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Original article

Gaps promote plant diversity in beech forests (*Luzulo-Fagetum*), North Vosges, France

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Abstract – Windstorms are major disturbance factors in temperate forests of Western Europe. With climatic changes those events are likely to become more frequent. The study of their impacts on plant communities is essential. Therefore our objective was to evaluate the differences of the plant community after the 1999 windstorm that blew down approximately 968 000 ha across France. This study took place in the North Vosges (36 800 ha destroyed). The differences in species diversity, resource requirements and functional plant traits were analysed, with floristic surveys, between undisturbed forest (10 plots) and gaps ranging from 250 m^2 and 1.8 ha (65 plots). The results showed a higher plant diversity in the gaps. This increase was mainly due to the presence of more light-requiring forest species and more species with high dispersal abilities (anemochorous or long-term persistent seedbank species). On the contrary, species with greater competitive abilities increased their cover and decreased the diversity. The other resource requirements were not modified in the gaps. This short-term study showed that functional traits and their interactions play a major role to determine the species composition in gaps, especially compared to the species requirements for the resources, except light.

forest gaps / vegetation changes / species diversity / functional traits / Ellenberg indicator values

Résumé – Les trouées favorisent la diversité végétale en hêtraie (*Luzulo-Fagetum*), dans les Vosges du Nord, France. Les tempêtes sont un facteur perturbateur principal des forêts tempérées d'Europe de l'Ouest. Suite aux changements climatiques, celles-ci deviennent de plus en plus fréquentes. Il apparaît essentiel de mieux comprendre leurs impacts sur les communautés végétales. Notre objectif était donc d'étudier les variations de la communauté végétale, en terme de diversité spécifique, d'exigences écologiques et de traits de vie des espèces. Cette étude fait suite à la tempête de 1999 ayant ravagé la France et provoqué des chablis massifs de l'ordre de 968 000 ha, dont 36 800 ha dans les Vosges du Nord. Des relevés de végétation ont été réalisés, dans une hêtraie des Vosges du Nord, dans 65 placettes au sein de trouées de 250 m^2 à 1,8 ha et dans 10 placettes sous forêt non perturbée. Les résultats ont mis en évidence une plus grande diversité végétale au sein des trouées. Cette augmentation résultait essentiellement d'une augmentation du nombre d'espèces forestières héliophiles (telles que les espèces de lisières) et d'espèces à grande capacité de dissémination (espèces anemochores ou à banque de graines permanente). Par contre, le recouvrement des espèces à plus grande capacité compétitrice augmente, ce qui provoque une diminution de la diversité. Les autres caractéristiques écologiques de la communauté végétale ont été peu modifiées par l'apparition des trouées. Cette étude à court terme a mis en évidence que la composition spécifique des trouées résulte essentiellement des traits fonctionnels et leur interaction, surtout en comparaison avec leurs exigences écologiques hormis celle pour la lumière.

trouées / changement de végétation / diversité spécifique / traits fonctionnels / coefficients d'Ellenberg

1. INTRODUCTION

In December 1999, two catastrophic windstorms occurred across Northern and Southern France respectively, with wind speed reaching 140 to 170 km/h, and locally up to 200 km/h. Numerous forests were blew down, with approximately 968 000 ha partially or totally destroyed. Fifty percent of this area showed weak damage (windthrow of 10 to 50% of the forest), 30% important damage (50 to 90% of the forest) and 20% with severe problems (more than 90% of the forest). The total damage was estimated in volume to be about 139.6 millions cubic meters corresponding to more than three times the average annual harvest [66]. In North Vosges, 38 635 ha were partially or totally blew down, including 8 941 ha of beech forest. The estimated destroyed volume was about 566 598 m^3, with 203 518 m^3 of beech, corresponding to 5% of the total volume of the region, and 4.4% of the total volume of beech. Such event, with a sudden change of the environment, may play a critical role on forest plant community related to its structure and dynamics. Indeed, several studies showed that disturbing

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events, especially wind in the temperate forests in Western Europe, play an important role in the dynamic of natural forests, by creating sites for growth of new individuals or species [32, 42, 44]. Moreover due to climatic changes, such events are getting more frequent and their frequency is likely to increase. It is therefore important to understand their impacts on the forest as well as the component of the forest ecosystem such as diversity and structure of the plant community.

The major impact of such events is the creation of large windthrows as well as canopy gaps of different sizes. The effect of such canopy gaps on the tree regeneration has received some attention, particularly in natural and managed forest of North America [3, 11, 48]. However, the effect of canopy gaps on the ground layer vegetation has been less studied, and studies have focused on small to medium gaps, produced by the fall of a single tree or groups of trees, ranging from several square meters to about 2000 m^2 [12, 13, 23, 37]. Those studies showed that plant richness increases already in small gaps. The effect of canopy gaps on the environmental factors is also quite well known [10, 45, 56]. Forest gaps are characterized by a strong change of many factors such as air and soil temperatures, air and soil moistures, irradiance, wind speed and soil properties (e.g., humus mineralization and humification) [10, 45, 56]. The resource availability (light, water and nutrients) increases with disturbances [7, 11]. Those environmental variations interact with plant physiology and have thus an effect on species diversity [61]. This increase in resource availability promotes a fast growth of the early successional tree species [4, 46]. However, the impact of windstorm on the resource requirement of the plant community is less known.

To understand the plant community response after a major disturbance like a windstorm, it is necessary to focus not only on its quantitative aspects (number and distribution) or its composition but also on the life traits of the species [57]. Life traits and functional ecology have recently received attention [14, 24, 33, 34, 60, 65]. The study of functional diversity in different ecosystems has to be emphasized because it plays an important role in ecosystem processes [15, 60]. The functioning of an ecosystem is governed by the functional traits of individuals, the distribution and abundance of these individuals and their biological activities [38]. The functional traits may also be helpful to understand and predict the distribution and abundance of plant species in forest habitat [26, 65]. Moreover some authors demonstrated a relation between functional traits and disturbance or management practices and assumed that there is a pattern of response according to the species traits [15, 24, 34]. Therefore the functional and compositional parts of the diversity are crucial for conservation purposes. The functional part may be approached by the species strategies relative to regeneration, growth and dispersal [33]. According to Weiher et al. [65] the following functional “core” traits are believed to be biologically significant and important for plant dynamics: dispersal type, seed mass and seed bank (reproductive traits) and life cycle, maximum canopy height at maturity and vegetative spread (vegetative traits). The compositional part of the plant community may be examined by the species autecological attributes [51].

