18,4	20,9	30,5	14	9	3535,2	1903,5	562,7	60	1009,1	0,53	-0,15	0,47	-0,01	0,85**
CHP 40¤†	45,6	23,4	22,6	22,9	18,8	11	7	4745,3	3173,8	939,2	444	188,3	-0,39	-0,61	-0,25	0,21	-0,11
CHP 49¤	70,8	29,6	22,7	30,9	42,95	7	13	5805,2	2498,6	1088,4	273,2	1945,1	-0,05	0,00	-0,20	-0,06	0,24
CHP 55¤	99,3	19,4	7,0	20,8	26,9	30	12	4781,9	1068,9	507	242	2964	0,52°	0,64*	0,57°	0,55°	0,20
CHP 59¤	69,7	21	18,7	24,1	-	-	15	5423,8	2315,2	1045,2	174,8	1888,5	-0,10	-0,26	-0,11	0,25	0,26
CHP 65¤	54	22	18,8	20,5	3,24	10	12	4084,2	2357,4	873,9	318,2	534,8	0,09	0,12	0,18	0,10	0,88***
CHP 70¤	34,8	19,6	20,9	21,7	14,76	31	14	4481,2	2027,4	785,9	227,6	1440,3	0,12	-0,29	-0,22	0,30	0,64*
CHP 71¤	66,7	25,9	16,6	28,8	8,57	8	14	5458,5	2144,6	1034,2	191,4	2088,3	-0,5°	-0,37	-0,15	-0,01	-0,37
CHS 01¤	87,8	25,2	19,9	21,6	22,72	10	13	5418,4	2808,8	991,4	270,5	1347,7	0,21	-0,41	0,43	0,23	0,73**
CHS 03¤	114	29,7	29,1	33,8	17,77	35	11	4633,5	2822,6	906,3	247,3	657,3	-0,31	-0,6°	-0,08	-0,28	0,50
CHS 10¤	82	24,9	17,3	19,2	6,45	20	14	5307,9	2885,2	1019,6	291,7	1111,4	0,34	-0,23	-0,30	0,57*	0,89***
CHS 18¤	77,7	28,4	25,9	27,7	28,27	15	11	4958,1	2959,9	949,7	345,5	702,9	0,12	0,01	0,20	-0,11	0,10
CHS 21¤	86,6	28,1	21,5	24,6	20,7	1	14	5735,5	2784,5	1179	304,3	1467,7	-0,29	-0,52°	-0,29	-0,05	0,78**
CHS 27¤†	54,1	22,3	12,0	23,0	23,51	24	14	5461	1642,7	869,1	226,4	2722,7	0,20	0,44	0,00	0,13	0,26
CHS 35¤	100,8	30,3	22,4	29,6	18,64	44	9	5300,6	2335,8	1120,7	197	1647,1	0,20	0,00	0,50	0,47	-0,75*
CHS 41¤	91,5	29,6	23,9	25,8	12,69	6	14	5144,1	2966,6	1214,9	229,7	732,8	0,44	0,27	-0,16	-0,09	0,24
CHS 51†	138,7	24,1	18,2	26,9	44,89	41	11	4623,4	1331,1	431,9	170,4	2690,1	-0,56°	-0,62*	-0,45	0,39	-0,38
CHS 57a¤†	84	26,9	24,0	29,5	27,94	103	14	5466,7	2569,4	847	416,8	1633,5	0,6*	-0,20	0,34	0,34	0,85***
CHS 57b¤	127,8	27,6	23,3	27,2	43,07	145	14	4073,9	2162,9	727,1	124,6	1059,3	0,61*	-0,01	0,63*	0,62*	0,71**
CHS 58¤	61	22,3	19,3	23,4	45,82	33	12	5038,8	2392,4	807,5	316,1	1522,8	0,34	-0,20	0,29	0,12	0,41
CHS 60¤	59,8	23,8	21,0	27,0	13,61	34	14	6214	3119,4	1325,9	491	1277,7	0,49°	0,21	0,58*	0,34	-0,08
CHS 61¤†	87,3	27,6	22,0	27,5	43,99	76	13	5590,9	2862	1006	207,1	1515,8	0,47	0,37	0,02	0,14	0,75**
CHS 68¤†	136,6	21	10,4	23,6	14,8	11	13	4184,2	1018,5	269,5	94,6	2801,5	-0,35	-0,6*	-0,62*	0,22	-0,13
CHS 72¤	63,8	23,7	25,9	29,1	21,8	119	11	4581,8	2644,7	797,8	42	1097,3	0,41	0,03	-0,01	-0,06	0,61°
CHS 81¤	97,4	25,7	23,2	23,3	32,92	128	12	4584,1	2943,3	1045,1	290,6	305,1	0,03	0,36	-0,13	-0,01	0,52°
CHS 86¤†	81,3	25,5	21,5	24,9	15,66	1	13	5847,9	2850,5	1722,3	340,3	934,8	0,51°	0,15	0,40	0,03	0,6*
CHS 88¤†	128,7	26,6	19,0	28,1	44,49	30	12	4676,1	2041,6	795,1	155,2	1684,1	-0,64*	-0,78**	-0,52°	-0,24	0,06
CPS 67¤†	75,7	23,1	19,2	27,9	49,55	115	14	5489,9	1953,8	1029,2	436,3	2070,5	0,24	-0,47°	0,46°	0,32	0,21
CPS 77¤†	112,2	27,3	18,4	23,3	17,62	11	15	5242,2	2173	901,6	384,9	1782,8	0,03	-0,73**	-0,04	0,11	0,84***
DOU 23¤†	23	17,7	22,4	22,5	-	-	10	3064,9	2632,5	331	100,2	1,2	-0,30	-0,48	0,72*	0,6°	-0,81**
DOU 34¤	47,1	36,4	53,8	54,0	36,37	468	9	2568,3	2064,3	404,8	91,7	7,6	-0,93***	-0,95***	-0,67°	-0,23	-0,07
DOU 61¤	29,4	26,3	36,7	36,7	20	231	12	2346	2004,4	286,9	53,6	1,2	0,32	0,23	0,45	0,01	0,31
DOU 65	23,9	21,2	15,2	15,2	12,88	60	13	2462,7	2049,6	333,9	2,2	77,1	0,68*	0,71**	0,33	0,00	0,63*
DOU 69¤†	23	18,7	29,1	29,1	48,17	120	9	1700,9	1382	156,1	160,9	2	-0,17	-0,47	0,28	0,72*	0,39
DOU 71¤	19,6	17	35,0	36,1	18,75	347	13	2300,4	2029,3	192,7	67	11,4	0,35	0,19	0,63*	0,78**	0,51°

Plot	MeanAge in 94	Mean Ho (91 à93)	Basal area I	Basal area all	Weather station distance	Weather station altitude difference	Nb years	Mean litterfall in Kg.ha^{-1}.y^{-1}					Trends - Spearman Correlation Coefficient				
		(m)	m².ha-1		(km)	(m)		Total	Leaves	Branches	Fruits	Rest	Total	Leaves	Branches	Fruits	Rest
EPC 08¤	34,8	20	34,9	34,9	22,05	331	14	3430,5	2709,4	508,9	212,2	0	-0,23	-0,11	-0,51°	0,14	0,00
EPC 34¤	26,1	14,5	45,1	45,1	-	-	10	4217,9	2963	303,2	947,2	4,5	0,58°	0,53	0,45	0,24	0,83**
EPC 39a¤	57,6	29,3	44,2	44,2	30,51	690	14	4008,4	2898,2	459,2	624,6	26,3	0,27	0,16	-0,09	0,42	0,67*
EPC 39b¤	110,8	24	33,9	34,8	34.48	834				No valid data							
EPC 63¤	27,4	18,2	36,4	37,4	5.66	60	15	4390,4	3353	382,7	591	63,7	0,23	0,23	0,40	0,16	-0,20
EPC 71¤	47,1	26,5	28,4	29,2	11.64	297	13	3181	2133,8	570,8	424,9	51,5	-0,49°	-0,63*	0,00	0,34	-0,42
EPC 73¤†	181,2	21,6	39,9	39,9	3,64	835	13	1968,6	1385,8	293,4	217,4	71,9	0,30	0,30	-0,44	0,08	0,32
EPC 74¤	72,7	29,1	64,7	64,7	17,45	824	12	4542,3	2983,7	631,6	700,8	226,2	0,02	-0,15	0,03	0,37	0,53°
EPC 81¤	42	21,9	35,2	41,0	17,35	588	11	3775	2847,5	642,1	211,6	73,9	-0,03	-0,30	-0,23	0,27	0,35
EPC 87¤†	22,7	14,9	24,8	26,7	49,65	248	14	4048,4	3116,1	453,3	470,7	8,3	-0,12	-0,35	0,46	0,29	-0,30
EPC 88	88,1	34,4	60,0	61,4	18,11	351	5	3138,9	2174,3	645,4	195,8	123,4	-0,20	0,20	-0,40	0,50	0,70
HET 02¤	53,1	27,6	21,8	29,1	48,08	37	13	5557,5	3227,6	1064,1	178	1087,8	-0,02	0,21	0,07	0,22	-0,73**
HET 03¤	86,4	27,5	27,3	32,2	31,2	341	13	4567,3	3176,8	731,9	134,5	524,2	-0,18	0,38	-0,55°	-0,09	-0,26
HET 04	87,6	23,6	19,2	19,3	21,14	735	13	4746,8	3608,8	923,8	176,1	38,1	0,62*	0,66*	0,23	0,35	-0,55°
HET 09¤	151,6	20,9	27,9	27,9	16,55	839	9	3755,7	2534,8	926,7	280,2	14	0,37	0,40	0,17	0,43	0,13
HET 14¤	82,5	26,7	23,8	23,9	28,72	26	11	5197,6	3400,4	1289,2	464	44	-0,25	-0,43	-0,25	-0,26	0,01
HET 21†	127,6	28,3	23,0	24,3	20,76	138	12	2651,5	1903,8	465,9	82,9	198,9	-0,71*	-0,69*	-0,28	-0,21	0,17
HET 25¤	40,4	18,6	15,5	20,0	22,82	263	12	3949,8	2655,2	438,8	55	800,9	0,52°	0,42	0,64*	0,61*	-0,17
HET 26¤	157,1	22,9	17,6	31,6	16,2	935	13	3235,8	1541,6	575,3	79,4	1039,6	0,12	-0,04	0,58*	0,02	-0,49°
HET 29¤	63,1	23,7	20,5	24,7	10,71	8	11	4832	2691,4	830,9	228,4	1081,3	-0,29	-0,06	-0,05	-0,13	-0,48
HET 30¤	142,6	18,8	35,6	35,6	41,9	685	14	3566	2785,4	720,5	50,5	9,6	0,40	0,68**	-0,29	0,40	0,7**
HET 52¤†	106	27,7	26,9	28,9	20,87	27	5	3980,8	2967,9	563,4	75,6	373,9	-0,20	0,70	-0,20	-0,11	-0,9°
HET 54a¤	94,3	28,5	26,7	30,0	38,1	8	5	4535,3	3086	908,4	115,2	425,7	0,00	0,10	0,10	-0,60	-0,30
HET 54b	98,8	27,6	19,6	20,7	12,17	178	4	4286,8	3332	752	78	124,8	-0,20	1°	-1°	-0,60	-0,40
HET 55†	88,1	29,3	17,7	23,8	49,46	148	11	4129,2	2496,3	553	154,8	925,1	0,15	0,05	0,00	0,19	-0,25
HET 60¤†	61,9	25,9	24,2	25,9	42,16	30	14	4808,1	3341	1072,9	223,5	170,7	-0,07	-0,04	-0,22	0,29	0,46°
HET 64¤†	66	26,1	24,0	29,7	32,78	217	14	3723,2	2443,1	599,9	58,2	622	0,20	0,29	-0,18	-0,27	-0,42
HET 65¤	160	27,6	38,8	38,8	12,46	250	10	3189,5	2042,1	823,2	301	23,2	0,31	0,45	0,10	-0,14	0,27
HET 76¤	86,8	29,1	22,2	24,1	37,93	59	14	5425,6	3408,9	1391,3	390	235,4	0,09	0,13	0,06	-0,05	-0,19
HET 81¤	107,2	28	32,3	32,6	9,7	466	10	4881,2	3476,7	1100,5	277	27	-0,25	-0,18	-0,25	-0,08	-0,46
HET 88¤†	67,8	24,3	21,4	23,3	19,29	83	13	3901,8	3003,8	523	60,6	314,4	-0,14	0,24	-0,45	0,15	0,49°
HET L1	-	-	17,4	21,3	-	-	14	5304,9	2917,8	1274,8	391,7	720,6	0,43	0,48°	0,27	0,06	0,32
HET L2¤	-	-	29,8	30,0	-	-	9	5149,2	3494,4	1327	280,2	47,6	-0,07	-0,07	-0,12	0,14	-0,40
MEL 05¤	131,3	25,7	31,7	31,7	15,96	979	13	3026,4	2251,5	580,1	136	58,7	0,76**	0,65*	0,10	0,77**	0,36
PL 20¤	173	37,9	57,5	57,5	27,65	738	11	5331,1	2912,6	1405,5	806,1	206,8	-0,25	0,02	-0,55°	-0,07	0,27
PL 41¤†	44,6	22,7	27,1	29,5	43,38	15	10	4090,6	1935,4	391,4	655,8	1108,1	0,28	-0,48	-0,73*	0,14	0,72*

