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Depth distribution and composition of seed banks under different tree layers in a managed temperate forest ecosystem

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ABSTRACT

In the present work we examined the composition and distribution across three soil layers of the buried soil seed bank under three different overstory types (*Fagus sylvatica*, *Quercus robur*, *Pinus sylvestris*) and in logging areas in a 4383-ha forest in central Belgium. The objectives were: (1) to investigate whether species composition and species richness of soil seed banks are affected by different forest stands; (2) to examine how abundant are habitat-specific forest species in seed banks under different planted tree layers. The study was carried out in stands which are replicated, managed in the same way (even-aged high forest), and growing on the same soil type with the same land-use history. In the investigated area, the seed bank did show significant differences under oak, beech, pine and in logging areas, respectively in terms of size, composition and depth occurrence. All species and layers taken together, the seed bank size ranked as follows: oak-wood > beechwood > logging area > pinewood. The same pattern was found for forest species. Seed numbers of *Betula pendula*, *Calluna vulgaris*, *Dryopteris dilatata* and *Rubus fruticosus* were significantly higher under the beech canopy. *Carex remota*, *Impatiens parviflora* and *Lotus* sp. showed a significantly denser seed bank in logging areas, while *Digitalis purpurea* seeds were significantly more abundant in soils under the oak canopy. The fact that the seed bank of an originally homogeneous forest varies under different planted stands highlights that a long period of canopy conversion can affect the composition and depth of buried seeds.

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1. Introduction

Many European temperate forests are intensively managed and have been transformed into high-yielding monospecific plantations of either native or exotic species. Plantations even dominate in many European countries like Belgium, Denmark or United Kingdom (UNECE/FAO 2003). There is currently ample evidence for the existence of an influence of ca-

nopy structure and tree species composition on the growing conditions for herb and shrub species (e.g. Boncina, 2000). Management-related variables may explain more variation in understory vegetation than soil and microclimate variables together (Aude and Lawesson, 1998). Influence of canopy species on understory plants may be due to their effect on soil properties. More than 50 years ago, Ovington (1953) already suggested that tree species influence soils differently. Trees can influence soil properties due to canopy interception of atmospheric deposition, weathering of soil minerals, nutrient output via water seepage or biomass removal (leaching), quality of litterfall, mineralization, stemflow, throughfall and root activity (Sydes and Grime, 1981a,

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1981b; Binkley, 1995; Neiryneck et al., 2000; Augusto et al., 2002).

The influence of the canopy on soil properties, temperature, light transmittance, and therefore on the nature of the field layer vegetation raises some questions related to the composition of diaspores in the soil. What are the long-term effects of the afforestation program on the composition of the seed bank? Under some canopies, there may be almost no plants or, at most, a few scattered ferns and mosses. Studying the seed bank in plantation forestry is therefore essential for understanding the processes of forest regeneration. However, there is still a considerable lack of knowledge concerning seed bank characteristics of typical forest species as outlined by Bossuyt and Hermy (2001). Contrary to grasslands and arable fields, there are relatively few data available from woodland communities (Thompson et al., 1997), and for most species, both early and late-successional, virtually nothing is known about the capacity of their seeds to survive storage in forest soils (Granström, 1987). Yet effects on seed viability and longevity of storage under different types of management are of major concerns (Thompson et al., 1997). In different forests of north-eastern France, Augusto et al. (2001) found that seed banks were influenced by silviculture practices, but as there were no internal replicates for tree species, the authors think that the effect of tree species on seed banks as they reported it should be considered with caution. As very few other studies examined this topic (but see Hill and Stevens, 1981; Amezaga and Onaindia, 1997), we may reasonably consider that further studies are needed in order to assess whether and to what extent tree species may influence the seed bank composition.

In the present work we examined the composition and distribution across three soil layers of the buried soil seed bank under three different overstory types (*Fagus sylvatica*, *Quercus robur*, *Pinus sylvestris*) and logging areas (at least 4 years old), in a 4383-ha forest in central Belgium. In the great majority of seed bank studies, a single soil layer is tested for the presence of viable seeds, while two or three layers are rarely sampled (Thompson et al., 1997). In order to increase the level of confidence of this study, analyses were carried out in stands which are replicated, managed in the same way (even-aged high forest), and growing on the same soil type with the same land-use history. The objectives were:

- to investigate whether species composition and species richness of soil seed banks are affected by different forest stands;
- to examine how abundant are habitat-specific forest species in seed banks under different planted tree layers.

