

Dynamic Response of Herbaceous Vegetation to Gap Opening in a Central European Beech Stand

Kristóf Kelemen, Barbara Mihók, László Gálhidy and Tibor Standovár

Kelemen, K., Mihók, B., Gálhidy, L. & Standovár, T. 2012. Dynamic response of herbaceous vegetation to gap opening in a Central European beech stand. *Silva Fennica* 46(1): 53–65.

Herbaceous ground vegetation in artificially-created gaps was studied in a managed beech (*Fagus sylvatica* L.) forest over a period of eight years in Northern Hungary, Central Europe. These gaps were being used as an alternative to the regular shelterwood system to create uneven-aged stands. The effects of gap size (15 and 40 m diameter) and canopy openness on herbaceous species colonization and persistence were assessed in a systematic grid of 5 × 5 m. Overall, herbaceous cover was low before gap creation, increased soon afterwards, and continued to rise over time. The number of herb species increased in the gaps and, to a lesser extent, in adjacent areas under the remaining tree canopy. Colonization of gaps was rapid and there was substantial turnover of species i.e. various species disappeared from the gaps over time whilst others colonized. Species with both long-term persistent seed banks and long distance dispersal abilities were the most successful types colonizing gaps. Six species occurred preferentially in large gaps, while only one species was found to prefer small gaps. Species present before gap creation survived in both gap sizes. Smaller gaps with a diameter of half the height of canopy trees also tended to remain free of common weed species, whereas large cover of *Rubus fruticosus* L. and *Calamagrostis epigejos* (L.) Roth could hamper natural regeneration in larger gaps. For the successful regeneration of beech we recommend the use of small gaps complemented by few large gaps.

Keywords continuous cover forestry, dispersal, gap colonization, herbs, seed bank type, species richness

Addresses Loránd Eötvös University, Institute of Biology, Dept. of Plant Systematics, Ecology and Theoretical Biology, Budapest, Hungary

E-mail standy@ludens.elte.hu

Received 5 July 2012 **Revised** 12 January 2012 **Accepted** 12 January 2012

Available at <http://www.metla.fi/silvafennica/full/sf46/sf461053.pdf>

1 Introduction

Natural dynamics of Central European deciduous forests are typically characterized by small-scale disturbance mainly from wind, ice and, to a lesser extent, pathogens (Peterken 1996, Kenderes and Standovár 2003, Zeibig et al. 2005). The death of one or several trees creates small patches or gaps characterized by greater light and nutrients levels than is found in the surrounding forest (Canham et al. 1990, Ritter et al. 2005). It is well established that both tree seedlings and herbaceous species are adapted to the patchy distribution of resources resulting from this disturbance regime (e.g. Watt 1923, Sousa 1984, McIntyre et al. 1999, Laska 2001). The herbaceous layer is important to look at, because it plays a central role in maintaining species diversity and ecosystem functioning (Roberts 2004).

In Central Europe, the vast majority of deciduous forests are managed under even-aged forestry systems (Ellenberg 1988, UN/ECE-FAO 2000). Beech forests in Hungary are usually managed under the uniform shelterwood system with short regeneration period and relatively large subcompartments (1–10 ha), which typically results in an even-aged structure (Brunet et al. 2010). Under this type of management, forests tend to be a patchwork of closed canopy and contrasting open areas distributed evenly at the landscape scale. Beneath the closed canopy, with the lack of regular thinning, there can be little if any herbaceous vegetation; herbaceous vegetation is abundant in open areas, but disappears rapidly upon canopy closure. Continuous cover forestry, such as selection felling and other multi-aged stands are generally better in providing heterogeneous stand structure at the fine scale, but the extent of their current use is negligible (O'Hara et al. 2007). In beech forests, most shade-tolerant species seem to survive under both shelterwood and selection cutting, but heavy regeneration cutting and soil compaction by mechanized timber harvest have an impact on many common species (Brunet et al. 2010).