Plot	MeanAge in 94	Mean Ho (91 à93)	Basal area I	Basal area all	Weather station distance	Weather station altitude difference	Nb years	Mean litterfall in Kg.ha^{-1}.y^{-1}					Trends - Spearman Correlation Coefficient				
		(m)	m².ha-1		(km)	(m)		Total	Leaves	Branches	Fruits	Rest	Total	Leaves	Branches	Fruits	Rest
PM 17¤†	22,7	10,5	26,1	26,1	25,31	2	12	3385,4	2421,7	360	440,4	163,3	-0,67*	-0,49	-0,31	-0,39	0,15
PM 20¤	41,5	21,6	71,7	72,8	28,45	828	13	5381,2	4055	783,7	392,8	149,7	-0,46	-0,37	-0,71**	0,03	-0,33
PM 40a¤	28,7	15,7	33,2	33,2	35,96	4	13	4899,5	3905,3	490	465,1	39,2	-0,18	-0,23	0,28	0,18	0,67*
PM 40b¤†	16,1	13	19,7	19,7	39,62	51	12	4213,9	3697	290,8	195,7	30,4	-0,57°	-0,63*	0,20	-0,31	0,63*
PM 40c¤†	14,1	11,9	18,7	18,7	42,6	91	11	3925,4	3147	452,5	299,4	26,5	0,25	-0,08	0,71*	-0,06	0,93***
PM 72¤†	25,7	17	19,0	19,0	24,63	102	13	3526,1	2617	315,8	356,7	236,6	0,19	0,23	0,42	0,06	0,74**
PM 85¤	61,1	12,6	22,1	22,1	49	2	13	3780,3	2362,6	764,4	492,5	160,8	0,03	-0,21	0,18	0,10	0,47
PS 04†	68,9	16,2	44,9	44,9	-	-	13	3503	2280,8	812,1	289,4	120,7	0,21	0,27	-0,10	0,73**	0,19
PS 15¤†	59,1	21,1	37,4	37,6	40,04	55	12	3573,4	1976,4	643,7	341,7	611,6	-0,69*	-0,76**	-0,71*	-0,59*	0,87***
PS 35¤	40,2	16,7	16,9	21,4	19,31	44	8	5351,8	1826,4	1114,3	697	1714	-0,26	-0,36	0,14	-0,43	0,14
PS 41¤†	38,3	20,1	27,3	27,4	43,72	15	13	3838,4	2097	966,7	513,9	260,9	-0,21	-0,51°	-0,30	-0,57*	0,98***
PS 44¤	55,3	19,6	29,5	29,6	27,13	50	12	4166,3	2133,5	1112,5	544,1	376,2	-0,28	-0,27	-0,23	-0,14	0,01
PS 45¤	53	20,4	25,1	32,2	-	-	9	3650,9	1070,9	595,3	401,4	1583,2	-0,05	-0,57	0,35	-0,58	0,65°
PS 61	42,9	22,2	22,9	23,6	49,06	116	4	3588,7	2447,1	483,8	547,2	110,5	-0,40	-0,40	-0,20	-0,20	0,80
PS 63¤†	93	24,4	27,5	28,3	12,91	195	14	3714,6	2264,9	869	480	100,7	0,02	0,13	0,26	-0,44	0,45
PS 67a¤†	64,3	23,4	30,1	35,0	33,82	25	9	4209,6	1426,5	689,7	366,1	1727,2	-0,63°	-0,67°	-0,65°	-0,88**	0,45
PS 67b¤†	63,1	26,2	34,0	35,2	33,66	175	12	4519,8	1880,8	1087,2	722,6	829,2	-0,17	-0,73**	-0,12	-0,10	0,69*
PS 76¤†	42,9	22,4	24,1	24,1	32,48	81	9	2766,4	1566,3	568,9	497,2	134	-0,72*	-0,83**	-0,47	-0,13	0,82*
PS 78†	43	21,1	30,6	30,8	22,35	3	10	3582	1990,7	778,6	747,9	64,8	0,32	0,54	0,27	-0,59°	0,53
PS 88¤†	65,1	24,2	25,2	25,5	18,11	183	12	2211,4	1171,4	523,5	340,4	176,1	-0,65*	-0,64*	-0,71*	-0,56°	0,89***
PS 89¤	57,3	27,5	29,9	35,1	20,84	87	5	4568,1	1721,1	925,4	893,9	1027,7	-0,20	-0,80	0,50	-0,50	0,30
SP 05¤	98,1	27,5	26,7	30,8	9,33	489	14	3086,4	1736,4	477,3	426	446,7	0,18	-0,02	-0,25	-0,02	0,42
SP 07¤†	79,8	24,9	54,5	56,4	19,33	152	12	3206,6	1685,8	563,4	693,8	263,6	0,31	0,18	-0,76**	0,49	0,20
SP 09¤†	167,6	24,9	39,5	39,5	24,99	689	9	1490,3	1005,3	364,1	92,7	28,1	0,72*	0,98***	-0,13	0,52	0,63°
SP 11¤	79,2	27,8	57,0	57,5	42,35	824	13	3523,9	2267,4	645,2	475	136,3	0,10	0,10	-0,10	0,12	0,8**
SP 25¤	80,2	23,9	29,6	38,2	47	693	14	3857,3	2166,9	678,9	296,6	714,9	0,08	-0,27	0,20	0,11	0,7**
SP 26¤	119,7	22,2	21,8	30,2	19,15	765	13	2662	834,5	213,4	98,9	1515,2	-0,15	-0,47	0,05	0,48	-0,12
SP 38¤	93,3	26,8	36,0	37,9	30,53	865	13	2800,7	1592,2	517,5	435,8	255,2	0,00	-0,03	-0,08	0,30	0,57*
SP 39¤	40,8	21,7	41,7	42,6	27,21	280	14	3520,6	2443,9	483,2	439,4	154	0,29	0,37	0,62*	-0,10	0,04
SP 57¤†	53,7	26,7	25,3	36,2	13,38	65	15	2951,7	1795,2	307,5	163,5	685,5	-0,12	-0,68**	-0,40	0,05	0,78***
SP 63¤	107,4	26,3	41,2	41,7	18,61	485	14	4490,3	2682,5	895,5	573,7	338,6	0,02	-0,17	0,30	0,08	0,48°
SP 68¤	103,9	29,5	49,0	55,2	12,62	395	14	3629,4	2194,8	986,7	376,6	71,3	-0,16	-0,34	0,38	-0,09	0,03

Relationship with stand basal area

Concerning relationships between total or leaf litterfall and the stand basal area of a year n for the main species, only Douglas fir and Norway spruce don't show any significant correlation (Table 5). Beech shows the lowest significant correlation (r=0.28) while common oak and maritime pine have highest correlations (r=0.83; r=0.85). There are no results concerning the fruits, branches and rest groups. Single Regression Analysis (Detailed calculations and test in Annex 3) show that stand basal area explains a large part of the leaf litterfall variance for common oak (R^2=0.73), sessile oak (R^2=0.46), oak species together (R^2=0.54), maritime pine (R^2=0.59) and Scots pine (R^2=0.25) species (Figure 6a). It explains less than 17% litterfall for other species and nothing for Norway spruce. Concerning the maritime pine species which has a large range of stand basal area (10 to 70 $m^2.ha^{-1}$), we tried to transformed data by a logarithm and a polynomial function (Figure 6b). Best fitting is obtained with logarithm function (R^2=0.67), then by second degree polynomial function (R^2=0.66) and finally by linear function (R^2=0.58). But the relationship is different if we exclude data from PM 20 that corresponds by far to the densest stand. (R^2_{linear}=0.67 and R^2_{log}=0.61; Annex 3c). European Larch and Corsican Pine plots were not used for analysis because few data were related to those and were just compared to other species.

Relationship with stand basal area disturbances

All relationships are negative for both leaf and total litterfall (Table 6/Figure 7). At "species scale" only oak species together and silver fir show a significant correlation (α<0.05) with leaves (r_{CH}=-0.68; r_{fir}=-0.46 p<0.5). Both broadleaves (r=-0.44) and coniferous (r=-0.33) show also significant correlations. Disturbances have no influence if the loss in stand basal area is less than 10%. Correlations with total litterfall are identical excepted for oak which is no longer significant (Annex 4).

Regressions confirmed that disturbances influence oak leaf litterfall (R^2=0.21; R^2=0.35 for sessile oak), Silver fir leaf litterfall (R^2=0.41) and also Scots pine leaf litterfall (R^2=0.41). But the part explained for other species is less than 20 % (Table 6/ Figure 7).

Relationship with defoliation

At "species scale", only fir shows a significant relationship between LF_{leaves} and defoliation (Spearman test r=-0.53; p<10^{-3}) (Table 7). However, negative relationships also occur for 13 plots (r < -0.7; p<10^{-3}). Only the HET 25 plot shows a positive relationship (r=0.78; p=10^{-2}). For those 13 plots, defoliation can explain more than 30% of the leaf litterfall (single regression R^2>0.3). Concerning LF_{fruits}, no general trends can be outlined. Among eleven significant correlations, seven are positive, the others negative. Moreover, linear regression and a graphical view of the results confirmed that LF_{fruits} relationships revealed by spearman correlations are noised by punctual events. But for LF_{leaves} relationships, regression confirmed previous links (Figure 8).

Relationship with climatic factors

According to Spearman's rank correlation, sessile oak plots are negatively correlated with P, and positively with T and ETP (Table 8). Similar relationships are found for beech species excepted for Tmax that is negatively correlated. Compared to sessile oak, common oak species show some positive correlations with P. Douglas fir and spruce are only correlated to T; maritime pine is mostly correlated to T and ETP. Finally Scots pine and Silver fir plots are negatively correlated to P and ETP only for years n-1 and n-2.
Best fitting models developed with multiple linear regressions for each species are displayed in Table 9. The selected factors for

best relationships much depend on tree species and LF_{leaves}. We can underline that there is a post-effect of meteorological conditions on litterfall for at least two years.

