



To what extent do forest herbs recover after clearcutting in beech forest?

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Abstract

We studied the occurrence of 22 plant functional groups and the distribution patterns of 12 forest herbs in four clear-felled areas of different ages, and across ecotones between the forest and clearcuts in a 4383 ha beech forest in central Belgium. The main goal was to improve our knowledge on the clearcut harvesting system and its possible influence on herb vegetation. Within each study site, the herbaceous vegetation was sampled along a north–south and an east–west transect with points at 20 or at 10 m intervals. We studied a total of 82 vegetation relevés (4 m²) on 18 transects according to the Braun–Blanquet method. Around the study sites, the abundance of each species present was noted according to a grid-map with cells of 50 m × 50 m, up to a distance of 150 m from the clearcut edges. Differences in species' cover percentage and frequency between the clearcuts and the surrounding matrix were tested. The colonisation rate for each species was calculated and possible effect of clearcut age on the plant composition was examined. Results of this study show that plant functional groups with a high conservation value, such as ancient-forest species, stress-tolerant species and autochorous species showed a progressive decrease in time after clearcutting. Most of the studied forest herbs had a lower frequency and/or cover in the clearcut areas than in the surrounding forest matrix. For some of these species, we found a progressive abundance decrease along a 150 m-gradient within the forest towards the clearcut (e.g. *Dryopteris dilatata*, *Luzula pilosa*, *L. sylvatica*, *Oxalis acetosella*). Others, such as *Anemone nemorosa* and *Circaea lutetiana*, are characterised by a regular cover in the forest which suddenly drops at the edge and sustains a very low level throughout the clearcut. If some forest herbs recover better than others, data collected so far indicate that most of the studied species are not able to recover such disturbed sites within a few years. We conclude that silvicultural systems should be adapted to the dispersal and recruitment limitations of forest herbs in order to enable their long-term conservation. To achieve this goal, management without large clear fellings and harvesting methods that never leave the ground completely bare are proposed as alternatives to the clearcutting system.

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1. Introduction

One of the most widespread forms of forest disturbance is clearcutting, i.e. the complete removal

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of a stand in a single harvest (Hubbard et al., 1998). Clearcutting may reduce the diversity of forest understory species (Halpern and Spies, 1995), and after harvesting plant communities are often dominated by a few species able to tolerate the new environment created by logging. When logs are removed using heavy machinery, soil compaction and loss of seedlings, seeds and nutrients may further damage plant habitats and reduce the capacity for forest regeneration (Van der Hout, 2000). Previous studies indicate that recovery of forest understory after logging may require half a century or more. In hardwood stands in New Brunswick, Mac Lean and Wein (1977) found little evidence of recovery of late-successional herbaceous species several decades after canopy opening. Duffy and Meier (1992) found no evidence of recovery of vernal herbs in secondary hardwood forests ranging from 45- to 87-year-old. According to Halpern and Spies (1995), early recovery of diversity following logging reflects two underlying successional processes: (1) rapid colonisation by ruderal, non-forest species; and (2) gradual reestablishment or recovery of characteristic understory taxa. The effects of clearcutting on herb layer species have been well documented for North America (Reader, 1987; Collins and Pickett, 1988; Gilliam et al., 1995; Meier et al., 1995; Bock and Van Rees, 2002) where there is a considerable interest in minimising the impact of tree harvesting on understory plants in the forests managed for timber production. In mature deciduous forests in southern Ontario, Reader (1987) observed that harvesting trees increased the rate at which species were lost from the understory, but the extent of this increase depended on the type of species, its initial abundance and the cutting intensity. In Canada, Bock and Van Rees (2002) observed an increased abundance of shrub and herb species and minimal changes to species composition after harvesting in boreal mixedwood forests. In different mature deciduous forest from Canada and USA, no consistent relationship between opening size and understory response was found (Reader, 1987; Collins and Pickett, 1988). The invasion of some disturbance species has been highlighted in experimental canopy gaps from Pennsylvania hardwood forests (Collins and Pickett, 1988). In West Virginia, findings of Gilliam et al. (1995) suggested a temporal shift in processes influencing species composition following clearcutting from allogenic factors (e.g. soil characteristics) to autogenic factors (e.g. stand char-

acteristics), which lead to a linkage between forest strata later in succession.

In Europe, clearcut studies mainly focus on the influence of logging on the soil degradation rather than on the flora (Herbauts et al., 1996, 1998; Rohand et al., 2000), and except some works in Sweden (Brunet et al., 1996, 1997; Hannerz and Hånell, 1997), in France (Deconchat and Balent, 2001), in Germany (Dierschke, 1988) and in England (Ash and Barkham, 1976; Kirby, 1990), little is currently known concerning the response of the European woodland flora to forest clearcutting. It has been known that the distribution of species depends on the availability of suitable habitats, the capacity to disperse to these habitats, and the capacity of populations to persist after establishment (Ehrlén and Eriksson, 2000). These three aspects will be examined in the framework of this study, with special emphasis on the species recovery from surrounding populations (i.e. the dispersal capacity). The colonisation, dispersal, migration or recovery of forest species is well documented for many countries, such as Sweden (Brunet and Von Oheimb, 1998), Belgium (Bossuyt et al., 1999b; Butaye et al., 2001; Verheyen and Hermy, 2001; Dumortier et al., 2002), the Netherlands (Grashof-Bokdam, 1997; Grashof-Bokdam and Geertsema, 1998; Poland (Dzwonko and Loster, 1992), and the United States (Matlack, 1994; Singleton et al., 2001), but for postagricultural forests. As ancient forests which have never been under agriculture often have larger ecological and pedological value than later established forests (Bossuyt et al., 1999a), the present study dealing with forest species' behaviour within a large ancient forest may bring new insights to the problematic of the recovering capacity of the woodland flora. The ultimate goal was to improve our knowledge on the clearcut harvesting system and its possible influence on herb vegetation, in order to help the interpretation and the prediction of biological phenomena associated with logging areas and to improve present forest management practices for a sustainable forestry.

2. 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 Habitat Directive 92/43/EEC). It is a remnant of the huge forest that is supposed to have covered the whole of Western Europe after the last Ice Age. The circumstances that have permitted the survival of the Sonian Forest are historical and related to its proximity to Brussels (huge source of income for construction timber and charcoal) and to its use as a hunting area around the 12th century, whereas the majority of the forests in Western Europe were cut at that time. 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 the area taken into consideration in the present study. 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, 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. Originally, the Sonian Forest was an oak-hornbeam forest (dominated by *Quercus robur* and *Carpinus betulus*). Since the plantation work of the Austrian administration at the end of the 18th century, it is now composed of 74% of beech trees (*Fagus sylvatica*). These trees are usually planted in mono-

cultural even-aged stands, thinned many times during the tree-generation, and harvested around 180 years. Because natural regeneration does not work in the study area (high predation on the seeds and presence of a compacted soil), the forest is currently managed with a clearcut system with small areas (mostly ≤ 2 ha each) which are clear felled and artificially regenerated. Except beech, few other woody species are found. Sixteen percent of the forest surface is occupied by oak stands (*Quercus robur*) and 8% is represented by introduced conifer stands (*Pinus sylvestris*, *Larix decidua*, *Picea abies*) (Vanwijnsberghe, 2002). Although the Sonian Forest has its original tree cover replaced with newer plantings, it has always been continuously wooded. It therefore belongs to the ancient replanted forests which have potentially far greater biodiversity than more recently established forests. While forests of this type may have suffered a much greater level of disturbance than ancient semi-natural forests, they still retain many of the plant species characteristic of ancient forests.