The transition of even-aged stands to continuous cover forestry involves the creation of relatively small gaps at an industrial scale (Bradshaw et al. 1994, Pommerening and Murphy 2004). Since

response of herbaceous species to disturbance can vary greatly, it is important to identify the factors influencing herbs before gaps will be used widely. Early investigations in canopy gaps showed that extant species survived, but colonization also played a role in the composition of canopy gaps of sizes similar to natural disturbance (Metzger and Schultz 1981, Collins and Pickett 1988). Light and soil moisture have been identified as important factors affecting regeneration processes early on (e.g. Moore and Vankat 1986), but biotic factors and site history have gained attention only recently (Fahey and Puettmann 2007, Naaf and Wulf 2007). Although there are a few recent studies that have looked at the herbaceous vegetation in gaps (e.g. Pavlovic et al. 2006, Naaf and Wulf 2007, Falk et al. 2008), the use of permanent plots for the study of vegetation dynamics within gaps is rare in temperate forest ecosystems.

In this paper we present results of a long term gap experiment in a temperate beech forest stand being used to study conversion from an even-aged to a multi-aged stand structure. Our objective was to document the dynamic patterns in vegetation cover and species occurrences after gap creation. More specifically, we wanted to answer the following:

- 1) how do gaps affect herbaceous vegetation cover over time;
- 2) what is the rate of species colonization and disappearance;
- 3) what traits do successful colonizers have in both early and later phases of gap succession;
- and 4) how do herbaceous species partition gaps in space and time?

2 Materials and Methods

2.1 Study Site and Experimental Design

The study site, located in the Börzsöny Mountains, Northern Hungary (47.9°N, 18.9°E), is a submontane beech forest. Deep brown forest soils overlay andesite bedrock. Mean annual temperature is 8°C with mean monthly temperatures of –3.5°C and 18°C in January and July, respectively. Mean annual precipitation is 700–800 mm. Elevation is 540–610 m. As a result of management there are only two layers of vegetation. The homogeneous canopy is dominated by European beech (*Fagus*

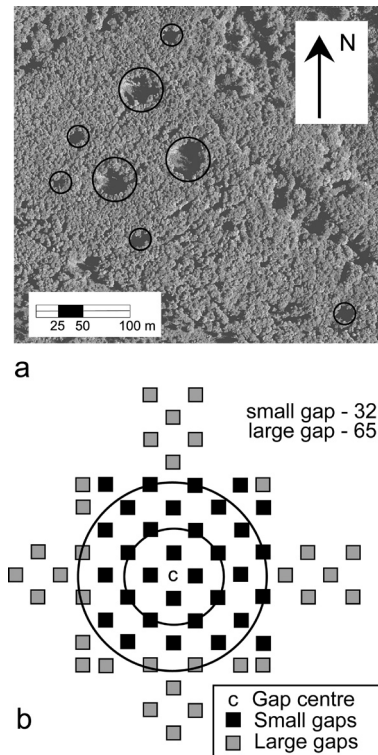


Fig. 1. a: Aerial photograph taken in summer 2007, 7 years after the creation of the gaps. Black circles show large and small gaps. b: Systematic sampling design. Each quadrat is 1 × 1 m in a 5 m grid. Black and grey squares constituted the sample grid: black – small gaps; black and grey – large gaps. Circles show approx. diameters.

sylvatica L.) trees that are approximately 100 years old according to old management plans. Stand density is high resulting in small canopy diameter of tree individuals. The closed canopy creates low light levels (4–5% of above canopy light (Mihók et al. 2005)) and thus light dependent vascular species are absent. No shrub layer is present. Under the canopy, the herbaceous vegetation consists of very few species and percentage cover is low. The most frequent species include *Carex pilosa* Scop., *Mercurialis perennis* L. and *Athyrium filix-femina* (L.) Roth. For a more detailed description of the study site see Gálhidy et al. (2006). The stand has been managed under the regular shelterwood system for

at least two rotations. We have indirect evidence that the present forest was regenerated together with its neighbouring stands over a period of about 20 years.

