Does moder development along a pure beech (*Fagus sylvatica* L.) chronosequence result from changes in litter production or in decomposition rates?

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Abstract

The development of temperate deciduous and conifers forests stands usually results in accumulation of forest floor organic matter and a shift from mull to moder humus forms. It has been suggested that an increase in nutrient uptake by trees during their rapid growth phase leads to topsoil acidification, decrease in earthworm density and thereby a decrease in litter turnover. The focus question of the paper is whether the mull-moder shift occurring along forest ageing is due to higher leaf litter production and/or to lower decay rates of litter. The objectives of this research were to determine (1) changes in macro-morphological properties of humus forms, leaf litter production, litter decay rates, soil nutrients content and pH along a 130-year pure beech (*Fagus sylvatica* L.) chronosequence in Normandy (Northwest France), (2) if humus form varied from mull to moder with increasing stand age, and (3) if a shift from mull to moder resulted from increased litter production, decreased litter decay rates, or both. Annual litter production did not change significantly along the chronosequence (mean 2.41 t.ha⁻¹). In contrast, litter decay rates decreased significantly during the rapid growth phase of trees. In consequence, the litter turnover time ($1/k$) was lower in the youngest stands (20 months) compared to the oldest ones (31 months). Even in the absence of a significant pattern of variation, litter production was positively correlated with the thickness of the OF (Oi) horizon. In contrast, litter decay was strongly negatively correlated with maximum thickness of the OH (Oa) horizon, suggesting that the appearance of the humification layer was mainly due to a decrease in litter decay rate. We did not find significant changes in the main properties of the organo-mineral horizon, suggesting that soil nutrient availability may not directly affect litter dynamics. We concluded that moder development along the chronosequence resulted in decreasing litter decay rates during the

aggradation phase while litter production was stable. Further studies are required to identify the ecological factors responsible for moder development along forest ageing.

Keywords

Litter production, litter decomposition rate, humus form, nutrient availability, 130-yr chronosequence, *Fagus sylvatica*, loamy acidic soil, forest management.

1. Introduction

Successional patterns of humus forms have often been described along both temperate deciduous and conifers managed (Aubert et al., 2004; Chauvat et al., 2007) and native forest maturation (Bernier and Ponge, 1994; Ponge and Delhay, 1995). Early successional stages have been associated with fast organic matter turnover (translated into mull humus form) while lower organic matter (OM) recycling (expressed as moder occurrence) has been frequently observed under older forest on acidic soils (soil pH < 5.0) (Ponge, 2003; Salmon et al., 2006). More precisely, the appearance of moder with stands ageing consists in development of both fragmentation and humification litter layers, including high proportions of fine organic matter from fauna faeces.

Accumulation of organic materials on the forest floor results from unbalanced rates of two ecological processes: litter production and litter decomposition. For instance, the gradually higher amount of organic matter falling each year along stands ageing may not be fully incorporated within mineral horizons by soil organisms. Only soluble and non-lignified cell carbohydrates are totally utilized during the early phases of leaf litter decomposition (Lavelle and Spain, 2001; Berg and McClaugherty, 2003). Each year, more and more recalcitrant compounds (lignified carbohydrates) may accumulate within the forest floor and promote the formation of fragmented and humified horizons (Lebret et al., 2001).

Besides litter production, changes in litter decay rates may also lead to the appearance of a humification horizon. Ponge (2003) and Ponge et al. (1998) assumed that higher uptake of nutrients by trees during their phase of intense growth, for wood production, may lead to lower nutrient availability in the soil thereby affecting soil biological activity, especially earthworms

activity. Indeed, there is also a global trend of decreasing abundance of earthworms during the phase of intense growth of temperate trees (Bernier and Ponge, 1994; Arpin et al., 1998). This may lead to a decrease in litter decay rates promoting the accumulation of fragmentation and humification litter layers. Nevertheless, Hedde et al. (2007) did not find any significant changes in macrofaunal species turnover along a 200 years old pure beech chronosequence in France despite clear changes in humus forms suggesting that others factors than earthworm occurrence may be implicated.