3. Methodology

3.1. Choice and demarcation of study sites

Orthophotos, soil maps and stand maps of the whole forest were examined in the G.I.S. Arc View (ESRI, 1996), in order to detect the presence and age of clearcuts and to select the study sites. Four clearcuts were chosen in areas with comparable combinations of (a)biotic factors, i.e. pedological and botanical aspects (Table 1). Because former land use is expected to influence the suitability of forest habitat (Peterken

Table 1
Physical and historical characteristics of the studied clearcuts (A, B, C, D) in the Sonian Forest

Variable	A	B	C	D
Area (m ²)	9029	20852	5313	7897
Perimeter (m)	459	786	380	477
Fractal dimension	1.35	1.34	1.38	1.37
Age (years)	13	5	5	13
Aspect	E	NE	NNW	NE
Elevation (m)	110–120	107–116	110–120	110–120
Soil type	Silt loam	Silt loam	Silt loam	Silt loam
Mean slope (%)	6.3	3.9	9.0	8.1
Former stand	<i>Fagus</i>	<i>Fagus</i> , <i>Quercus</i>	<i>Fagus</i>	<i>Fagus</i>
Surrounding stands	<i>Fagus</i>	<i>Fagus</i>	<i>Fagus</i> , <i>Quercus</i>	<i>Fagus</i>

and Game, 1984; Grashof-Bokdam and Geertsema, 1998; Dupouey et al., 2002), all the clearcut areas were selected on former beech stands. Clearcut borders were determined by examining orthophotos in Arc View. The crown of the last surrounding trees was used as criterion to demarcate the clearcuts. At the moment of the sampling, they were not replanted and, except a few scarce seedlings of *Betula pendula* resulting from natural recolonisation, no woody vegetation was present. The vegetation of each selected clearcut was represented by a mosaic of species belonging mainly to three phytosociological classes, i.e. the *Querco-Fagetea*, the *Quercetea robori-petraeae* and the *Epilobietea angustifolii* (Van der Meijden, 1999).

3.2. Vegetation sampling

Within the four study sites, the herbaceous vegetation was sampled along a north–south and an east–west transect with points at 20 m intervals for the biggest sites (A and B) or at 10 m intervals for the smallest ones (C and D). Because clearcut B was characterised by an elongated shape in the NE–SW direction, the vegetation was also sampled along two more transects (NE–SW and NW–SE). We studied a

total of 82 vegetation relevés on 18 transects according to the Braun–Blanquet method (e.g. Westhoff and van der Maarel, 1973) on 4 m² plots, which is the recommended area for grassland-like vegetation types (Kent and Coker, 1992). Around the study sites, we used the grid-map method in order to have a full coverage around each clearcut. So, instead of using 4 m² plots along line-transects, we recorded the species abundance (expressed in cover percentage) in all the grid-cells (50 m × 50 m; $n = 219$) surrounding the study sites, and this up to a distance of 150 m from the clearcut edges, divided into three buffer zones (Fig. 1). This choice is justified by the probability of occurrence of many forest plant species which drops almost to zero when the nearest source patch is situated further than 200 m (Butaye et al., 2001).

3.3. Data analyses

We characterised the shape of each selected clearcut by the Fractal Dimension as defined by McGarigal and Marks (1995), i.e. two times the logarithm of patch perimeter (m) divided by the logarithm of patch area (m²). A fractal dimension greater than 1 indicates a departure from Euclidean geometry (that is, an increase

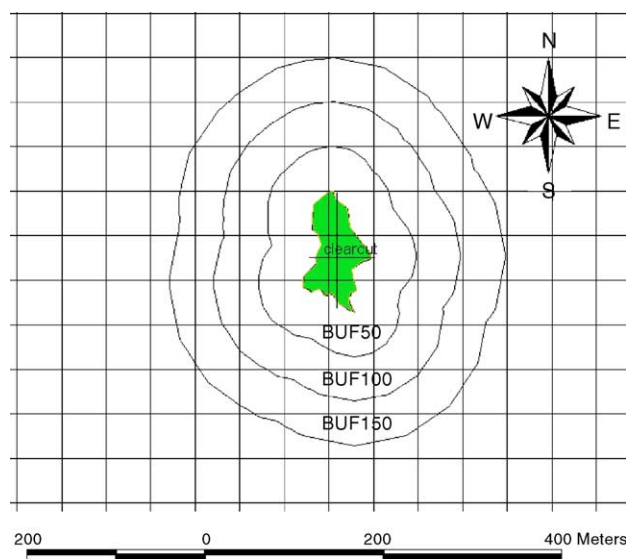


Fig. 1. Diagram showing the sampling design used for the study of forest herb distribution in and around clearcuts in the Sonian Forest. Within a clearcut (grey area), the herbaceous vegetation was sampled along a north–south and an east–west transect with points at 10 or 20 m intervals, depending on the size of the study site. The presence and abundance of forest herbs outside the clearcut was censused within grid cells of 50 m × 50 m. According to the distance to the clearcut (50, 100 and 150 m), three buffer zones were defined (BUF50, BUF100, BUF150).

in shape complexity). It approaches 1 for shapes with very simple perimeters such as circles, and approaches 2 for shapes with highly convoluted perimeters (McGarigal and Marks, 1995).

Because any assessment of a woodland flora should be relevant to woodlands and should not be affected by the typical grassland and ruderal species found on rides and disturbed ground (Peterken, 1974), we focused on the forest flora for most of the analyses. Indeed, generalist and opportunistic species respond more successfully to change than specialists (Gibb and Hochuli, 2002), and their survival ability is much higher than specialists. In this study, we used as forest species those defined for Belgium by Stieperaere and Fransen (1982).

Since Braun–Blanquet cover-abundance values are not suitable for mathematical treatment, raw data were transformed into cover percentages by taking the median of each scale interval: 87.5, 62.5, 37.5, 15, 2.5, 0.5 and 0.2, accounting respectively for 5, 4, 3, 2, 1, + and r (arbitrary values were taken for r , + and 1). By this way, the mean percentage cover of each species could be compared inside and outside the clearcuts. Mann–Whitney U non-parametric tests were used to test for differences in species' cover percentage between the clearcuts and the surrounding matrix. Fisher exact probability tests were used to test for differences in species' frequency between the clearcuts and the surrounding matrix. The species' frequency is defined as the proportion of vegetation relevés (inside the clearcut) or grid cells (outside the clearcut) where the species has been noted.

In order to detect possible migration patterns in the species data, we first calculate the similarity between vegetation samples along the transects within the clearcuts. As similarity measure between the vegetation relevés, we used Sørensen's similarity coefficient, because it gives more weight to the species that are in common to the samples rather than those that only occur in either sample (Kent and Coker, 1992). To evaluate the possible influence of the distance from the forest edge upon clearcut vegetation, we used an Analysis of Variance followed by a Student Newman Keuls test on Sørensen's similarity coefficients calculated between all clearcut relevés situated at 0, 10, 20 and 30 m of the forest edge.

Given that the forest surrounding of the clearcuts was the likely source area for herbs growing in these

clearcuts, we calculated the colonisation rate for each species studied. The species' colonisation rate in the clearcuts was defined as the percentage of the total number of target plots which were occupied, divided by the percentage of the total number of grid cells in the surrounding forest matrix (likely source area) which were occupied (Grashof-Bokdam and Geertsema, 1998). In order to test species' migration abilities, colonisation rates were also calculated according to the distance clearcut-forest, i.e. compared with three buffer zones (50, 100 and 150 m) defined around each clearcut (Fig. 1). Differences were tested by the Kruskal–Wallis analysis of ranks.

In order to test for a possible effect of clearcut age on the plant composition, Mann–Whitney U -tests were performed for individual species cover and plant traits or functional groups between “old” (13 years) and “young” (5 years) clearcuts. We used data on plant traits that are available in the literature. Forest species and clearcut species are determined according to Stieperaere and Fransen (1982). Together with the woodland flora, we also focused on ancient-forest species, as defined by Honnay et al. (1998) for Belgium, which 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 recreatability (Peterken, 1977). Due to their poor colonising 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.