The aim of this study was to evaluate the effect of gap formation on the plant diversity (in species number and composition) after a windstorm in a (*Luzulo-Fagetum*) beech forest (North Vosges, France). On the hypothesis of a higher species richness in the gaps compare to the species richness under undisturbed forest, the study addressed the following questions: (1) is there any indicator species of forest and gaps, (2) are there some changes of the resource requirements of the plant community, (3) does the functional diversity (proportion of species traits) differ between forest and gaps?

2. MATERIALS AND METHODS

2.1. Study site

The study site took place in the forest of “La Petite Pierre Sud” located in the North Vosges, France (7° 19’ lat. N., 48° 51’ long. E.). It is part of the low sandstone Vosges, a hilly landscape composed of pastures and woodlands. It is characterized by a temperate semi-continental climate with a mean annual rainfall of 835 mm and a mean annual temperature of 8.9 °C. The altitude ranges from 280 to 377 m and the forest lays on acidic brown soil with a good drainage. The study site is situated in a forest of 4600 ha dominated at 75% of total cover by beech (*Fagus sylvatica* L.), with other species e.g. oak (*Quercus petraea* (Mattme.) Liebl.) at 15%, fir (*Abies alba* Mill.) at 5% and in smaller proportions, spruce (*Picea abies* (L.) Karst.), larch (*Larix decidua* Mill.), Scots pine (*Pinus sylvestris* L.), and other broadleaved species. The potential vegetation belongs to the *Luzulo-Fagetum* [50].

The forest of “La Petite Pierre Sud” was severely damaged during the December 1999 windstorm. Eight hundred ha were blew down, from which 600 ha had more than 60% of fallen trees. In this study, a sample site of 100 ha was selected in the forest where numerous gaps of various sizes were found.

2.2. Sampling design and data collection

A total of 65 study plots were set in 42 different forest gaps ranging from 250 m^2 to 1.8 ha, with a mean size of 3100 m^2. Ten additional plots were set under the undisturbed forest. Almost every gap of the site was sampled except those at lower altitude and with a different tree composition before windstorm. We used a stratified sampling design directed to the gaps with a random distribution of plots inside the gaps. Proximity to forest roads and tracks was avoided. The damages that occurred in the gaps were characterized by windfall, with few broken trees. Almost all trunks were removed and crown branches were left on the ground. The undisturbed forest plots were selected so that topography, forest structure and tree species composition before windstorm were homogenous on the whole study area. Moreover, to avoid edge effects, undisturbed forest plots were set at a distance of the nearest gap higher than 35 meters. The number of forest plots was sufficient according to the Species-area curve, analysed by PcOrd [36].

Floristic surveys, using the Braun-Blanquet method [8] were carried out in 400 m^2 plots as this is the size recommended by Noirfalise [39] for surveys in forest. Data were recorded both in July–August 2002, and in May–June 2003. The second survey was useful to focus on vernal species, and therefore the total number of species is the sum of the two surveys and the cover is the maximum of the two. The soil characteristics were investigated in five spots of each plot (one in the centre and four at five meters in the four cardinal directions). We characterized the humus type as dysmull, hemimoder and eumoder [31]. The humus layer thickness, as well as the sub-horizons (Ol, Of and Oh) if present, were also measured. Ah horizons were sampled for pH ($CaCl_2$) determination [1] because soil pH is a good estimator of the nutrient status of the soil [16]. The total carbon and nitrogen contents of those Ah samples were determined with a dry combustion method (CHON analyser). To ensure that the topography was homogeneous

Table I. Plant attributes used for the study of the plant community.

Plant attribute	Classification
Reproductive traits	
Dispersal type	11 classes from Grime et al. [26] anemochory (small seeds held above the surrounding vegetation, very small seeds (ferns), hairy seeds or winged seeds); zoochory (endo-, epi-, or dys-, myrmecochory), hydrochory, autochory and unspecialized.
Seed mass (mg)	7 classes from Verheyen et al. [63] and modified from Grime et al. [26]: 0 : too small to be measured; 1: < 0.20; 2: 0.21–0.50; 3: 0.51–1.00; 4: 1.01–2.00; 5: 2.01–10.00; 6: ≥ 10.01.
Seed bank	3 classes defined by Thompson et al. [58]: transient, short-term persistent, long-term persistent.
Vegetative traits	
Life cycle	Annual; biennial and perennial.
Maximum height (m)	8 classes from Grime et al. [26]: 1: ≤ 0.1; 2: 0.11–0.29; 3: 0.3–0.59; 4: 0.6–0.99; 5: 1.0–3.0; 6: 3.1–6.0; 7: 6.1–15.0; 8: > 15.0
Vegetative spread	5 classes from Grime et al. [26]. 1 : annual, 2 : perennial and small tussocks (diameter < 100 mm), 3 : perennial attaining diameter of 100 to 250 mm, 4: perennial attaining diameter of 251 to 1000 mm, 5: perennial attaining diameter more than 1000 mm.

between undisturbed forest and gaps, the slope inclination and orientation were measured by means of an electronic compass, the Impulse 200 combined with the Mapstar Compass, developed by Lasertech Inc. The altitude of all plot centres was also determined with the compass.

2.3. Plant community characteristics

The Ellenberg's indicator values, for pH, water, nitrogen and light, were used for the analysis of resource changes [20], as they are well suited to study the environmental resources [16, 22, 50, 62]. We also focused on the plant functional traits, described as "core" traits [65], that are likely to modify the presence or the abundance of the species in respond to disturbance. Those functional traits were classified according to the reproductive and vegetative strategies (Tab. I).

2.4. Data transformation and data analysis

To assess the change of the vegetation between undisturbed forest and gaps, several indexes were computed for each plot. The Shannon diversity index was used to estimate the plant diversity. The Braun-Blanquet coefficients (BB) were transformed in numeric coefficients using the Van der Maarel [62] transformation (BB+:2, BB1:3, BB2:5, BB3:7, BB4:8, BB5:9) and the Shannon index was calculated as follow:

$$H = -\sum_{i=1}^{n} p_i \cdot \log_2(p_i),$$

where $p_i = Iv_i / Iv_{tot}$, with n the number of species, Iv_i the Van denMaarel index for species i and $Iv_{tot} = \sum_{i=1}^{n} Iv_i$.