The question of the paper was whether the shift mull-moder occurring along beech forest ageing is due to changes in leaf litter production and/or decay rates. More exactly, the objectives of this research were to determine (1) changes in macro-morphological properties of humus forms, leaf litter production, litter decay rates, soil nutrients content and pH along a 130-year pure beech (*Fagus sylvatica* L.) chronosequence Normandy (Northwest France), (2) if humus form changed from mull to moder with increasing stand age, (3) if a shift from mull moder resulted from increased litter production, decreased litter decay rates, or both. We also aimed at validating in a managed context the hypothesis developed by Ponge (2003) about soil properties (nutrients content and pH) impact on moder appearance. We tested the hypothesis that fragmented and humified organic materials would accumulate within the forest floor due to decreasing litter decay rates and increasing litter production (Lebret et al., 2001). We also expected the decrease in nutrients availability and pH within the organo-mineral horizon with moder appearance (Ponge, 2003; Aubert et al., 2004).

2. Materials and methods

2.1. Study site

The study site was located in the Eawy state forest (France, Upper Normandy, 01°18' E; 49°44' N; 7200 ha). The climate is temperate oceanic with a mean annual temperature of +10°C and a mean annual precipitation of 800 mm. A space-for-time substitution procedure (Pickett, 1989) was used to empirically reconstitute an even-aged forest chronosequence: sixteen pure beech stands were selected to represent four silvicultural phases (SP) (Aubert et al., 2003) of different ages: 13-18 years (SP15), 65-66 years (SP65), 91-103 years (SP95) and 121-135 years (SP130) (Table 1). Each phase was comprised of four replicated stands. All stands were managed as even-aged full-grown forest by the French Forestry Service (Office National des Forêts – ONF) and were located on a flat (plateau) topography at 205 m (a.s.l). The soil was an endogleyic dystic Luvisol (FAO, 2006) developed on more than 80 cm of loess (lamellated silt of aeolian origin) lying on clay with flints (Laignel et al., 1998). Understory vegetation was defined as a characteristic *Endymio-Fagetum* according to phytosociological classification (Durin et al., 1967). At the centre of each stand, a 16 m² square plot was delimited away from vehicle tracks and base of trees to avoid any local acidification due to the influence of tree stems (Beniamino et al., 1991).

2.2. Morphology of organic and organo-mineral horizons

Macro-morphological descriptions of organic and organo-mineral horizons were previously conducted within frames (25 cm x 25 cm) at three corners of the central plot according to the French nomenclature of soil horizons (Jabiol et al., 2007) in May 2007 (Table 2). We distinguished mull (mainly dysmull) and moder (hemimoder + eumoder + dysmoder) humus

forms on the basis of morphological characters (Table 2). A total of 36 macro-morphological variables were described in the field on the basis of variation visible to the naked eye (Appendix 1) and 48 humus profiles were described (3 profiles per stand $\times$ 16 stands). We differentiated (1) the OL horizon consisting of almost unmodified leaf and woody fragments; (2) the OF horizon consisting of a mixture of coarse plant debris and fine organic matter (humus); (3) the OH horizon, which is an organic horizon characterized by an accumulation of decomposed plant litter and (4) the organo-mineral (A) horizon which vary in depth and structure among humus forms.

2.3. Chemical properties of the organo-mineral horizon

Four subsamples of the organo-mineral horizon were collected in May 2007 within frames (25 x 25 cm) located at each corner of the central square plot. In the laboratory, samples were sieved to 2 mm and air-dried until stable weight. Subsamples were dried at 105°C during 24h to determine water content. In air-dried samples of the organo-mineral horizon, concentrations of total C and N were measured by gas chromatography with a CHN pyrolysis micro-analyser (Flash 2000 Series, CHNS/O Analysers Thermo Scientific, IRCOF, France). C-to-N ratio, pH_{water} and pH_{KCl} (soil-to-solvent ratio = 1/2.5, WTW pH Meter 340, Weilheim, Germany) (Baize, 2000), available P (Duchaufour and Bonneau, 1959), and Cation Exchange Capacity (CEC) were also determined in the samples as well as total elements (Ca, Mg, K, Mn, Na, Al, Fe) by the cobalt hexamine exchange method (Ciesielski and Sterckeman, 1997).

2.4. Litter production

Litterfall collectors, 1m² surface (1m side), 30cm deep and 1m height, were installed in order to characterize the annual litter production. Three collectors were placed in each stand near to the 16m² plot (less than 20m) along a 40m transect at 0, 20 and 40m. Litter was sampled every month from October 2007 to October 2008. A total of 48 collectors were installed (3 collectors per stand x 16 stands). Litterfall samples were oven-dried at 65°C for 48h (Gardner, 2006). Dry samples were sorted and litter components were classified into categories then weighed. Litter categories were leaves, wood fragments and reproductive organs. The wood category included dead wood and bark. Reproductive organs included beech mast and male flowers. Litter was stored at room temperature for litterbag experiment described below.