C–S–R strategies were obtained from Grime et al. (1988). Intermediate strategies were pooled according to Graae and Sunde (2000) using the following categories:

- C+ (competitors): C, C/CR, C/CSR, C/SC;
- CSR+ (competitive and stress-tolerant ruderals): CR, CR/CSR, CSR, SC, SC/CSR, SR, SR/CSR;
- R+ (ruderals): R, R/CR, R/CSR, R/SR;
- S+ (stress tolerants): S, S/CSR, S/SC, S/SR.

The database of Kleyer (1995) was used to provide information on diaspore's dispersal, number per shoot, weight and shape. Seed bank persistence was obtained

from the extensive database of Thompson et al. (1997): (1) transient ($t < 1$ year); (2) short-term persistent ($1 < t < 5$ years); (3) long-term persistent ($t > 5$ years).

The contribution of the different plant functional groups to the total species richness in the plot was calculated as the number of species in the group divided by the total number of species in the plot (i.e. relative number of species).

If not stated otherwise, all statistical analyses were carried out with Statistica Version 6.0 (Statsoft Inc., 2001). The 0.05 level of probability was accepted as significant throughout the work.

Nomenclature and species life forms are given by Lambinon et al. (1998).

4. Results

A total of 47 species was found in the clearcuts (Appendix A). Eighteen are forest species, of which 12 are shared with the surrounding forest matrix. Overall, *Carex pilulifera*, *Pteridium aquilinum* and *Teucrium scorodonia* were significantly more frequent in the clearcuts than in the forest matrix, while the opposite was observed for *Carex remota*, *Circaea lutetiana*, *Dryopteris dilatata*, *Luzula sylvatica* and *L. pilosa* (Fig. 2). Some species having a higher frequency in the clearcut may show a higher abundance in the forest matrix, such as *Pteridium aquilinum* and *Teucrium scorodonia*. Furthermore, as might be expected, there is no forest species which is significantly more abundant in the clearcut than in the surrounding forest (Fig. 3).

The occurrence of 22 plant functional groups was compared in young (5 years) and old (13 years) clearcuts (Table 2). For six of these groups, their proportion was found to be significantly different according to the clearcut age. The percentage of ancient-forest species, competitive and stress-tolerant ruderals, stress tolerants, autochores and species with light diaspores ($0.21 < \text{weight} < 0.5$ mg) was higher in the younger clearcuts. Conversely, the percentage of competitive species was lower in the younger clearcut. Other parameters were not statistically different between 5-year and 13-year-old clearcuts. The cover of three of the investigated forest species also varied significantly according to the clearcut age (Table 3): *Carex remota* was more abundant in the older areas, while *Circaea lutetiana* and *Luzula pilosa* showed a

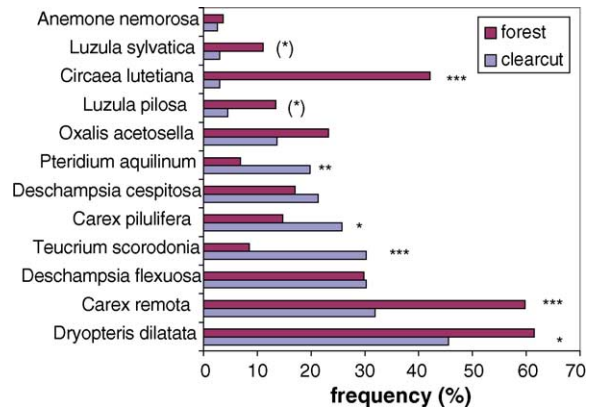


Fig. 2. Frequency of forest species in four clearcuts and surrounding forest (up to 150 m around the clearcut). Species are ranked by frequency in clearcuts. Asterisks indicate significance of Chi-square tests between clearcuts and surroundings: (*) $P < 0.06$; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

higher abundance in the recently cut areas. Results for *Carex pilulifera* and *Dryopteris dilatata* were marginally significant. Cover differences of *Pteridium aquilinum* were particularly striking (30.40 and 3.74% in old versus young clearcuts, respectively), but these are not significant due to a small sample size. Recovery occurred in clearcuts of both age classes for most species studied (Table 4). Five species (*Anemone nemorosa*, *Carex remota*, *Deschampsia cespitosa*,

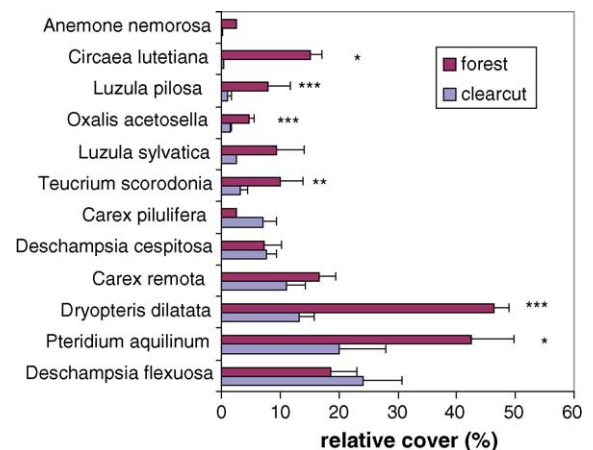


Fig. 3. Relative cover (mean + 1 S.E.) of forest species in four clearcuts and surrounding forest (up to 150 m around the clearcut). Species are ranked by cover in clearcuts. Asterisks indicate significance of Mann–Whitney U -test between clearcuts and surroundings: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

Table 2

Mann–Whitney *U*-test for plant functional groups between old (13 years) and young (5 years) clearcuts

	Mean		S.D.		Z	
	Old	Young	Old	Young	Adjusted	<i>P</i> -level
Sp richn	5.23	5.65	3.36	2.88	−0.6874	0.4917
%anc	19.71	35.72	23.32	25.76	−2.7807	0.0054
%forsp	38.68	45.88	25.36	27.74	−0.8449	0.3981
%clearcutsp	12.35	10.27	14.07	16.17	−0.8614	0.3889
%C+	22.18	11.93	20.13	12.37	−2.4209	0.0154
%CSR+	25.27	35.97	20.33	21.36	−2.4687	0.0135
%R+	2.05	2.22	5.10	6.21	−0.2420	0.8087
%S+	8.51	20.46	10.08	22.15	−2.3913	0.0167
%WIND	33.01	25.92	25.03	21.39	−1.5612	0.1184
%ANIM	6.92	3.46	11.21	6.47	−1.0376	0.2994
%AUTO	5.97	13.58	8.73	14.44	−2.2339	0.0254
%NUM_1000	10.41	13.86	13.95	16.15	−0.7613	0.4464
%NUM_10000	3.80	4.14	8.09	8.59	−0.0268	0.9785
%MASS_02	8.49	7.22	9.68	9.14	−0.6196	0.5355
%MASS_05	3.80	9.96	6.57	12.50	−2.1244	0.0336
%MASS_10	0.70	1.55	2.50	4.28	−0.7120	0.4764
%MASS_20	2.67	1.62	5.18	5.27	−1.3148	0.1885
%MASS_100	4.79	3.39	7.65	6.47	−0.7776	0.4367
%FORM_25	11.44	12.68	15.96	14.31	−0.4981	0.6183
%LON_LPER	13.54	15.04	15.33	14.77	−0.3175	0.7508
%LON_SPER	2.09	5.08	5.15	8.26	−1.5018	0.1331
%LON_TRAN	5.15	4.66	9.05	9.57	−0.5634	0.5731

Except for the mean species number per plot (Sp richn), all other parameters are relative numbers (%); anc: ancient-forest species; forsp: forest species; clearcutsp: clearcut species; C+: competitors; CSR+: competitive and stress-tolerant ruderals; R+: ruderals; S+: stress tolerants; WIND: species with wind-dispersed diaspores; ANIM: species with animal-dispersed diaspores; AUTO: diaspores with self-dispersion; NUM_1000: species with less than 1000 diaspores per shoot; NUM_10000: species with 1001 to 10000 diaspores per shoot; MASS_02: species with diaspores of less than 0.2 mg; MASS_05: species with diaspores between 0.21 and 0.5 mg; MASS_10: species with diaspores between 0.51 and 1.00 mg; MASS_20: species with diaspores between 1.01 and 2.00 mg; MASS_100: species with diaspores between 2.01 and 10.00 mg; FORM_25: species with diaspores of length/breadth ratio between 1.5 and 2.5; LON_LPER: species with long-term persistent seeds (>5 years); LON_SPER: species with short-term persistent seeds (>1 year but <5 years); LON_TRAN: species with transient diaspores (<1 year).