The mean Ellenberg value was calculated on the basis of the Ellenberg index [25] of the different species, for each plot and each resource (pH, nitrogen, water and light). The mean Ellenberg value is then:

$$\bar{E} = \sum_{i=1}^{n} e_i \cdot c_i \Big/ \sum_{i=1}^{n} c_i,$$

with e_i the value of the Ellenberg index and c_i the number or the cover of species with the i value of the Ellenberg index. The same data computation was performed with the seed mass, the canopy height and the vegetative spread classes.

The seed longevity index was calculated following Hodkinson et al. [28], on the basis of the seed persistence data from Thompson et al. [58]:

$$SL = \frac{\sum(SP2 + SP3)}{\sum(SP1 + SP2 + SP3)}.$$

Three classes have been established by the authors according to the seed persistence records: $SP1$ for transient (persistence < 1 year), $SP2$ for short-term persistent (persistence > 1 year but < 5 years) and $SP3$ for long-term persistent (persistence > 5 years). This index ranges from 0 (strictly transient) to 1 (strictly persistent).

All indexes (Ellenberg, seed mass, canopy height, vegetative spread and seed longevity) were calculated twice: (1) using the number of species (presence/absence data) and (2) using the species cover. For the other functional traits, the species proportions in the different classes were also calculated twice.

According to the results obtained with the normality tests, two different statistical methods were used to analyse the differences between gaps and forest. One way ANOVA [55] was performed, using SAS [49], for parameters that followed a normal distribution: Shannon Index, number of species and environmental factors without transformation; and Ellenberg indexes after a square-root transformation. Non-parametric tests of Wilcoxon [55] were performed, using SAS [49], for parameters that did not follow a normal distribution, even after transformation: seed mass, seed longevity, canopy height and vegetative spread indexes; as well as for the species proportion in the different classes determined for the other functional traits (dispersal type, life cycle). The descriptive statistics, means and standard errors [55] were also computed with the SAS software [49].

The differences in species composition between forest and gaps and the investigation of indicator species were analysed by the INDVAL method [18], using PcOrd [36].This method provides a way to find indicator species between different groups, based on the relative abundance and the relative frequency of species in the groups. The indicator value of a species is $IndVal_{ij} = A_{ij} \times B_{ij} \times 100$, with A_{ij} the *specificity* in a group and B_{ij} is the *fidelity* to a group. $A_{ij} = Nindividuals_{ij}/Nindividuals_{i.}$ with $Nindividuals_{ij}$ the mean number of individuals of species i across sites of group j, and $Nindividuals_{i.}$ is the sum of the mean numbers of individuals of species i over all groups. $B_{ij} = Nsites_{ij}/Nsites_i$ where $Nsites_{ij}$ is the number of sites of the group j where species i is present, while $Nsites_{.j}$ is the total number of sites in that group. If all plots are taken into account, the indicator value corresponds to the presence index of the species, the proportion of plots where the species is present.

Table II. Mean values (± standard error) of topography and soil characteristics under forest and in the gaps. The *p*-values of the analysis of variance are also given.

	Forest	Gaps	*p*
Altitude	338.1 ± 7.74	330.4 ± 3.35	0.4216
Slope	26.2 ± 5.45	28.8 ± 1.97	0.6294
Orientation	149.8 ± 35.63	208.3 ± 12.32	0.0931
pH	3.50 ± 0.03	3.60 ± 0.02	**0.0059**
C/N	17.24 ± 0.35	17.4 ± 0.24	0.7685
Organic matter (%)	6.2 ± 0.41	6.7 ± 0.43	0.9625
Humus thickness (cm)	3.2 ± 0.28	2.1 ± 0.12	**0.0003**
Litter thickness (cm)	1.6 ± 0.25	0.8 ± 0.09	**0.0006**
Of thickness (cm)	1.6 ± 0.14	1.3 ± 0.07	0.0633

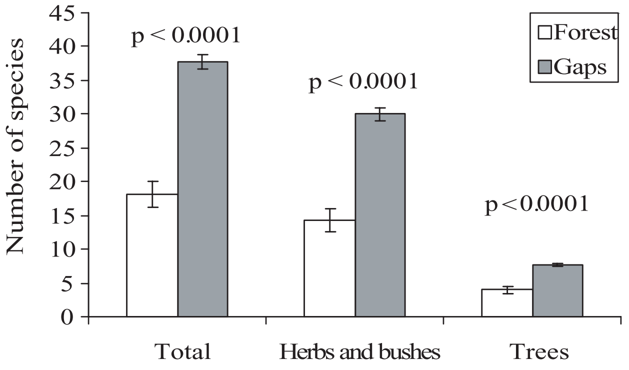

Figure 1. Mean values (and standard errors) of the total species, the herbaceous and bush species and the tree species richness in the undisturbed forest and in the gaps. *p*-values obtained by one-way ANOVA are given on the figure.

3. RESULTS

3.1. Environmental factors

No significant differences were detected for altitude, slope and orientation and confirmed the homogeneity between gaps and undisturbed forest (p = 0.42, 0.63 and 0.07 respectively, Tab. II). The gaps were characterised by a significant (p = 0.0059) higher value of soil pH. They were also characterized by a significant lower humus thickness (p = 0.0059) and a significant lower litter thickness (p = 0.0045). The C/N ratio (p = 0.96) and the Of thickness (p = 0.17) did not differ between gaps and forest (Tab. II).

3.2. Species richness and species profile

A total of 127 species, including 17 tree species, were observed. Sixty-four species among those 127 were found in the forest and in the gaps, three only under forest (*Geranium robertianum* L., *Polygonatum multiflorum* (L.) All. and *Viola riviniana* Reichb.) and 60 in the gaps. As shown by the list of the mean abundance indices (Appendix), most of the species were more frequent in the gaps. The gaps had a significant (p < 0.0001) higher number of species; the mean number of species (± standard error) by plot was of 37.7 (± 1.05) in the gaps and of 18.2 (± 1.90) under forest (Fig. 1). Similar results were obtained for the number of herbaceous and bush species (30.0 ± 0.97 in the gaps and 14.2 ± 1.69 in the forest; p < 0.0001) as well as for the number of tree species (7.7 ± 0.25 and 4.0 ± 0.39; p < 0.0001). The Shannon diversity index was significantly higher (p < 0.0001) in the gaps with a value of 3.5 (± 0.07) vs. 2.8 (± 0.05) in the forest. The cover of herbaceous and bush layer was also significantly (p < 0.0001) higher in the gaps (97.8% (± 2.72) vs. 27.4% (± 5.25) in the forest).