2.5. Litter decay

We sampled leaf litter in one stand of each silvicultural phase in November 2007 using a net (24m² surface) tight one meter above the forest floor in order to avoid any colonization by soil organisms. Litterfall samples were oven-dried at 65°C for 48h (Gardner, 2006) and stored at room temperature before the experiment. Litter decay was assessed in each silvicultural phase using the litterbag method (Bocock and Gilbert, 1957; Verhoef, 1995). Litterbags (15 x 20cm) were made from nylon net with 0.175 mm mesh size to only exclude macrofaunal activity (Gartner and Cardon, 2004; Aubert et al., 2010). They were filled with 10g of dried leaves. This amount of litter corresponds to the mean annual leaf litter production in French beech forests according to Lebreton et al. (2001). Four different litterbag types were prepared, consisting of litter from four tree age-classes (15, 65, 95 and 130 years). In each stand, litterbags filled with the respective litter were inserted in the forest floor between OL and OF horizons. Litterbags were

placed in the field in December 2007. For each silvicultural stage, 4 replicate bags (one per stand) were removed 12 months after the start of the experiment. When removed, litterbags were packed in plastic bags and transported to the laboratory for analyses. The content was then oven dried at 65°C for 48h to determine litter dry mass (Gardner, 2006).

2.6. Data treatment and statistical analyses

The decay rate coefficient (k) estimates the disappearance of litter on an annual basis, using the following negative exponential decay function:

$$X_t/X_0=e^{-kt}$$

where X_0 is the original mass of litter and X_t is the mass remaining at time t (Olson 1963). The k value (month^{-1}) was used to assess the turnover time of litter ($1/k$) (Olson, 1963).

All tests were computed with the R freeware (R Development Core Team, 2008) and statistical significance was set at $P < 0.05$. Means and standard deviations were calculated for each silvicultural phases ($n=4$ replicates). Comparisons of means were done among silvicultural phases using one-way ANOVA and Tukey HSD post-hoc tests. The normality of data and the homogeneity of variances were previously checked using Wilk-Shapiro (Royston, 1982) and Bartlett tests (Bartlett, 1937), respectively. A Principal Component Analysis (PCA) was performed on organo-mineral horizon properties in order to present a clearer representation of topsoil parameters variations along the beech chronosequence (variables are listed in table 3). We also performed backward-stepwise multiple regressions to discern soil morphological variables that were significantly related to both litter production and litter decay along the chronosequence, after screening potential independent variables for significant co-variation ($R^2 > 0.90$).

3. Results

3.1. Litter production along the chronosequence

Due to high inherent variability, leaf production did not vary among silvicultural phases (Figure 1). It exhibited the lowest average value in SP15 (2.08 t.ha^{-1}) and the maximal one in SP65 (2.58 t.ha^{-1}). Similarly to leaf litter, wood production did not change between silvicultural phases. In contrast, the production of reproductive organs show significant variations with higher values in SP130 and lower ones in SP65. Leaf was the most abundant component of litterfall in all silvicultural phases. Wood was the second one except for SP130 where reproductive organs were most abundant (Figure 1). Total litter production (leaves + reproductive organs + wood) did not vary significantly among silvicultural phases (Figure 2) but exhibited its highest values in SP130 (2.82 t.ha^{-1}) and its lowest ones in SP15 (2.27 t.ha^{-1}).

3.2. Litter decomposition along the chronosequence

After 12 months of litterbag experiment, SP95 and SP130 exhibited a significantly higher remaining mass percentage (68 and 65%, respectively) compared to SP15 (53%) (Figure 2). The decay rate coefficient (k) was significantly higher in SP15 (0.050 month^{-1}) compared to SP95 (0.032 month^{-1}) while the turnover time ($1/k$) was significantly lower in SP15 (20 months) compared to older stands (31 and 28 months in SP95 and SP130, respectively) (Figure 3).

3.3. Chemical properties of the organo-mineral horizon

We did not observe any significant change in chemical properties in the organo-mineral horizon, except for the Mg pool (Table 3). Soil Mg content was higher in SP15 compared to SP65 and SP130. Even insignificant, CEC, Ca and Na contents as well as pH_{water} and pH_{KCl} decreased slightly along the chronosequence, while P, H and Al contents and ΔpH tended to increase.

