

Variation in the herb species response and the humus quality across a 200-year chronosequence of beech and oak plantations in Belgium

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The present study aimed at exploring the long-term impact of pure and mixed beech *Fagus sylvatica* and oak *Quercus robur* stands on the forest floor by documenting changes in the herb species' behaviour and in humus index across a 200-yr chronosequence of forest stands. The research was conducted in central Belgium, in a 4383 ha beech-dominated forest. Analyses were carried out in stands which are replicated, of the same age, managed in the same way, and growing on the same soil type with the same land-use history. The results of this study indicate that stand aging is an important determinant of herb species occurrence in the studied area. Most of the species studied show a different response to stand age in pure compared to mixed stands. Our results clearly show a decrease of the humus quality with age in pure stands (beech as well as oak). On the other hand, we found that mixing beech and oak maintained or improved the humus status along the chronosequence according to the proportion of each tree. So the addition of some oak to the beech made it possible to keep a constant quality of the humus. We found that, even if the understory tree species is very scarce, it may be sufficient to maintain the humus status on the long term. In the present study, a cover of 1% oak in a beech stand was sufficient to show an effect of the minor species on these soils. This pattern contrasts with the widespread idea that substantial effects of the minor tree species on soils might not develop if the ratio of major/minor species is low.

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Due to its sensitivity to soil fertility and site conditions (Siccama et al. 1970), the herb layer has been used as an indicator of general edaphic factors and forest site quality (Cserep et al. 1991, Strong et al. 1991). Forestry treatments also appeared to alter the distribution and abundance of particular ground flora species (Kirby 1988). This author highlighted that changing tree species does have a major effect on the ground flora. He found large differences between sites in the response of the ground flora to changing the tree species, and his study suggests that the effects may be greater on more base-rich sites.

There is currently enough evidence for the existence of an influence of canopy structure and tree species composition on the growing conditions for herb and shrub species (Boncina 2000). Influence of canopy species on understory plants may be due to their effect on soil properties. Twenty years ago, Miles (1985) suggested that tree species should be expected to influence soils differently, based on differences in nutrient uptake, litter quality, and growth. Trees can influence soil properties due to canopy interception of atmospheric deposition, weathering of soil minerals, nutrient output via water seepage or biomass removal

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(leaching), amount of litterfall, mineralisation and nitrification, stemflow, throughfall and root activity (Sydes and Grime 1981a, b, Binkley 1995, Augusto et al. 1998, 2002, Neiryneck et al. 2000).

Although there is enough evidence for the effect of forest tree species on the forest floor, this is often difficult to demonstrate (Binkley 1995). Most of the time, the influence of this factor is expected to be unimportant compared to other factors (e.g. soil type) to be significant (Augusto et al. 1998), and confounding effects of site and prior history obscure any effect of species (Binkley 1995). Various studies have highlighted large differences in the quantity and chemistry of litterfall in forests of different species composition (see the review of Binkley 1995). Comparisons across different sites, however, may not provide adequate information on the differences between species when grown on a single site (Binkley 1995). The impact of monocultures on forest soils has been addressed by many studies, but few of them have examined the effects of varying ratios of species within stands (Ewers et al. 1996).

Many of the studies carried out in Europe compared the effect of conifers vs broad-leaved species, mainly *Picea abies* vs *Fagus sylvatica* (Sohet et al. 1988, Koch and Matzner 1993, Bergkvist and Folkesson 1995, Fichter et al. 1998, Augusto et al. 2000, Rothe et al. 2000, Klimo 2002). Very few studies did the same for *Fagus sylvatica* vs *Quercus robur* (but see Norden 1994). As highlighted by Binkley (1995), much of the beech research in Europe is characterised by unreplicated studies both in terms of species treatments and in terms of within-stand sampling (one plot/stand).

Few long-term, replicated experiments are available to provide information on the effects of tree species on soil chemistry (Binkley and Valentine 1991). A wide range of studies have documented changes in soil pH over time (Hallbäck and Tamm 1986, Falkengren-Grerup 1987, Tyler 1987), but the longest timespan taken into consideration mostly does not exceed 55 yr. The limited temporal duration of most studies constrains our understanding of the interactions between the canopy and soil properties. Inferences about long-term impact based on short-term studies may not accurately predict the effect of tree species on forest floor. In the present study, we have attempted to avoid the limitations of short-term investigations through a chronosequence approach. By using one homogenous site, critical assumptions of the chronosequence method are met, i.e. 1) all sites have been subjected to similar processes, and 2) the patterns among sites reflect temporal change (Pickett 1989, Glenn-Lewin and van der Maarel 1992).

In the present paper, we assessed the long-term impact of particular tree species on the forest floor by documenting changes in the herb species' behaviour and in humus quality across a 200-yr chronosequence of forest stands. The objectives are: 1) to analyse the effect of

stand aging on the presence of forest herb species; 2) to test for long-term effects of beech and oak on the humus quality; 3) to investigate whether mixed stands influence the forest floor in a different way as pure stands. In the present study, analyses were carried out in stands which are replicated, of the same age, managed in the same way, and growing on the same soil type with the same land-use history. A recent review of Augusto et al. (2002) highlighted that there are few studies with this level of confidence.

Study area

The research was conducted in the Sonian Forest, south of Brussels (50°47'N, 4°26'E). This area has been proposed as a Site of Community Importance (Natura 2000 area, in fulfilment of the EC-Habitat Directive 92/43/EEC). It is a remnant of the huge forest that is supposed to have covered much of western Europe after the last ice age. The forest actually covers an area of 4383 ha, 1654 ha of which are situated within the administrative limits of the Brussels Capital Region, this constituting a management unit and being the area considered in the present study.

Some 20 000 yr ago, sandstone and flintstone formed the upper layer in the area of the Sonian Forest. After the last ice age, this layer was covered with loess. Today, almost the whole surface of the forest (95%) is composed of a 3–4 m thick calcareous loessic deposit of the Würm age (Herbauts et al. 1996). The prevailing soil type has an "Abc" profile, i.e. silt loam soil with textural B horizon according to the Belgian soil map (Louis 1959) (USDA: Hapludalf; FAO: Luvisol; French classification: Sol lessivé acide). The forest ranges in altitude from 65 to 130 m a.s.l. The climate of the area is temperate and humid, with a growing season of 7 months (April–October). Mean annual temperature is 9.9°C, annual precipitation is 835 mm.