2. Material and methods

2.1. Study area

The research was conducted in a 4383-ha forest, the Sonian Forest (50°47'N; 4°26'E), located in the Brussels Capital Region. Some 20,000 years 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 silt layer (pH_{H2O} around 4.0 in the upper 10 cm), which corresponds to the loess deposition. 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 mixed deciduous forest in which oaks (*Quercus robur* and *Quercus petraea*) and beech (*Fagus sylvatica*) are the main species. At the end of the 18th century, the Austrian administration undertook plantation work. Due to the species selected in these times, the forest is nowadays composed of 74% beech (*Fagus sylvatica*) with only a few other woody species: 16% is occupied by oak stands (*Quercus robur*), 8% by introduced conifers (*Pinus sylvestris*, *Larix decidua*, *Picea abies*), the remaining 2% are represented by diverse broadleaved stands, such as chestnut (*Castanea sativa*), ash (*Fraxinus excelsior*), maple (*Acer pseudoplatanus*), etc.

2.2. Choice of sampling areas

In order to be sure that differences observed under different tree species are only linked to tree species, sampling areas were chosen to meet certain prerequisites:

- same soil type; the prevailing soil type with an “Abc” profile was chosen;
- same topography (i.e. flat and horizontal);
- stands older than 50 years, in order to remove the effect of former overstory types, as Bossuyt and Hermy (2001) showed, for temperate forest ecosystems, that the effect of historical land use decreases after 50 year, due to seed senescence.

A map of the areas meeting these conditions was drawn by overlaying the soil map, the stand map and a Digital Elevation Model of the whole forest in the GIS Arc View (ESRI, 1996). For detecting the presence and age of clearcuts, orthophotos were added to and examined in our GIS, in order to localize logging areas of at least 4 years old. Finally, eight areas (two beech stands, two oak stands, two pine stands and two logging areas) were selected within those that exactly met the previously mentioned criteria.

2.3. Vegetation sampling

Within each selected area, field layer vegetation was surveyed in 400 m²-quadrats (20 × 20 m) in the spring and summer of 2001. Abundance of all vascular species occurring was estimated in three classes according to a simplified Tansley-scale (1 = rare; 3 = frequent; 5 = dominant). Data of spring and summer surveys were pooled into one dataset whereby for each species the maximum abundance class was taken into account.

2.4. Soil sampling

Soil sampling for investigation of the seed bank was done in December 2001. Within each selected quadrat, soil samplings were collected in eight subplots of 20 × 20 cm in three layers (0–5, 5–10 and 10–15 cm depth) positioned in a regular way along the diagonals of the quadrat. After manual removal of the litter layer as well as roots and plant fragments, soil samples (2000 cm³ each) were spread in 192 seed trays of 16 × 25 × 5 cm, one tray for each of the individual samples (4 areas × 2 replicates × 8 subplots × 3 layers). Each tray had small holes in its bottom in order to prevent the soil from becoming water-saturated.

Soil samples were divided in two equal parts, after being homogenized. The first half was incubated for direct seed germination in trays in a greenhouse at 20–25 °C with 12/12 hours light/dark condition. The second half of each sample was incubated in the same environmental conditions but after cold moist stratification (soil layer in each tray was therefore 2.5-cm thick). Because species differ greatly in germination requirements, and therefore greenhouse conditions are not always suitable for the germination of all species (Galinato and Van der Valk, 1986), we stratified the seeds for breaking dormancy by putting half of the samples into a cold chamber at 5 °C for 3 months, as suggested by Gross (1990). According to this author, using these two pre-treatment methods provides a more complete listing of species present in the soil seed bank than elutriation. No seed separation method (i.e. by flotation and by washing) was used. Indeed, if these methods seem very effective in finding large-seeded species (Malone, 1967; Fay and Olsen, 1978), they are, however, ineffective and time consuming for small-seeded species and for soil including much organic matter (Gross and Renner, 1989; Ter Heerdt et al., 1996).