Maritime pine species is the most influenced by meteorology (R^2=0.49; R^2=0.53 without data from PM 20), followed by common oak (R^2=0.28), spruce (R^2=0.23), Douglas fir (R^2=0.16), beech (R^2=0.16) and sessile oak (R^2=0.13) species. For Scots pine and Silver fir, no significant models are found (R^2=0.05).

Year n	**Leaves**	**Total**	**regression**					
Species	**r**	**r**	**a**	**b**	**R^2**	**Min G**	**Max G**	**n**
All species	**0,17**	**-0,18**	**12,4**	**2037**	0,04	7,11	75,57	254
CHP	**0,83**	**0,64**	**86,7**	**506,8**	0,7	7,11	25,77	21
CHS	**0,60**	0,00	**83,5**	**744,1**	0,46	8,41	30,28	54
CH	**0,67**	0,20	**88**	**601,7**	0,54	7,11	30,28	75
DOU	0,22	0,22	36,7	871,5	0,16	16,09	46,30	12
EPC	0,06	-0,03	**1,9**	2309,1	0	24,37	61,29	29
HET	**0,28**	0,16	**43,4**	**1865,9**	0,1	9,50	38,11	50
PM	**0,85**	**0,88**	**40**	**1900,7**	0,59	12,17	75,57	16
PS	**0,44**	0,06	**34,4**	**986,2**	0,25	8,86	51,56	34
SP	**0,49**	0,32	**23,8**	**872,1**	0,2	16,32	61,82	31
Broadleaves	**0,52**	**0,18**	**77**	**931,7**	0,34	7,11	38,11	125
Coniferous	**0,37**	0,14	**29,8**	**1343,6**	0,19	8,86	75,57	91

Year n+1	**Leaves**	**Total**	**regression**					
Species	**r**	**r**	**a**	**b**	**R^2**	**Min G**	**Max G**	**n**
All species	**0,18**	**-0,15**	**16,4**	**1890,8**	0,06	7,11	75,57	259
CHP	**0,67**	**0,59**	78,2	**685,5**	0,39	7,11	25,77	22
CHS	**0,52**	-0,02	**89,6**	**531,8**	0,46	8,41	30,28	52
CH	**0,56**	0,15	**87,6**	**556,2**	0,46	7,11	30,28	74
DOU	0,18	0,20	**10,8**	1601,3	0,07	16,09	46,30	16
EPC	-0,12	-0,05	**-6,3**	2847,3	0,01	24,37	61,29	25
HET	**0,33**	0,11	**39,3**	**1820,6**	0,15	9,50	38,11	55
PM	**0,64**	**0,63**	**33,7**	**2075,2**	0,41	12,17	75,57	18
PS	**0,49**	0,04	**28,8**	**1013,7**	0,23	8,86	51,56	35
SP	**0,43**	0,28	**24**	**931,1**	0,18	16,32	61,82	30
Broadleaves	**0,56**	0,15	**70,9**	**978,6**	0,35	7,11	38,11	74
Coniferous	**0,47**	0,01	**30,1**	**1314,4**	0,2	8,86	75,57	129

Table 5: *Spearman correlation coefficient r between Litterfall and Basal Tree Area for the year n (left) and the year n+1 following measurements (right). Significant values (α=0.05) are in bold. Regression form is* $LF_{leaves}=aG_{year\ n}+b$. *Min G and Max G represents Basal Tree Area extremum and n the number of data used for the*

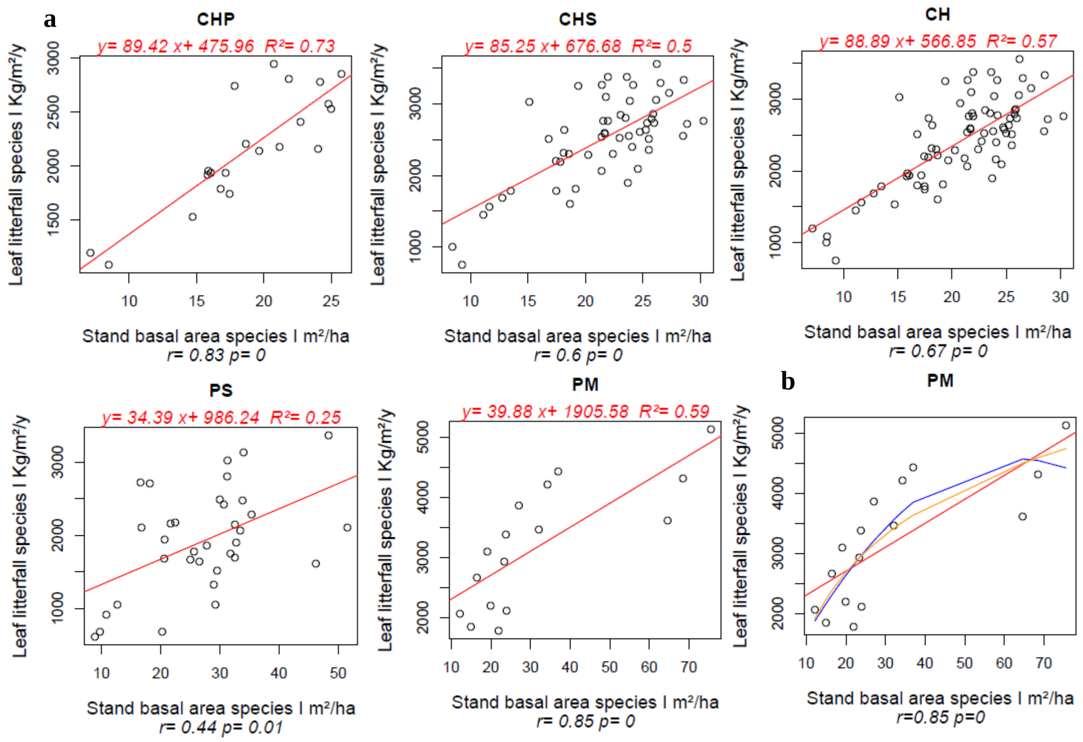

Figure 6: a) *Relationships between basal tree area ($m^2.ha^{-1}$) of the year n and Leaves litterfall ($Kg.m^{-2}.y^{-1}$) of the year n for two broadleaves species CHP and CHS and for two coniferous species PS and PM. It is data from dominant tree species of plots. The fitting model expression (y=ax+b) is written in red on the top of the plot. Spearman correlation r and the corresponding p-value p are written on the bottom of the plot (α=0.05).*

b) *Linear (red), logarithmic (orange) and polynomial (blue) fitting models for PM species. Expressions are respectively*

$y=39.88x + 1905.58$ (R^2=0.59); $y=1552.1\log(x) -1968.9$ (R^2=0.67) and $y=119.97x -0.9x^2+559.05$ (R^2=0.66).

	Spearman coefficient r			Disturbances informations			Regression y=ax+b		
Species	**Leaves**	**Fruits**	**Total**	**Min %**	**Max %**	**n**	**a**	**b**	**R²**
All species	**-0,40**	-0,01	**-0,34**	0,83	68,30	99	**-1,09**	10,49	0,16
CHP	-0,37	-0,01	-0,31	0,83	33,31	13	-0,70	0,88	0,13
CHS	-0,49	-0,22	-0,44	1,81	35,56	15	**-0,92**	7,68	0,35
CH	**-0,46**	-0,03	-0,34	0,83	35,56	28	**-0,79**	3,69	0,21
DOU	-0,25	0,50	-0,25	11,88	32,20	7	-3,10	49,88	0,20
EPC	0,15	0,19	0,10	9,01	30,12	10	-0,91	4,95	0,03
HET	-0,35	0,20	-0,19	6,44	55,56	18	-0,83	11,25	0,16
PM	-0,33	0,13	-0,32	11,06	26,20	9	-3,90	72,33	0,17
PS	-0,36	-0,20	-0,26	1,52	68,30	13	**-0,98**	4,23	0,41
SP	**-0,68**	-0,14	**-0,55**	6,56	31,61	13	**-1,64**	15,15	0,41
Feuillus	**-0,44**	0,04	**-0,30**	0,83	55,56	46	**-0,78**	6,12	0,17
Résineux	**-0,33**	0,10	**-0,32**	1,52	68,30	39	**-1,23**	13,14	0,14

***Table 6**: Relationships between leaves, fruits, total litterfall and G disturbances. Significant values are in bold (p<0.05). Min% and Max% are respectively minimum and maximum disturbances in percent. n represents the number of disturbances data available for analysis. Regression form is:*
$LF = a*(\Delta G) + b$

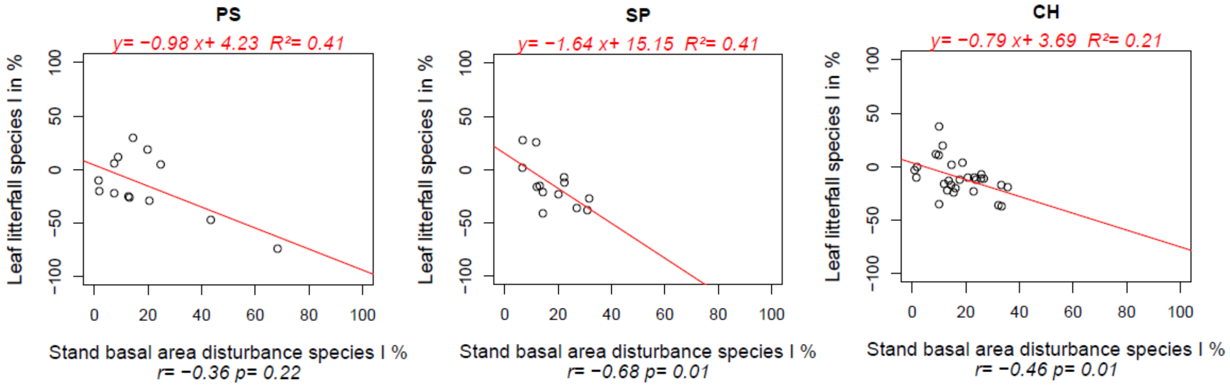

***Figure 7**: Representation of $\%LF_{Leaves}$ versus %G loss for PS, SP and CH. r is the Spearman coefficient and p the corresponding p-value (α=0.05). The regression expression and the correlation coefficient R² are written in red on the top of the plot.*

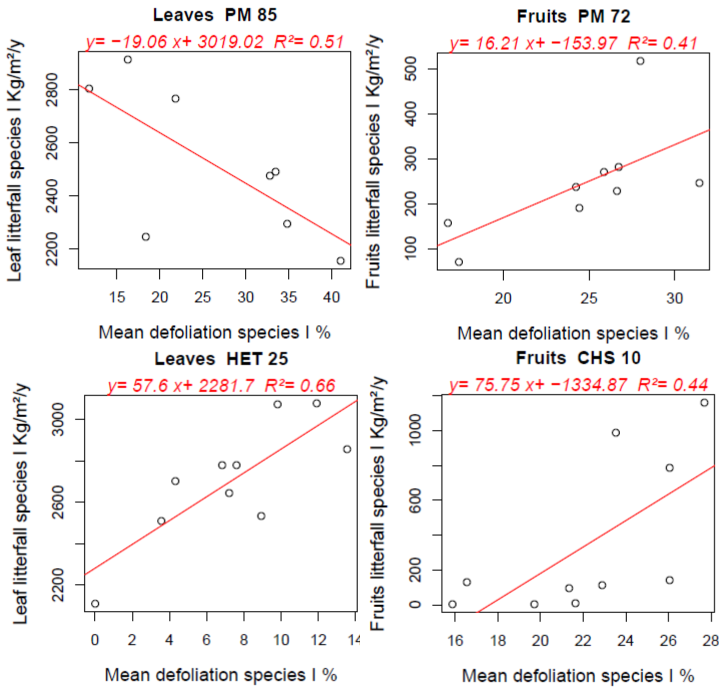

***Figure 8**:*
Representation of LF_{Leaves} versus %defoliations for PM 85 and HET 25. We can see here differences in defoliation range and trends.