The natural vegetation is a deciduous forest in which oaks (*Quercus robur* and *Quercus petraea*) and beech *Fagus sylvatica* are the main species (Herbauts et al. 1996). Since the plantation work of the Austrian administration at the end of the 18th century, it is now composed of 74% beech *Fagus sylvatica* with only a few other woody species. Sixteen percent is occupied by oak stands (*Quercus robur*) and 8% by introduced conifers (*Pinus sylvestris*, *Larix decidua*, *Picea abies*). Beech is frequently planted in monocultural even-aged stands, thinned many times during the tree regeneration, and harvested when it is ca 160 yr old. Some stands have however not been harvested at this stage and the oldest trees are 240 yr old. The variety of age-classes present suggests that the Sonian Forest is an excellent study area for determining the influence of overstorey age on the ground flora and the humus quality. As we studied

stands of the same soil type and history within one site, we can assume that differences observed under two tree species were only linked to tree species, other differences being considered non-existent.

Methods

Data collection

The taxa which were taken into consideration in the framework of this study belong to two categories: 1) plant species which are good indicators of the high ecological value of the forests, i.e. true and ancient forest species as defined by Honnay et al. (1998), and 2) plant species indicating a disturbance of the biotope, such as eutrophication (*Urtica dioica*), clear-felled areas (*Rubus fruticosus*) or soil compaction with pseudogleyification (*Juncus effusus*, *Carex remota*).

Field sampling was carried out from April to June 2001. We chose this period because it allows at the same time the location of the vernal species as well as the summer species. As seasonal differences may affect the recorded abundance of particular species (most obviously vernal plants such as *Anemone nemorosa* for instance), the sampling period was kept as short as possible (3 months).

Within the Brussels part of the Sonian Forest (1654 ha), the presence of each one of these key-species was noted according to a grid-map of 6500 cells of 50 × 50 m. The species' abundance is estimated according to the Tansley-scale (1 = rare; 2 = occasional; 3 = frequent; 4 = abundant; 5 = dominant). The five classes of the Tansley-scale were interpreted as follows: 1: a few individuals or tufts (<10); 2: a few m²; 3: many tens or hundreds of individuals; 4: many tens or hundreds of tufts; 5: many tens or hundreds of m². The abundance of each species could be estimated by prospecting the whole grid cell according to parallel strips while counting the number of individuals, tufts and square meters. The resulting vegetation map was processed in the GIS ArcView (Anon. 1996), and it was overlaid with the digitised soil and stand maps.

Evaluation of the humus quality

Soil nutrient regime is a composite gradient of several soil chemical variables, of which the pH value and the availability of mineral nitrogen are the most important. The occurrence of the major humus types (mor, moder and mull) is broadly related to soil nutrient regime defined in this way (Wilson et al. 2001). An index of humus quality was attributed to the grid cells according the method of Rogister (1978) i.e. by calculating their mean indicator value for acidity (soil reaction; mR) and nitrification (soil nitrogen; mN). These mean indicator

values were calculated by averaging the Hill's et al. (1999) indicator value of each species for acidity (R) and nitrification (N), weighted by their respective abundance coefficient. Species are not always constant in their ecological requirements and ought in principle to have different indicator values in different parts of their range (Hill et al. 1999). The original Ellenberg's values were developed for central Europe (much more continental than our study area). The Hill's values are recalibrated for the British Isles (phytogeographically closer to our study area: Atlantic region) and reflect therefore much more accurately the species' ecological behaviour in our study area. The indicator values have been widely employed and validated for the interpretation of the variation among plant communities in space and time in many northern European countries (Ter Braak and Gremmen 1987, van der Maarel 1993, Diekmann and Dupré 1997).

The product mR × mN was then calculated. Rogister (1978) showed a very reliable positive relationship between this product and the quality of the humus layer. For calculating the humus index (mR × mN), this author took the N-values from the original tables of Ellenberg (1974) and the R-values from Noirfalise and Dethioux (1970) the latter being converted into the scale of Ellenberg. This implies that the range for the index of Rogister (1978) is slightly different than this calculated by us with the most recent values. In order to overcome this problem and to be able to identify humus types in the classification of Rogister (1978), we recalibrated our indices with a correction factor of 0.642857143, which is the ratio between the maximum value in Rogister's scale (36) and the maximum value in our results (56).

The classification developed by Rogister (1978) recognises six humus types: mor (humus index <6.4), moder (6.4–14.4), oligomull (14.4–18.2), oligomull-eumull (18.2–23.0), eumull (23.0–27.5), carbonate eumull (27.5–36). These six classes correspond to those given by the Biogeoclimatic Ecosystem Classification in British Columbia (Wilson et al. 2001).

In the present study, we focused on humus types because: 1) it is recognised as being a useful and integrative parameter for inferring the level of plant-available soil nutrients of forest ecosystems (Pojar et al. 1987, Wilson et al. 2001), and 2) the impact of tree species is highest in the topsoil (Binkley and Valentine 1991, Augusto et al. 1998, 2002, Neiryneck et al. 2000).

Data analysis

In order to study long-term changes expediently, we used a chronosequence approach, i.e. we investigated stand development with trees from 6 to 243 yr. In order to maintain uniform soil conditions, data processing was performed only on areas sharing the same soil type

(Abc) and for which the stand age was known. Within these areas, all grid cells situated within pure (monocultural) even-aged beech *Fagus sylvatica* stands were selected in order to test for a possible effect of stand age on the humus form. The same was done for pure (monocultural) even-aged oak *Quercus robur* stands. Other overstory species were not taken into consideration in the framework of this work as they are scarce in the study area. From the original 6500 grid cells, only 2128 fulfilled these prerequisites and were used in the analyses. In order to investigate the effect of mixed stands on the temporal variation of the humus form, grid cells containing beech overstories with an oak understory (mostly very scarce with a cover of 1% oak), and conversely oak overstories with a beech understory (mostly between 10 and 40% cover) were also analysed. The number of grid cells used per age class and forest type is given in Table 1.

Using Canoco 4.5 (Ter Braak and Šmilauer 2002), a Generalised Additive Modelling regression (GAM; Hastie and Tibshirani 1990) was used with a cubic smooth spline function, in order to assess the response of the herb species to overstory age within different stand types. GAM regression has been used in numerous studies of species-environment relationships (Bio et al. 1998, Austin 1999, Guisan and Zimmermann 2000, Vetaas 2002) and was chosen because it does not assume any general shape of the response prior to the estimation (Austin and Meyers 1996). A Poisson distribution was assumed with a logistic link function.

Relationships between the calculated (and recalibrated) humus index and the stand age were analysed by linear regression analyses (Spearman rank correlation coefficient r_s), using the package Statistica ver. 6.0 (Anon. 2001). The same test was used to explore the relationship between the varying amount of the minor species and the humus index. The 0.05 level of probability was accepted as significance limit throughout the work.