Vegetation was surveyed in the autumn of 2000; during the winter of 2000–2001 eight circular artificial gaps were created (Fig. 1a). These gaps were either 15 or 40 m in diameter corresponding to 0.5 times average tree height or 1.5 times average tree height in the surrounding stand. There were 5 small (S) gaps and 3 large (L) gaps. The gaps were all created in one relatively large (9.18 hectare) subcompartment and are similar with respect to altitude, slope and aspect. Systematic sampling was carried out on six occasions between 2000 and 2008 taking every second 1 × 1-m quadrat of a 5 × 5-m grid (Fig. 1b). In large gaps, the sampling penetrated into the stand around the gap and 65 quadrats were sampled. In small gaps, 32 quadrats were placed (33 were used in one of them). Thus a total of 356 1 × 1 m quadrats were used to measure temporal changes in the herbaceous vegetation.

In each quadrat, data on vegetation and light were collected. We determined percentage cover of herbaceous species using visual estimation. Tutin et al. (1964–1993) was used for botanical nomenclature. Light measurements were made using a densiometer (Robert E. Lemmon, Bartlesville, USA). This instrument is used to measure canopy openness (CO) by visual estimation from four different angles. The average of these measurements gives the percentage canopy openness above the quadrat. Canopy openness correlates with direct (Lemmon 1956) and indirect light measurements (Englund et al. 2000, Tinya et al. 2009a). High correlations between light levels measured with hemispherical photography and CO were confirmed on site ($r=0.88$, $p<0.01$) in 2003 (Mihók, unpublished data). Measurements were taken in 2006 and since lateral expansion of the canopy did not alter light conditions considerably, they were used for the characterization of light levels in quadrats throughout the study period. Based on the frequency distribution of CO values, three groups emerged and thus each quadrat was ordered into light zones. These light zones correspond to different parts of the gap as follows: Z1 = under-canopy (0–20% CO); Z2 = centre of small and edge of large gaps (20–40% CO); Z3 = centre of large gaps (>40% CO).

2.2 Ecological Traits

Seed traits for each species observed more than once over the course of the study were determined using existing plant databases. Seed dispersal was assessed based on two databases (Csontos et al. 2002, Klotz et al. 2002) and two categories were created: long-distance dispersal (LongD) and non-LongD. Anemochorous species as well as zoochorous species dispersed by either mammals or birds were included in the LongD category, while herbs without such abilities (e.g. autochorous species) were included in the non-LongD category. Seed bank traits were compiled using two other databases (Thompson et al. 1997, Liu et al. 2008). Long-term persistent seed bank (LP) was attributed if at least one such reference was found. The rest were categorized as non-LP seed bank species. Where no data were available, we categorized seed bank type by reference to similar species.

2.3 Data Analysis

Percentage cover for sampling units was calculated as the sum of herb species cover, which could exceed 100% where multiple layers of herbaceous vegetation existed. The relationship between herb cover and canopy openness and gap size was tested using linear mixed effects models with gap and quadrat membership as random factor (Pinheiro and Bates 2000). Year was included as a fixed effect, because we also wanted to test the effect of time on the relationship. Herb cover values were log transformed to ensure homogeneity of residuals. Restricted maximum likelihood estimation (REML) was applied using the nlme package of R (Pinheiro et al. 2011). Spatial autocorrelation was tested on empirical semi-variograms of the residuals (Zuur et al. 2009) using the gstat package for R, and was found to be unsubstantial (<10% of total variance).

Species number was calculated for each year as the total number of species occurring in the 356 quadrats. The earliest appearance of any given species was used as the date of colonization and the latest appearance as the date of disappearance. Absolute turnover was then determined for

each survey as the mean of the colonizing and disappearing species (Schoener 1988, Virola et al. 1999). To determine the possible ways of colonization the number of new occurrences was traced for each species and these numbers were summed for each seed trait category group.