The first two axes of the PCA performed on organo-mineral horizon data explained 61.1% of the total variation (Fig. 4.A). The first axis (relative inertia = 39.1%) was highly correlated with organic matter content, total C, total N, CEC and C/N ratio (positives scores). The second one (relative inertia = 21.9%) was highly correlated with pH, pH_{water} , Al (negative scores) and Ca, Mg and Na (positive scores) (Fig. 4.A.). The individual factor maps (Figure 4.B) did not discriminate the silvicultural phases and humus forms.

3.4. Humus forms and litter dynamics co-variation patterns

Litter production was positively related to the percentage of bleached leaves in OLv, the maximum thickness of OF layer, the abundance of live roots and negatively related to the number of earthworm casts in OLn ($P < 0.01$, $R^2 = 0.89$) (Table 4.). In contrast, the litter decay rate (k) was negatively related to the maximum thickness of OF and OH horizons, the percentage of skeletonized and brown leaves in OLv ($P < 0.05$, $R^2 = 0.62$) (Table 4).

4. Discussion

4.1. Litter dynamics along the beech chronosequence

Our results showed that litterfall production did not change significantly along the pure beech chronosequence. The absence of significant differences agrees with Starr et al. (2005) who did not find any correlation between stand age and litterfall production in Scots pine forest in Finland. Nevertheless, even insignificant, litterfall production tended to increase during the rapid growth phase of trees. This trend was also observed by Lebret et al. (2001). In their study, beech litter production varied from 1.15 t ha⁻¹ yr⁻¹ in a thicket stand (10-yr-old) to 3.13 t ha⁻¹ yr⁻¹ in a mature stand (147-yr-old) from the Fougères forest in western France.

Besides climate and soil conditions, changes in litter production were often related to stand structure such as relative basal area, breast height diameter of trees or mean height and thinning intensity (Ranger et al., 1995; Lebret et al., 2001; Saarsalmi et al., 2007). In the present study, we did not find any significant relationship between stand structure variables and litter production. Higher foliar biomass per tree in mature stands may compensate for decrease in tree density along the chronosequence, leading to constant litter production. However, we showed that the litter decomposition rate varied to a great extent along the chronosequence, the mean residence time of beech leaves passing from 20 months at 15 years to more than 30 months at 95 years, i.e. during the phase of rapid growth of beech trees. These changes in litter decay may be related to changes in the activity of soil organisms (Berg and Laskowski, 2006). For instance, Ponge (2003) explained that anecic earthworms populations are particularly sensitive to tree development due to soil acidification in the vicinity of tree trunks (Ponge and Delhay, 1995; Salmon et al., 2006). The abundance of anecic earthworms tends to decrease during the phase of intense growth of trees followed by progressive recovery as trees reach maturity then senesce (Bernier and Ponge, 1994). However, Hedde et al. (2007) did not find any significant macrofaunal species turnover along 200 years of pure beech chronosequence, using the same site

as in the present study. The authors assessed that the lack of change in species composition along the chronosequence might reflect the confounding effect of silvicultural practices, i.e. monoculture of a soil-acidifying tree species on acidic soils and the use of tillage to assist natural regeneration. Those practices may have dramatic impacts on burrowing earthworms. The soil pH might be too much acid even in youngest stands ($\text{pH}_{\text{water}} 3.97$) to permit high anecic earthworm abundance. Finally, according to Hedde et al. (2007) results, the observed changes in litter decay rates may not be related to earthworm community structure and activity.

Other explanation lies on the high lignin content of beech litter (Karroum et al., 2005; Sariyildiz and Anderson, 2005; Hobbie et al., 2006). *Fagus sylvatica* is a woody species which produces low quality leaf litter with a high content of lignin and a low content of nitrogen (Sariyildiz and Anderson, 2003b; Hobbie et al., 2006) compared to early successional species such as birch (*Betula pendula*) or hornbeam (*Carpinus betulus*). Karroum et al. (2004; 2005) showed that lignin degradation occurring in organic layers of beech forests consists in an increase in the vanillic acid/aldehyde ratio. The production of phenolic monomers during lignin degradation probably leads to strong acidification in both organic and organo mineral horizons during forest development. Consequently, microbial activity may vary and thus may affect litter decay rates. An investigation of litter quality along the chronosequence may provide insights in our understanding in moder development with forest ageing. It would be also interesting to investigate the structure and function of soil microbial communities in both the organic and organo mineral layers to validate this hypothesis (Idol et al., 2002).