Results

The results of the regression analyses for overstory age in different stands are summarised in Table 2. Of the 65 herb species which were searched for, 57 occurred in the grid cells fulfilling the prerequisites, among which 47 (82%) are significantly related to stand age in at least one out of the four stand types studied. The response curves of those species which show a significant response to stand age are given in Figs 1–6. Among species which characterise a mor humus (Fig. 1), *Pteridium aquilinum* shows a progressive decreasing trend when stand age increases in oak stands, while it has the opposite behaviour in mixed oak-beech stands. *Deschampsia flexuosa* shows an increasing trend with age in beech-oak stands, whereas it has a bell-shaped curve in the other stands with a maximum occurrence in 150 yr old stands under pure oak or beech, and in 75 yr old stands in mixed oak-beech stands. *Carex pilulifera* also has opposite behaviours under pure beech stands and when beech is accompanied by some oaks in understory. Among moder species (Fig. 2), *Anemone nemorosa* shows a decreasing occurrence under pure oak stands and the opposite when oak is mixed with some beech. The probability of occurrence of *Juncus effusus* increases with stand age under pure oak and mixed beech-oak, while it has bell-shaped curves in the other cases. Among the species which characterise an oligomull humus (Fig. 3), *Dryopteris filix-mas* has a maximum occurrence under 100 yr old beech stands (either pure or mixed), while its presence progressively decreases with age under oak-beech stands. Among oligomull-eumull species (Fig. 4), *Convallaria majalis* shows a bell-shaped curve under pure beech with a maximum occurrence around 70 yr old stands, while it has an increasing trend under mixed oak-beech canopy. *Milium effusum* has a constant behaviour in the different stand types, but *Hyacinthoides non-scripta* shows a decreasing trend under pure oak, the opposite in mixed oak-beech stands, whereas under a beech canopy it reaches its maximum occurrence in

Table 1. Distribution of the number of grid cells per age class and forest type used in the data processing.

Stand age (yr)	Number of grid cells				Total
	<i>Fagus</i>	<i>Quercus</i>	<i>Fagus/Quercus</i>	<i>Quercus/Fagus</i>	
0–20	89	22	56	4	171
21–40	65	5	18	2	90
41–60	132	26	2	3	163
61–80	49	0	1	0	50
81–100	3	0	18	21	42
101–120	92	1	76	2	171
121–140	191	5	54	13	263
141–160	118	0	231	1	350
161–180	428	0	119	0	547
181–200	193	2	0	79	274
201–220	3	0	0	0	3
221–240	0	0	0	0	0
241–260	4	0	0	0	4
Total	1367	61	575	125	2128

Table 2. Regression results (F-test) for all investigated species on stand age, within pure and mixed beech and oak stands, according to a Generalised Additive Modelling regression with a cubic smooth spline function and a Poisson distribution with a logistic link function.

	n	R × N correc.	<i>Fagus</i>	<i>Fagus-Quercus</i>	<i>Quercus-Fagus</i>	<i>Quercus</i>
Mor species						
<i>Calluna vulgaris</i>	4	2,57	0.013a	3.47*	0.035a	–
<i>Vaccinium myrtillus</i>	4	2,57	0.006a	–	40.23***	–
<i>Carex pilulifera</i>	475	3,86	16.54***	28.65***	1.55	3.16*
<i>Deschampsia flexuosa</i>	382	3,86	17.53***	5.51**	26.91***	3.50*
<i>Festuca filiformis</i>	2	3,86	3.17*	3.47a	–	–
<i>Molinia caerulea</i>	4	3,86	–	–	55.95***	–
<i>Blechnum spicant</i>	39	5,79	2.88	0.134	0.496	–
<i>Maianthemum bifolium</i>	11	5,79	0.923	2.2	0.073a	–
<i>Pteridium aquilinum</i>	541	5,79	15.58***	3.93*	5.90**	6.39**
Moder species						
<i>Hypericum pulchrum</i>	6	7,71	8.25***	1.71	–	–
<i>Oreopteris limbosperma</i>	2	7,71	0.433a	–	–	–
<i>Teucrium scorodonia</i>	357	7,71	9.24***	2.28	2.09	0.692
<i>Luzula pilosa</i>	369	9,64	15.68***	18.22***	3.84*	1.27
<i>Cytisus scoparius</i>	34	10,29	2.98	2.85	–	0.065a
<i>Juncus effusus</i>	1411	10,29	48.85***	13.23***	7.73***	3.78*
<i>Luzula sylvatica</i>	693	10,29	18.10***	6.56**	5.39**	1.62
<i>Oxalis acetosella</i>	667	10,29	60.79***	4.13*	52.97***	1.43
<i>Anemone nemorosa</i>	341	12,86	30.43***	14.25***	5.90**	11.36***
<i>Carex ovalis</i>	38	12,86	16.18a	1.31a	–	–
<i>Carex pallescens</i>	5	12,86	9.45***	10.82a	–	–
<i>Deschampsia cespitosa</i>	468	12,86	12.75***	1.13	3.89*	0.416
<i>Dryopteris carthusiana</i>	30	12,86	2.08	3.05*	–	–
<i>Dryopteris dilatata</i>	1729	12,86	68.96***	5.77*	14.08***	10.42***
<i>Lysimachia nemorum</i>	105	12,86	3.38*	1.06	2.04	0.39
<i>Viola riviniana</i>	9	12,86	1.61	–	12.17***	–
Oligomull species						
<i>Chrysosplenium oppositifolium</i>	40	16,07	6.04**	0.319	9.04a	–
<i>Dryopteris filix-mas</i>	75	16,07	9.69***	4.55*	3.60*	3.64*
<i>Lonicera periclymenum</i>	45	16,07	1.90	9.21***	1.04	1.3
<i>Epipactis helleborine</i>	10	18,00	21.03***	0.862	–	–
Oligomull-eumull species						
<i>Adoxa moschatellina</i>	20	19,29	2.21	2.56	1.05	0.366
<i>Brachypodium sylvaticum</i>	110	19,29	2.24	2.19	0.162	0.065a
<i>Convallaria majalis</i>	23	19,29	4.26*	2.3	9.45***	0.894
<i>Hyacinthoides non-scripta</i>	109	19,29	23.17***	7.90***	12.90***	6.16**
<i>Milium effusum</i>	723	19,29	15.52***	6.39**	24.41***	2.95
<i>Narcissus pseudonarcissus</i>	7	19,29	0.006a	0.052a	1.52	–
<i>Hypericum hirsutum</i>	2	22,50	3.17*	–	–	25.67***
<i>Listera ovata</i>	1	22,50	–	–	2.68	–
<i>Melica uniflora</i>	2	22,50	3.17*	11.91***	–	–
<i>Sanicula europaea</i>	11	22,50	2.83	0.016a	1.10	0.065a
Eumull species						
<i>Carex remota</i>	1500	23,14	4.70**	4.47*	13.96***	2.74
<i>Ranunculus ficaria</i>	126	23,14	4.50*	11.95***	0.417	0.883
<i>Rubus fruticosus</i>	1715	23,14	20.81***	17.82***	3.45*	1.74
<i>Veronica montana</i>	238	23,14	0.976a	6.24**	1.75	2.55
<i>Carex pendula</i>	45	27,00	3.44*	5.47**	60.10a	6.25**
<i>Carex strigosa</i>	48	27,00	7.26***	2.31	0.035a	6.84**
<i>Circaea lutetiana</i>	876	27,00	5.44**	7.11**	0.856	2.25
<i>Equisetum telmateia</i>	9	27,00	10.79***	0.016a	24.39***	–
<i>Lamium galeobdolon</i>	157	27,00	17.58***	3.05	2.46	3.72*
<i>Paris quadrifolia</i>	17	27,00	0.313	–	3.68*	0.614
<i>Polygonatum multiflorum</i>	25	27,00	3.25*	5.35**	3.15*	0.175a
<i>Primula elatior</i>	6	27,00	0.82	19.07***	2.68	–
Calbonate mull species						
<i>Allium ursinum</i>	3	31,50	–	22.32***	5.45**	–
<i>Arum maculatum</i>	93	31,50	4.79**	2.34	17.34***	3.99*
<i>Mercurialis perennis</i>	5	31,50	15.27***	–	2.68	–
<i>Urtica dioica</i>	1432	36,00	10.61***	6.14**	3.73*	3.53*
No humus index						
<i>Phyteuma</i> sp.	4	–	6.99***	62.33***	–	0.065a
<i>Senecio ovatus</i>	2	–	0.006a	–	–	24.40a