Representation of LF_{Fruits} versus %defoliations for PM 72 and CHS 10. Regression expression is written in red. We can see here that trends are noised and do not reflect real trends.

Species / plot	Spearman r Leaves	Spearman r Fruits	Leaves a	Leaves b	Leaves R²	Fruits a	Fruits b	Fruits R²
All species	-0,04	**-0,15**						
PM	**-0,27**	0,17	-26,32	**3688,15**	0,05			
PS	**-0,23**	**-0,23**	-6,47	**1917,83**	0,01	-4,60	**508,81**	0,02
SP	**-0,53**	-0,19	**-27,80**	**2214,08**	0,20			
CHP 55	0,12	**-0,89**				-85,19	**2344,95**	0,47
CHP 70	**-0,64**	-0,37	**-59,50**	**3701,76**	0,39			
CHS 03	**-0,86**	-0,57	-40,24	**3302,73**	0,49			
CHS 10	0,30	**0,83**				**75,75**	-1334,87	0,44
CHS 51	-0,54	**0,79**				14,31	-404,89	0,15
DOU 69	-0,43	**0,94**				**23,54**	-79,05	0,75
DOU 71	0,38	**0,78**				31,93	24,65	0,21
EPC 08	0,10	**0,78**				**67,45**	-232,32	0,59
EPC 34	0,40	**0,74**				76,81	-561,24	0,36
EPC 39a	0,26	**-0,65**				-64,76	**1231,38**	0,17
HET 14	-0,76	**0,33**	-53,50	4570,71	0,71			
HET 21	-0,79	**-0,08**	-25,37	2587,03	0,66			
HET 25	0,78	**-0,01**	57,60	2281,70	0,66			
HET 26	-0,72	**0,24**	-29,83	2271,62	0,39			
MEL 05	-0,73	**-0,54**	-38,98	3094,89	0,46			
PM 72	0,58	**0,78**				16,21	**-153,97**	0,41
PM 85	-0,71	**0,67**	-19,06	3019,02	0,51			
PS 15	-0,73	**-0,74**	-81,24	2446,12	0,53	-16,80	**392,45**	0,36
PS 44	-0,85	**-0,01**	-44,44	2893,20	0,49			
PS 67a	-0,90	**-0,60**	-68,17	2742,60	0,78			
SP 07	-0,83	**-0,08**	-227,57	5317,24	0,50			
SP 25	-0,71	**0,20**	-1029,98	2443,75	0,34			
SP 26	-0,67	**0,22**	-39,16	1486,73	0,40			
PS 78	-0,03	**-0,89**				-55,66	**1204,76**	0,59

Table 7 (left): *Significant Spearman correlation results between litterfall (leaves and fruits) and defoliation percentage. Regressions are performed in case of significant Spearman correlations. Regression form is y=ax + b with y = litterfall masses and x = defoliation percentage. Significant values (α<0.05) are in bold.*

parameters	period	CH	CHP	CHS	DOU	EPC	HET	PM	PS	SP	Broadleaves	Coniferous
P (mm)	Annual n	**-0,19**	0,12	**-0,23**	-0,05	0,09	**-0,22**	0,17	-0,13	-0,09	**-0,18**	-0,05
Tmin (°C)	Annual n	**0,22**	**0,30**	**0,23**	-0,01	**0,29**	**0,31**	0,18	0,17	0,03	**0,26**	**0,30**
Tmax (°C)	Annual n	**0,19**	**0,23**	**0,20**	**0,35**	-0,09	-0,07	**0,31**	0,08	0,15	0,08	**0,21**
Tmean (°C)	Annual n	**0,32**	**0,41**	**0,35**	0,16	0,12	0,13	**0,51**	0,07	0,07	**0,25**	**0,34**
ETP (mm)	Annual n	**0,29**	**0,29**	**0,28**	0,15	0,12	**-0,20**	**0,39**	0,14	-0,02	**0,11**	**0,27**
P-ETP (mm)	Annual n	**-0,25**	0,01	**-0,29**	-0,11	0,05	**-0,15**	0,00	-0,13	-0,06	**-0,20**	**-0,14**
P_S (mm)	Summer n	**-0,21**	-0,12	**-0,20**	-0,08	0,12	-0,10	0,12	0,00	-0,09	**-0,15**	**-0,10**
T_s min (°C)	Summer n	-0,06	0,14	-0,08	-0,08	0,06	**0,25**	**0,34**	0,05	0,07	**0,09**	**0,18**
T_s max (°C)	Summer n	**0,19**	**0,23**	**0,20**	**0,35**	-0,09	-0,07	**0,31**	0,08	0,15	0,08	**0,21**
T_s mean (°C)	Summer n	**0,13**	0,11	**0,15**	**0,32**	-0,02	0,01	**0,48**	-0,07	0,06	0,08	**0,25**
ETP_s (mm)	Summer n	**0,23**	0,13	**0,21**	0,30	0,05	**-0,17**	**0,30**	0,11	-0,03	0,08	**0,21**
$P\text{-}ETP_s$ (mm)	Summer n	**-0,26**	-0,17	**-0,25**	-0,20	0,11	-0,02	0,01	-0,02	-0,05	**-0,16**	**-0,14**
P_1 (mm)	Annual n-1	-0,09	**0,24**	-0,12	0,14	0,02	**-0,24**	0,17	-0,06	-0,06	**-0,12**	-0,02
T_1min (°C)	Annual n-1	**0,30**	**0,47**	**0,28**	0,08	**0,20**	**0,27**	0,09	0,18	0,08	**0,29**	**0,30**
T_1max (°C)	Annual n-1	**0,17**	0,11	**0,19**	-0,02	**-0,28**	0,02	**0,34**	0,13	-0,08	**0,10**	**0,10**
T_1mean (°C)	Annual n-1	**0,33**	**0,41**	**0,34**	0,07	-0,01	0,09	**0,58**	0,11	-0,06	**0,24**	**0,29**
ETP_1 (mm)	Annual n-1	**0,29**	**0,31**	**0,27**	0,10	-0,04	**-0,19**	**0,41**	0,18	-0,11	**0,12**	**0,22**
$P\text{-}ETP_1$ (mm)	Annual n-1	**-0,16**	0,16	**-0,19**	0,12	0,07	**-0,16**	-0,01	-0,08	-0,02	**-0,14**	-0,08
P_2 (mm)	Annual n-2	**-0,15**	0,07	**-0,17**	-0,08	-0,14	**-0,30**	0,12	**-0,26**	**-0,18**	**-0,16**	**-0,11**
T_2min (°C)	Annual n-2	**0,19**	**0,29**	**0,17**	-0,08	0,13	**0,18**	0,20	0,16	0,04	**0,21**	**0,27**
T_2max (°C)	Annual n-2	**0,11**	-0,03	**0,13**	0,00	**-0,20**	**-0,15**	0,13	-0,05	-0,09	0,00	0,07
T_2mean (°C)	Annual n-2	**0,31**	**0,39**	**0,33**	0,06	-0,03	-0,01	**0,63**	0,05	-0,09	**0,20**	**0,28**
ETP_2 (mm)	Annual n-2	**0,28**	**0,30**	**0,28**	0,15	0,00	**-0,21**	**0,51**	0,16	-0,13	**0,11**	**0,22**
$P\text{-}ETP_2$ (mm)	Annual n-2	**-0,20**	0,02	**-0,23**	-0,11	-0,12	**-0,22**	-0,04	**-0,26**	-0,12	**-0,19**	**-0,17**
P_{s1} (mm)	Summer n-1	**-0,13**	0,07	**-0,16**	0,28	0,07	**-0,22**	0,15	**0,05**	-0,02	**-0,13**	**-0,05**
T_{s1}min (°C)	Summer n-1	**0,05**	0,29	**0,05**	0,01	0,05	**0,26**	0,37	**0,04**	0,10	**0,17**	**0,19**
T_{s1}max (°C)	Summer n-1	**0,17**	0,11	**0,19**	-0,02	-0,28	**0,02**	0,34	**0,13**	-0,08	**0,10**	**0,10**
T_{s1}mean (°C)	Summer n-1	**0,15**	0,03	**0,20**	0,07	-0,22	**0,04**	0,55	**0,04**	-0,17	**0,10**	**0,15**
ETP_{s1} (mm)	Summer n-1	**0,21**	0,03	**0,21**	0,06	-0,16	**-0,13**	0,23	**0,14**	-0,19	**0,08**	**0,10**
$P\text{-}ETP_{s1}$ (mm)	Summer n-1	**-0,17**	0,07	**-0,20**	0,29	0,15	**-0,13**	0,05	**0,00**	0,07	**-0,14**	**-0,06**
P_{s2} (mm)	Summer n-2	**-0,13**	-0,01	**-0,15**	0,05	0,10	**-0,19**	0,16	**-0,18**	-0,03	**-0,12**	**-0,06**
T_{s2}min (°C)	Summer n-2	**0,07**	0,32	**0,09**	0,09	0,06	**0,27**	0,33	**0,06**	0,05	**0,18**	**0,19**
T_{s2}max (°C)	Summer n-2	**0,11**	-0,03	**0,13**	0,00	-0,20	**-0,15**	0,13	**-0,05**	-0,09	**0,00**	**0,07**
T_{s2}mean (°C)	Summer n-2	**0,11**	-0,01	**0,17**	0,00	-0,14	**-0,07**	0,50	**-0,01**	-0,15	**0,04**	**0,16**
ETP_{s2} (mm)	Summer n-2	**0,21**	0,12	**0,21**	0,08	-0,04	**-0,21**	0,28	**0,13**	-0,18	**0,06**	**0,13**
$P\text{-}ETP_{s2}$ (mm)	Summer n-2	**-0,18**	-0,01	**-0,21**	-0,01	0,09	**-0,08**	0,06	**-0,11**	0,07	**-0,13**	**-0,07**

Table 8 (right): *This table displays Spearman correlation coefficient between leaf litterfall and meteorological data for each species. Significant values (α<0.05) are in bold.*
Tmin = minimum temperature, Tmax = maximum temperature…
s index is related to parameters calculated on summer period (from june 1st to September 31st). Parameters without s index are calculated on the whole year.
1 and 2 index are related to parameters calculated respectively for the previous n-1 year and n-2 year. Otherwise parameters are calculated for the current year.

