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► To cite this version:

Jean Trap, Fabrice Bureau, Alain Brêthes, Bernard Jabiol, Jean-François Ponge, et al.. Does moder development along a pure beech (*Fagus sylvatica* L.) chronosequence result from changes in litter production or in decomposition rates?. *Soil Biology and Biochemistry*, 2011, 43 (7), pp.1490-1497. 10.1016/j.soilbio.2011.03.025 . hal-00593548

HAL Id: hal-00593548

<https://hal.science/hal-00593548>

Submitted on 16 May 2011

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1 Type of contribution: regular paper

2 Date of preparation: August, 2010

3 Number of text pages: 26

4 Number of figures: 4

5 Number of tables: 4

6 Number of appendixes: 1

7

8 Title

9

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

12

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29

30

31 **Abstract**

32

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

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

56

57 **Keywords**

58

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

61

62

63 1. Introduction

64
65 Successional patterns of humus forms have often been described along both temperate
66 deciduous and conifers managed (Aubert et al., 2004; Chauvat et al., 2007) and native forest
67 maturation (Bernier and Ponge, 1994; Ponge and Delhaye, 1995). Early successional stages have
68 been associated with fast organic matter turnover (translated into mull humus form) while lower
69 organic matter (OM) recycling (expressed as moder occurrence) has been frequently observed
70 under older forest on acidic soils (soil pH < 5.0) (Ponge, 2003; Salmon et al., 2006). More
71 precisely, the appearance of moder with stands ageing consists in development of both
72 fragmentation and humification litter layers, including high proportions of fine organic matter
73 from fauna faeces.

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

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

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

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

106

107 **2. Materials and methods**

108 *2.1. Study site*

109

110 The study site was located in the Eawy state forest (France, Upper Normandy, 01°18' E;
111 49°44' N; 7200 ha). The climate is temperate oceanic with a mean annual temperature of +10°C
112 and a mean annual precipitation of 800 mm. A space-for-time substitution procedure (Pickett,
113 1989) was used to empirically reconstitute an even-aged forest chronosequence: sixteen pure
114 beech stands were selected to represent four silvicultural phases (SP) (Aubert et al., 2003) of
115 different ages: 13-18 years (SP15), 65-66 years (SP65), 91-103 years (SP95) and 121-135 years
116 (SP130) (Table 1). Each phase was comprised of four replicated stands. All stands were managed
117 as even-aged full-grown forest by the French Forestry Service (Office National des Forêts –
118 ONF) and were located on a flat (plateau) topography at 205 m (a.s.l). The soil was an endogleyic
119 dystric Luvisol (FAO, 2006) developed on more than 80 cm of loess (lamellated silt of aeolian
120 origin) lying on clay with flints (Laignel et al., 1998). Understory vegetation was defined as a
121 characteristic *Endymio-Fagetum* according to phytosociological classification (Durin et al.,
122 1967). At the centre of each stand, a 16 m² square plot was delimited away from vehicle tracks
123 and base of trees to avoid any local acidification due to the influence of tree stems (Beniamino et
124 al., 1991).

125

126 2.2. Morphology of organic and organo-mineral horizons

127

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

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

139

140 *2.3. Chemical properties of the organo-mineral horizon*

141

142 Four subsamples of the organo-mineral horizon were collected in May 2007 within
143 frames (25 x 25 cm) located at each corner of the central square plot. In the laboratory, samples
144 were sieved to 2 mm and air-dried until stable weight. Subsamples were dried at 105°C during
145 24h to determine water content. In air-dried samples of the organo-mineral horizon,
146 concentrations of total C and N were measured by gas chromatography with a CHN pyrolysis
147 micro-analyser (Flash 2000 Series, CHNS/O Analysers Thermo Scientific, IRCOF, France). C-
148 to-N ratio, pH_{water} and pH_{KCl} (soil-to-solvent ratio = 1/2.5, WTW pH Meter 340, Weilheim,
149 Germany) (Baize, 2000), available P (Duchaufour and Bonneau, 1959), and Cation Exchange
150 Capacity (CEC) were also determined in the samples as well as total elements (Ca, Mg, K, Mn,
151 Na, Al, Fe) by the cobalt hexamine exchange method (Ciesielski and Sterckeman, 1997).