Table 3

Mann–Whitney *U*-test for forest species cover between old (13 years) and young (5 years) clearcuts

	Mean		S.D.		Z	
	Old	Young	Old	Young	Adjusted	<i>P</i> -level
<i>Anemone nemorosa</i>	0.20	0.20	0.00	0.00	0.0000	1.0000
<i>Carex pilulifera</i>	3.74	8.54	6.36	10.68	−1.8982	0.0576
<i>Carex remota</i>	18.61	5.62	19.72	5.65	−2.0546	0.0399
<i>Circaea lutetiana</i>	0.00	0.50	0.00	0.00	−2.5587	0.0105
<i>Deschampsia cespitosa</i>	5.62	8.55	6.25	6.82	−0.5533	0.5799
<i>Deschampsia flexuosa</i>	2.50	26.52	0.00	30.09	−1.3519	0.1763
<i>Dryopteris dilatata</i>	19.59	9.71	15.21	11.58	−1.8128	0.0698
<i>Luzula pilosa</i>	0.35	2.50	0.21	0.00	−3.0136	0.0025
<i>Luzula sylvatica</i>	0.00	2.50	0.00	0.00	−0.7236	0.4696
<i>Oxalis acetosella</i>	1.00	1.70	1.00	1.09	−0.9899	0.3222
<i>Pteridium aquilinum</i>	30.40	3.74	32.10	6.36	−1.5542	0.1201
<i>Teucrium scorodonia</i>	1.35	3.47	1.62	5.37	−0.7530	0.4513

Table 4
Colonisation rate of studied species in old (13 years) and young (5 years) clearcuts

Species	Colonisation rate (%) in clearcuts	
	Old	Young
<i>Anemone nemorosa</i>	36	22
<i>Carex pilulifera</i>	117	331
<i>Carex remota</i>	72	60
<i>Circaea lutetiana</i>	0	24
<i>Deschampsia cespitosa</i>	232	183
<i>Deschampsia flexuosa</i>	15	194
<i>Dryopteris dilatata</i>	58	95
<i>Luzula pilosa</i>	83	22
<i>Luzula sylvatica</i>	0	51
<i>Oxalis acetosella</i>	91	132
<i>Pteridium aquilinum</i>	563	339
<i>Teucrium scorodonia</i>	53	443

Species' colonisation rate in clearcuts was calculated as the percentage of the total number of target plots which were occupied, divided by the percentage of the total number of grid cells in the surrounding forest matrix (likely source area) which were occupied.

Luzula pilosa, *Pteridium aquilinum*) showed a higher colonisation rate in the oldest patches, while the opposite pattern was observed for the other seven species (Table 4).

The similarity between vegetation samples along the transects within the clearcuts (Fig. 4) shows that the more the plots are located inside the clearcuts, the more they are similar with each other. The mean similarity index of 0.17 for plots situated at the forest edges gradually increased up to 0.31 for samples located at 30 m from the edge in the clearcuts. The

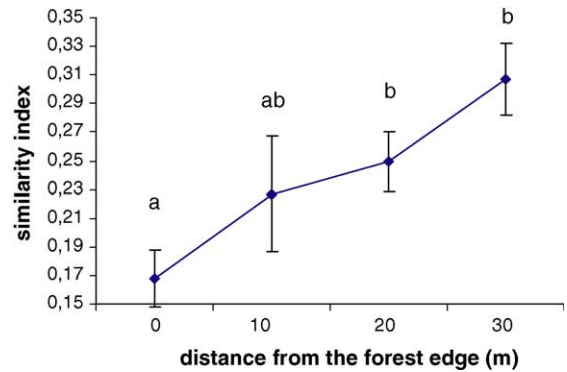


Fig. 4. Mean values (+S.E.) of the Sørensen's similarity index along gradients from the forest edge into the clearcut ($F = 4.52$; d.f. 3,106; $P = 0.0050$). Differing letters indicate significant differences using a one-way ANOVA followed by a Student's Newman Keuls test.

spatial variability in the species cover along gradients up to 40 m into the clearcuts and 150 m into the forest are given in Fig. 5. Some species showed a progressive decrease in their abundance within the forest as they progress towards the clearcut (e.g. *Dryopteris dilatata*, *Luzula pilosa*, *L. sylvatica*, *Oxalis acetosella*). Others, such as *Anemone nemorosa* and *Circaea lutetiana*, are characterised by a regular cover in the forest which suddenly drops at the edge and sustains a very low level throughout the clearcut. Striking is the fact that the abundance of most of the species shows a higher variability in the clearcuts in comparison with the forest. These results are confirmed when examining the colonisation rate of each species, calculated on the

Table 5

Kruskal–Wallis test for the colonisation rate of forest species in clearcuts compared with three buffer zones (50, 100, 150 m from the edge) in the surrounding matrix

	colonisation rate			Kruskal–Wallis		
	BUF50	BUF100	BUF150	<i>H</i>	<i>n</i>	<i>P</i> -level
<i>Anemone nemorosa</i>	43	72	0	3.00	4	0.2231
<i>Carex pilulifera</i>	270	202	271	0.56	8	0.7575
<i>Carex remota</i>	70	54	73	0.04	12	0.9807
<i>Circaea lutetiana</i>	12	10	13	0.04	12	0.9783
<i>Deschampsia cespitosa</i>	106	191	275	2.85	11	0.2407
<i>Deschampsia flexuosa</i>	198	123	72	2.71	10	0.2586
<i>Dryopteris dilatata</i>	89	74	65	0.97	12	0.6141
<i>Luzula pilosa</i>	21	0	52	1.48	8	0.4779
<i>Luzula sylvatica</i>	45	35	25	0.31	7	0.8569
<i>Oxalis acetosella</i>	158	102	76	2.93	10	0.2314
<i>Pteridium aquilinum</i>	238	293	375	0.04	8	0.9819
<i>Teucrium scorodonia</i>	405	338	52	2.57	8	0.2773