			Residuals normality Shapiro-Wilk test		Homoscedasticity Breusch-Pagan test		Auto-correlation Durbin-Watson test	
Species	**Best model**	**R²**	**W**	**p**	**BP/df**	**p**	**DW**	**p**
Oak	**-0.98** (P-ETP_s) + **158.1** (T_1mean) + 417.9	0.1	0.96	7.10^{-8}	1.6/2	0.5	0.89	2.10^{-16}
Common Oak	**0.97** (P_1) + **166.2** (T_2mean) + **2.6** (ETP_1) **-2499**	0.28	0.98	0.2	3.9/3	0.3	0.74	3.10^{-11}
Sessile Oak	**2.8** (ETP) + **64.2** (T_1min) + **1174.8**	0.13	0.95	3.10^{-7}	2.8/2	0.2	0.97	1.10^{-15}
Douglas fir	**85.9** ($T_s$max) – 935.4	0.16	0.98	0.8	0.92/1	0.3	2.2	0.74
Spruce	**90.9** (Tmin) – **77.4** (T_{s1}max) – **99.9** (T_{s2}max) + **9516.6**	0.23	0.99	0.7	1.5/3	0.7	1.13	3.10^{-6}
Beech	**97.2** (T_{s1}min) – **1.1** (P_2) – **1.6** (ETP_2) + **4602.3**	0.16	0.87	4.10^{-12}	8.6/3	0.03	1.1	6.10^{-11}
Maritime Pine (PM)	**376.5** (T_{s1}mean) – **14.4** (ETP_{s1}) – **10.1** (ETP_{s2}) + **11** (ETP_2) **-2390.2**	0.49	0.97	0.03	1.9/4	0.7	1.9	0.3
PM (- PM20)	**295.6** (Ts1mean) – **9.1** (Ps1) + **2.9** (Ps2) + **5.3** (ETP2) + **11.5** (P-ETPs1) - **3106.5**	0.53	0.97	0.06	2.4/5	0.8	2.1	0.6
Scot Pine	**2** (P_2) **-2.2** (P-ETP_2) + 1092.7	0.05	0.93	2.10^{-8}	0.86/2	0.65	0.95	5.10^{-16}
Silver fir	**-2.4** (ETP_{s1}) **– 0.5** (P_2) + **3414.8**	0.05	0.97	0.02	1.25/2	0.5	1	8.10^{-9}

Table 9: *Best fitting climatic models for each species. Significant coefficients (α < 0.05) are in bold.*
Tmin = minimum temperature, Tmax = maximum temperature…
s index is related to parameters calculated on summer period (from june 1st to September 31st). Parameters without s index are calculated on the whole year.
1 and 2 index are related to parameters calculated respectively for the previous n-1 year and n-2 year. Otherwise parameters are calculated for the current year.

Discussion

Potentialities and limits with RENECOFOR data

In all tests, sampling is a major parameter influencing correlations and the interpretation of the results must include some limits. A first limit is due to the 5 m² sampling area that can lead to a biased representation of litterfall over the 0.5ha central part of the plot. This is particularly important for plots where stands became more heterogeneous with windthrow events and must be taken into account in interpreting the effects of disturbances.
A second limit is due to the distribution of the tree species in French forests. This leads for each dominant tree species to a variable number of plots within the RENECOFOR network and to different ranges in explanatory factors. Moreover results at the 'species scale' must be carefully interpreted as they integrate both effects of various environmental constraints and of different specific responses to these constraints. For example Norway spruce plots are mostly distributed in mountains whereas maritime pine plots are mostly distributed in flatlands.
A third limit rises from the considered time period. This study is based on an exceptionally long dataset collected over 13 years. But this remains quite short compared to forest ecosystem and global change time scales.

All these limits are mostly kind to impair correlation detection rather than lead to detect wrong correlations. Thus the following discussion will mainly focus on the detected relationships and not conclude from non detections.

Litterfall rates and trends

In European temperate forests (Liu et al. 2004), leaf and total litterfall values available for broadleaves (3.4 and 4.4 $t.ha^{-1}.y^{-1}$) and coniferous (2.9 and 3.5 $kg.ha^{-1}.y^{-1}$) are higher than results obtained on the RENECOFOR network. Differences are respectively about 18.3% for coniferous and 30% for broadleaves. Most part of those differences can be explained by spatial dispersion of forests (Latitude and altitude playing a great part on it, (Vogt et al. 1986), differences in stand management and time period analysis. Indeed, other studies found similar results as ours, as for example in New Zealand (Enright 1999), where annual litterfall rates are 2200 $Kg.ha^{-1}$ for coniferous and 2400 $Kg.ha^{-1}$ for broadleaves. If we look at species scale, results obtained for oak, beech, spruce, pines and fir forests, leaf and total litterfall are similar to those in literature (Table 10). Only results for Douglas-fir plots are lower in range with mean annual leaf litterfall.
Wood compartment is the second most abundant constituent of litterfall and has been shown as dependent of the stand age and probably stand density (Lebret, Nys, et Forgeard 2001).
There were difficulties to precisely estimate fruit litterfall because of balance precision (± 1g). Thus, some years, fruit mass is null even if one fruit is measured and some other years, fruit mass is at least of 2$kg.ha^{-1}$ (1g/5m² reported to 1ha) for the same fruits quantity.

There is disagreement among studies about litterfall trends over time. On one hand, Gloaguen et Touffet (1982) or Bray et Gorham (1964) explain that no specifics trends can be outlined. On the other hand, Hughes et Fahey (1994) or Ranger et al. (1995) show slight leaf litterfall increase followed by a stabilization over stand ageing. But we cannot affirm that no specific trends exist because of all parameters influencing litterfall and lifting changes. However, looking at significant trends, positives and negatives, interesting results can be compared to literature. On beech plots for example, we can see positive correlations when no particular events outcome. This result is the opposite of those find by Lebret et al. (2001), a two year study on an Atlantic beech stand. It clearly demonstrates here the impact of the time period considered and justifies the choice of longer study to detect trends. But the 13 year time period used for this work remains too short to erase strong inter-annual variations. Indeed it noised statistical tests despite a net graphical view of those trends. Annual litterfall data are sufficient to detect trends on plots without disturbances but not on all plots and with the hypothesis that the time period analysis is long enough to prevent cyclic phenomena. Moreover, strong events can lead to stand changes, which stands can react differently after disturbance. Indeed some interesting relationships appear by looking at plot scale. For example, plots HET 21, PS 15, PS 76 and PS 88 show negative leaf litterfall trends while litterfall trends of the rest compartment are positive. Those plots were severely stroke by storm of December 1999 (Table 5), and secondary tree species took place of dominant tree species explaining the increase of litterfall of the rest compartment. To prevent these results, we could have performed two analyses (before and after disturbance) for plots encountering special events but in this case, analysis would have been based on a little number of observations. In addition, fixed seasonal or monthly collections could have permit finest analyses by allowing the observation of quick stand responses.

Wood and fruits compartments show no specific trends because of a strong inter-annual variation in amount of litterfall. In addition both positive and negative significant trends appear. Inter-annual variations are the strongest for fruits litterfall and graphically seem to follow meteorological or storm events (Figure 9) for several plots. A comparison of fertile years could lead us to more significant results and prevent measurement precision problems.

As a perspective, this exploratory study makes evidence for a need for further investigation at the plot scale, because of the potential importance of stand management and history on litterfall changes.

Litterfall and stand basal area

In literature, stand basal area vs. litterfall shows curvilinear relations (Bray et Gorham 1964; Hennessey et al. 1992). Here most significant relations are linear excepted for maritime pine species that is logarithmic. This result can be explain because of the range of basal area data available for each species, maritime pine being the only one with values more than 60 $m^2.ha^{-1}$. Moreover, relation to basal area can depend on species. We obtain best relations for heliophilic species (oaks and pines) than for sciaphilic species (beech, spruce or firs).

The use of basal area growth could have been a better way to study litterfall dynamics but measurement being spaced of a five years period (about 4 measures during the campaign), calculation of growth rate for each plot would not have been precise.

For all species, disturbances have a negative impact on litterfall despite the fact we did not take disturbances more than 68%. Graphically, disturbances less than 10~15% seems to have no influence on the mean annual litterfall. We did not use statistical test on this hypothesis because a selection of disturbances could have induced sampling biases.

Aber et al. (1979) showed that for any harvesting regime, nutrient return to the soil was reduced after disturbance for a period of 15-30 year. According to Roig et al. (2005), thinning intensity in Maritime pine stands is negatively correlated with litterfall but this effect disappears 5 years after disturbance. These results reinforce our choice to consider the year n+1 or n+2 after disturbance to calculate litterfall mass differences. Among the 102 plots, disturbances rarely happened at the same date. Thus, it becomes hard to observe stress following thinning. Disturbances less than 30% of the total basal area may have no bad effects on remaining trees (Inagaki et al. 2003). But in order to investigate possible stress effects (climatic, biologic…) on remaining trees after thinning more than 30%, a plot by plot analysis would be more appropriate. However, those results must be weighted in relation to initial stand density and basal area that are closely correlated to litterfall and thus greatly depend to plots (Hennessey et al. 1992; Guo et Sims 1999).

Litterfall and Defoliation

Results obtained at plot scale show better correlations than at 'species scale' (group of plots with the same dominant tree species). In contrast to J. Bille-Hansen et K. Hansen (2001), all significant relations are negative excepted for HET 25 plot. Relationships between defoliation and litterfall are complex and greatly depend of the observation date. If defoliation is caused by a stress as parasitic processes for example, it can boost productivity (March et Watson 2007) and lead to positive correlation with litterfall. On the other hand, if defoliation is intrinsic, then it should be negatively correlated to litterfall.

In addition, differences in relationships can be explained by the range of mean defoliation (for example from 0 to 14% for HET 25 and from 10 to 40 for PM 85; Figure 8), while in other cases defoliation percentage is high.

Defoliation closely depends on tree age (Anon 1997) and other parameters as soil composition (Thomsen 1996). Moreover biological attacks and hard meteorological conditions have an impact on defoliation. It is the case of several plots (SP 26 and HET 88 for example) where crown drying appears after 2003 dryness. These parameters can explain here strong leaf litterfall variations between plots and thus the absence of results at species scale.

Defoliation percentage has no effect on fruits litterfall. But, as for leaves, relations can be masked by other.

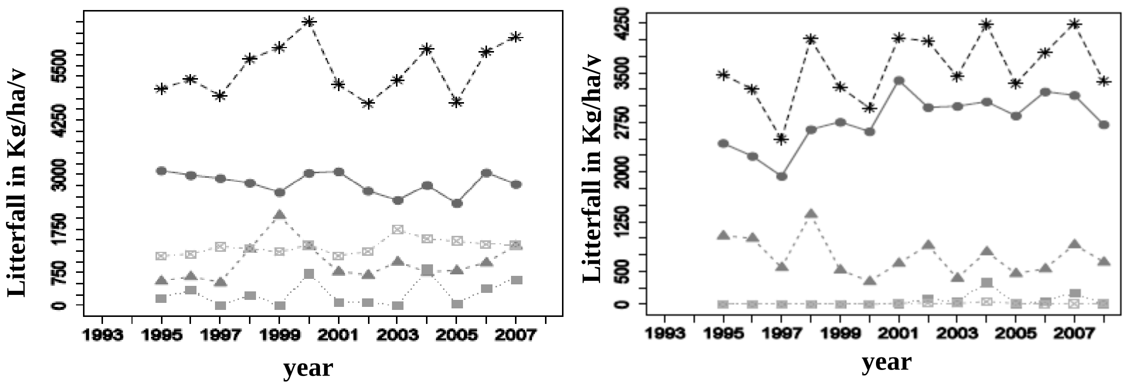

Figure 9: *Litterfall in Kg.ha^{-1}.y^{-1} vs. timeLitterfall. Trends for leaf compartment (circle); branches compartment (triangle); fruits compartment (fill square); rest compartment (empty square)and total litterfall (stars). Two pikes appear for fruits compartment following storm of 1999 and dryness of 2003 on CHS01 (sessile oak) plot, one pike after 2003 on HET 30 (beech).*