The floristic surveys showed that there was a clear change in species composition in the gaps. It was possible to distinguish a core of 20 species frequently present both in the gaps and under forest, and a core of 67 species more frequently present in the gaps. The 40 other species were present in less than 5% of the plots. No indicator species were found for the undisturbed forest (Tab. III). However, some species such as *Quercus petraea (*Mattus.) Liebl. (INDVAL = 45.98), *Impatiens parviflora* DC. (INDVAL = 36.40) and *Dryopteris dilatata* (Hoffm.) A. Gray (INDVAL = 21.11) had greater indicator values in those plots than in the gaps. Twenty-one indicator species were identified for the gaps, including 11 with a maximum indicator value for the gaps (Tab. III). Some of those species were only confined in the gaps (specificity equal to 1) such as (in decreasing order of indicator values) *Betula pendula* Roth., *Eupatorium cannabinum* L., *Pinus sylvestris* L., *Atropa belladonna* L., *Populus tremula* L., *Agrostis capillaris* L. and *Holcus lanatus* L.

According to the mean Ellenberg values (Fig. 2), gaps were characterized by a significant higher light index. This difference was noticed when calculated using the presence/absence data (light index of 5.5 in the gaps vs. 4.7 in the forest), as well as when taking the cover into account (light index of 5.6 vs. 4.3). This higher index value was the result of more light-requiring species and less shade and semi-shade tolerant species within the gaps. The mean relative cover of light-requiring species was of 17.5% and 50.4% and for the shade tolerant of 75.3% and 30% respectively under the forest and in the gaps. The gaps were also characterized by a significant greater pH index (4.8 in the gaps vs. 4.2 in the forest) when calculated with the presence/absence data, which confirmed the result obtained by soil analyses. No significant changes were observed between gaps and forest for the water and nitrogen indexes.

3.3. Plant strategies

The mean number of anemochorous species, and especially the species with hairy seeds, was significantly higher in the gaps (15.5 species vs. 6.0 under forest, Tab. IV). It corresponded respectively to 32.4% and 41.4% of the mean total species and this increase in species percentage was highly significant (p = 0.0072). The species percentage was also significantly higher (p = 0.0147) for the species without specific dispersal abilities. In cover proportions, the most important increase was observed for the endozoochorous species (33.6% in the gaps vs. 3.2% in the forest). The cover proportion of the species with

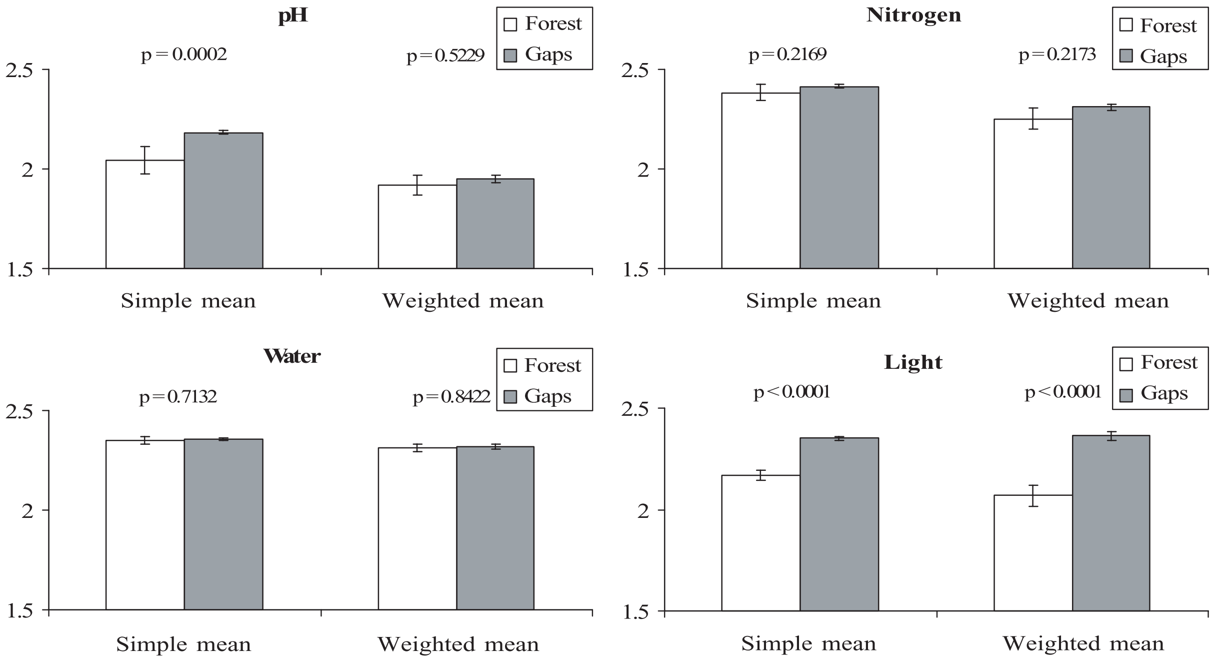

Figure 2. Mean values (and standard errors), using presence/absence data (simple mean) and using species cover (weighted mean), of the square root transformation of the Ellenberg indexes for pH, nitrogen, water and light under forest and in the gaps. *p*-values obtained by one-way ANOVA are given on the figure.

Table III. Species with significant (* $p < 0.05$) or highly significant (** $p < 0.01$) indicator value in the gaps, given by the INDVAL method [18]. The species are set in decreasing order for gaps indicator values. The indicator values for all the plots (or presence index) are also given and maximum values are shown in bold.

	Indicator values			Indicator values	
Species	All plots	Gaps	Species	All plots	Gaps
Salix caprea L.	85.3	**87.9** **	*Cytisus scoparius* (L.) Link	62.7	**64.0** **
Juncus effusus L.	**86.7**	84.8 **	*Calamagrostis epigejos* (L.) Roth	58.7	**59.1** *
Rubus idaeus L.	**93.3**	80.7 **	*Luzula luzuloides* (Lam.) Dandy & Willm.	**100.0**	57.9 *
Rubus fruticosus L.	**94.7**	80.1 **	*Dryopteris filix-mas* (L.) Schott.	**70.7**	56.9 *
Digitalis purpurea L.	**82.7**	**77.3** **	*Epilobium ciliatum* Rafin.	**54.7**	52.9 *
Pinus sylvestris L.	62.7	**72.3** **	*Urtica dioica* L.	**53.3**	51.6 *
Senecio sylvaticus	70.7	**71.6** **	*Atropa bella-donna* L.	37.3	**43.1** *
Epilobium angustifolium L.	70.7	**71.2** **	*Agrostis capillaris* L.	36.0	**41.5** *
Betula pendula Roth.	61.3	**70.8** **	*Populus tremula* L.	30.7	**36.4** *
Sambucus racemosa L.	**80.0**	66.2 **	*Dryopteris carthusiana* (Villar) H.P. Fuchs	**85.3**	55.2 *
Eupatorium cannabinum L.	57.3	**66.2** **			

no specific abilities was also higher ($p = 0.0404$) in the gaps. The number and cover of autochorous and barochorous species did not differ between forest and gaps. Therefore their number percentage was significantly lower in the gaps ($p = 0.0066$ and $p < 0.0001$ for autochorous and barochorous respectively) as well as their cover proportions ($p = 0.0330$ and $p < 0.0001$). The proportions of epizoochorous, hydrochorous or myrmecochorous species did not differ, in number of species and in cover (Tab. IV).