152

153 *2.4. Litter production*

154

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

164

165 *2.5. Litter decay*

166

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

178 placed in the field in December 2007. For each silvicultural stage, 4 replicate bags (one per stand)
179 were removed 12 months after the start of the experiment. When removed, litterbags were packed
180 in plastic bags and transported to the laboratory for analyses. The content was then oven dried at
181 65°C for 48h to determine litter dry mass (Gardner, 2006).

182

183 *2.6. Data treatment and statistical analyses*

184

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

$$187 \quad X_t/X_0=e^{-kt}$$

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

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

201

202 **3. Results**

203 *3.1. Litter production along the chronosequence*

204

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

214

215 *3.2. Litter decomposition along the chronosequence*

216

217 After 12 months of litterbag experiment, SP95 and SP130 exhibited a significantly higher
218 remaining mass percentage (68 and 65%, respectively) compared to SP15 (53%) (Figure 2). The
219 decay rate coefficient (k) was significantly higher in SP15 (0.050 month⁻¹) compared to SP95
220 (0.032 month⁻¹) while the turnover time ($1/k$) was significantly lower in SP15 (20 months)
221 compared to older stands (31 and 28 months in SP95 and SP130, respectively) (Figure 3).

222

223 *3.3. Chemical properties of the organo-mineral horizon*

224

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

229 The first two axes of the PCA performed on organo-mineral horizon data explained
230 61.1% of the total variation (Fig. 4.A). The first axis (relative inertia = 39.1%) was highly
231 correlated with organic matter content, total C, total N, CEC and C/N ratio (positives scores). The
232 second one (relative inertia = 21.9%) was highly correlated with pH, pH_{water} , Al (negative scores)
233 and Ca, Mg and Na (positive scores) (Fig. 4.A.). The individual factor maps (Figure 4.B) did not
234 discriminate the silvicultural phases and humus forms.

235

236 *3.4. Humus forms and litter dynamics co-variation patterns*

237

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

243

244 **4. Discussion**

245 *4.1. Litter dynamics along the beech chronosequence*

246

247 Our results showed that litterfall production did not change significantly along the pure
248 beech chronosequence. The absence of significant differences agrees with Starr et al. (2005) who
249 did not find any correlation between stand age and litterfall production in Scots pine forest in
250 Finland. Nevertheless, even insignificant, litterfall production tended to increase during the rapid
251 growth phase of trees. This trend was also observed by Lebet et al. (2001). In their study, beech
252 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
253 mature stand (147-yr-old) from the Fougères forest in western France.

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

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

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

290

291 *4.2. Humus forms and litter dynamics co-variation patterns*

292

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

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

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

324

325 *4.3. Soil nutrient availability as a controlling factor of humus form development?*

326

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

333 However, even insignificant, we observed a trend of decreasing soil quality (pH and
334 nutrient availability) along the chronosequence, i.e. pH_{water} was maximum in SP15 and minimum
335 in SP95, pH_{KCl} showed the same pattern, with 3.33 in SP15 and 3.09 in SP95, the Ca content in
336 the organo mineral horizon was maximum in SP15 ($1.43 \text{ cmol+ kg}^{-1}$) and minimum in SP95
337 ($0.71 \text{ cmol+ kg}^{-1}$) while the Al content showed an inverse pattern. This trend agrees with results
338 by Aubert et al. (2004) and Chauvat et al. (2009). They both observed an acidification of the

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

350

351 **5. Conclusions**

352

353 Our results showed that the appearance of moder under the oldest stands was likely to be
354 due to decreasing litter decay rates during the rapid growth phase of trees while litter production
355 was constant. The first hypothesis formulated in the introduction is thus partially validated.
356 However, we cannot validate the second hypothesis concerning topsoil nutrients concentration
357 and pH which should decrease along the pure beech chronosequence and limits soil biological
358 activity (direct effect) and consequently litter decomposition rates. Indeed, we did not find any
359 significant linear correlations between litter dynamics and organo-mineral horizon properties, and
360 the PCA performed on those latter did not discriminate the silvicultural phases and humus forms.
361 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.