Patterns in vegetation response to gap creation were assessed by multivariate analysis of the CO zones as well as by testing individual species preferences. Linear discriminant analysis was performed to test for the main compositional differences between the zones of small and large gaps in 2008. This method maximizes the variance between the groups and thus enabled us to focus on the species whose abundance explained the separation of the zones. The limitation of this method is that the number of variables has to be less than the number of observations. Therefore only the most abundant 12 species were included in this analysis. Zone 1 of one of the small gaps was excluded, because of the absence of herbs. The total cover in each zone was log transformed to assure normal distribution. Normality was tested with Doornik and Hansen omnibus (Doornik and Hansen 2008).

Indicator species analysis was used to test for the relative abundance of herbaceous species in the light zones of small and large gaps (Dufrene and Legendre 1997) using the labdsv package for R (Roberts 2010). This analysis was carried out separately for each year after gap creation for average cover data.

All results were considered significant at $p < 0.05$. SYN-TAX 2000 (Podani 2001) and PAST software (Hammer et al. 2001) were used for LDA and R was used for all further analyses (R Development Core 2011).

3 Results

3.1 Vegetation Cover

The cover of the herbaceous layer was < 5% before gap creation (Fig. 2). It increased steadily reaching 100% cover in the centre of all gaps six years after gap creation. The mixed effects model showed that both canopy openness ($t = 5.08$, $df = 346$, $p < 0.0001$) and year ($t = 2.34$,

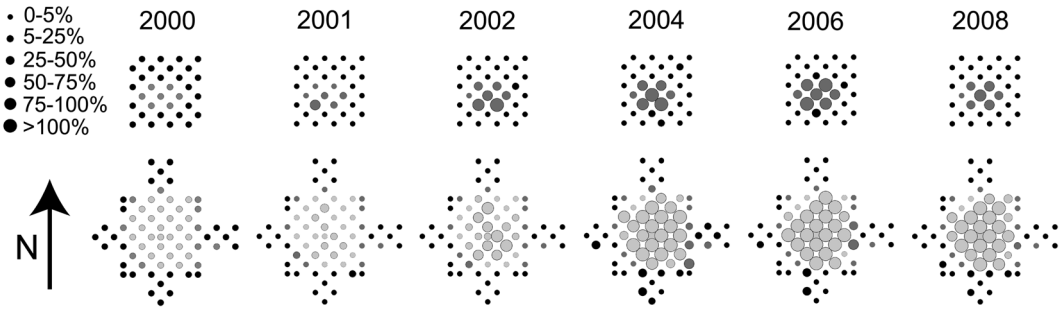


Fig. 2. Graphical representation of the total herbaceous species cover in each quadrat of one small and one large gap during the entire study period. Circle size shows the sum of estimated percent cover for all species, while circle colour is according to the different canopy openness (CO) zones: black-Z1 (0–20% CO); dark grey-Z2 (20–40% CO); light grey-Z3 (>40% CO).

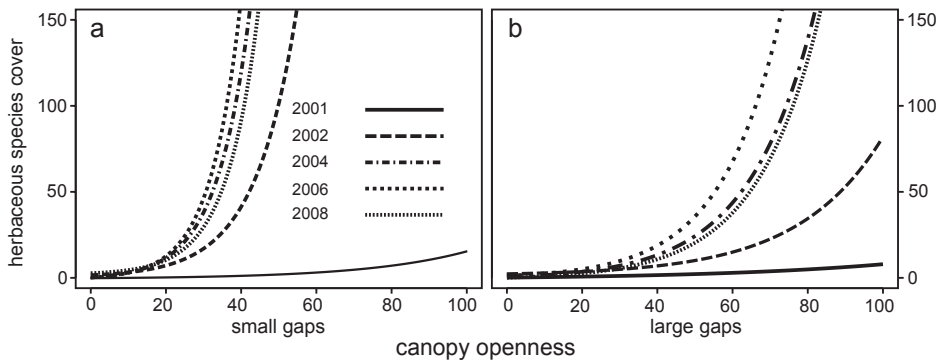


Fig. 3. Relationship between total herbaceous cover and canopy openness in (a) small and (b) large gaps. Total herbaceous cover is expressed as the sum of estimated percent cover allowing superposition of species. Only the fitted models are shown for each year.