*: $p < 0.05$; **: $p < 0.01$; ***: $p < 0.001$; n: number of grid cells where each species was present; “–” means that the regression model could not be fitted because the response variable has only one value; “a” means that there were too small arguments.

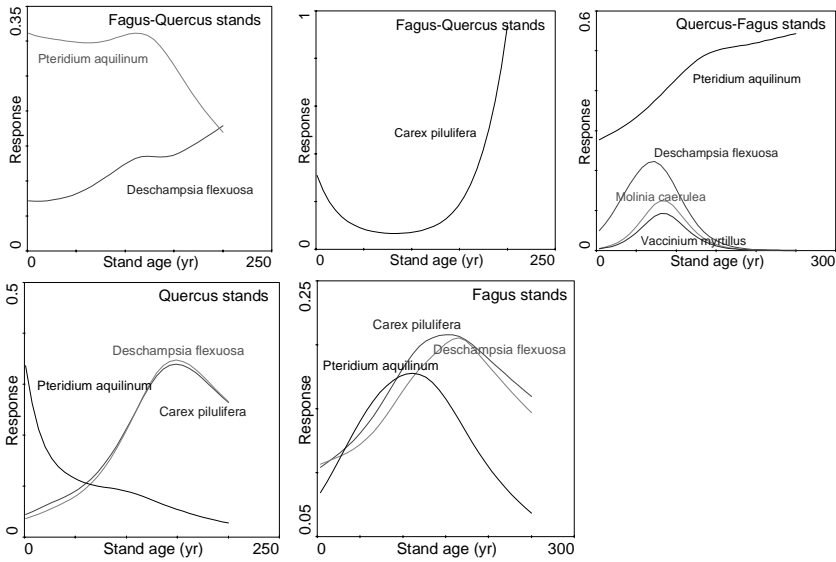


Fig. 1. The response (probability of occurrence) of mor species significantly related to stand age within pure and mixed beech and oak stands.

100 yr old pure stands or 150 yr old mixed stands. Among species which indicate a eumull (Fig. 5), *Carex remota* shows also different response curves according to stand type. Under oak-beech canopy, it reaches its maximum development in 100 yr old stands, while under

pure beech its occurrence decreases with stand age. *Carex pendula* has a bell-shaped curve in pure stands (either beech or oak) with a maximum occurrence when the stands are 80–100 yr old, whereas it increases under mixed beech-oak stands. *Rubus fruticosus* shows oppo-

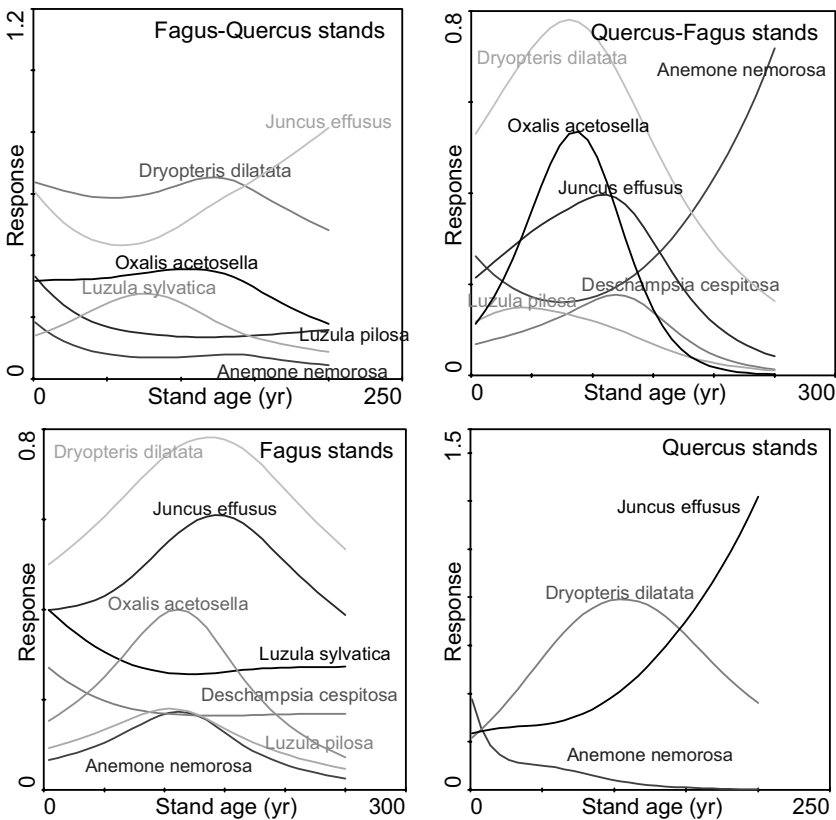
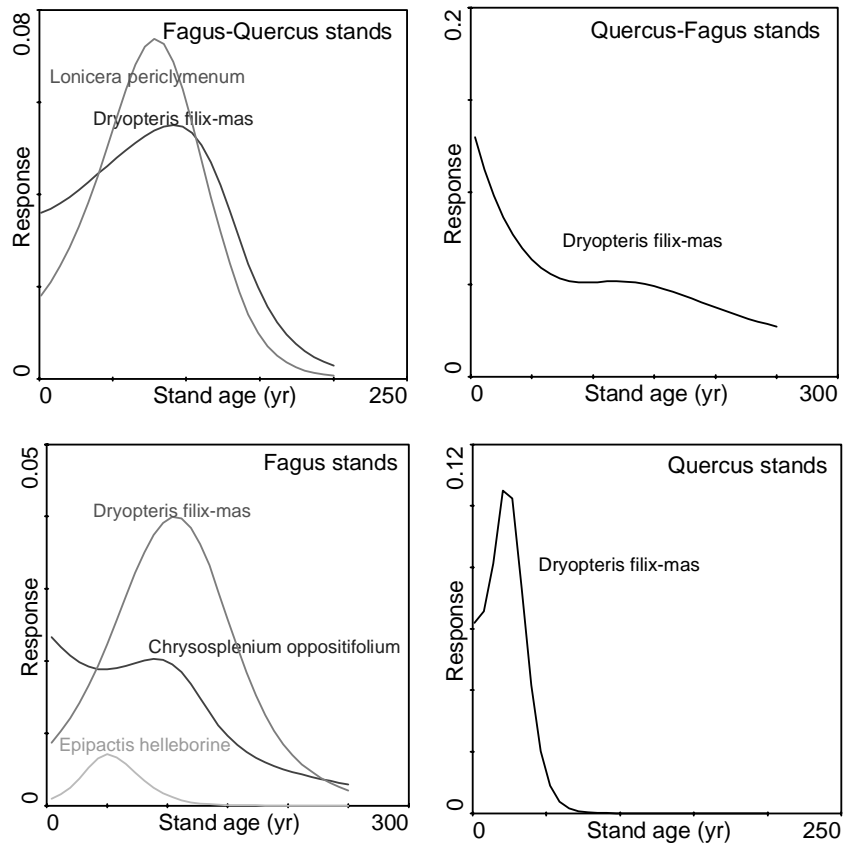