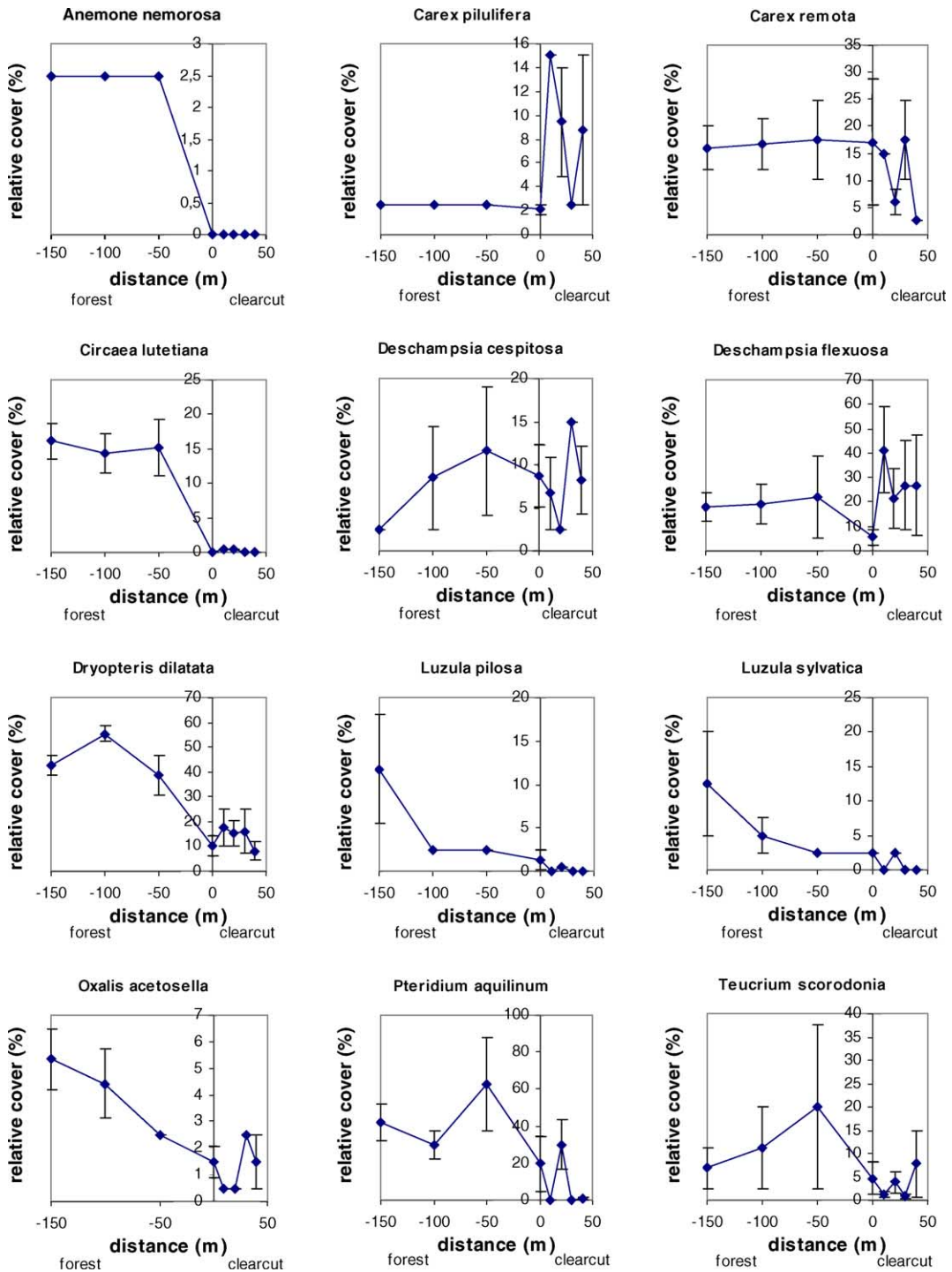


Fig. 5. Spatial variability of the relative cover (mean + 1 S.E.) of forest species in four clearcuts and surrounding forest (up to 150 m around the clearcut).

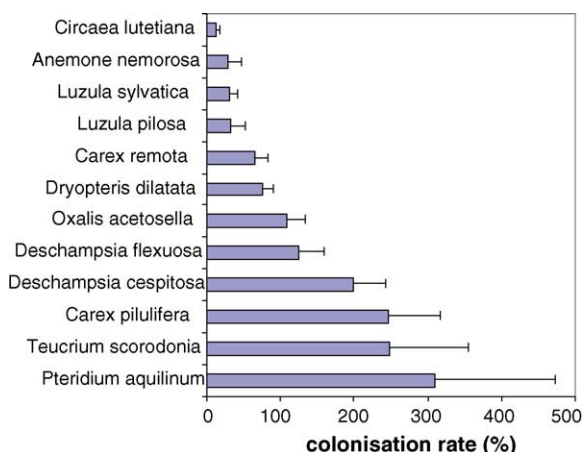


Fig. 6. Mean values (+S.E.) of the colonisation rate of studied species (Kruskal–Wallis $H = 38.02$; d.f. = 9; $n = 94$; $P < 0.0001$). Species' colonisation rate in clearcuts was calculated as the percentage of the total number of target plots which were occupied, divided by the percentage of the total number of grid cells in the surrounding forest matrix (likely source area) which were occupied.

basis of their frequency inside and outside the clearcut (Fig. 6). This diagram illustrates the high colonisation rate of *Pteridium aquilinum*, *Teucrium scorodonia*, *Carex pilulifera*, *Deschampsia cespitosa*, while it clearly appears that taxa such as *Circaea lutetiana*, *Anemone nemorosa*, *Luzula sylvatica* and *L. pilosa* have a very poor recovery according to these criteria. Colonisation rates calculated according to the distance clearcut-forest, i.e. compared with the three buffer zones (50, 100 and 150 m) defined in the surrounding matrix, progressively increased with the distance for *Deschampsia cespitosa* and *Pteridium aquilinum*, while they showed a decreasing trend for *Deschampsia flexuosa*, *Dryopteris dilatata*, *Luzula sylvatica*, *Oxalis acetosella* and *Teucrium scorodonia*. However, due to a small sample size, these results are not significant according to the Kruskal–Wallis test (Table 5).

5. Discussion

5.1. Effects of clearcutting on forest herbs

Of the 12 forest species analysed, 8 showed significantly different frequencies and/or abundances between clearcuts and forest. With a dramatic decrease in cover and/or frequency, most of these

species seem to be affected by clearcutting. This is consistent with the results of Hannerz and Hånell (1997) who have shown, for Swedish Norway spruce forests, that forest species which are relatively common before harvesting are greatly reduced in the clearcut. The causes may vary from one species to the other, but it is likely that microclimate is of paramount importance. Under higher levels of light, shade-tolerant herbs are known to be competitively inferior, and microclimate created after clearcutting produces high light flux to the ground which may cause local extinction of field layer species that survived the clearcutting. Another possible explanation is that the increased sunlight may dry out the humus layer in the clearcut and the water balance of the species could be affected (Atlegrim and Sjöberg, 1996). Moisture deficiency may reduce photosynthesis and growth (Atlegrim and Sjöberg, 1996) and may be an explanation for the low cover of *Circaea lutetiana*, *Dryopteris dilatata*, *Luzula pilosa*, *Oxalis acetosella*, *Pteridium aquilinum* and *Teucrium scorodonia* in clearcuts. Harvesting machines which drive over the species may induce severe mechanical damage, and can also be responsible for the low cover of these species in the clearcut. Nevertheless, competition from other competitive species (e.g. grasses) cannot be excluded (Hester et al., 1991), certainly for species with a low stature such as *Luzula pilosa* and *Oxalis acetosella*.

Meier et al. (1995) suggest five possible ecological mechanisms for reducing or limiting alpha diversity of forest herbs in logged stands, three of which may also account for the slow recovery of some herbaceous species: (1) logging reduces populations of rarer herbs. This is for example the case with *Anemone nemorosa* in this study; (2) populations of forest-floor species are further reduced during the successional stages following logging, either by inability to adapt to changed microclimate or by competition with r -selected species that are better dispersers and better able to tolerate desiccation and increased radiation. We already showed this phenomenon in another study (Godefroid et al., in preparation) where it was found that species such as *Dryopteris dilatata* and *Luzula sylvatica* are not able to survive a low level of air humidity; (3) forest-floor herbs have slow growth and reproduction rates, thus population densities increase slowly; (4) many forest-floor herbs are clonal (e.g.

Anemone nemorosa or *Oxalis acetosella* in our study sites), ant-dispersed (e.g. *Luzula pilosa* or *L. sylvatica*), or gravity-dispersed, thus they are slow to reoccupy suitable habitat once extirpated or greatly reduced in population numbers; and (5) logging results in less-than-optimal conditions for forest-floor herb reproduction by modifying microhabitats on the forest floor and by temporarily eliminating gap-phase succession.