4.2. Humus forms and litter dynamics co-variation patterns

Even if litter production changes were not significant at $P < 0.05$, we showed that they were positively correlated with the maximum thickness of the OF layer, suggesting a possible effect of litterfall increase on moder development. They were also highly correlated with the percentage of bleached leaves (discolored leaves due to fungal activity) in the OL_v horizon and were negatively correlated with the number of earthworm casts in the OL_n horizon. It is probable that a higher beech leaf litter production favored the fungal community, in particular white-rot fungi (Karroum et al., 2005) due to a higher amount of phenolic recalcitrant compounds (lignified carbohydrates and polyphenol-protein complexes) in litter, which may accumulate within the forest floor along the chronosequence. This hypothesis is supported by Karroum et al. (2005) who investigated the morphological evolution of beech litter and biopolymer transformation in humus forms from the Fougères forest (northwestern France). They showed that fungal attacks occurred mainly within the OL and OF horizons while bacterial activity was high within the OF and especially the OH horizons where they were responsible for the structural degradation of polysaccharides. The gradually higher amount with stands ageing of lignin-rich leaf litter falling each year may promote the fungal community within the OL layer, a spatial segregation of soil decomposers and consequently the thickening of the fragmentation layer in the absence of anecic earthworm activity (Lebret et al., 2001; Salmon et al., 2006). Our results also showed that litter production was significantly correlated with the abundance of live roots in the OL_v horizon. We indeed observed a higher root colonization in OF and OH horizons along the studied chronosequence. This statement corroborated results by Ehrenfeld et al. (1992) who found that as forest floor material accumulates along coniferous forest development, the percentage of fine roots increases within organic horizons. Since beech is a strongly ectomycorrhizal species (Taylor et al., 2000), the presence of roots in OF and OH horizons may promote the

ectomycorrhizal fungal community in organic litter layers and in turn limits decomposer activity (Ehrenfeld et al., 1997).

We showed that litter decay rates were highly correlated with the maximum thickness of OH horizons, suggesting that the development of moder may result from the decrease in litter decay rates observed in SP95. The litter decay rate was also negatively correlated with the maximum thickness of the OF horizon and the percentage of skeletonized and brown leaves in the OL_v horizon, suggesting that changes in mesofaunal and enchytraeid communities may take place along the chronosequence and greatly affect litter decay rates (Chauvat et al., 2007).

4.3. Soil nutrient availability as a controlling factor of humus form development?

We did not observe significant changes in nutrient availability within the organo-mineral horizon along the chronosequence. Furthermore, the PCA did not discriminate the four silvicultural phases and the humus forms. The first principal component described changes in organic matter content and CEC while the second one reflected changes in soil acidity. These results suggest that the variability in organo –mineral horizon properties among stands was not related to forest ageing.

However, even insignificant, we observed a trend of decreasing soil quality (pH and nutrient availability) along the chronosequence, i.e. pH_{water} was maximum in SP15 and minimum in SP95, pH_{KCl} showed the same pattern, with 3.33 in SP15 and 3.09 in SP95, the Ca content in the organo mineral horizon was maximum in SP15 (1.43 cmol+ kg⁻¹) and minimum in SP95 (0.71 cmol+ kg⁻¹) while the Al content showed an inverse pattern. This trend agrees with results by Aubert et al. (2004) and Chauvat et al. (2009). They both observed an acidification of the

organo mineral horizon along chronosequences of pure beech stands. The decrease in soil nutrient availability along forest maturation was often related to higher nutrient uptake by trees during the phase of intense growth of trees in response to nutrient requirements for wood building (Brais et al. 1995, Ponge 2003). Since mineral weathering (a stable process in mineral element production along forest maturation) may not supply enough nutrients (base cations) for beech tree requirements, soil quality might decrease along a pure beech chronosequence (Brais et al., 1995; Trap et al., 2009), affecting in turn litter decay. This hypothesis is supported by Sariyildiz and Anderson (2003a) who showed that after 12 months of laboratory incubation, both oak (*Quercus robur* L.) and beech litter decomposition rates varied greatly according to soil quality. It can be wondered whether these changes in soil nutrient availability were significant enough to be responsible for the accumulation of organic material along the pure beech chronosequence.