366

367 **Acknowledgements**

368

369 We are grateful to the “Conseil Régional de Haute-Normandie” for providing a PhD grant
370 to J. Trap through the SCALE network of the GRR SER. This research was funded by both the
371 SCALE network and the GIP ECOFOR (Viflorhum program). We want to thank P. Delporte, T.
372 Tallec, B. Richard, G. Perez and P. Margerie (University of Rouen) for their assistance during
373 litter collection and J.-F. Cheny (ONF) for his help in stand choice.

374

375

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377

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508

509 **Figure captions**

510

511 Figure 1. Leaves, reproductive organs and wood production (expressed in $t\ ha^{-1}\ yr^{-1}$) according to
512 silvicultural phases in a pure beech chronosequence in Eawy forest, France. Data are means.

513 Vertical bars correspond to standard deviation. Letters (a and b) refer to significant differences
514 between silvicultural phases according to one-way ANOVA and Tukey HSD test ($P < 0.05$ level,
515 $n=4$).

516

517 Figure 2. Total litter production ($t\ ha^{-1}\ yr^{-1}$) and final litter remaining mass (% of initial mass)
518 according to silvicultural phases in a pure beech chronosequence in Eawy forest, France. Data are
519 means. Vertical bars correspond to standard deviation. Letters (a, b, x and y) refer to significant
520 differences between silvicultural phases according to one-way ANOVA and Tukey HSD test ($P <$
521 0.05 level, $n=4$).

522

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

528

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. 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 (m ² /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. 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	×	
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 (k)
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	OLvsk	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	OLvro	From 0 to 3 (0: absent, 1: rare, 2: moderately present, 3: abundant)
	OF	Maximum thickness	OFMt
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)
Living roots		OFro	From 0 to 3 (0: absent, 1: rare, 2: moderately present, 3: abundant)
OH	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