Species	Publication	Information (period analysis /development stage)	Leaf litterfall (kg.ha^{-1}.y^{-1})	Woody litter-fall (kg.ha^{-1})	Fruits litter-fall (kg.ha^{-1})	Total litter-fall (kg.ha^{-1})
Oak	(Rapp 1969)	Two years	1709 to 2674	-	-	3055 to 7943
	(Christensen 1978)	Three years	-	577.5 to 903.5	-	-
	(Hernandez et al. 1992)	Three years	1850	280	100	2230
	(Rapp et al. 1999)	Two years	2088 to 2830	278 to 649	106 to 440	2549 to 3998
	(Hansen et al. 2009)	Six years	2566	595	53	3344
Beech	(Parmentier et Re-macle 1981)	Three years	2905 to 2933	137 to 434	96 to 2125	3526 to 5664
	(Gloaguen et Touffet 1974; 1982)	Three&ten years/4stages	3000 and 2700	-	0.3 to 106	2500 to 5600
	(Lebret et al. 2001)	Two year/ 4 stages (10y to 147y)	1200 to 3000	106 to 764	4.8 to 103.6	2000 to 4700
	(Hansen et al. 2009)	Six years	2665	262	50	3186
Spruce	(Aussenac 1969)	Two years	1608	57	24	1879
	(Parmentier et Re-macle 1981)	One year	2300	776	449	3581
	(Saarsalmi et al. 2007)	Four years	2700 to 4650	-	-	4400 to 6770
	(Hansen et al. 2009)	Six years	2634 to 3117	149 to 165	380 to 477	3328 to 3706
Scot Pine	(Aussenac 1969)	Two years	4127	1005	152	5626
	(Finér 1996)	Nine years	1477	-	-	1995
	(Starr et al. 2005)	Three years/ stand 35 to 200y	220 to 1570	-	-	320 to 2300
Maritime Pine	(Hernandez et al. 1992)	Three years	1670	26	18	1728
	(Roig et al. 2005)	Ten years	-	-	-	3284
fir	(Aussenac 1969)	Two years	1503	1016	106	3186
Douglas fir	(Gessel et Turner 1976)	Eight years/Four stages (30y to 160y)	926 to 2497	42 to 858	16 to 71	1276 to 3014
	(Aussenac 1979)	One year	3284 to 3500	-	-	3434 to 3705
	(Ranger et al. 2003)	Seven years	2374 to 3321	317 to 628	10 to 78	3350 to 3950
	(Hansen et al. 2009)	Six years	2696	184	380	3294
Broadleaves	(Enright 1999)	Five years	2390 to 2460	-	-	3310 to 3560
	(Liu et al. 2004)	-	3440	-	-	4420
Coniferous	(Enright 1999)	Five years	1650 to 2230	-	-	3460 to 5290
	(Liu et al. 2004)	-	2860	-	-	3470

Table 10: *This table displays litterfall mass results available in literature for some temperate tree species. Values are mean values. Several values can be available in one study; in this case mass range is displayed.*

Litterfall and Meteorology

According to Liu et al. (2004), temperate forests closely depends on temperature, and responses highly differ between coniferous and broadleaves species at a continental scale. In European temperate forests, coniferous responses to climate are well correlated to evapotranspiration, less with precipitations and temperature (B. Berg et Meentemeyer 2001). Indeed, evapotranspiration explains in our work a great part of litterfall variations for maritime pine and oaks (Table 9). But this result differs for Scots pine litterfall, which is related to temperature of previous summer in Kouki et Tatu Hokkanen (1992) study.

In several studies about conifers, litterfall production is influenced by meteorological data of the preceding years (Kouki et Tatu Hokkanen 1992; Starr et al. 2005). Moreover, Bille-Hansen et Hansen (2001) showed that the temperature and precipitation condi-

tions during the formation of needles had an influence on the year when they fell.
As for Saarsalmi et al. (2007) our results for Norway spruce show effective relationship with summer temperatures of previous years.

Conclusions and perspectives

The main results of this study on the litterfall data from the RENECOFOR network can be summarized as following.

- No general trends in litterfall production can be found in this 13-year analysis. Both positive and negative trends can occur for any litterfall compartment. But their interpretation needs further investigation at the plot scale, especially for stand management and history.
- The correlations between annual leaf litterfall and defoliation are significant only for some plots. But they can be whether negative or positive, so that complex processes could have impaired the possibility to detect relationships.
- On the other hand strong relationships are found between leaf litterfall and stand basal area for heliophilic tree species. Moreover stand disturbances (logging and windthrows) are negatively related to interannual litterfall changes, with significant linear regressions at the scale of some tree species.
- In addition significant regressions are calculated with meteorological parameters considered up to two years before leaf litterfall. R^2 can reach 0.53 for maritime pine and only Scots pine and Silver fir show no significant regression.

This exploratory approach gives a first insight into litterfall changes and relationships over time.
Further analysis should focus on the plot scale for proper interpretation of these relationships and especially for distinction between time and spatial effects over French forests. And then meta-analysis tools could be used to summarize the results obtained at the plot scale and to include the effect of plot variables (geographical localisation, tree species…).
Another challenge would consist in modelling annual litterfall changes with all explanatory factors together in order to take their interactions into account and to compare their respective weights. And new statistical tools like PLS could greatly help for this purpose.
Finally intra-annual changes could be now explored with monthly litterfall data collected since 2008 on 14 plots.

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Annexes

Annex 1: French Permanent Plot Network for the Monitoring of Forest Ecosystems (1992 - 2022) - RENECOFOR

The RENECOFOR network was created by the French National Forest Board (Office National des Forêts, ONF) in 1992 in order to complete the existing French forest health monitoring activities. It is part of a European network of permanent plots for the monitoring of forest ecosystems in compliance with the S1 resolution of the ministerial conference for the protection of forests in Europe, held in 1990 in Strasbourg. It is one of 3 coherent and collaborating French monitoring networks and the one with the highest number of observations.

The main objective of the RENECOFOR network is to detect possible long-term changes in the functioning of a great variety of French forest ecosystems, selected as regionally representative stands, and to determine the reasons for the changes. Between 1992 and 2007, the network's objectives were directly related to the resolution n°1 of the first ministerial conference for the protection of forests in Europe. Since 2008, and as a result of a two audits (by a special commission and by the scientific committee of ONF in 2006 and 2007), the objectives are until 2013:
• monitor with precision, continuously and on the long term the evolution of forest ecosystems, which are principally of interest for wood production, under the effect of external factors, especially climate change (observatory function),
• contribute to the understanding and to the comprehension of cause-effect relationships between external factors and the observed evolutions, and use this knowledge for predictions and the development of scenarios, based on models,
• to be in line with the continuum of forest ecosystem observation systems, helping thus necessary extrapolations and generalizations, linked with other monitoring systems or relevant experimentations and by developing partnerships,
• help forest managers in their sustainable management choices within a changing and uncertain environment.

The phenomena to be measured and observed are:
• the reaction of forest ecosystems to climate change,
• the nutrient cycle of forests, especially linked to atmospheric deposition,
• the evolution of certain aspects of biodiversity.
RENECOFOR was co-funded by the European Union between 1991 and 2006 (40-50%). Currently the network is funded by ONF, the ministries of agriculture and environment and the environmental agency (ADEME). It consists of 102 permanent plots (Figure A1) which are to be monitored for at least 30 years. Each plot has a surface of about 2 hectares, the central 0.5 hectare of which is fenced. The network is co-ordinated by a team based in Fontainebleau, which is part of ONF's research department. At a more regional level specialised technicians of ONF's 10 territorial management offices carry out and supervise the work. Regular local work is carried out by some 200 local foresters. For the work demanding a higher degree of knowledge, ONF collaborates with several scientific partners, like INRA, CNRS, CEMAGREF, universities, private engineer companies, associations and partners in other European countries. Scientific projects are carried out on the permanent plots in addition to the monitoring activities because the scientists can take advantage of an already quite complete database.
RENECOFOR covers the following fields and operations, the frequency and intensity of which vary depending on the monitoring intensity defined for each plot : forest health survey (entomological and pathological observations, defoliation and abnormal

coloration), full stand inventories (girth and tree species) and specific tree mensuration, dendrochronology, foliar analysis (tree nutrition), phenological observations, estimation of annual litterfall, soil chemical evolution, floristic inventories, inventory of soil macro-fauna and of mushroom diversity, automatic meteorological measurements, bulk and throughfall deposition measurements and soil solution analysis, ozone and ammonia air concentration measurements and ozone symptom observations.

The data of all these measurements, observations and analysis are stored in a specially developed central database, which contains at the end of 2007 approximately 65 million raw data. The results are published regularly in the "RENECOFOR" series and in scientific and popular science journals. These publications give the state of knowledge at the start of the network and show ever since the evolutions of many parameters as a result of the analysis of ever longer time series. Multi-disciplinary studies are more frequent nowadays in order to understand the interactions between several variables and their influence on the forest ecosystems.

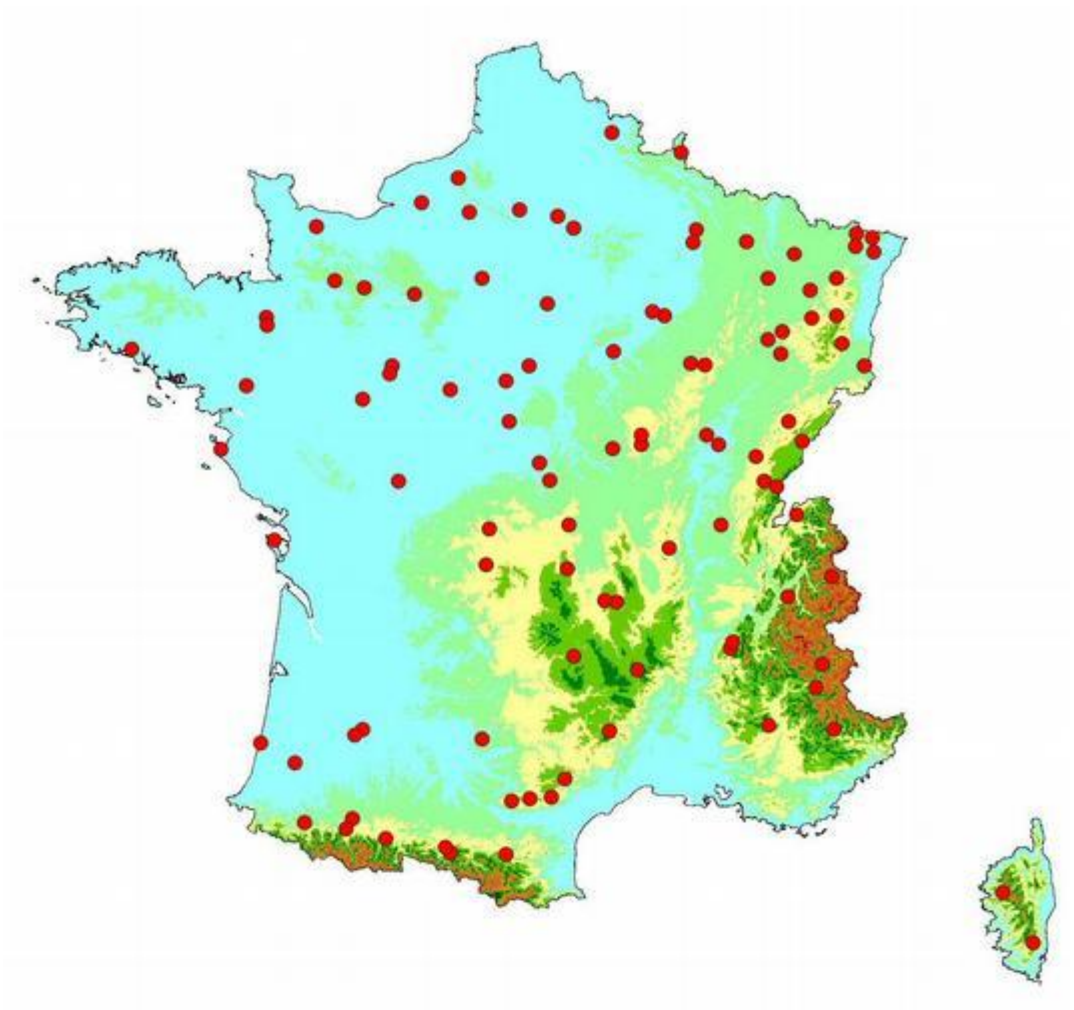


Figure A1: *Location of the 102 RENECOFOR plots throughout France.*

Annex 2: Template example of the plot CHP 10.