5. Conclusions

Our results showed that the appearance of moder under the oldest stands was likely to be due to decreasing litter decay rates during the rapid growth phase of trees while litter production was constant. The first hypothesis formulated in the introduction is thus partially validated. However, we cannot validate the second hypothesis concerning topsoil nutrients concentration and pH which should decrease along the pure beech chronosequence and limits soil biological activity (direct effect) and consequently litter decomposition rates. Indeed, we did not find any significant linear correlations between litter dynamics and organo-mineral horizon properties, and the PCA performed on those latter did not discriminate the silvicultural phases and humus forms. Finally, we can conclude that soil nutrient availability effects on litter decay rates were either

362 limited or not linear. These findings raise questions about the ecological factors responsible for
363 the decrease of litter decay rates and thereby moder development with stand ageing which remain
364 unknown. In the challenge to improve forest soil health and quality, further investigations are
365 thus required, maybe by manipulating potential causative factors in long-term experiments.

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507

508

Figure captions

Figure 1. Leaves, reproductive organs and wood production (expressed in $\text{t ha}^{-1} \text{yr}^{-1}$) according to silvicultural phases in a pure beech chronosequence in Eawy forest, France. Data are means. Vertical bars correspond to standard deviation. Letters (a and b) refer to significant differences between silvicultural phases according to one-way ANOVA and Tukey HSD test ($P < 0.05$ level, $n=4$).

Figure 2. Total litter production ($\text{t ha}^{-1} \text{yr}^{-1}$) and final litter remaining mass (% of initial mass) according to silvicultural phases in a pure beech chronosequence in Eawy forest, France. Data are means. Vertical bars correspond to standard deviation. Letters (a, b, x and y) refer to significant differences between silvicultural phases according to one-way ANOVA and Tukey HSD test ($P < 0.05$ level, $n=4$).

Figure 3. Litter decomposition parameters according to silvicultural phases. Data are means. Vertical bars correspond to standard deviation. The decomposition constant k (month^{-1}) was calculated from $(X_t/X_0)=e^{-kt}$, where X_0 is the original amount of litter and X_t is the amount of litter remaining at time t . Letters (a, b, x and y) refer to significant differences between silvicultural phases according to one-way ANOVA and Tukey HSD test ($P < 0.05$ level, $n=4$).

529 Figure 4. Principal Component Analysis (PCA) performed on organo-mineral horizon properties.
530 (A) Correlations circle showing organo-mineral horizon variables (variables factor map). (B)
531 Scatter diagrams onto the PCA factorial plan (individuals factor maps, silvicultural phase or
532 humus forms are labeled) (C). PCA eigenvalue diagram.

Table 1

Table 1. Stand and soil characteristics of the stands in four silvicultural phases along the 130 year pure beech chronosequence in Eawy Forest, France.

Silvicultural phases	15-yr-old (SP15)				65-yr-old (SP65)				95-yr-old (SP95)				130-yr-old (SP130)				
	Stands	1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4
Age in 2009 (years)		15	20	15	15	67	67	67	68	105	93	103	93	137	137	123	123
Last year cut		2004	2003	2003	2003	2003	2003	2003	2004	2003	2004	2002	2004	2002	2003	2004	2004
Area (ha)		14.5	8.0	4.6	4.4	10.8	9.5	9.2	12.1	4.5	16.4	18.1	13.5	3.6	13.8	16.2	18.7
Basal area (m²/ha)		15	21	22	17	26	30	27	30	20	29	30	22	20	23	20	24
Percentage of beech (G/ha) ^a		100	100	100	100	100	100	100	90	90	100	100	100	90	90	100	100
Humus forms ^b		Du	Du	H	Du	E	E	E	H	Do	E	E	H	E	Do	E	E
Vertical sequence ^c																	
OLn		x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
OLv		x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
OF		x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
OH						x / (x)	x / (x)	x / (x)		x	x / (x)	x / (x)		x / (x)	x	x / (x)	x / (x)
						<1cm	<1cm	<1cm		>1cm	<1cm	<1cm		<1cm	>1cm	<1cm	<1cm
A structure ^d		BM	BM	J	BM	J	J	J	J	J	J	J	J	J	J	J	J
Topsoil pH ^e		4.47	3.83	3.56	3.99	3.87	3.83	3.91	4.24	3.80	3.85	3.83	3.72	3.83	3.97	3.73	3.91
Topsoil C/N ^e		15.1	16.6	17.8	15.7	16.3	15.4	16.9	15.0	15.5	15.4	18.5	15.9	15.4	15.8	15.0	14.8
Topsoil P (g kg ⁻¹) ^e		0.13	0.23	0.18	0.16	0.18	0.12	0.10	0.20	0.18	0.21	0.22	0.23	0.48	0.12	0.12	0.15
Topsoil CEC (cmol ⁺ kg ⁻¹) ^e		5.21	6.19	7.43	6.95	5.69	5.66	4.99	5.25	5.74	5.56	7.09	5.60	6.17	5.71	5.28	5.75