5.2. Recovery in clearcut areas

Development of the vegetation following clear-felling depends on seeds and established plants already present (Hill and Stevens, 1981). However, many forest species do not accumulate persistent soil seed banks (Kjellsson, 1992). Therefore, their re-establishment is dependent on migration from adjacent areas (Brunet and Von Oheimb, 1998). In our experiment, the cover of most of the studied species was not significantly different according to the clearcut age. It seems therefore that clearcutting may have a persistent effect on residual species. This result contrasts with a number of previous studies. In forest dominated by mature and old-growth *Pseudotsuga menziesii*, Halpern and Spies (1995) found that residual forest taxa regained dominance within 5–10 years after logging and burning, and according to these authors the regenerative structure (e.g. tubers, roots, rhizomes) of most plants are buried deeply enough to ensure survival. Most of the species studied by Grashof-Bokdam and Geertsema (1998) in secondary woodland in the Netherlands had a colonisation rate higher in the oldest target patches compared to young patches. The overall patterns observed in our study do not confirm this, and it corroborates the statement of Hannerz and Hånell (1997) that the level of the impact caused by clearcutting is related to the forest type and disturbance history.

In our system of beech high forest on acidic silty soil, the recovery of forest herbs is generally not better 13 years than 5 years after clearcutting. This pattern indicates either recruitment or dispersal limitation. As highlighted by Brunet and Von Oheimb (1998), who found maximum dispersal distances of 50 m in 30–75 years, local development of a typical woodland field layer vegetation is a slow process, advancing on average at a rate of some dm year^{-1} . So, the poor dispersal

abilities of most forest species, combined with the fact that growth conditions for the (re)establishment of forest herbs (high light intensity and low air humidity, nutrient leaching, competition by grasses and grass-like plants) are not yet favourable after 13 years, likely account for the absence of fast recovery. Severe root or shoot competition with early successional species or tree regeneration after clearcutting probably also play a key role in the cover decrease of some species (e.g. *Carex pilulifera*, *Circaea lutetiana*, *Luzula pilosa*) in older areas. Exceptions to the overall pattern found are *Carex remota*, *Dryopteris dilatata* and *Pteridium aquilinum* which show a higher cover in older clearcuts, indicating a certain recovery. A possible explanation for this is that these species have better dispersal capacities or regenerative strategies. *Dryopteris dilatata* regenerates by means of numerous wind-dispersed spores which may become incorporated into a persistent spore bank, while *Pteridium aquilinum* is known to regenerate mainly by vegetative means from deep underground rhizome (Grime et al., 1988). This confirms Hill and Stevens (1981)' statement that immigration is largely confined to species with air-borne propagules.

When looking at the colonisation rate, based on the frequency data, we found some species having a rate over 100%, which indicates that they are more frequent in target patches (clearcuts) than in source patches (surrounding forest). For instance, the high colonisation rates of *Carex pilulifera* and *Teucrium scorodonia* are remarkable in comparison with the other species. This is consistent with previous studies that have found that both species produce a persistent seed bank (Hill and Stevens, 1981; Kjellsson, 1985; Thompson et al., 1997).

The progressive cover decrease of some species within the forest in the direction of the clearcut indicates that they do not tolerate small microclimatic changes. It is likely that these species need particular forest microclimatic conditions as we highlighted in a previous experiment for *Dryopteris dilatata* and *Luzula sylvatica* which were found to be restricted to those sites with a high level of air humidity (Godefroid et al., in preparation). Conversely, other species such as *Anemone nemorosa* and *Circaea lutetiana* seem to better tolerate small shifts in air and soil temperature and moisture within the forest (i.e. have a higher tolerance threshold) as they keep a constant abundance there till they reach the edge

where they undergo a sudden cover reduction as a consequence of the abrupt microclimate change.

The absence of significant patterns in colonisation rates between different buffer zones may be explained partly by the low number of studied sites that did not provide enough variation in the data, which makes the comparisons more difficult. It could also be argued that this result reflects the absence of a real pattern, but we believe that the progressive downward or upward trend of most of the studied species is ecologically meaningful. For instance, the downward trend in the colonisation rate of *Deschampsia flexuosa*, *Dryopteris dilatata*, *Luzula sylvatica*, *Oxalis acetosella* and *Teucrium scorodonia*, compared with the distance to the clearcut, can be attributed to dispersal and/or recruitment limitation. This is in accordance with Grashof-Bokdam and Geertsema (1998) who have shown that the probability of occurrence of many forest species drops to around 0.2 when distance from target patch to source patch increases from 0 to 100 m. However, this pattern is not so easy to explain as, like us, these authors also found no clear differences in colonisation rate between different dispersal groups. We had indeed expected that species having minute wind-dispersed diaspores would not have shown any trend in their colonisation rate through the three buffer zones as they can be dispersed at long distances. This is not the case as, even for these species, we found a clear trend. Additional studies are therefore needed to investigate the persistence of these patterns and to determine which of these limitation factors is predominant for each species.

5.3. Conclusion and management implications

Data collected so far indicate that clearcutting has an expected overall negative impact on shade-tolerant species. Results of this study show that many plant functional groups with a high conservation value, such as ancient-forest species, stress-tolerant species and species with dispersal limitation (autochorous) show a progressive decrease in time after clearcutting. Species frequencies, covers and colonisation rates calculated in our experiment show that most of the studied species are not able to recover such disturbed sites within a few years. This failing recovery is a matter of dispersal capacity and/or a problem of habitat quality. Both are likely acting in combination,

as all species are to some extent dispersal and recruitment-limited although the degree varies between species (Eriksson and Ehrlén, 1992). In order to reduce the dispersal limitation problem, management without large clear fellings may be necessary to facilitate the recovery of dispersal-limited plant species from the surrounding forest matrix. Remedial measures to facilitate forest regeneration in the old gaps may include shallow tillage. This measure is used, particularly in Scandinavia, to encourage natural regeneration, and to improve the survival and early growth of seedlings (Matthews, 1999). This technique has been experimentally implemented in our study area, with promising results for the regeneration of forest herbs (Godefroid et al., in preparation). For overcoming the main disadvantage of low habitat quality, we believe that harvesting methods that never leave the ground completely bare have to be promoted in the future. For instance, slash and coarse woody debris can be left to break down slowly; by this way, the release of nutrients and the improvement of the microclimate near the ground can aid young plant to survive and grow (Matthews, 1999). Areas with shelterwood cutting usually provide relatively undisturbed microsites where sensitive species survive better than in clearcut areas (Reader, 1987; Hannerz and Hånell, 1997). This silvicultural system preserves also the forest microclimate as well as soil properties, and reduces the risk of invasion by competitive weeds (Matthews, 1999).

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Appendix A

Species which were found in the investigated clearcuts. Anc. for. sp.: ancient-forest species according to Honnay et al. (1998); strategy: pooled Grime's strategies according to Graae and Sunde (2000): C+: competitors; CSR+: competitive and stress-tolerant ruderals; R+: ruderals; S+: stress tolerants; ecol. gr.:

Table A.1

Species	Plant traits				Diaspore traits			
	Anc. for. sp.	Strategy	Ecol. gr.	Dispersal	Number	Weight (mg)	Shape	Longevity
<i>Agrostis stolonifera</i>		CSR+	2	WING	1–1000	<0.2	1.5–2.5	LP
<i>Anemone nemorosa</i>		S+	9	ELAI	1–1000	1.01–2.00	>2.5	TR
<i>Athyrium filix-femina</i>		C+	9					
<i>Cardamine flexuosa</i>		R+	9					
<i>Carex pallescens</i>	x		8					
<i>Carex pilulifera</i>	x	S+	7					
<i>Carex remota</i>			9					
<i>Centaurium erythraea</i>		CSR+	8					
<i>Circaea lutetiana</i>	x	CSR+	9					
<i>Dactylis glomerata</i>		C+	5	SHED	1–1000	0.51–1.00	1.5–2.5	TR
<i>Deschampsia cespitosa</i>	x	CSR+	2	SHED	>100000	0.21–0.50	>2.5	SP
<i>Deschampsia flexuosa</i>	x	S+	9					
<i>Digitalis purpurea</i>		CSR+	8					
<i>Dryopteris carthusiana</i>			9					
<i>Dryopteris dilatata</i>		CSR+	9					
<i>Dryopteris filix-mas</i>		CSR+	9	SHED	>100000	Too small	<1.5	SP
<i>Epilobium angustifolium</i>		C+	8					
<i>Epilobium roseum</i>			8					
<i>Epilobium tetragonum</i>			8	PLUM	1001–10000	<0.2	1.5–2.5	LP
<i>Galeopsis tetrahit</i>		R+	8	BURR	1–1000	0.51–1.000	<1.5	LP
<i>Galium aparine</i>		CSR+	8	BURR	1–1000	0.51–1.000	<1.5	TR
<i>Hieracium umbellatum</i>		S+	7	PAPP	1001–10000	0.21–0.50	>2.5	TR
<i>Holcus lanatus</i>		CSR+	5	SHED	1–1000	0.21–0.50	1.5–2.5	LP
<i>Hypericum perforatum</i>		CSR+	6	SHED	>100000	<0.2	1.5–2.5	LP
<i>Impatiens parviflora</i>			8	MAN	1–1000	0.51–1.000	1.5–2.5	TR
<i>Juncus effuses</i>		C+	2					
<i>Lapsana communis</i>		R+	8	SHED	1–1000	1.01–2.00	>2.5	LP
<i>Lonicera periclymenum</i>	x	CSR+	9					
<i>Lotus corniculatus</i>		S+	6	EXPL	1–1000	1.01–2.00	<1.5	LP
<i>Lotus pedunculatus</i>		CSR+	5					
<i>Luzula campestris</i>		S+	6	ELAI	1–1000	0.51–1.00	1.5–2.5	LP
<i>Luzula multiflora</i>			7					
<i>Luzula pilosa</i>	x	S+	9					
<i>Luzula sylvatica</i>	x		9					
<i>Moehringia trinervia</i>		CSR+	9	ELAI	1–1000	0.21–0.50	<1.5	SP
<i>Myosotis arvensis</i>		R+	8	BURR	1–1000	0.21–0.50	1.5–2.5	LP
<i>Oxalis acetosella</i>	x	S+	9					
<i>Polygonum hydropiper</i>			2					
<i>Pteridium aquilinum</i>	x	C+	9					
<i>Ranunculus repens</i>		CSR+	2	SHED	1–1000	0.51–1.000	1.5–2.5	LP
<i>Rubus fruticosus s.l.</i>								
<i>Rumex acetosella</i>		CSR+	6	WING	1–1000	0.21–0.50	1.5–2.5	LP
<i>Scrophularia nodosa</i>			9					
<i>Stachys sylvatica</i>		C+	9	BURR		1.01–2.00	<1.5	LP
<i>Stellaria media</i>		R+	1	DISBERRY	>100000	0.21–0.50	<1.5	LP
<i>Teucrium scorodonia</i>	x	CSR+	9					
<i>Urtica dioica</i>		C+	8	WING	1001–10000	<0.2	<1.5	LP

ecological group according to Stieperaere and Fransen (1982): 1: pioneers from disturbed, artificial, anthropised habitats; 2: pioneers from disturbed semi-natural habitats, on open humid soils; 5: plants from mesotrophic to eutrophic humid to damp grasslands; 6: plants from dry grasslands; 7: plants from heathlands; 8: plants from clear-felled areas; 9: forest plants. Diaspore traits according to Kleyer (1995). BURR: burrs; DISBERRY: fleshy berries; ELAI: elaiosomes; EXPL: explosive discharge; MAN: dispersal by man; PAPP: diaspores with umbrella-like structures (i.e. pappus); PLUM: plumed diaspores; SHED: light diaspores; WING: winged diaspores. Shape: length/breadth ratio; LP: species with long-term persistent seeds (>5 years); SP: species with short-term persistent seeds (>1 year but <5 years); TR: species with transient diaspores (<1 year). Missing values mean that no information is available. See Table A.1.

References

- Ash, J.E., Barkham, J.P., 1976. Changes and variability in the field layer of a coppiced woodland in Norfolk. England. *J. Ecol.* 64, 697–712.
- Atlegrim, O., Sjöberg, K., 1996. Response of bilberry (*Vaccinium myrtillus*) to clearcutting and single-tree selection harvests in uneven-aged boreal *Picea abies* forests. *For. Ecol. Manage.* 86, 39–50.
- Bock, M.D., Van Rees, K.C.J., 2002. Forest harvesting impacts on soil properties and vegetation communities in the northwest territories. *Can. J. For. Res.* 32, 713–724.
- Bossuyt, B., Deckers, J., Hermy, M., 1999a. A field methodology for assessing man-made disturbance in forest soils developed in loess. *Soil Use Manage.* 15, 14–20.
- Bossuyt, B., Hermy, M., Deckers, J., 1999b. Migration of herbaceous plant species across ancient-recent forest ecotones in central Belgium. *J. Ecol.* 87, 628–638.
- Brunet, J., Von Oheimb, G., 1998. Migration of vascular plants to secondary woodlands in southern Sweden. *J. Ecol.* 86, 429–438.
- Brunet, J., Falkengren-Grerup, U., Tyler, G., 1996. Herb layer vegetation of south Swedish beech and oak forests – effects of management and soil acidity during one decade. *For. Ecol. Manage.* 88, 259–272.
- Brunet, J., Falkengren-Grerup, U., Tyler, G., 1997. Pattern and dynamics of the ground vegetation in south Swedish *Carpinus betulus* forests: importance of soil chemistry and management. *Ecography* 20, 513–520.
- Butaye, J., Jacquemyn, H., Hermy, M., 2001. Differential colonization causing non-random forest plant community structure in a fragmented agricultural landscape. *Ecography* 24, 369–380.
- Collins, B.S., Pickett, S.T.A., 1988. Demographic responses of herb layer species to experimental canopy gaps in a northern hardwoods forest. *J. Ecol.* 76, 437–450.
- Deconchat, M., Balent, G., 2001. Effect of logging on vegetation at a fine scale. *Ann. For. Sci.* 58, 315–328.
- Dierschke, H., 1988. Pflanzensoziologische und ökologische Untersuchungen in Wäldern Süd-Niedersachsens. IV. Vegetationsentwicklung auf langfristigen Dauerflächen von Buchenwald-Kählschlägen. *Tuexenia* 8, 307–326.
- Duffy, D.C., Meier, A.J., 1992. Do Appalachian herbaceous understories ever recover from clearcutting. *Conserv. Biol.* 6, 196–201.
- Dumortier, M., Butaye, J., Jacquemyn, H., Van Camp, N., Lust, N., Hermy, M., 2002. Predicting vascular plant species richness of fragmented forests in agricultural landscapes in central Belgium. *For. Ecol. Manage.* 158, 85–102.
- Dupouey, J.L., Dambrine, E., Laffite, J.D., Moares, C., 2002. Irreversible impact of past land use on forest soils and biodiversity. *Ecology* 83, 2978–2984.
- Dzwonko, Z., Loster, S., 1992. Species richness and seed dispersal to secondary woods in southwestern Poland. *J. Biogeogr.* 19, 195–204.
- Ehrlén, J., Eriksson, O., 2000. Dispersal limitation and patch occupancy in forest herbs. *Ecology* 81, 1667–1674.
- Eriksson, O., Ehrlén, J., 1992. Seed and microsite limitation of recruitment in plant populations. *Oecologia* 91, 360–364.
- ESRI, 1996. ArcView GIS. Environmental Systems Research Institute.
- Gibb, H., Hochuli, D.F., 2002. Habitat fragmentation in an urban environment: large and small fragments support different arthropod assemblages. *Biol. Conserv.* 106, 91–100.
- Gilliam, F.S., Turrill, N.L., Adams, M.B., 1995. Herbaceous-layer and overstory species in clearcut and mature central Appalachian hardwood forests. *Ecol. Appl.* 5, 947–955.
- Graae, B.J., Sunde, P.B., 2000. The impact of forest continuity and management on forest floor vegetation evaluated by species traits. *Ecography* 23, 720–731.
- Grashof-Bokdam, C.J., 1997. Forest species in an agricultural landscape in the Netherlands: effects of habitat fragmentation. *J. Veg. Sci.* 8, 21–28.
- Grashof-Bokdam, C.J., Geertsema, W., 1998. The effect of isolation and history on colonization patterns of plant species in secondary woodland. *J. Biogeogr.* 25, 837–846.
- Grime, J.P., Hodgson, J.G., Hunt, R., 1988. Comparative plant ecology. A functional approach to common British species. Unwin-Hyman, London.
- Halpern, C.B., Spies, T.A., 1995. Plant species diversity in natural and managed forests of the Pacific Northwest. *Ecol. Appl.* 5, 913–934.
- Hannerz, M., Hånell, B., 1997. Effects on the flora in Norway spruce forests following clearcutting and shelterwood cutting. *For. Ecol. Manage.* 90, 29–49.
- Herbauts, J., El Bayad, J., Gruber, W., 1996. Influence of logging traffic on the hydromorphic degradation of acid forest soils developed on loessic loam in middle Belgium. *For. Ecol. Manage.* 87, 193–207.
- Herbauts, J., El Bayad, J., Gruber, W., 1998. The impact of mechanized forestry techniques on the physical deterioration of soils –