df = 1420, p = 0.019) had a significant effect on herbaceous cover. Although gap size had a non-significant effect on cover alone, its interaction with CO was found to be significant ($t = 2.06$, df = 346, p = 0.040) suggesting that gap size influenced the relationship between herbaceous cover and canopy openness. Furthermore, small gaps showed a faster change in herbaceous cover as can be seen in Fig. 3 presenting the fitted functions for each year for the two gap sizes. In large gaps, more light is required for the same herbaceous vegetation cover and in 2002 many quadrats showed low herbaceous cover values despite the elevated light levels (Fig. 3b).

3.2 Species Richness and Composition

A total of 117 herbaceous species were found in the study quadrats. Species included both common shade tolerant herbs and those inhabiting canopy openings and meadows in forested landscapes. The species that were most frequently observed included *Epilobium montanum* L., *Mycelis muralis* (L.) Dumort., *Scrophularia nodosa* L. and *Urtica dioica* L. Only 16 species were found in the 356 quadrats prior to gap creation; all with low frequencies. This number increased dramatically after gap formation with 63 recorded at the first sampling. The total species richness remained high, while species turnover decreased slightly. By the end of the observation period, colonization and disappearance rates became equal (Fig. 4).

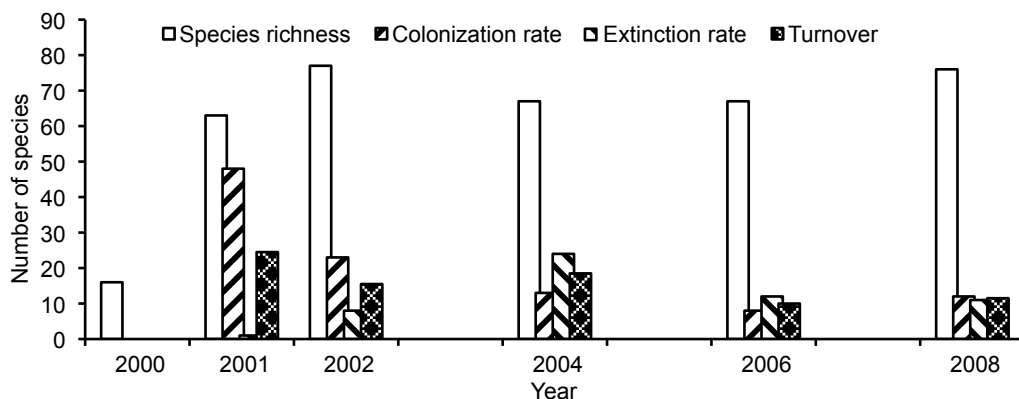


Fig. 4. Species richness and turnover during the investigation period. All numbers refer to the 356 1 × 1 m sampling units. Rates are expressed as the number of species new or missing as compared to the previous sample year. Turnover is the arithmetic mean of colonization and disappearance rates.

Eight years after gap creation the relative turnover rate exceeded 20% showing that there was still a dynamic species pool. Although species composition changed over time, all species present before gap formation survived eight years later.

After 2004 the total number of new occurrences diminished (Table 1). The analysis of seed traits showed that new colonization following gap creation came from species with both long distance dispersal and long-term persistent seed banks (such as *Scrophularia nodosa*). Later, not only did the number of new occurrences in this group decline, but their relative importance became smaller. New occurrences increased in the groups with non-LP seed banks with a maximum in 2004.

The change in species number was unevenly distributed among the light zones within the gaps (Fig. 5). In large gaps, most species appeared near the centre by 2004 (over 8 species per quadrat on average), only 4 years after gap formation. As early as two years after gap creation, the gap edges showed less species richness when compared to the gap centre. The centre of the small gaps showed greater number of species than the edge of large gaps, although individual gaps varied. The under-canopy zones of both large and small gaps showed limited increase in species richness and did not differ in species number.