^a Percentage of basal area of beech (G/ha) compared to the total species present in the stand

^b With Du : Dysmull; H : Hemimoder; E : Eumoder; Do : Dysmoder (Jabiol et al. 2007)

^c With OLn : unmodified leaves less than one year old, OLv : unmodified leaves more than one year old, OF : coarse plant fragments with fine organic matter (FOM), OH : more than 70% FOM, A : organic-mineral horizon. x : continuous; (x) : discontinuous

^d BM : Biomacrostructured; J : Juxtaposition A (A with massive or single-grain structure but no biological or chemical structure)

^e Data are means (n=3)

Table 2

Table 2. Main properties of humus forms occurring along beech forest chronosequences according to Brêthes et al. (1995); Jabiol et al. (2007); Gobat et al., (1998) and correspondence with Green et al. (1993) classification.

Properties	Humus forms				
	Mull Dysmull	Moder Hemimoder	Eumoder	Dysmoder	
OLn	×	×	×	×	
OLv	×	×	×	×	
OF	×	×	×	×	
OH			×/(×) <1cm	×	>1cm
O/A transition	Discontinuity between O and A		O – A progressive transition		
A structure	Biomacrostructured		juxtaposition A ^{\$}		
A pH	<5		<4.5	<4.5	<4.5
A C/N ratio	15-20		20-25	20-25	≤25
Soil fauna main groups	Anecic earthworms White rot fungi		Macro- arthropods	Mesofauna and insecta larvae	
Bacterial activity	+ ←—————→ -				
Fungal activity	- —————→ +				
Green et al (1993)	Lepto-moder		Leptomoder / mormoder		

× : continuous horizon; (×) discontinuous horizon

^{\$}juxtaposition A : A with massive or single-grain structure but no biological or chemical structure; humified organic matter is juxtaposed to mineral matter

Table 3. Main properties of the organo mineral horizon (A) according to silvicultural phases in a pure beech chronosequence in Eawy forest, France.

Topsoil (A) properties	Silvicultural Phases			
	SP15	SP65	SP95	SP130
Total C (g kg ⁻¹)	54.42 (24.92) a	41.81 (4.63) a	50.38 (14.80) a	45.92 (8.93) a
Total N (g kg ⁻¹)	3.26 (1.29) a	2.62 (0.28) a	3.04 (0.71) a	2.97 (0.52) a
C/N (g kg ⁻¹)	16.31 (1.16) a	15.92 (0.88) a	16.37 (1.46) a	15.29 (0.41) a
P (g kg ⁻¹)	0.17 (0.04) a	0.15 (0.05) a	0.21 (0.02) a	0.22 (0.17) a
CEC (cmol+ kg ⁻¹)	6.45 (0.97) a	5.40 (0.34) a	6.00 (0.73) a	5.73 (0.36) a
H (cmol+ kg ⁻¹)	0.90 (0.30) a	0.90 (0.05) a	1.14 (0.13) a	1.10 (0.15) a
Ca (cmol+ kg ⁻¹)	1.44 (1.05) a	0.54 (0.25) a	0.72 (0.39) a	0.39 (0.15) a
Mg (cmol+ kg ⁻¹)	0.37 (0.07) a	0.21 (0.03) b	0.27 (0.07) ab	0.22 (0.04) b
Na (cmol+.kg ⁻¹)	0.09 (0.05) a	0.06 (0.01) a	0.07 (0.01) a	0.07 (0.01) a
K (cmol+ kg ⁻¹)	0.21 (0.04) a	0.18 (0.03) a	0.26 (0.06) a	0.21 (0.05) a
Fer (cmol+ kg ⁻¹)	0.07 (0.06) a	0.07 (0.04) a	0.05 (0.02) a	0.08 (0.03) a
Mn (cmol+ kg ⁻¹)	0.19 (0.10) a	0.21 (0.10) a	0.23 (0.07) a	0.19 (0.05) a
Al (cmol+ kg ⁻¹)	3.79 (1.52) a	3.91 (0.49) a	4.14 (0.37) a	4.11 (0.32) a
pH _{water}	3.97 (0.38) a	3.97 (0.19) a	3.80 (0.06) a	3.86 (0.10) a
pH _{KCl}	3.33 (0.25) a	3.20 (0.06) a	3.09 (0.04) a	3.10 (0.09) a
ΔpH	0.64 (0.14) a	0.77 (0.14) a	0.71 (0.06) a	0.76 (0.12) a