Seedlings that were identified at the species level were counted and removed. Seedlings that could not be identified were individually transplanted to pots and grown, where necessary, until flowering. After 6 months, germination in most trays ceased, partly due to colonization of the trays by mosses and liverworts. By that time, the soil samples were stirred in order to expose seeds to the light that resided in lower sections of the soil layer within the trays, which might have hampered germination. After 12 months, few additional seeds were germinating even immediately after stirring the soil, and the experiment was concluded. Very few seedlings died before they could be identified. Control trays with commercial organic soil were placed in order to record contamination by wind-borne seeds or spores. From August 2002 onwards seedlings of *Betula* emerged in the control trays. Records of this taxon have therefore been excluded from the results from this date onwards. No attempt was made to assess the number of ungerminated seeds possibly remaining in the samples.

2.5. Data analyses

Seedling counts per exposed soil surface (400 cm²) were multiplied by 25 to convert them to equivalent density on the forest floor (seeds per square meter). For some analyses, we focused on two species groups with a particularly high con-

servation value, such as forest species which are determined according to Stieperaere and Franssen (1982), and ancient forest species which are defined by Honnay et al. (1998) for Belgium. The latter are generally considered to be the most valuable as they can be called extinction-prone (Terborgh, 1974), and are part of ecosystems of very low degree of ability to re-create (Peterken, 1977). Due to their poor colonizing ability (Whitney and Foster, 1988; Honnay et al., 1998), these species are limited to primary or ‘ancient’ woodland areas, i.e. “woodland sites which have been continuously wooded since about the year 1775, the approximate date of the publication of the Ferraris maps” (Hermy and Stieperaere, 1981), the earliest reliable mapping of this area.

In order to detect the patterns of variation in the seed bank and vegetation data, we performed a detrended correspondence analysis (DCA) using Canoco 4.5 for Windows (Ter Braak and Šmilauer, 2002) for both datasets (presence/absence data), where the unit is the stand. In case of a gradient length shorter than 3.0, we used principal component analysis (PCA), as advised by Lepš and Šmilauer (1999). In the same way, using the Canoco redundancy analysis (RDA) allowed us to explore the influence of tree species and soil layers on the seed bank composition as a whole (abundance data, without any transformation). Forward selection was used to select significant variables, the Monte Carlo test being used to assess significance. Variables exhibiting collinearity were removed from the model.

The data under different overstory types were compared by Median tests on the total number of species and seed density at each depth. Seed density and vertical distribution were also analyzed separately for each species encountered in the samples. This results in two replicates (two quadrats per stand type) and the eight samples within each stand are repetitions that serve to estimate the statistics of within stand variation. Statistical analyses were carried out using the computer package Statistica 6.0 (Statsoft Inc., 2001).

Nomenclature is given by Lambinon et al. (1998). The highly variable and taxonomically disputed *Rubus fruticosus* s.l. was considered a single species. For convenience, the terms seeds and seedlings are used in the text for seed plants as well as for pteridophytes.

3. Results

A total of 47,064 seedlings germinated, corresponding to an average seed density of 9192 seeds/m² over a 15 cm depth. From the 37 species which emerged, the most abundant were *Carex remota* (69% of the total seedling number) and *Dryopteris dilatata* (21%) (Table 1).

A total of 34 species were found in the above-ground vegetation, of which 35% were present in the seed bank. Only 39% of the species present in the seed bank were also a component of the above-ground vegetation (Table 2). Most of the dominant or frequent species from the herb layer rarely or never emerged from the soil samples, such as *Athyrium filix-femina*, *Luzula sylvatica*, *Urtica dioica*, *Rubus fruticosus* and *Circaea lutetiana*. Striking is the fact that *Carex remota*, which has a high density in the seed bank, never appears in the vegetation. The ordination of the established (vegetation) and

“below-ground” (seed bank) communities of sampling plots displays a clear pattern (Fig. 1). Along the second axis of the DCA ordination, established vegetation plots and seed bank samples are clearly separated and the distances between them are greater in the case of *Quercus* stands and shorter in the case of *Pinus* stands, indicating a decrease in the similarity between vegetation and the seed bank from pine to oak plantations.

The ordination of the seed bank data (Fig. 2) shows that below-ground communities under different overstory types are not clearly separated from each other along the first two axes of the PCA. The highest variability is represented under beech canopy together with logging areas. The composition of the seed bank under oak overstory is much less heterogeneous and this under pine is remarkably homogeneous.