The effects of gap size and within-gap position on species composition were assessed in 2008, eight years after gap formation (Fig. 6). The linear

Table 1. New occurrences of herbaceous species in the study gaps grouped by seed dispersal and seed bank traits. LP = long-term persistent seed bank, LongD = long distance seed dispersal. New occurrences were calculated from surplus frequencies as compared to the previous survey that were summed by trait groups.

LP	LongD	2001	2002	2004	2006	2008
+	+	373	254	239	57	47
+	-	73	58	76	35	23
-	+	47	89	133	69	28
-	-	43	16	105	15	67
Sum		536	417	553	176	165

discriminant analysis clearly separated the centre of the large gaps from the other light zones, while the others zones overlapped as a result of the large variance among individual gaps. The first two axes covered 92% and 5% of total variance, respectively. Intermediate openness created the largest variance as shown by the length the different zones occupy on Axis 1 of Fig. 6. The under-canopy of small gaps varied more in composition than Z1 of large gaps.

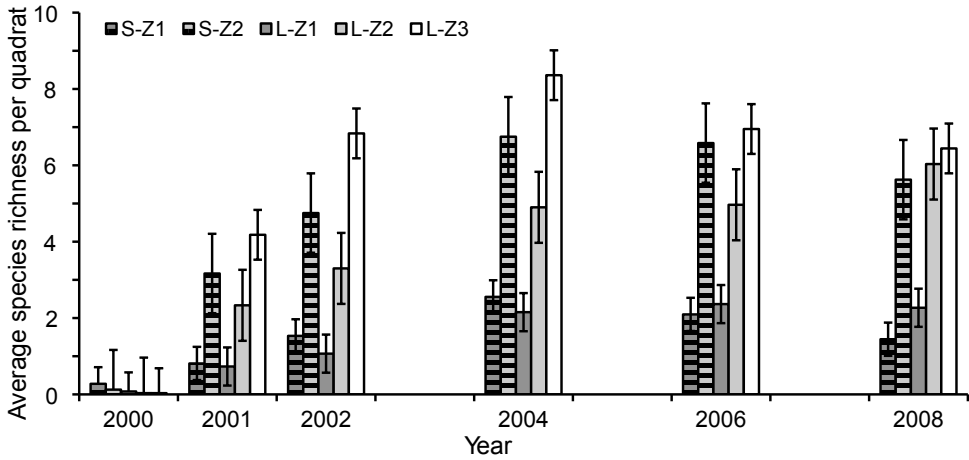


Fig. 5. Changes in species richness in different positions of small and large gaps. Average number of species per quadrat was calculated for each canopy openness (CO) zone. S – small; L – large; Z1: 0–20% CO; Z2: 20–40% CO; Z3: >40% CO. Whiskers denote 0.95 confidence intervals.