The gaps were characterized by a higher seed longevity index based on presence/absence data ($p < 0.0001$) as well as using the species cover ($p = 0.0303$, Fig. 3). The higher proportion of species with a long-term persistent seed bank contributed to this greater seed longevity index was, in species number (42.8% in the gaps vs. 28.5% in forest, $p < 0.0001$) and in cover (50.2% vs. 21.4%, $p = 0.0004$). Moreover, it was combined with a lower proportion of species with transient seed bank, in species number (32.1% in the gaps vs. 49.0% in forest,

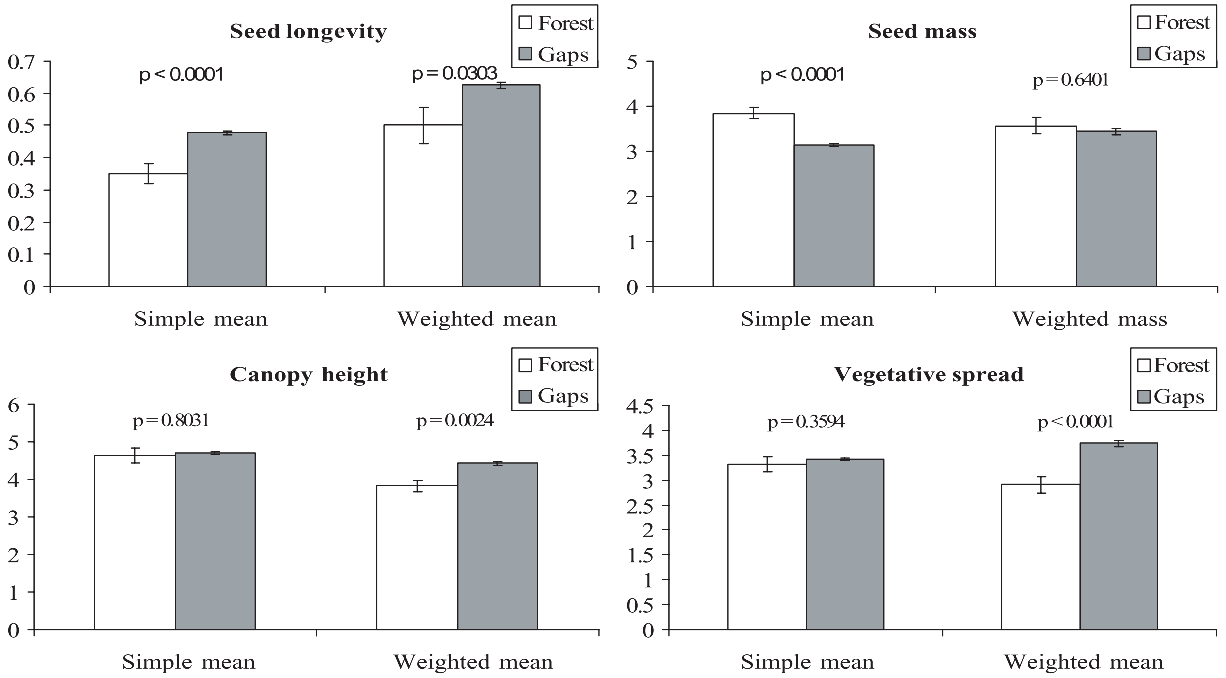

Figure 3. Mean values (and standard errors) for the seed longevity, the seed mass, the canopy height and the vegetative spread indexes of the herbaceous and bush layer, using presence/absence data (simple mean) and using species cover (weighted mean), in forest and in gaps. *p*-values obtained by the Wilcoxon tests are given on the figure.

Table IV. Mean number of species (± standard error) and mean cover values (± standard error) and their relative proportions (%) for the dispersal strategies in the undisturbed forest and in the gaps. *p*-values obtained by the Wilcoxon tests on their relative proportions are also given.

	Number of species					Cover				
	Forest	%	Gaps	%	Test	Forest	%	Gaps	%	Test
Anemochore	6.0 ± 0.92	32.4	15.5 ± 0.45	41.4	**0.0072**	6.7 ± 3.07	20.7	16.0 ± 1.41	16.8	0.4358
Autochore	1.4 ± 0.32	6.6	1.3 ± 0.10	3.3	**0.0066**	2.9 ± 1.45	9.1	2.8 ± 0.52	2.8	**0.0330**
Barochore	1.9 ± 0.09	11.9	1.9 ± 0.05	5.1	**< 0.0001**	1.0 ± 0.06	5.6	1.0 ± 0.05	1.1	**< 0.0001**
Endozoochore	1.8 ± 0.51	8.2	3.9 ± 0.12	10.8	0.2423	0.9 ± 0.25	3.2	33.5 ± 2.77	33.6	**< 0.0001**
Epizoochore	2.5 ± 0.44	12.3	4.4 ± 0.21	11.6	0.3825	5.2 ± 1.90	15.4	11.5 ± 1.74	11.2	0.1306
Hydrochore	1.7 ± 0.38	8.7	2.2 ± 0.15	5.7	0.0572	1.1 ± 0.41	5.3	2.7 ± 0.69	2.6	0.0504
Myrmecochore	2.2 ± 0.19	13.5	3.9 ± 0.20	10.6	0.3259	8.9 ± 2.31	37.2	24.8 ± 2.25	26.7	0.2271
Unspecified	1.3 ± 0.44	6.2	4.5 ± 0.35	11.4	**0.0147**	0.9 ± 0.44	3.5	5.5 ± 0.74	5.3	**0.0404**

$p < 0.0001$), as well as in cover (31.9% vs. 58.6%, $p = 0.0008$). The plant community was dominated by transient seed bank species in the forest, and by long-term persistent seed bank species within the gaps. Vegetation in the gaps was also characterized by a significantly lower mean seed mass than under forest (Fig. 3), when calculated with the number of species ($p < 0.0001$), but not with the species cover ($p = 0.6401$).