All species and layers taken together, the seed bank size ranked as follows: oakwood (12,047 viable seeds/m²) > beechwood (10,774 viable seeds/m²) > logging area (8208 viable seeds/m²) > pinewood (5740 viable seeds/m²). The differences were only significant for the two upper soil layers (Fig. 3a). In oak stands, logging areas and beech stands, the seedling number decreased gradually with soil depth, though not significantly for the latter. In pine stands, the highest number of seedlings emerged from the second layer (5–10 cm depth). When looking at species groups, there were more seedlings of forest species which emerged from the seed bank under oak stands than from the other overstory types (Fig. 4a). In that case, the ranking was: oakwood > logging area > beechwood >> pinewood. The differences were significant only for the upper soil layer. Results gathered for the ancient forest species show the same trend but they were not significant (Fig. 4b). From the point of view of species richness, we found, however, more forest species and ancient forest species in the seed banks under beech than in the other stand types (results not shown).

There were also significant differences among the different overstories in the number of species detected per tray (Fig. 3b). In the upper soil layer, the species richness per tray ranked as follows: beechwood > logging area > oakwood > pinewood. In the intermediary layer, the ranking was different with oakwood = beechwood > logging area > pinewood. Here also, the deepest soil layer did not give significant differences. In all overstory types, the species number decreased gradually with soil depth, although results were not significant for pine stands.

Tree species and soil depth explain only 14% of the variation in the seed bank composition (Table 3). The lowest (10–15 cm) soil layer, *Quercus* overstory and the upper (0–5 cm) soil layer explained 7%, 3% and 2% of the variation, respectively ($P < 0.05$). *Pinus* and *Fagus* stands did not significantly contribute to the overall variation.

The results at the species level showed that there is a significant gradual decrease in the seed density from the upper layer to the intermediate and the lowest one for species like *Betula pendula*, *Carex remota*, *Dryopteris dilatata* and *Rubus fruticosus* (Table 1). The same trend has been observed for most of the other species but they were so scarce that the differences were not significant. Within the upper layer (0–5 cm), 11 species (30% of the total number of species) showed a significant overstory-effect. Seed numbers of *Betula pendula*, *Cal-*

luna vulgaris, *Dryopteris dilatata* and *Rubus fruticosus* were significantly higher under the beech canopy. *Carex remota*, *Impatiens parviflora* and *Lotus* sp. showed a significantly denser seed bank in logging areas, while *Digitalis purpurea* seeds were significantly more abundant in soils under the oak canopy. The overstory-effect is less pronounced in the intermediate and lowest soil layers where respectively six and five species (16% and 14% of the total number of species) were significantly related to the overstory type.

4. Discussion

4.1. Seed bank composition and depth

Almost 40% of the seed bank of our sampling areas was composed of forest species. This is quite surprising as it is commonly argued that shade-tolerant understory herbs do not appear in forest seed banks (e.g. Olano et al., 2002), and that these species rely on clonal growth to expand under the canopy (Grime, 2001). Even if the forest species we found appear in relatively low densities (except *Carex remota* and *Dryopteris dilatata*), these results indicate that for at least some shade-tolerant species, survival involving a bank of seeds or spores may be a feasible strategy.

Our results showed a significant correlation in species richness and density with depth. Overall species and seed numbers were lower in the lower layers than in the upper layer. This is consistent with what has been found in other studies (e.g. Bossuyt et al., 2002; Olano et al., 2002). This pattern can be attributed to historical changes in above-ground vegetation and seed bank regime (McGraw, 1987), seed mass and shape (Bekker et al., 1998), as well as the vertical transport of seeds by earthworms (Willems and Huijsmans, 1994). As there is some evidence that deeply buried seeds are older than shallow ones (Thompson et al., 1997), our results therefore suggest that not all forest species form a transient seed bank and that at least some of them (e.g. *Carex remota*, *Dryopteris dilatata*, *Hypericum humifusum*, *Luzula* sp., *Oxalis acetosella*) appear to form a long-term persistent seed bank, as they were still recorded in the lowest soil layer.