Fig. 2. The response (probability of occurrence) of moder species significantly related to stand age within pure and mixed beech and oak stands.

Fig. 3. The response (probability of occurrence) of oligomull species significantly related to stand age within pure and mixed beech and oak stands.



site behaviours in mixed beech-oak and oak-beech stands. For carbonate mull species (Fig. 6), *Allium ursinum* has a peak of occurrence in 25 yr old beech-oak stands while the same peak occurs at 180 yr in oak-beech stands. The response of *Arum maculatum* shows a decreasing trend in pure oak stands while it progressively increases in mixed oak-beech stands. The response of *Urtica dioica* continuously decreases with stand age under beech and oak-beech canopy, but it fluctuates in oak and beech-oak stands.

Relationships between the calculated humus index and stand age are shown in Fig. 7. In pure beech stands, the humus index slightly decreased across the chronosequence ($r_s = -0.09$; $n = 1367$; $p = 0.0005$; Fig. 7a). We found the same trend in pure oak stands, but due to a small sample size this pattern was not significant ($r_s = -0.08$; $n = 61$; $p = 0.5515$; Fig. 7d). In mixed beech-oak stands, the humus index was kept constant through the chronosequence ($r_s = 0.03$; $n = 575$; $p = 0.3815$; Fig. 7b), whereas in mixed oak-beech stands the humus index increased across the chronosequence ($r_s = 0.15$; $n = 125$; $p = 0.0972$; Fig. 7c). The varying amount of beech in the oak-beech stands did affect the humus index, but the relationship was significant only for one of the two considered age classes (Fig. 8).

Discussion

The results of this study indicate that stand aging is an important determinant of herb species occurrence in the studied area. It could be argued that the chronosequence approach is inadequate without taking into account the historical composition of the stand. For example, 6 yr of beech plantation will likely not delete 200 yr impact of oak, but we can assume that 50 yr do as Binkley and Valentine (1991) showed that 50 yr of stand growth led to substantial biogeochemical changes in the topsoil of different forest plantations in Connecticut. Hagen-Thorn et al. (2004) came to the same conclusion after 30–40 yr of stand growth of various tree species in northern Europe. To test whether our data are biased by young stands, we calculated for 20-yr interval age classes the overall variability of the humus index using the coefficient of variation (standard deviation expressed as a percentage of the mean). The variability of the humus index decreased with increasing stand age, though the trend was not significant (Fig. 9). This suggests an influence of the species composition of the tree layer in the past, particularly for stands up to 40 yr old. We therefore re-analysed our data after discarding all the stands younger than 50 yr (16% of the dataset), but it did not provide consistent results as the relationship between

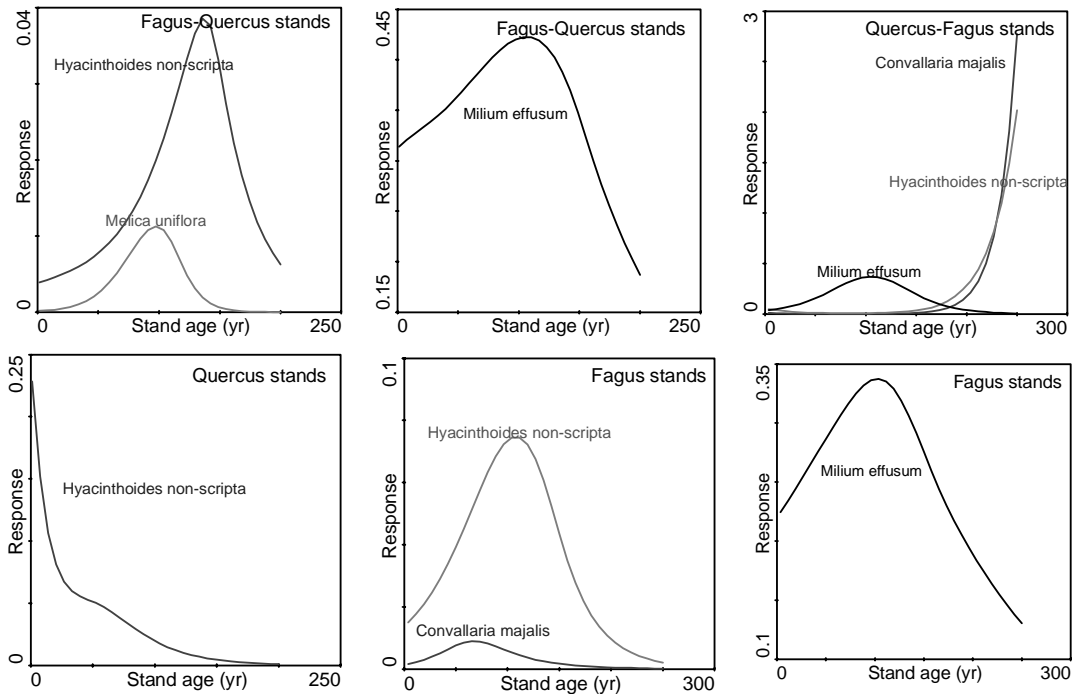


Fig. 4. The response (probability of occurrence) of oligomull-eumull species significantly related to stand age within pure and mixed beech and oak stands.

stand age and humus index was improved for pure *Quercus* stands, remained the same for mixed *Fagus-Quercus* stands, and was less good for pure *Fagus* and mixed *Quercus-Fagus* stands. This a posteriori analysis

suggests therefore that the tree species planted in the past does not significantly affect our analysis.