As far as the life cycle is concerned, the plant community is clearly dominated by perennial species, both in the gaps (92.8% of the cover and 85.7% of the total species, Tab. V) and under forest (84.2% of the cover and 83.1% of the total species). The mean number of annual species in the community was low (4.6 in the gaps and 3.1 under the forest, which represents respectively 6.4 and 4.3% in cover). The cover proportion of those species was then significantly ($p = 0.0113$) lower in the gaps (Tab. V).

The mean maximum canopy height of the species present in the herbaceous and bush layer based on their cover was significantly higher ($\text{Chi}^2 = 9.24$, $p = 0.0024$) in the gaps (Fig. 3). It was the result of a significantly greater relative cover of species with a maximum height of 1.0 to 3.0 m, reaching 40% in the gaps vs. 14% under forest ($p = 0.0002$). The relative cover also increased for the species with a height of 3.0 to 6.0 m, (12% in the gaps vs. 1% under the forest, $p = 0.0001$). It was also combined with a minder relative cover of species of height less than 10 cm (3% in gaps vs. 9% under forest, $p = 0.0396$). The understorey

Table V. Mean number of species (± standard error) and mean cover values (± standard error) and their relative proportions (%) for the life cycle in the undisturbed forest and in the gaps. *p*-values obtained by the Wilcoxon tests on their relative proportions are also given.

	Number of species					Cover				
	Forest	%	Gaps	%	Test	Forest	%	Gaps	%	Test
Annual	3.1 ± 0.57	15.6	4.6 ± 0.28	11.8	0.185	4.3 ± 1.51	15.1	6.4 ± 0.91	6.2	**0.011**
Biennial	0.3 ± 0.21	1.3	0.9 ± 0.03	2.5	**0.005**	0.2 ± 0.11	0.7	1.0 ± 0.13	1.0	**0.003**
Perennial	15.4 ± 1.74	83.1	32.1 ± 0.83	85.7	0.543	23.0 ± 4.41	84.2	90.4 ± 2.51	92.8	**0.019**

plant community was strongly represented in the gaps by species with a maximum height of 1.0 to 3.0 m (40% of the herbaceous and bush cover) and under closed canopy by the species with a maximum height of 30 to 60 cm (42% of the herbaceous and bush cover). Otherwise, for the species number, the mean maximum canopy height was not significantly different between forest and gaps ($p = 0.1306$).

No significant differences ($p = 0.0782$) were observed for lateral spread index between forest and gaps calculated with the presence/absence data (simple mean, Fig. 3). However, the vegetative spread index was significantly higher ($\text{Chi}^2 = 15.92$, $p < 0.0001$) when the cover was taken into account (weighted mean). In that case, species with a large development (diameter greater than 1.0 m) had a most important relative cover, as their proportion increased from 17% under forest to 45% in the gaps ($p = 0.0004$). Moreover, the relative cover of perennial species forming tussocks with a diameter of 10 to 25 cm, dominating the community under the forest (44% of the herbaceous and bush cover) decreased ($p = 0.0280$) in the gaps (relative cover of 28%).

4. DISCUSSION

4.1. Soil characteristics

Our results showed a clear decrease of the humus thickness due to a decrease in litter thickness. However, there was no change of the Of horizon thickness and thus no effect on the organic decomposition, which is confirmed by the similar C/N ratio in gaps and in undisturbed forest. As far as litter is concerned, the decrease in thickness is somewhat expected as gap creation reduced the number of trees in the surroundings and leaded to a smaller annual litter fall in the gaps. Such result has also been recorded in other studies [2, 54]. The observed lack of change in Of thickness seems to be contradictory with the study of Arpin et al. [2] who observed thinner Of horizons in clearings. However, Shure and Philips [54] observed a change of the Of thickness after 15 years but not just after gap creation. Gap creation has a rapid first impact on the first humus layer (litter thickness) that will affect the second humus layer (Of thickness) only after some years. Therefore, in our short-term study, the effect on the Of thickness was not yet observable.

When looking to the soil acidity, it is difficult to understand the observed slight pH increase. In the short-term, forest harvesting has, for example, different impacts on soil pH that can increase, decrease or stay unchanged [40]. Our slight increase in pH may however be related to the presence of branches and decaying woods on the forest floor, that can increase the nutrient availability in the top soil.

4.2. Species richness and species profile

As expected, a higher plant diversity was observed within the gaps in terms of species number, Shannon index, and herbaceous and bush cover. Our results confirmed similar findings recorded in natural and managed forests [6, 12, 13, 30]. In an American beech forest, a herbaceous cover increase has already been noticed in small gaps resulting of single tree falls [37]. As shown in other studies, gaps are critical for establishment, growth and reproduction of plant species [12, 13]. Our study clearly showed that the higher species richness observed in forest gaps resulted from two phenomenons: the survival of the understorey species through disturbance and the establishment of new species after disturbance [27, 52, 53]. Survival can be estimated by the low number of species (only three) present under the forest but absent from the gaps. Arrival of new species had a major contribution on the higher diversity in gaps (almost half of the species were present only in gaps). This may contribute to an increase of species richness over long periods as the spatial distribution of plants may be maintained for many years and several generations [30].

Species composition indicated that, except for *Dryopteris carthusiana*, *Dryopteris filix-mas* and *Luzula luzuloides*, the gap-species required light for their growth. Moreover, gap indicator species with a higher specificity to gaps (maximum Indval values in gaps) were forest species typical to edges and clearings [29] such as: *Calamagrositis epigejos*, *Cytisus scoparius*, *Epilobium angustifolium* and *Senecio sylvaticus*. Gaps create favourable microclimatic conditions for the growth of these edge species particularly through the increase of light [52]. The other indicator species characterized early successional forest vegetation groups of the *Epilobion angustifolii*, *Sambuco-salicion capreae* and *Fragarion vescae* [39]. Three tree indicator species of gaps, *Betula pendula*, *Salix caprea* and *Populus tremula*, were observed in absence of tree seeds in the sampled area (minimum distance to the nearest tree greater than 250 m). Those trees are pioneer species and frequently take part to the first tree stages in linear and cyclic dynamics [47]. Gaps are thus sites of particular interest for the establishment of early successional tree species [52]. The absence of indicator species for undisturbed forest is interesting to note because some of the observed species are called true-forest species [29] as they are confined to the internal core of the forest and prefer deeper shadow. Those species are, for example, *Athyrium filix-femina, Carex pendula*, *C. remota*, *C. sylvatica*, *Dryopteris* sp., *Festuca gigantea*, *Millium effusum*, *Oxalis acetosella* or *Poa nemoralis*.