4.2. Relationship between vegetation and seed bank composition

There was no close relationship between the relative proportion of species in the seed bank and the species composition of the established vegetation at each stand. Correlations between vegetation and the seed bank composition have usually been found to be weak (Pratt et al., 1984; Falinska, 1999; Olano et al., 2002) and this is often ascribed to disturbance, with closer relationships found for more stable communities (Williams, 1984). Nevertheless, even in plant communities with a long history of stable species composition, it is well known that many species present in the vegetation may be absent from the seed bank (Thompson, 2000). The fact that the most abundant seed bank species (*Carex remota*) was not found in the vegetation can be related to its historic occurrence and/or its present occurrence in the vicinity. This

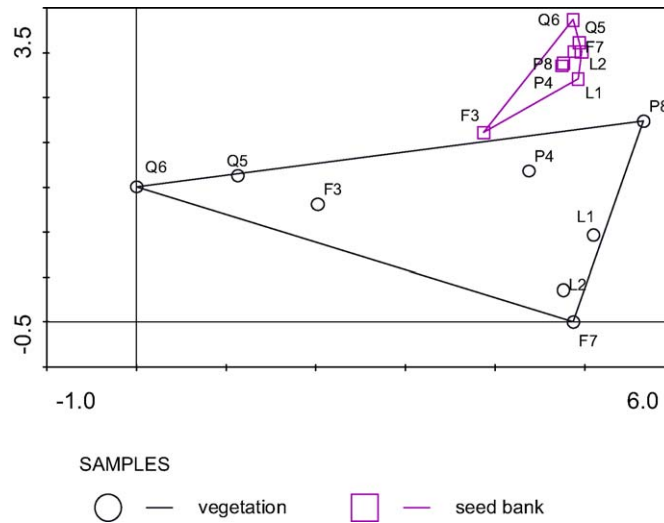


Fig. 1 – Ordination of the established (vegetation) and “below-ground” (seed bank) communities (presence/absence data) of sampling plots relative to the first two axes of a Detrended Correspondence Analysis. Units of the DCA axes are S.D., i.e. average standard deviation of species turnover (Gauch, 1982). Eigenvalues for axes 1 and 2 are 0.823 and 0.548, respectively. F: *Fagus* stands; P: *Pinus* stands; Q: *Quercus* stands; L: logging area.

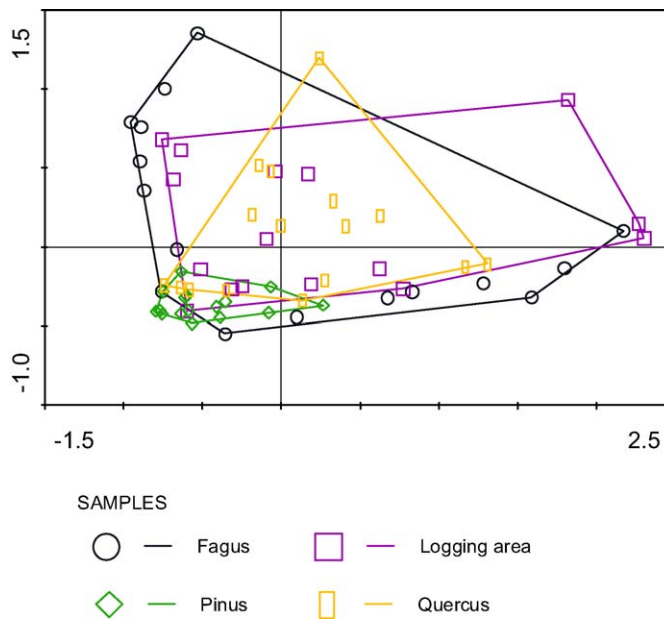


Fig. 2 – Ordination of seed bank data (abundance data without any transformation) relative to the first two axes of a Principal Component Analysis. Units of the PCA axes are S.D., i.e. average standard deviation of species turnover (Gauch, 1982). Eigenvalues for axes 1 and 2 are 0.721 and 0.204, respectively.

means that the seed bank contains not only species from the existing vegetation but also:

- species from the surrounding forest stands (*Carex remota* is a frequent species in beech stands in the study area);
- species that were present in the vegetation in former stages, as suggested by Falinska (1999).

4.3. Relationship between overstory type and seed bank composition

Our experiment may bring new insights to the exploration of the possible effect of stand conversion on the soil seed bank in a forest ecosystem. In the investigated area, the seed bank did show significant differences under oak, beech, pine and in logging areas, in terms of size, composition and depth oc-