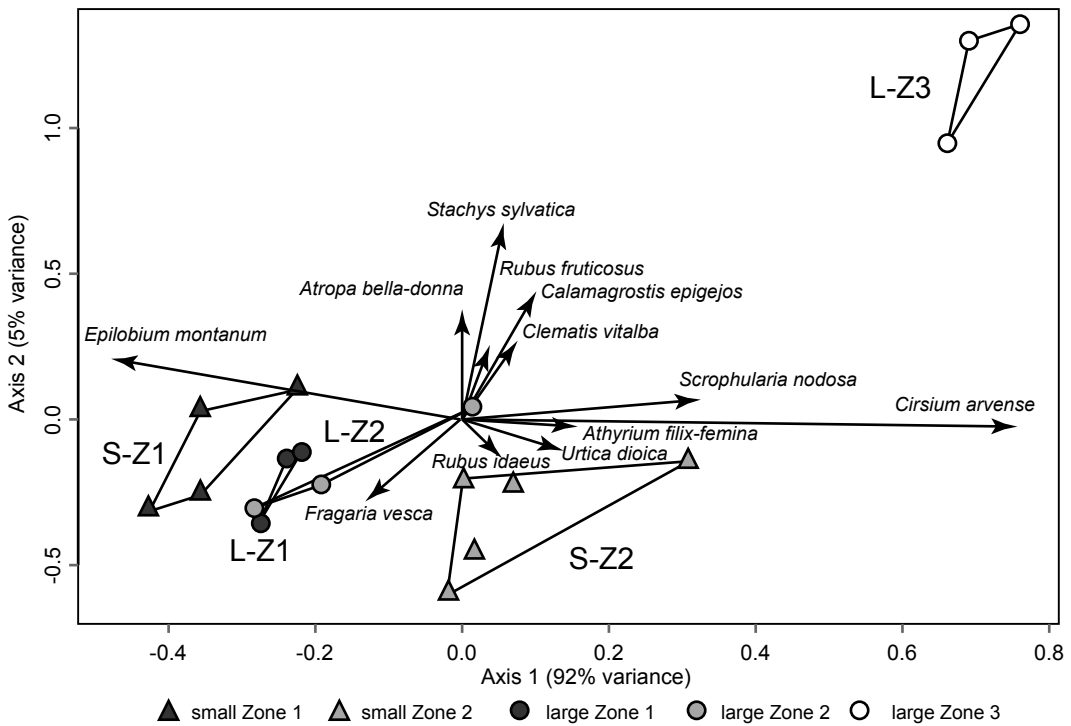


Fig. 6. Biplot of Linear Discriminant Analysis (LDA) for the canopy openness zones in 2008 (eight years after gap creation). Species are represented by the arrows (the scale is arbitrary) and places by triangles for small gaps and circles for large gaps. Species cover data were added up for each zone and log transformed for the 12 most abundant vascular species.

Table 2. Individual species preferences on gap size and within-gap position. For each species and year the result of the indicator species analysis is shown including the maximum indicator value (calculated as the product of relative frequency and relative abundance within each cluster) and the canopy openness (CO) zone that the species indicated. Significant results are marked by an asterisk ($p < 0.05$). S = small gaps, L = large gaps, Z1: 0–20% CO, Z2: 20–40% CO, Z3: >40% CO.

Species	2001	2002	2004	2006	2008
<i>Athyrium filix-femina</i>	–	L-Z3 0.80*	L-Z3 0.63*	L-Z3 0.44	S-Z2 0.41
<i>Atropa bella donna</i>	L-Z3 0.35	L-Z3 0.45	L-Z3 0.47	L-Z3 0.55*	L-Z3 0.64
<i>Calamagrostis epigejos</i>	–	L-Z3 0.81*	L-Z3 0.78*	L-Z3 0.94*	L-Z3 0.65*
<i>Carex divulsa</i>	–	L-Z3 0.99*	L-Z2 0.57	L-Z2 0.56	L-Z2 0.59
<i>Carex pilosa</i>	S-Z1 0.49	–	L-Z3 0.34	–	–
<i>Cirsium arvense</i>	L-Z3 0.67	L-Z3 0.90*	L-Z3 0.87*	L-Z3 0.85*	L-Z3 0.33
<i>Clematis vitalba</i>	–	L-Z3 0.47	L-Z3 0.52*	L-Z3 0.42	L-Z3 0.39
<i>Epilobium montanum</i>	–	L-Z2 0.40	L-Z2 0.37	S-Z2 0.46	–
<i>Eupatorium cannabinum</i>	–	L-Z3 0.49	L-Z3 0.62*	L-Z3 0.96*	L-Z3 0.90*
<i>Fragaria vesca</i>	L-Z3 0.33	L-Z3 0.80*	L-Z3 0.72*	L-Z3 0.36	L-Z3 0.53
<i>Galium odoratum</i>	–	–	L-Z2 0.54*	–	S-Z2 0.35
<i>Geranium robertianum</i>	L-Z1 0.38	L-Z1 0.33	–	–	L-Z3 0.32
<i>Hypericum perforatum</i>	L-Z3 0.64*	L-Z3 0.62*	L-Z3 0.40	L-Z3 0.36	L-Z2 0.56
<i>Impatiens noli tangere</i>	–	–	–	–	S-Z2 0.30
<i>Mycelis muralis</i>	–	S-Z2 0.32	–	–	–
<i>Poa nemoralis</i>	–	L-Z3 0.31	L-Z2 0.54	–	L-Z2 0.85
<i>Rubus fruticosus</i>	S-Z2 0.39	S-Z2 0.34	L-Z3 0.61*	L-Z3 0.66*	L-Z3 0.81*
<i>Rubus idaeus</i>	L-Z3 0.49	L-Z3 0.65*	L-Z3 0.70*	L-Z3 0.69*	L-Z3 0.74*
<i>Scrophularia nodosa</i>	L-Z3 0.42	L-Z3 0.43	S-Z2 0.43	–	–
<i>Stachys sylvatica</i>	–	S-Z2 0.49	S-Z2 0.36	S-Z2 0.46	L-Z3 0.91*
<i>Urtica dioica</i>	S-Z2 0.64*	S-Z2 0.63*	S-Z2 0.62*	S-Z2 0.58*	L-Z3 0.67*
<i>Veronica officinalis</i>	L-Z3 0.63*	L-Z3 0.65*	L-Z2 0.31	L-Z2 0.58	–