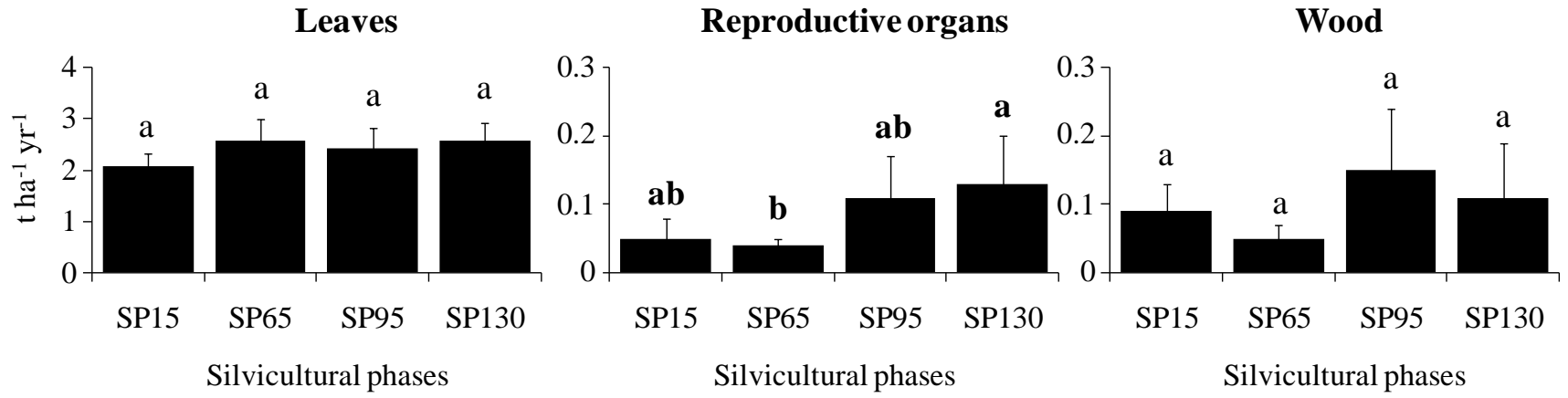


Figure 2

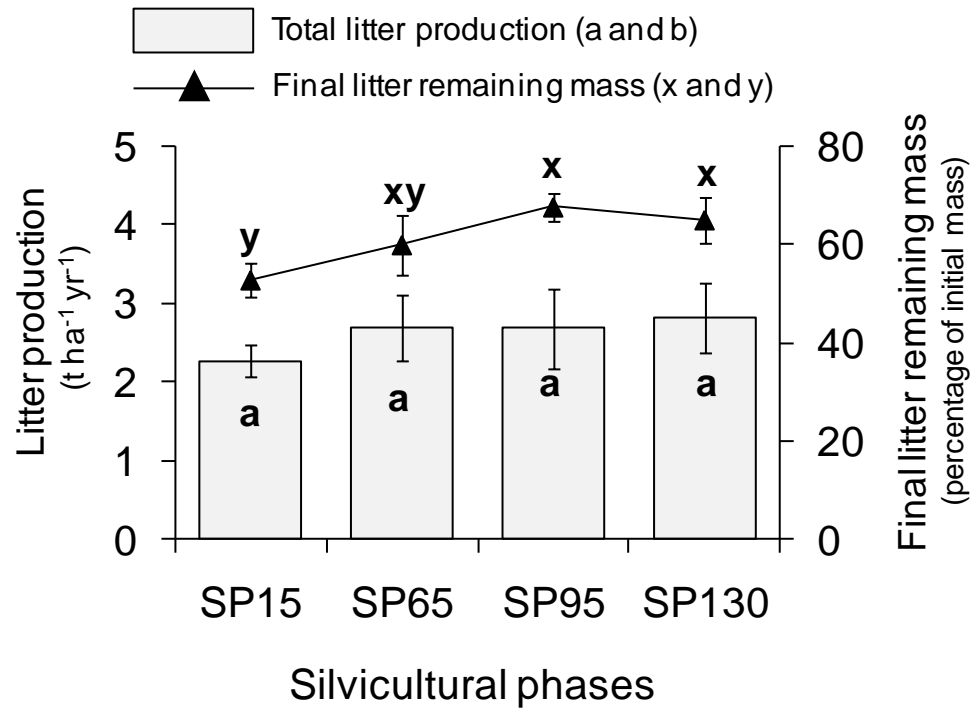


Figure 3

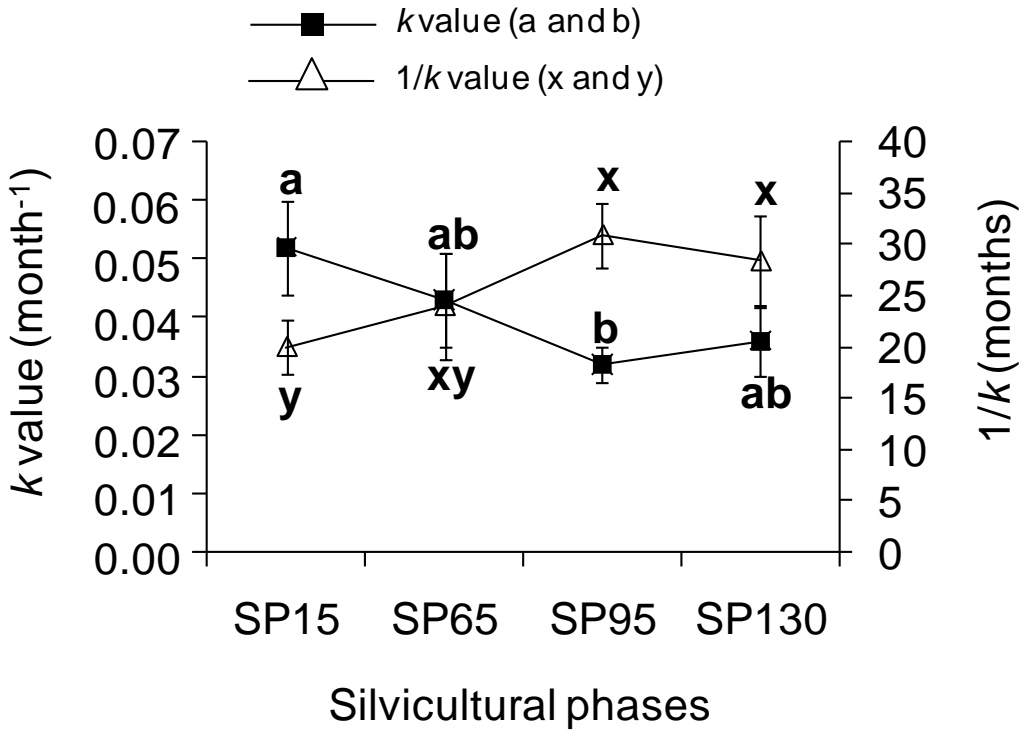


Figure 4