Our results confirm these found by Whitney and Foster (1988), for old white pine mixed hardwood

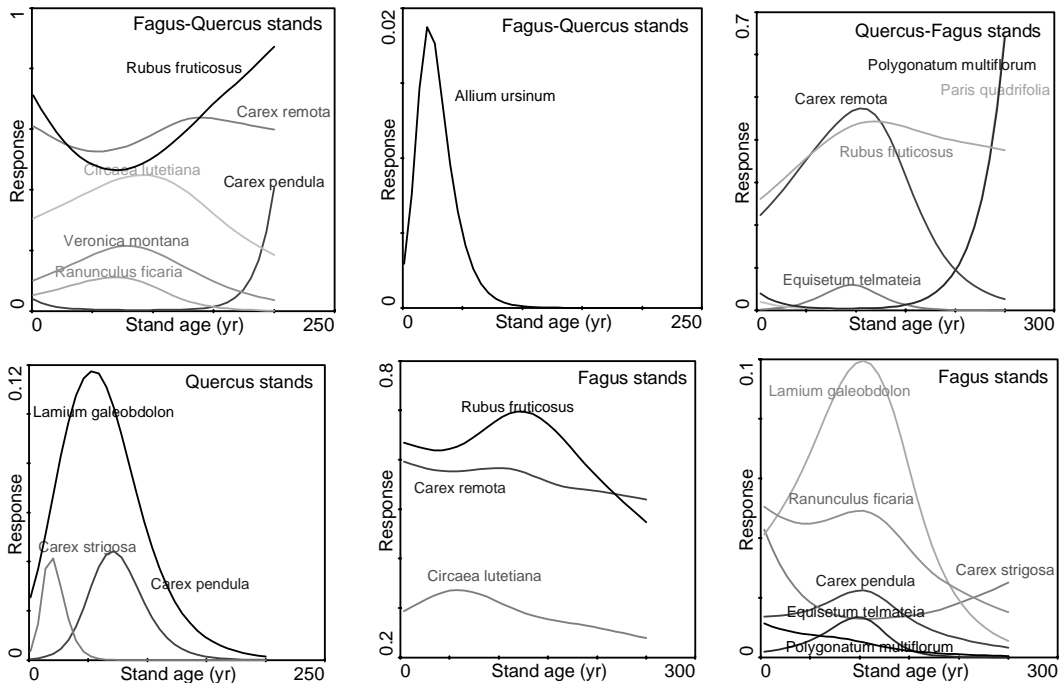


Fig. 5. The response (probability of occurrence) of eumull species significantly related to stand age within pure and mixed beech and oak stands.

successions in Massachusetts and New Hampshire, highlighting the importance of stand age for the occurrence of some common understory species. The mechanisms by which developing tree crops influence the ground flora are imperfectly understood. Shading is commonly assumed to be the major factor, but this parameter was found to be constant throughout the age classes and stand types. The mean light index for each grid cell, calculated with Hill's indicator values, was remarkably homogeneous, with 95% of the values being 5 or 6 on a 9-point scale (results not shown).

The litter characteristics of the tree species may also affect the growth and distribution of ground flora species (Sydes and Grime 1981a, b). Augusto et al. (2000) found, for different tree species, linear relations between aerial biomass and nutrient amount in adult stands. This suggests that the amount of nutrient in the litter is not constant through the chronosequence, and

this is confirmed by Fisher and Binkley (2000) who found that nutrient concentrations of leaves vary with stand age. Recently, Kennedy and Pitman (2004) found that soil nitrogen accumulates in beech forest as stands age due to a reduction in nitrogen demand of older trees. Soil pH seems also to be temporally variable, as Tamm and Hallbäck (1986) reported in a 50-yr study a strong acidification under beech canopy (ca 1 pH unit in the top soil). Striking is the fact that all species from the same humus type (having theoretically the same requirements regarding soil nutrient content and pH) do not show the same response to stand aging within a particular stand type. This would mean that other ecological factors vary with stand age. In a previous study on the same area, we found a significant positive correlation between compaction measurements and stand age, as well as different sensitivities of forest herbs to soil compaction (Godfred and Koedam 2004). Litter depth probably also