Those species can therefore persist in less favourable habitat, at least for some times after the disturbance (four years in our case). The unpronounced competition with other competitive species or the presence of local suitable habitat may explain their survival in this less favourable environment. Those species may be also more sensitive to environmental factors other than light that are not modified in windthrow such as, for example, phosphorus level [29]. For a methodological point of view, the Indval method was a useful tool for determining indicator species characteristic of particular habitats. This method, combined with the study of functional traits, can give a more precise characterization of a habitat, on the basis of an observed species composition.

As shown by the species composition, our results demonstrated that the light profile of the plant community is modified within the gaps. New species requiring more light were present in the gaps and their cover significantly extended. This result could be expected, as it is well known that the light regime increases in forest gaps [10, 21, 25] and enables the presence of light-requiring species [9, 10, 46]. This is particularly true in beech forests characterized by a relative darkness excepted during the gap phase [7, 21]. However, our study showed that the gap phase did not prevent the presence of shade tolerant species. Their number as well as their cover was higher in the gaps. The gaps have thus a positive effect on the diversity of shade tolerant species and light-requiring species, at least some years after disturbance. The lack of change for the other resource requirements of the plant community was unexpected as many studies have shown a change of resources within the gaps when directly measured [10, 45, 56]. In our case (a forest without water deficit or water surplus), the lack of variation for water needs suggested that the different species may find their water requirements in the gaps. It can be explain by the differences in soil moisture existing between gaps of various sizes, large gaps may even be drier than undisturbed forest [25], or the positions within the gaps [25, 37]. For nitrogen, a higher cover of nitrophilous species was expected as some studies have shown that the nitrogen availability for plants (mineral nitrogen) increases with decreasing overstorey [41]. This increase of available nitrogen was detected as early as two years after gap formation [41]. However, the increase of nitrogen availability in the gaps may not induce a change in plant composition but may increase plant growth. Therefore gaps do not necessarily promote nitrophilous species and the expansion of such species may be more dependent on anthropic activities. The differences in plant growth, between gaps and forest, may explain the lack of change observed with the Ellenberg values compared to previous studies using direct measures. The plant community can react to resource change by adapting its growth more than its species composition. Moreover, plant functional traits may be more important than abiotic factors to determine the species dynamics of the herbaceous community. A similar finding was obtained by Gondard and Deconchat [24].

4.3. Plant strategies

Our results showed that anemochorous species, and especially those with hairy seeds, were more present in the gaps than other species. Early successional or disturbed habitats are often dominated by wind-dispersed species that seem to be the most effective colonizers [19]. Moreover, several studies in secondary forests have shown that anemochorous species have the highest dispersal abilities [19, 35]. Those studies have also revealed that barochorous, myrmecochorous and autochorous species have the lowest dispersal abilities. Therefore, in our study, few new species with those dispersal abilities appeared in the gaps. The species without specific dispersal abilities tend to produce smaller seeds in larger amounts [67] that can explain their higher proportion in the gaps. Thompson et al. [59] have exposed that plants of unstable habitats generally have seeds with higher persistence in the soil. Therefore, gaps promote species with greater seed persistence. Moreover, in our study species belonging to the genera *Carex, Digitalis, Hypericum, Juncus, Poa, Rubus* or *Rumex* were found mainly in the gaps. These are light-requiring species that have a long-term persistent seed bank with a high number of seeds and therefore are frequently found in seed banks [64]. The establishment of species with a persistent seed bank also depends on the presence of bare ground [26] that can only be found locally in forest gaps but not in the undisturbed forest. In deciduous forest, seedbanks formation takes place during the first stages of vegetation succession and few new seeds are added after canopy closure [43]. Therefore, seed banks are mainly composed by species of those early successional stages. The observed decrease of the seed mass index may be explained by the positive relationship between tolerance to shade and size of the seeds [28] and the negative relationship between seed size and seed longevity in the soil [28]. In conclusion, species with high dispersal abilities in space and time (low seed mass, specific adaptation: with hairy or winged seeds, and high seed longevity index) tended to be proportionally more numerous within the gaps and therefore increased the plant diversity.

The low proportion of annual species observed in the gaps is unusual. In general, those species are common in disturbed habitats and in forest gaps in particular [5]. As the study started in the third growing season, we can hypothesize that these species have already been outcompeted by more competitive species and that their proportion was higher just after the windstorm. Moore and Vankat [37] found an increase in annual species in one or two years old gaps and a decrease in older gaps. For maximum height and vegetative spread, our results clearly showed that the number of species did not differ between forest and gaps unlike species cover. A greater competitive ability estimated by those two traits seems to be advantageous in term of space occupancy. This advantage is well illustrated by two species able of fast growth and vegetative spread, *Rubus idaeus* and *Rubus fruticosus*. Those species dominated the plant community in the gaps but were almost missing under closed canopy. It is known that those social light-requiring species, with greater plant height and quick expansion, are able to overgrow, outshade and outcompete smaller species when the conditions, such as light, are favourable [17, 30]. The development of such competitive species, may then characterize the plant community in gaps [2] and reduce the plant diversity by preventing establishment or growth of other species.

Our study showed that beech forest gaps are specific environments for establishment of new species and therefore windstorm had, at least in the short-term, a positive effect the plant diversity. This higher species diversity resulted mainly to an increase in light environment inside the gaps, with a vigorous reaction of light-requiring species. In the short-term, gaps seemed not to prevent the growth of the more shade tolerant species or true forest species. However the future is unknown and an important question is what those species will become. A long-term study would be therefore useful. Functional traits and their interactions play a major role to determine the species composition, especially compared to the species requirements for resources other than light. On the first hand, reproductive traits, and especially the dispersal in space and time, tended to promote the plant diversity in the gaps. On the other hand, vegetative traits tended to promote the occupancy of the available space by some particular species with great competitive abilities. It is likely that plant and functional diversity will be highest some years after gap creation, when the species with reproductive advantages are established and before the occupancy of all the growing space by competitive species. A high recurrence of such windstorm may then have a negative effect on plant diversity by facilitating the development of competitive species thanks to more favorable conditions for their growth. In terms of silvicultural practices, it is better to regularly create canopy gaps, in different places, instead of trying to maintain in the forest some open spaces over a long period of time. Those ones will be dominated by few species with high competitive abilities that will prevent the development of other species. We can also hypothesize that large clearcuts will have the same effects. In large clearcuts, forest recovering will take more time and therefore competitive species are more likely to dominate the plant community.