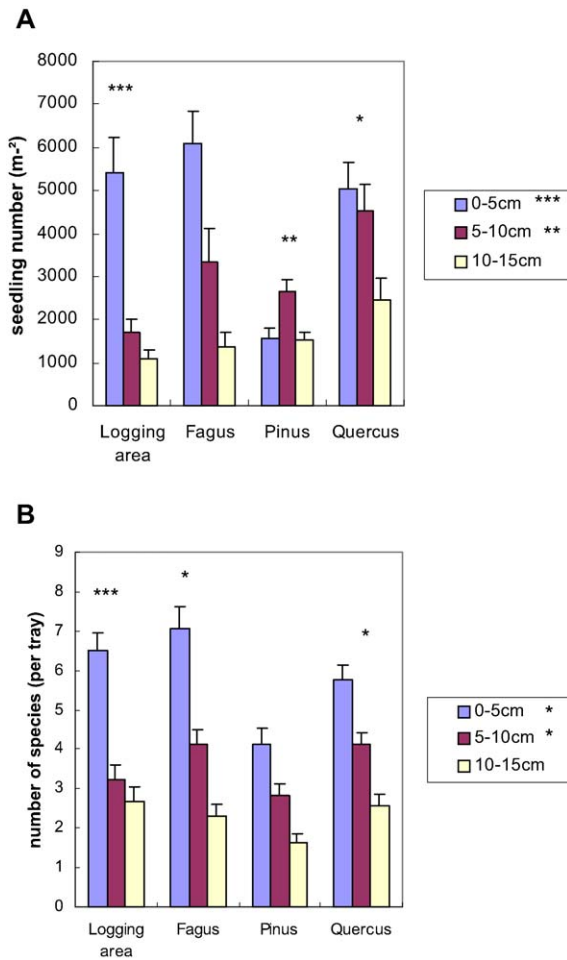


Fig. 3 – Seed density and species richness in the seed bank of different soil layers under various overstory types. The significance of differences between the soil layers for each overstory type (Median test) is indicated in the graph. The significance of differences between the overstory types for each soil layer (Median test) is indicated in the legend (***: $P < 0.001$; **: $P < 0.01$; *: $P < 0.05$). $N = 16$ (8 samples within each stand \times 2 replicates).

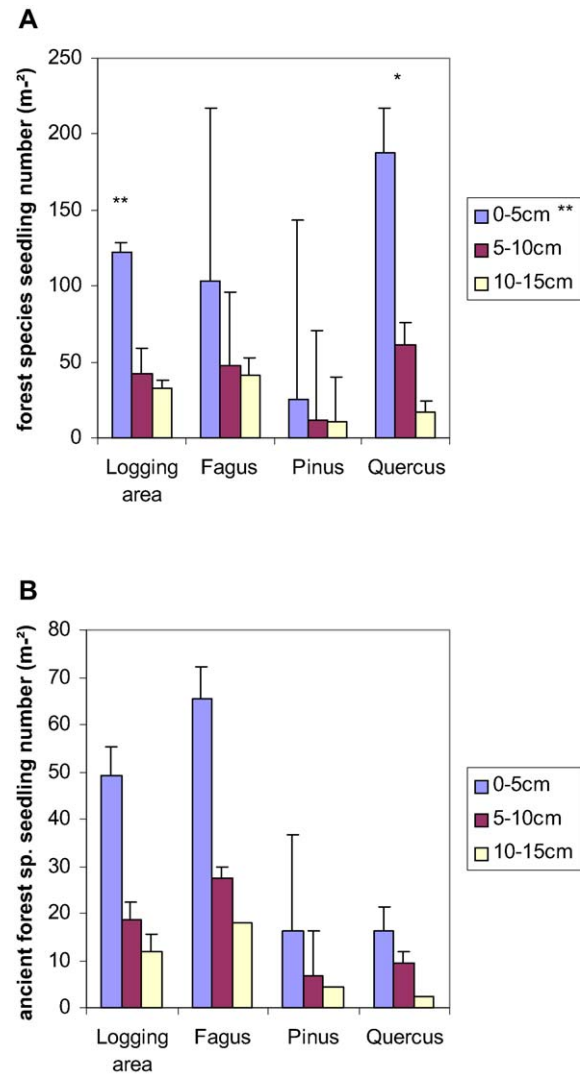


Fig. 4 – Seed density of forest species and ancient forest species in the seed bank of different soil layers under various overstory types. To avoid bias in the results, the analyses were performed without those forest species (*Carex remota* and *Dryopteris dilatata*) or ancient forest species (*Calluna vulgaris*) that largely dominate the seed banks. The significance of differences between the soil layers for each overstory type (Median test) is indicated in the graph. The significance of differences between the overstory types for each soil layer (Median test) is indicated in the legend (***: $P < 0.001$; **: $P < 0.01$; *: $P < 0.05$). $N = 16$ (8 samples within each stand \times 2 replicates).