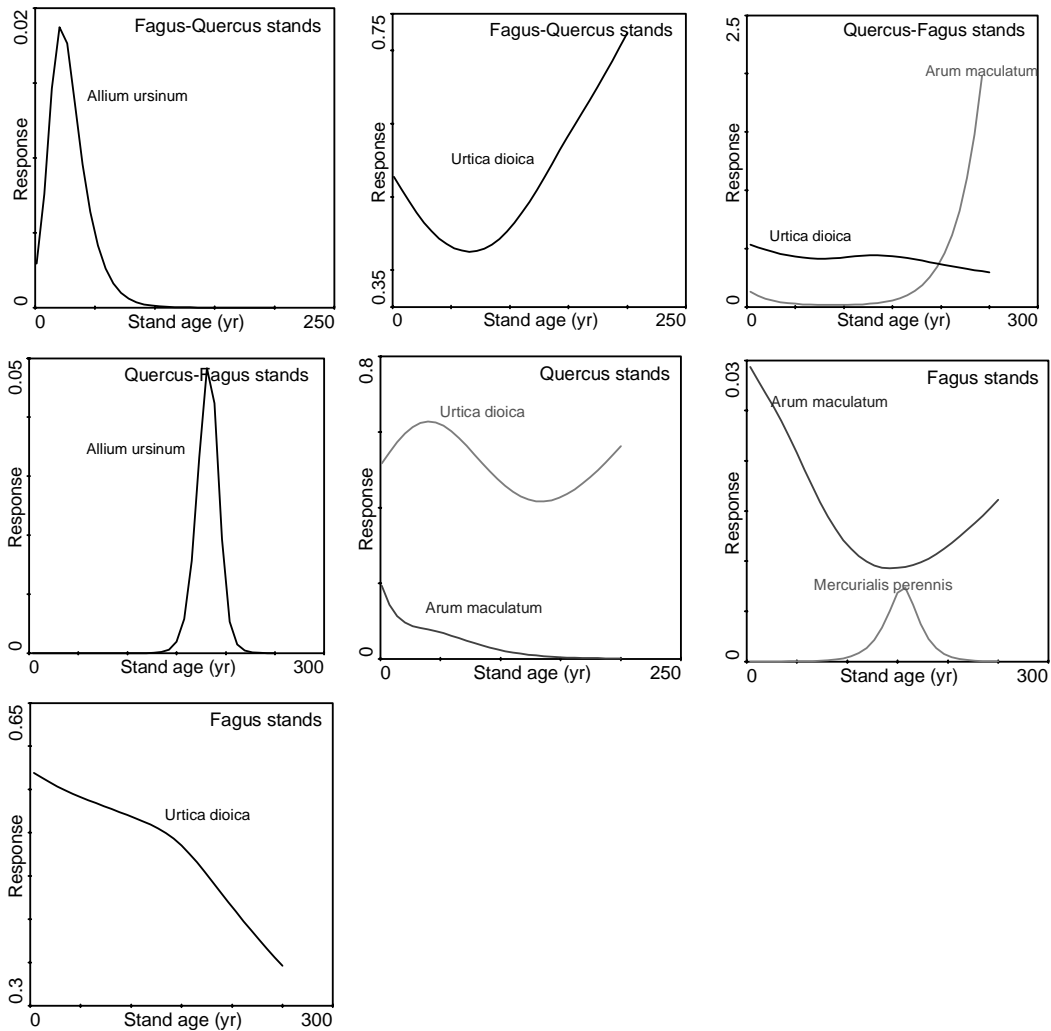


Fig. 6. The response (probability of occurrence) of carbonate mull species significantly related to stand age within pure and mixed beech and oak stands.

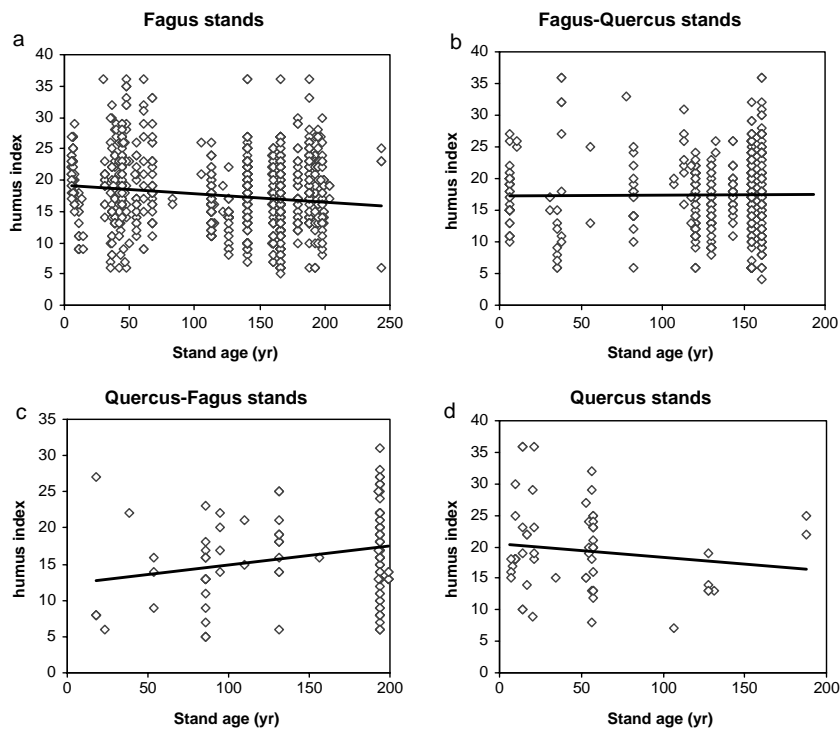


Fig. 7. Relationships between stand age and humus index for pure and mixed beech and oak stands. a) pure beech stands ($r_s = -0.09$; $n = 1367$; $p = 0.0005$); b) beech stands with oak understorey (mostly 1% cover) ($r_s = 0.03$; $n = 575$; $p = 0.3815$); c) oak stands with beech understorey (5–50% cover) ($r_s = 0.15$; $n = 125$; $p = 0.0972$); d) pure oak stands ($r_s = -0.08$; $n = 61$; $p = 0.5515$).

play a key role in the species response to stand age. On acid soil, beech litter accumulates as the stand ages in such a way that, at the end of the rotation, seedling survival may be poor (Deleporte 2001). Furthermore, high temperature and moisture, which could occur at a particular stage of stand development, together with active microbes and invertebrates, can lead to a faster litter decomposition and thus facilitate establishment of vegetation (Facelli and Pickett 1991). Soil temperature alone influences as well the growth of many forest herbs as we already highlighted for the same study area (Godefroid et al. unpubl.). Few data are available on the effects of tree species on soil temperature, but the influence of tree age on soil temperature regime should derive from differences in canopy leaf area, which attenuates both incoming radiation and long-wave emissions from the soil (Binkley 1995).

Most of the species studied have a different behaviour in pure compared to mixed stands. Our results clearly show a slight but steady decrease of the humus quality with age in pure stands (beech as well as oak), where the humus index moved from ca 20 down to 15 on average. This means that, in a 200-yr chronosequence, the original oligomull-eumull moved to an oligomull. Migration of humic acids and initiating podzolisation were often reported on oak-beech stands (Mackney 1961, Beyer et al. 1991). Patterns observed in our study are also similar to those found in other forest ecosystems. In conifer (*Pseudotsuga menziesii*) stands in British Columbia, Fons and Klinka (1998) also found a temporal

variation in humus forms changing progressively with stand development, and implying an increase in acidity and a decrease in soil nutrient availability. On the other hand, we found that mixing beech and oak maintained or improved the humus status along the chronosequence according to the proportion of each tree. So the addition of some oak to the beech made it possible to keep a constant quality of the humus. The results are even more conclusive when the oak is dominating and that one adds to it a beech understorey of 10–40% cover, which made it possible to go from a moder to an oligomull-eumull across the 200-yr chronosequence. Similar results are reported from Sweden for Norway spruce *Picea abies* stands where Brandtberg et al. (2000) found that the admixture of birch (*Betula pendula* and *B. pubescens*) induced a higher base saturation in the forest floor.