CHP 10

ANALYSE DES LITIERES

Campagne de mesures de 1995 à 2007

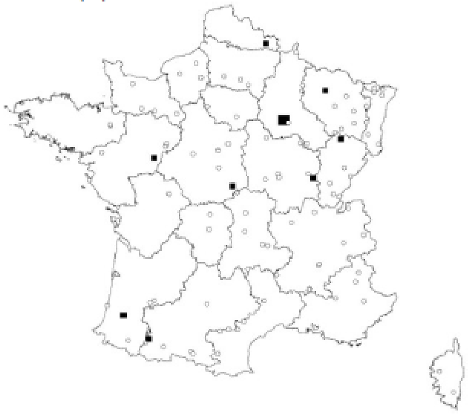
RENECOFOR

Informations générales

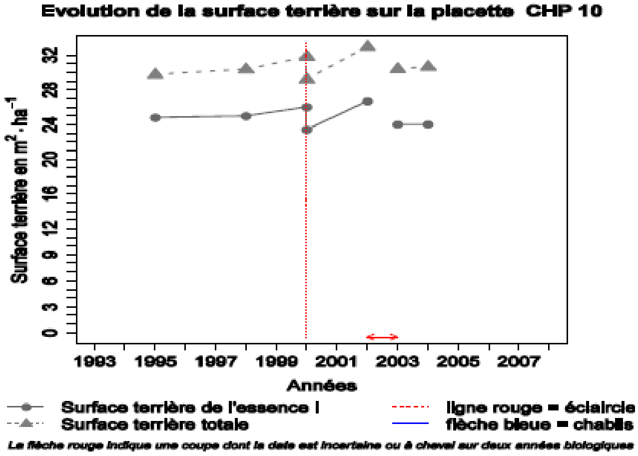
Forêt Domaniale de Larivour

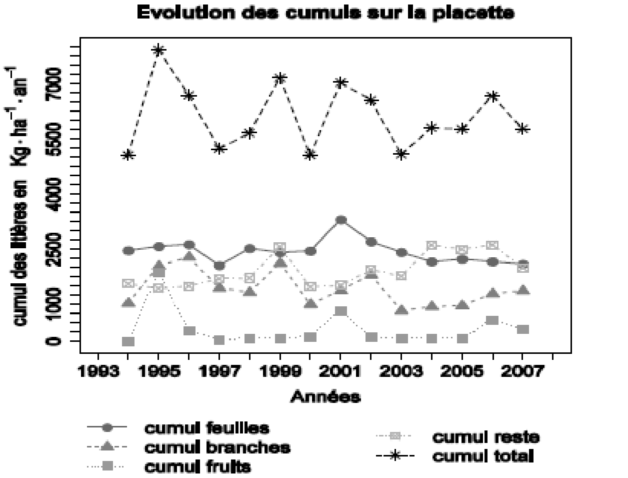
Commune de Rouilly-Sacey (Aube)

Latitude	: 48°20'51" N
Longitude	: 4°18'17" E
Altitude	: 115
Pente (%)	: 0
Exposition	: plat
Topographie	: terrain plat
Type de sol	: Type 3
Structure du peuplement	: tallis sous futaie vieilli
Essence principale	: *Quercus robur*
Essence secondaire	: *Carpinus betulus*
Age à 1,30m en1994	: 133
Ho en 1995 (m)	: 22,9



Evolution au cours du temps des chutes de litières





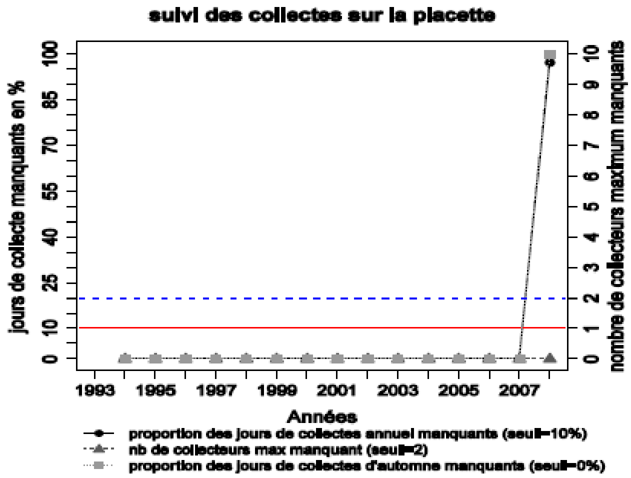
Analyse statistique

	feuilles	branches	fruits	reste	total
n	14	14	14	14	14
min	2057	832	2	1429	5055
moy	2444	1418	323	1920	6106
max	3310	2291	1876	2620	7928
CV %	14	36	168	26	16
rs	-0,45	-0,47°	0,2	0,72**	0,01

*seuil α: °0.1, *0.05, **0.01, ***0.001; donnés en Kg.m-2.an-1*

Donnés à l'échelle de l'essence

	feuilles	branches	fruits	reste	total
min	693	187	0	27	2047
moy	2185	940	245	1657	5026
max	3709	2291	1990	3620	7928
CV %	27	42	157	50	22



Perturbations

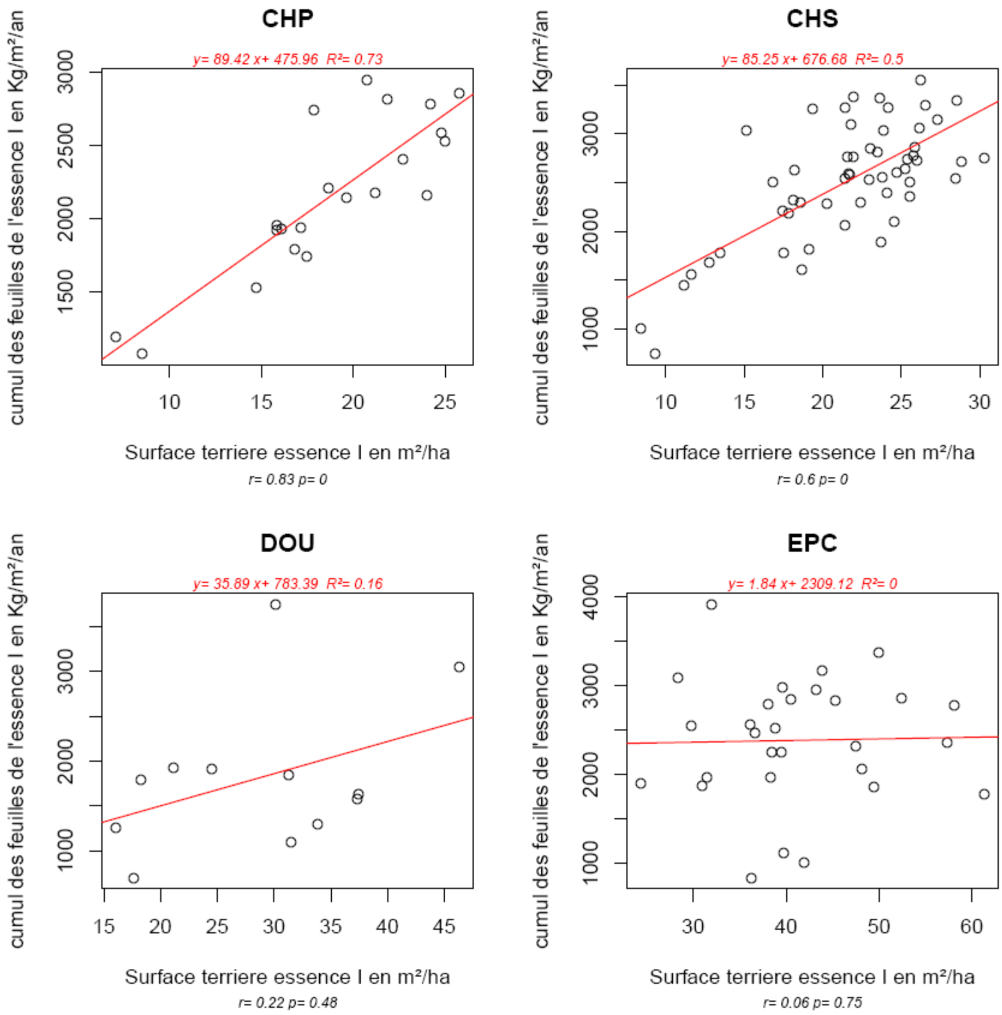
	Année	Amplitude (m².ha⁻¹)
coupes	21/11/2000	3
	18/03/2003	3
chablis		

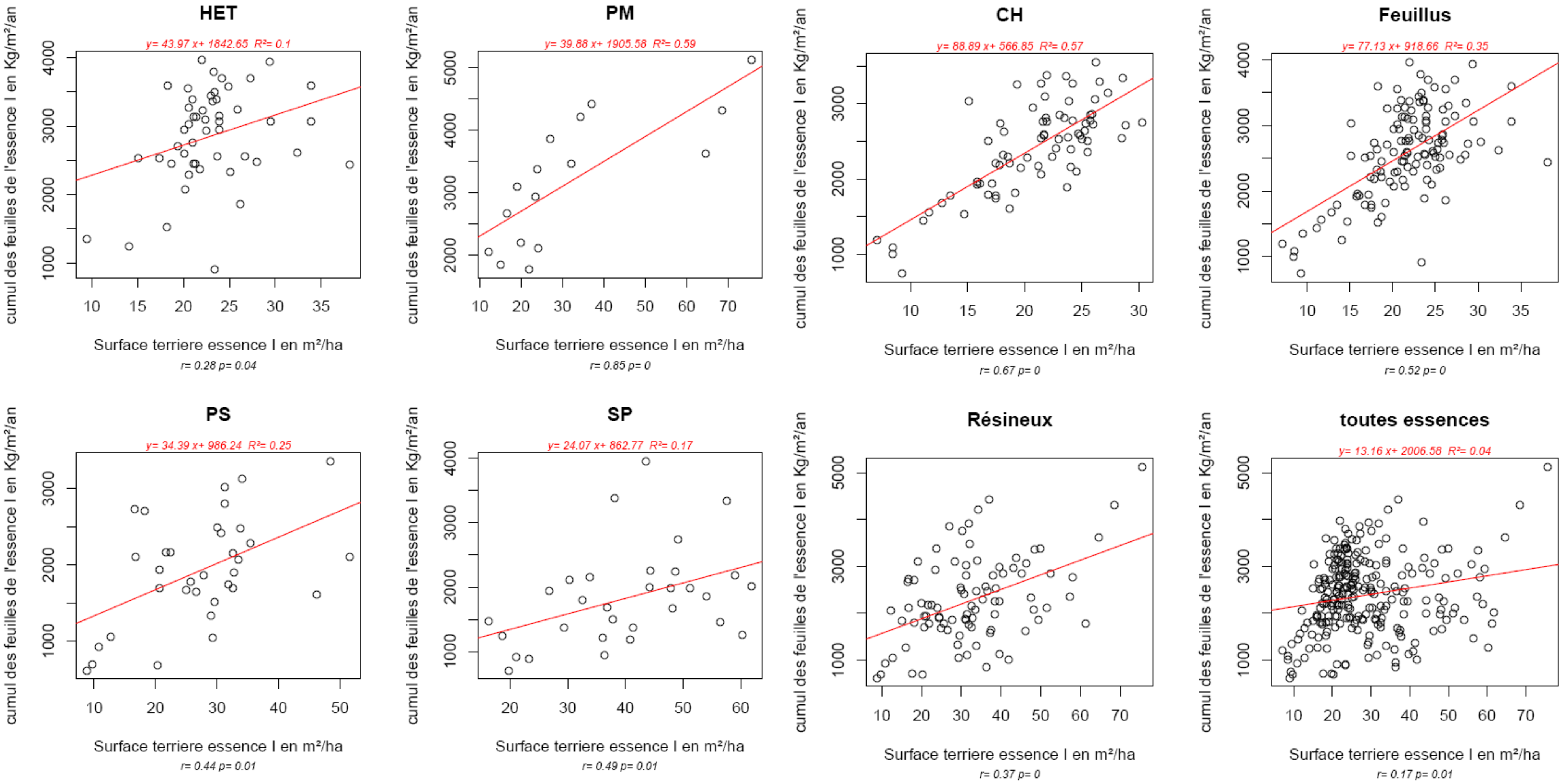
Commentaires

Annex 3: a) Details of regressions analysis of the relationships between basal tree area (G) and leaves litterfall (LF). Expression: LF=aG+b

a-p and b-p are p-values corresponding to the F-test for nullity. ShapiW and Shapi-p are respectively the ratio of two estimated variances of the population and the corresponding p-value applied to residual (Shapiro-Wilk test). White-p is the p-value corresponding to the White test for homoscedasticity applied to residuals. p-values under 0.05 are in bold. Plots are represented behind tables with spearman coefficient *r*, the corresponding p-value *p* and the regression expression *LF=a(G)+b R²* (in red).