- the case of acid, silty soils in the Soignes Forest (Belgium) (in French). *Rev. For. Fr.* 2, 124–137.
- Hermly, M., Stieperaere, H., 1981. An indirect gradient analysis of the ecological relationships between ancient and recent riverine woodlands to the south of Bruges (Flanders, Belgium). *Vegetatio* 44, 43–49.
- Hester, A.J., Miles, J., Gimingham, C.H., 1991. Succession from heather moorland to birch woodland. II. Growth and competition between *Vaccinium myrtillus*, *Deschampsia flexuosa* and *Agrostis capillaris*. *J. Ecol.* 79, 317–328.
- Hill, M.O., Stevens, P.A., 1981. The density of viable seed in soils of forest plantations in upland Britain. *J. Ecol.* 69, 693–709.
- Honnay, O., Degroote, B., Hermly, M., 1998. Ancient-forest plant species in Western Belgium: a species list and possible ecological mechanisms. *Belg. J. Bot.* 130, 139–154.
- Hubbard, W., Latt, C., Long, A., 1998. Forest Terminology for Multiple-use Management. SS-FOR-11, Series of the School of Forest Resources and Conservation. University of Florida, Gainesville.
- Kent, M., Coker, P., 1992. *Vegetation Description and Analysis. A Practical Approach*. Belhaven Press, London.
- Kirby, K.J., 1990. Changes in the ground flora of a broadleaved wood within a clear fell, group fells and a coppiced block. *Forestry* 63, 241–249.
- Kjellsson, G., 1985. Seed fate in a population of *Carex pilulifera* L. 2. Seed predation and its consequences for dispersal and seed bank. *Oecologia* 67, 424–429.
- Kjellsson, G., 1992. Seed banks in Danish deciduous forests: species composition, seed influx and distribution pattern in soil. *Ecography* 15, 86–100.
- Kleyer, M., 1995. Biological traits of vascular plants. A database. Arbeitsberichte Inst. f. Landschaftsplanung und Ökologie Univ. Stuttgart, N.F. Bd. 2.
- Lambinon, J., De Langhe, J.E., Delvosalle, L., Duvigneaud, J., 1998. Flora van België, het Groothertogdom Luxemburg, Noord-Frankrijk en de aangrenzende gebieden. Nationale Plantentuin van België, Meise.
- Louis, A., 1959. Carte des Sols de la Belgique. Texte explicatif de la planchette d'Uccle 102W. IRSIA.
- Mac Lean, D.A., Wein, R.W., 1977. Changes in understory vegetation with increasing stand age in New Brunswick forests: species composition, cover, biomass, and nutrients. *Can. J. Bot.* 55, 2818–2831.
- Matlack, G.R., 1994. Plant–species migration in a mixed-history forest landscape in eastern north-America. *Ecology* 75, 1491–1502.
- Matthews, J.D., 1999. *Sylvicultural Systems*. Oxford University Press, Oxford.
- McGarigal, K., Marks, B., 1995. FRAGSTATS: spatial pattern analysis program for quantifying landscape structure. Gen. Tech. Re PNW-GTR-351. US. Department of Agriculture, Forest Service, Pacific Northwest Research Station, Portland, OR.
- Meier, A.J., Bratton, S.P., Duffy, D.C., 1995. Possible ecological mechanisms for loss of vernal-herb diversity in logged eastern deciduous forests. *Ecol. Appl.* 5, 935–946.
- Peterken, G.F., 1974. A method for assessing woodland flora for conservation using indicator species. *Biol. Conserv.* 6, 239–245.
- Peterken, G.F., 1977. Habitat conservation priorities in British and European woodlands. *Biol. Conserv.* 11, 223–236.
- Peterken, G.F., Game, M., 1984. Historical factors affecting the number and distribution of vascular plant species in the woodlands of central Lincolnshire. *J. Ecol.* 72, 155–182.
- Reader, R.J., 1987. Loss of species from deciduous forest understory immediately following selective tree harvesting. *Biol. Conserv.* 42, 231–244.
- Rohand, K., Van Molle, M., Herbauts, J., Verbrugge, J.-C., 2000. Influence of logging traffic on physical and mechanical properties of a loamy leached soil in the Soignes Forest (in French). *Biotechnol. Agron. Soc. Environ.* 4, 181–189.
- Singleton, R., Gardescu, S., Marks, P.L., Geber, M.A., 2001. Forest herb colonization of postagricultural forests in central New York State, USA. *J. Ecol.* 89, 325–338.
- Statsoft Inc., 2001. STATISTICA (Data Analysis Software System), Version 6. Statsoft Inc., Tulsa, OK.
- Stieperaere, H., Fransen, K., 1982. Standaardlijst van de Belgische vaatplanten, met aanduiding van hun zeldzaamheid en socio-oecologische groep. *Dumortiera* 22, 1–41.
- Terborgh, J., 1974. The preservation of natural diversity: the problem of extinction prone species. *BioScience* 24, 715–722.
- Thompson, K., Bakker, J., Bekker, R., 1997. *The Soil Seed Bank of North West Europe: Methodology, Density and Longevity*. Cambridge University Press, Cambridge.
- Van der Hout, P., 2000. Testing the applicability of reduced impact logging in greenheart forest in Guyana. *Int. For. Rev.* 2, 24–32.
- Van der Meijden, R., 1999. *Heukels Interactive Flora van Nederland*. Wolters-Noordhoff, Groningen.
- Vanwijnsbergh, S., 2002. Management Plan Proposal for the Sonian Forest. Part Brussels Capital (in French and Dutch). Brussels Institute for Environmental Management, Forest Department, Brussels.
- Verheyen, K., Hermly, M., 2001. The relative importance of dispersal limitation of vascular plants in secondary forest succession in Muizen Forest. *Belgium J. Ecol.* 89, 829–840.
- Westhoff, V., van der Maarel, E., 1973. The Braun–Blanquet approach. In: Whittaker, R.H. (Ed.), *Handbook of Vegetation Science. Part V. Ordination and Classification of Vegetation*. Dr. W. Junk B.V. Publishers, The Hague, pp. 619–726.
- Whitney, G.G., Foster, D.R., 1988. Overstorey composition and age as determinants of the understory flora of woods of central New England. *J. Ecol.* 76, 867–876.