Data are means (SD). Letters (a and b) refer to significant differences among silvicultural phases according to Kruskal-Wallis rank sum test and Multiple comparison tests after Kruskal-Wallis test (P=0.05 level, n=4)

Table 4. Stepwise multiple regressions with backwards elimination of litter production or decay rate with soil morphological variables.

Soil morphological variables	Litter production	Litter decay rate (<i>k</i>)
Leaf fragments in OLn	X(+)	
Earthworm casts in OLn	X(-)*	
Bleached leaves in OLv	X(+)**	
Live roots in OLv	X(+)*	
Skeletonized leaves in OLv		X(-)
Brown leaves in OLv		X(-)
OF maximum thickness	X(+)*	X(-)**
OH maximum thickness		X(-)**
<i>P</i> value	**	*
R²	0.89	0.62

An “X” indicates that the variable was included in the model from the multiple regression analysis. The sign of the relationship between significant soil morphological variables and litter production or decay rates is indicated between brackets.

* *P* < 0.05.
** *P* < 0.01.
*** *P* < 0.001.

Appendix 1. Morphological variables used to determine humus forms within each stand of a 130-yr-old pure beech chronosequence in Eawy forest, France.

Soil layers ^a	Variables	Codes	Modalities
OLn	Leaf fragments	OLnfg	Percentage
	Skeletonized leaves	OLnsk	Percentage
	Macrofaunal faeces	OLnMfae	Number per square meters
OLv	Maximum thickness	OLvMt	Centimeters
	Minimum thickness	OLvmt	Centimeters
	Leaf fragments	OLvfg	Percentage
	Skeletonized leaves	Olvs k	Percentage
	Macrofaunal faeces	OLvMfae	Number per square meters
	Bleached leaves	OLvBl	Percentage
	Brown leaves	OLvBr	Percentage
	Cover	OLvrec	Percentage
	Compacted leaves	OLvCom	From 1 to 4 (1: no compact, 2: slightly compact, 3: moderately compact, 4: strongly compact)
	Mycelium	OLvmy	From 0 to 3 (0: absent, 1: rare, 2: moderately present, 3: abundant)
	Living roots	OLro	From 0 to 3 (0: absent, 1: rare, 2: moderately present, 3: abundant)
OF	Maximum thickness	OFMt	Centimeters
	Minimum thickness	OFmt	Centimeters
	Leaf fragments	OFfg	Pourcentage
	Fine organic matter	OFfog	Pourcentage
	Macrofaunal faeces	OFMfae	Number per square meters
	Bleached leaves	OFBl	Pourcentage
	Cover	OFrec	Pourcentage
	Compacted leaves	OFCom	From 1 to 4 (1: no compact, 2: slightly compact, 3: moderately compact, 4: strongly compact)
	Mycelium	OFmy	From 0 to 3 (0: absent, 1: rare, 2: moderately present, 3: abundant)
OH	Living roots	OFro	From 0 to 3 (0: absent, 1: rare, 2: moderately present, 3: abundant)
	Maximum thickness	OHMt	Centimeters
	Minimum thickness	OHmt	Centimeters
	Fine organic matter from faunal faeces	OHffog	Percentage
	Plant fine organic matter	OHvfog	Percentage
	Cover	OHrec	Percentage
	Mycelium	OHmy	From 0 to 3 (0: absent, 1: rare, 2: moderately present, 3: abundant)
	Living roots	OHro	From 0 to 3 (0: absent, 1: rare, 2: moderately present, 3: abundant)
A	Maximum thickness	AMt	Centimeters
	Minimum thickness	Amt	Centimeters
	Agregate size	Aas	Millimeters
	Structure	Ast	From 1 to 4 (1: without aggregate, 2: slightly aggregate, 3: moderately aggregate, 4: strongly aggregate)
	Living roots	Aro	From 0 to 3 (0: absent, 1: rare, 2: moderately present, 3: abundant)

^a According to Jabiol et al. 2007. OLn: New. OLv: slightly altered.

Figure 1

Figure 2

Figure 3

Figure 4