Species	a	b	R^2	a-p	b-p	ShapiW	Shapi-p	White-p
CHP	86,69	506,78	0,70	**0,05**	**0,00**	0,91	**0,04**	0,49
CHS	83,53	744,07	0,46	**0,01**	**0,00**	0,98	0,34	0,39
DOU	36,65	871,52	0,16	0,23	0,12	0,93	0,25	0,75
EPC	1,84	2309,12	0,00	**0,00**	0,90	0,97	0,64	0,44
HET	43,35	1865,87	0,10	**0,00**	**0,02**	0,96	0,11	0,87
PM	39,96	1900,75	0,59	**0,00**	**0,00**	0,97	0,65	0,81
PS	34,39	986,24	0,25	**0,00**	**0,00**	0,97	0,40	0,96
SP	23,80	872,09	0,20	**0,02**	**0,01**	0,92	**0,01**	0,37
CH	87,97	601,71	0,54	**0,00**	**0,00**	0,97	**0,04**	0,94
Broadleaves	76,98	931,71	0,34	**0,00**	**0,00**	0,99	0,17	0,17
Coniferous	29,75	1343,61	0,19	**0,00**	**0,00**	0,99	0,48	0,29
All species	12,42	2037,01	0,04	**0,00**	**0,00**	0,99	0,14	0,06




HET
y= 43.97 x+ 1842.65 R²= 0.1
r= 0.28 p= 0.04
PM
y= 39.88 x+ 1905.58 R²= 0.59
r= 0.85 p= 0
CH
y= 88.89 x+ 566.85 R²= 0.57
r= 0.67 p= 0
Feuillus
y= 77.13 x+ 918.66 R²= 0.35
r= 0.52 p= 0
PS
y= 34.39 x+ 986.24 R²= 0.25
r= 0.44 p= 0.01
SP
y= 24.07 x+ 862.77 R²= 0.17
r= 0.49 p= 0.01
Résineux
r= 0.37 p= 0
toutes essences
y= 13.16 x+ 2006.58 R²= 0.04
r= 0.17 p= 0.01
cumul des feuilles de l'essence I en Kg/m²/an
Surface terriere essence I en m²/ha

b) Fitting models applied to the PM species with PM20 data. In all case Durbin-Watson test shows no autocorrelation.

x=Leaves litterfall y=G Signif. codes: 0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

➔ **Single linear regression**

lm(formula = **y ~ x**)
Coefficients:

	Estimate	Std. Error	t value	Pr(>|t|)
(Intercept)	**1900.746**	281.321	6.757	**2.49e-06 *****
graph$ST1	**39.965**	7.901	5.058	**8.19e-05 *****

Residual standard error: 612.6 on 18 degrees of freedom
Multiple R-squared: **0.587**, Adjusted R-squared: 0.5641
F-statistic: 25.59 on 1 and 18 DF, p-value: 8.185e-05

Model validation:

Shapiro-Wilk normality test
data: reg$residuals
W = 0.965, p-value = **0.6483**

studentized Breusch-Pagan test
data: reg
BP = 0.06, df = 1, p-value = **0.8065**

➔ **Second degree polynomial fitting**

lm(formula **= y ~ x + I(x^2)**)
Coefficients:

	Estimate	Std. Error	t value	Pr(>|t|)
(Intercept)	**559.0473**	749.0479	0.746	**0.4657**
x	**119.9668**	42.4742	2.824	**0.0117 ***
I(x^2)	**-0.9042**	0.4727	-1.913	**0.0728** .

Residual standard error: 571.9 on 17 degrees of freedom
Multiple R-squared: **0.6602**, Adjusted R-squared: 0.6202
F-statistic: 16.51 on 2 and 17 DF, p-value: 0.0001037

Model validation:

Shapiro-Wilk normality test
data: c$residuals
W = 0.9378, p-value = **0.2183**

studentized Breusch-Pagan test
data: c
BP = 1.4801, df = 2, p-value = **0.4771**

➔ **After log transformation**

lm(formula = y ~ I(log(x)))
Coefficients:

	Estimate	Std. Error	t value	Pr(>|t|)
(Intercept)	**-1968.9**	991.0	-1.987	**0.066884** .
I(log(x))	**1552.1**	294.6	5.269	**0.000119 *****

Residual standard error: 617.4 on 14 degrees of freedom
Multiple R-squared: **0.6647**, Adjusted R-squared: 0.6408
F-statistic: 27.76 on 1 and 14 DF, p-value: 0.0001187

Model validation:

Shapiro-Wilk normality test
data: reg$residual
W = 0.9336, p-value = **0.2774**

studentized Breusch-Pagan test
data: reg
BP = 0.4113, df = 1, p-value = **0.5213**

c) Fitting models applied to the PM species without PM20 data. In all case Durbin-Watson test shows no autocorrelation.

➔ **Single linear regression**

lm(formula = y ~ x)
Coefficients:

	Estimate	Std. Error	t value	Pr(>|t|)
(Intercept)	**591.21**	516.38	1.145	**0.276547**
x	**98.92**	20.97	4.716	**0.000633 *****

Residual standard error: 542.8 on 11 degrees of freedom
Multiple R-squared: **0.6691**, Adjusted R-squared: 0.639

Model validation:

Shapiro-Wilk normality test
data: reg$residuals
W = 0.917, p-value = **0.2313**

studentized Breusch-Pagan test
data: reg
BP = 0.1733, df = 1, p-value = **0.6772**

F-statistic: 22.24 on 1 and 11 DF, p-value: 0.0006334

➔ Second degree polynomial fitting

lm(formula = y ~ x + I(x^2))

Coefficients:

	Estimate	Std. Error	t value	Pr(>|t|)
(Intercept)	**1862.351**	1691.095	1.101	**0.297**
x	**-13.046**	143.179	-0.091	**0.929**
I(x^2)	**2.253**	2.849	0.791	**0.447**

Residual standard error: 552.3 on 10 degrees of freedom
Multiple R-squared: **0.6886**,   Adjusted R-squared: 0.6263
F-statistic: 11.06 on 2 and 10 DF, p-value: 0.002930

Model validation:

Shapiro-Wilk normality test
data: reg$residuals
W = 0.954, p-value = **0.6679**

studentized Breusch-Pagan test
data: reg
BP = 5.2469, df = 2, p-value = **0.07255**

➔ Second degree polynomial fitting

lm(formula = y ~ I(log(x)))

Coefficients:

	Estimate	Std. Error	t value	Pr(>|t|)
(Intercept)	**-3828.0**	1627.1	-2.353	**0.03830 ***
I(log(x))	**2169.1**	520.3	4.169	**0.00157 ****

Residual standard error: 587.4 on 11 degrees of freedom
Multiple R-squared: **0.6124**,   Adjusted R-squared: 0.5772
F-statistic: 17.38 on 1 and 11 DF, p-value: 0.001566

Model validation:

Shapiro-Wilk normality test
data: reg$residuals
W = 0.847, p-value = **0.02622**

studentized Breusch-Pagan test
data: reg
BP = 0.0018, df = 1, p-value = **0.9657**

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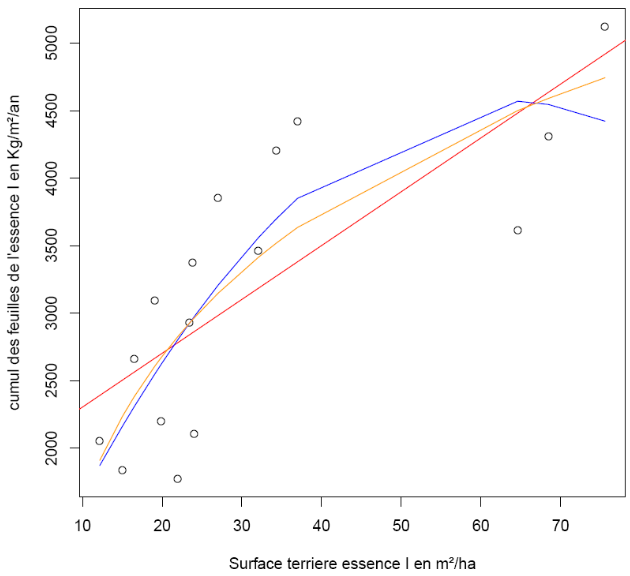
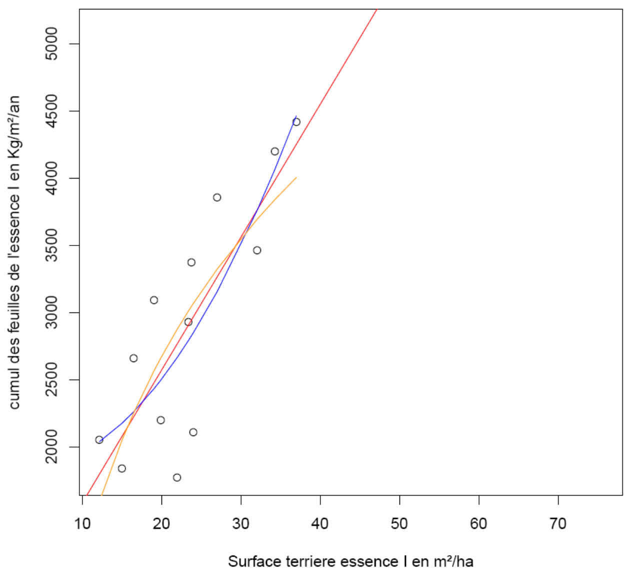


Plot with PM20



Plot without PM20

Linear fitting = red curve
Second degree polynomial fitting = blue curve
Logarithmic fitting = orange curve

<u>Annex 4:</u> Correlations between total litterfall and basal area disturbance. α : '°'<0.1; '*'<0.05; '**'<0.01; '***'<0.001
N represents the number of years used for the analysis.

Species	Spearman correlation coefficient	N
All species	-0,34***	99
CHP	-0,31	13
CHS	-0,44	15
DOU	-0,25	7
EPC	0,10	10
HET	-0,19	18
PM	-0,32	9
PS	-0,26	13
SP	-0,55*	13
CH	-0,34°	28
Broadleaves	-0,3*	46
Coniferous	-0,32	39