Table 3 – Percentage variation in the seed banks (abundance data without any transformation) explained by explanatory variables, and level of significance (Monte Carlo test), based on Redundancy Analysis, with respect to five variables (three tree species, *Fagus*, *Pinus* and *Quercus*, and two depths, 0–5 cm and 10–15 cm; logging areas and depth 5–10 cm were collinear and therefore removed from the model)

Explanatory variable	Variance explained by single variable (%)	Cumulative variance explained (%)	P
Depth 10–15 cm	7	7	0.0020
<i>Quercus</i> overstory	3	10	0.0040
Depth 0–5 cm	2	12	0.0160
<i>Pinus</i> overstory	1	13	0.0600
<i>Fagus</i> overstory	1	14	0.2720

currence. This confirms that seed persistence is a site-dependent variable, which strengthens the hypothesized influence of the plantation type on seed survival. The overlapping between the below-ground communities under the different overstory types along the PCA axes testifies to the common origin or the common seed rain of the planted stands, which makes it possible to better appreciate the differences purely related to the effect of the planted tree layer. Our results might suggest the presence of complex interactions between

canopy and seeds in the soil. Tree species may differ substantially in their effects on soils. A forest cover can significantly modify the temperature and moisture conditions of the soil below by its influence on the amounts of light and water that reach the soil surface, by a reduction in runoff and an increase in percolation, and by an increase in water loss as a result of evapotranspiration (Fisher and Binkley, 2000). Seeds may be exposed to different degrees of leaf-canopy-filtered light, where spectral composition is important. Light is known to affect germination (Murdoch and Ellis, 2000), but Pons (2000) also suggested that the dormancy-enforcing effect of leaf-canopy-filtered light is a result of a shift in the red/far red ratio.

The seed bank under *Pinus sylvestris* was the poorest (in terms of species number and seed density) when compared to the other plantation types. Soils under coniferous species are more acidic and have higher concentrations of aluminum than soils under hardwood (Augusto et al., 2003). These circumstances may induce an impoverishment of the understory and therefore of the seed rain which subsequently leads to a poorer seed bank. For logging areas, we could expect that seed banks be replenished after logging as the understory vegetation expands and seed production and seed rain increase. This pattern was not found in our study, as logging areas had seed numbers similar to those in beech stands. Although there is a general trend for increased emergence in canopy gaps (Bullock, 2000), there are also species differences in the degree to which gaps enhance emergence and in the effect of gap size on emergence (Silvertown and Wilkin, 1983; Ryser, 1993). Furthermore, water stress in gaps may also possibly play a role in the observed pattern. From the present study, it also appeared that there were more seeds in the seed bank under *Quercus robur* than under *Fagus sylvatica*. The cause of this may be that the soil under beech is more compacted (Godefroid et al., 2005), which induces waterlogging (Herbauts et al., 1996). This is likely unfavorable for seed preservation because increased humidity exacerbates fungal attack (Fowler, 1988).

4.4. Restoration

Present results suggest that the restoration of the original ground cover in a forest converted into plantation will be different according to the tree species that has been planted. Of course we know from previous studies that few climax woodland species have persistent seed banks, and that such seed banks play little part in regeneration of the mature vegetation after disturbance (Pickett and McDonnell, 1989). However, the present study showed that at least some of these species do form a seed bank, which is important for regeneration as typical forest species are generally poor dispersers (Bossuyt and Hermy, 2001). The fact that the seed bank of an originally homogeneous forest varies under different planted stands highlights that a long period of canopy conversion can affect the composition and depth of buried seeds, probably because of complex interactions between seeds, soil and microclimatic conditions. However, the fact that only 14% of the variance was explained by our variables shows that obviously other important factors not identified play a significant role in the observed pattern. Furthermore,

as the distribution of the species in the soil may be quite patchy (Thompson, 1986; Olano et al., 2002), this probably induced a significant part of the unexplained variation of the results. In our study area, *Quercus robur* (which was naturally dominating in the forest before its conversion) showed the highest seed number of forest species, while *Pinus sylvestris* gave the lowest seed bank density. This has interesting consequences for the restoration of the herb layer in forests which were converted into plantations. These results may also give some elements of reflection to feed the debate on the conversion of planted coniferous stands into broadleaved forests.

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