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APPENDIX. Mean abundance indices (Van der Maarel) of each species, in the different layers, under forests and in the gaps.

	Forest	Gaps
Number of plots	10	65
Species		
Tree layer (> 8 m)		
Fagus sylvatica	8.20	4.32
Quercus petraea	2.60	0.48
Picea abies	0.50	0.05
Pinus sylvestris	–	0.14
Shrub layer (3–8 m)		
Fagus sylvatica	4.80	2.80
Sambucus racemosa	–	0.67
Betula pendula	–	0.12
Salix caprea	–	0.18
Herbaceous and bush layer (< 3 m)		
Luzula luzuloides	3.70	5.09
Rubus idaeus	1.20	5.03
Rubus fruticosus	1.00	4.02
Athyrium filix-femina	1.80	2.42
Galeopsis tetrahit	2.10	2.23
Fagus sylvatica	2.00	2.03
Dryopteris carthusiana	1.30	2.11
Festuca altissima	1.70	1.97
Quercus petraea	1.80	1.72
Oxalis acetosella	1.80	1.72
Sambucus racemosa	0.60	1.85
Stellaria nemorum	1.60	1.63
Abies alba	1.40	1.60
Dryopteris filix-mas	0.60	1.71
Milium effusum	1.00	1.55
Impatiens parviflora	1.50	1.38
Mycelis muralis	0.80	1.37
Picea abies	0.80	1.35
Carex remota	0.70	1.35
Polygonum hydropiper	1.00	1.20
Carex pilulifera	0.80	1.18
Acer pseudoplatanus	0.90	1.06
Dryopteris dilatata	1.10	0.98
Carex ovalis	0.50	0.69
Juncus effusus	0.40	2.80
Digitalis purpurea	0.40	2.06
Scrophularia nodosa	0.40	0.92
Poa annua	0.40	0.86
Pteridium aquilinum	0.40	0.86
Poa nemoralis	0.40	0.78
Stachys sylvatica	0.40	0.58
Lysimachia numularia	0.40	0.09
Carpinus betulus	0.40	0.18
Salix caprea	0.20	1.94
Cytisus scoparius	0.20	1.89
Senecio sylvaticus	0.20	1.71
Calamagrostis epigejos	0.20	1.66
Epilobium angustifolium	0.20	1.62
Epilobium ciliatum	0.20	1.23
Urtica dioica	0.20	1.23
Larix decidua	0.20	0.94
Veronica officinalis	0.20	0.89
Juncus bufonius	0.20	0.77
Carex sylvatica	0.20	0.69
Prunus avium	0.20	0.65
Carex pendula	0.20	0.58
Hypericum pulchrum	0.20	0.55
Luzula sylvatica	0.20	0.51
Rumex acetosella	0.20	0.46
Stellaria media	0.20	0.37
Deschampsia flexuosa	0.20	0.31
Festuca gigantea	0.20	0.31
Rumex obtusifolius	0.20	0.29
Circea lutetiana	0.20	0.28
Calluna vulgaris	0.20	0.25
Myosoton aquaticum	0.20	0.15
Hedera helix	0.20	0.12
Deschampsia cespitosa	0.20	0.09
Fraxinus excelsior	0.20	0.09
Teucrium scorodonia	0.20	0.09
Anemone nemorosa	0.20	0.06
Melica uniflora	0.20	0.03
Ranunculus repens	0.20	0.03
Sambucus nigra	0.20	0.03
Geranium robertianum	0.20	–
Polygonatum multiflorum	0.20	–
Viola riviniana	0.20	–
Pinus sylvestris	–	1.45
Betula pendula	–	1.42
Eupatorium cannabinum	–	1.38
Atropa bella-donna	–	1.14
Agrostis capillaris	–	0.91
Populus tremula	–	0.71
Holcus lanatus	–	0.65
Carex pallescens	–	0.55
Taraxacum officinalis	–	0.49

APPENDIX. (continued).

	Forest	Gaps		Forest	Gaps
Number of plots	10	65	Number of plots	10	65
Species			Species		
Poa trivialis	–	0.35	*Veronica chamaedrys*	–	0.09
Hypericum perforatum	–	0.34	*Carex montana*	–	0.06
Rumex acetosa	–	0.31	*Asperula odorata*	–	0.06
Senecio fuchsii	–	0.31	*Calystegia sepium*	–	0.06
Dryopteris affinis	–	0.28	*Carex pilosa*	–	0.06
Fragaria vesca	–	0.28	*Linaria vulgaris*	–	0.06
Bromus benekenii	–	0.23	*Plantago major*	–	0.06
Euphorbia cyparissias	–	0.22	*Rumex sanguineus*	–	0.06
Lapsana communis	–	0.22	*Trifolium repens*	–	0.06
Viola canina	–	0.22	*Vicia pisiformis*	–	0.06
Epilobium montanum	–	0.18	*Carex paniculata*	–	0.05
Pseudotsuga mensiezii	–	0.18	*Aethusia cynapium*	–	0.03
Stellaria graminea	–	0.18	*Alopecurus pratensis*	–	0.03
Cirsium vulgare	–	0.15	*Chrysosplemium oppositifolium*	–	0.03
Gymnocarpium robertianum	–	0.14	*Epilobium palustre*	–	0.03
Artemisia vulgaris	–	0.12	*Galium saxatile*	–	0.03
Cirsium arvense	–	0.12	*Glechoma hederacea*	–	0.03
Sorbus aucuparia	–	0.12	*Lonicera peryclimenum*	–	0.03
Dactylis glomerata	–	0.09	*Lysimachia nemorum*	–	0.03
Galium aparine	–	0.09	*Malus sylvestris*	–	0.03
Holcus mollis	–	0.09	*Polygonum bistorta*	–	0.03
Impatiens noli-tangere	–	0.09	*Robinia pseudoacacia*	–	0.03
Oxalis corniculata	–	0.09	*Senecio jacobea*	–	0.03
Prenanthes purpurea	–	0.09	*Sonchus arvense*	–	0.03
Tanacetum vulgare	–	0.09	*Tussilago farfara*	–	0.03