We found that mixing *Fagus sylvatica* and *Quercus robur* allows to avoid a degradation of the humus in the long term, compared with pure stands of each of the two species. Most of the studies carried out up to now deal with mixed stands of tree species with high versus low quality litter. Interestingly, our study deals with two tree species having the same acidifying ability according to Augusto et al. (2002). One possible explanation for the observed pattern would be that oak, because of its deeper root system compared to beech, may take up nutrients from deeper soil horizons, thereby redistributing some of these nutrients to upper soil layers through litter fall and canopy leaching, and therefore increasing

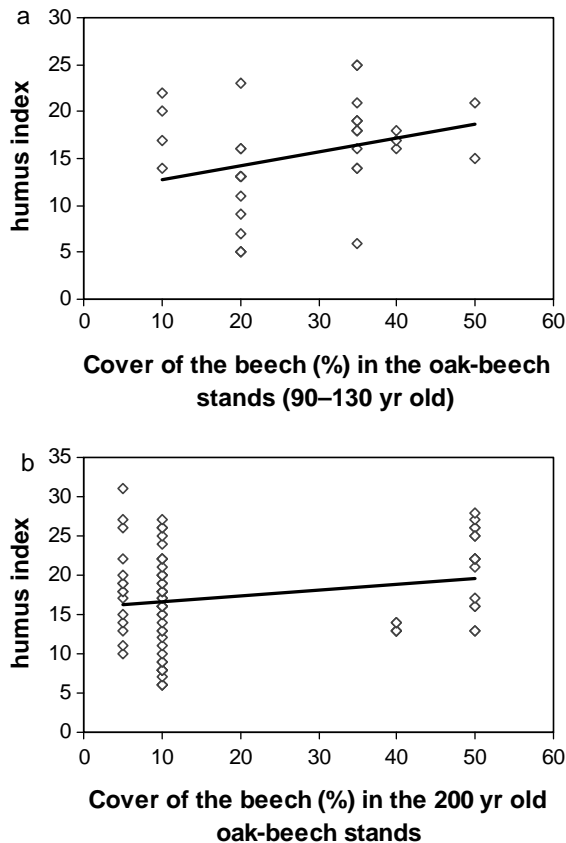


Fig. 8. Relationships between the varying amount of beech in the oak-beech stands and the humus index. a) 90–130-yr old stands ($r_s=0.32$; $n=36$; $p=0.0572$); b) 200-yr old stands ($r_s=0.11$; $n=79$; $p=0.3507$).

the nutrient availability and inducing the development of other herbaceous species. Nevertheless, this hypothesis is not fully satisfactory as it does not explain why pure oak stands influence the humus form in the same way as beech does. Beech may also tend to root deeper in the mixed stands compared with pure beech stands, as shown by Wittkopf (1995), cited by Rothe and Binkley (2001). According to Binkley and Giardina (1998), mixtures of species produce litter that fosters novel soil communities. The mixing of litters may promote decomposition and in turn nutrient availability (Briones and Ineson 1996, McTiernan et al. 1997), and resources with dissimilar availability in different litters can be shared when litters are mixed (Thelin et al. 2002).

An interesting result of the present contribution is that, in an acidophilous beech-oak forest, even if the understory tree species is very scarce, it may be sufficient to maintain the humus status on the long term. This pattern contrasts with the widespread idea that substantial effects of the minor tree species on soils might not develop if the ratio of major/minor species is low. In our case study, a cover of 1% oak in a beech stand did

show an effect of the minor species on these soils. It could be argued that such a very small amount cannot influence the humus, but if individual trees influence soil properties primarily within the radius of the canopy (Riha et al. 1986, Vogt et al. 1995, Ewers et al. 1996, Rhoades 1997), litter fall and microclimate may influence nutritional interactions up to one tree height (Shure and Phillips 1987, Ferrari and Sugita 1996). Rothe and Binkley (2001) specified that ca 90% of the litter of an average hardwood tree fell within ca 1000 m² (18 m radius). It means that the influence of an individual tree extends beyond the limits of its canopy and that a substantial part of the ground floor can be affected by only a few oak trees scattered in a beech-dominated stand.

Our results also showed that increasing the cover of the minor species has a positive influence on the humus index. In the 90–130-yr old oak-beech stands, the humus index significantly increased from 12.8 to 18.7 when increasing the amount of beech from 10 to 50%. In the 200-yr old oak-beech stands, the humus index increased from 16.2 to 19.4 when increasing the amount of beech from 5 to 50%, but this relationship was not significant, likely because of the high variability of the humus index. As abovementioned, this variability is partly due to the stand age, but it can also be explained by the fine scale of the grid combined with the large influence of individual trees.

The complex nature of mixed litter decomposition is revealed by the study of Wardle et al. (1997) who compared decomposition rates, N release, and microbial biomass of 70 litter mixtures containing two to eight species, with the values expected from pure litters. They concluded that decomposition of mixed litters shows non-additive effects that are difficult to generalise. The

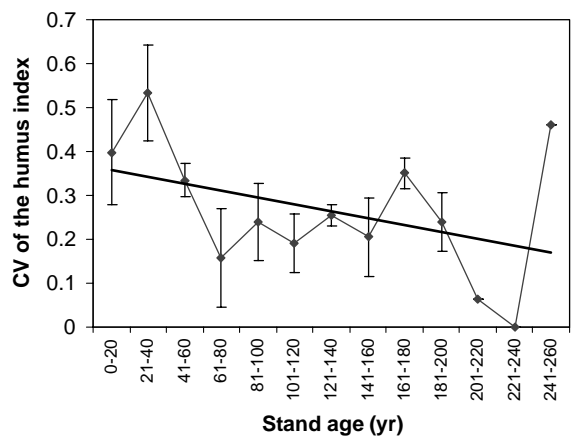


Fig. 9. Relationship between stand age and the coefficient of variation (CV) of the humus index for pure and mixed beech and oak stands. CV is calculated as the ratio between the standard deviation and the average of the humus index within each age class for the four investigated stand types ($r_s = -0.26$; $n=35$; $p=0.1305$).

biogeochemistry of mixed-species forests remains largely unexplored (Binkley and Giardina 1998), and general conclusions are limited by the small number of studies that directly addresses mixed-species effects in forests, and the wide variety of observed interactions (Rothe and Binkley 2001).

In conclusion, our results suggest that by mixing beech and oak, the humus quality of loessic soils can be maintained or improved in the long term, which is an important mitigating tool in soil rehabilitation and should be helpful in sustainable forest management. As a result, this would suggest that mixing two tree species has an effect on the ecosystem that is not equivalent to the sum of the effects produced by the separated species. It is actually much more than that, and it underlines the need for additional research in order to explain why the admixture of one species to another can lead to greater than expected influences on the humus quality relative to single species stands.

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