3.3 Species Preferences – Gap Size and Within-gap Position

Table 2 shows individual species preferences for gap size and within-gap position. Significant maximum indicator values were only found for species in the centres of large gaps with the exception of *Urtica dioica* that preferred the centres of small gaps until 2008. Only a few species (e.g. shade-tolerant herbs *Galium odoratum* (L.) Scop. and *Impatiens noli-tangere* L.) showed non-significant, but higher indicator values for the centres of small gaps, along with others that preferred the edge of large gaps (e.g. *Carex divulsa* Stokes, *Veronica officinalis* L.).

4 Discussion

4.1 Vegetation Cover

At our study site the herbaceous layer was very sparse prior to gap opening. This is likely an effect of the shelterwood forest management system that maintains a homogeneous closed canopy throughout most of the rotation. In near-natural beech stands the herbaceous layer tends to vary with respect to light conditions (Lysik 2008) and site heterogeneity (Kenderes and Standovár 2003). Soil conditions have a profound effect on the herbaceous layer below maturing closed stands. For example Tinya et al. (2009b) found the herbaceous layer was dense on alkaline soil derived from limestone, whereas on acidic volcanic soil there was little herbaceous vegetation even with higher light levels. Watt (1923) reported that in English beechwoods the herbaceous layer is generally more abundant as soil depth and fertility increase.

Gap formation led to a significant increase in herbaceous cover especially in the centre of gaps. Mountford et al. (2006) reported similar expansion of the herbaceous layer in a comparable beech forest on mesotrophic brown earth soils and studies from other forest types also generally show an increase in herbaceous cover (Moore and Vankat 1986, Falk et al. 2008). However, a study in Germany showed that herbaceous vegetation cover can decrease below canopy gaps even on limestone bedrock, if dominating species cannot recover after cutting (Schmidt 1997). The recorded increase in the ground vegetation cover was evidently related with an increase in light availability (Fig. 3), but canopy opening is also known to increase soil water and nutrient availability within canopy gap environments (Ritter et al. 2005, Gálhidy et al. 2006).

Herbaceous cover increased beneath the canopy in the areas immediately adjacent to the gap openings. This is consistent with the “light gap” theory (Canham et al. 1990) that states that the effects of gaps are extended beyond the physical boundaries of the actual gap opening.

4.2 Species Richness and Composition

Similar to earlier gap studies (e.g. Busing and White 1997, Schumann et al. 2003, Naaf and Wulf 2007) we found significant increases in species richness within gaps as compared to beneath the closed canopy (Fig. 5). Gap edges have been observed to support more species than gap centres (Fahey and Puettmann 2008), but most studies of forest gaps were undertaken in much larger gaps than the ones we created for our study (Euskirchen et al. 2001, Fahey and Puettmann 2008). Some studies did not detect an increase in species number in gaps (Goldblum 1997, Pavlovic et al. 2006), but the lack of change was either a result of very small gap size (i.e. single treefall gaps) or the presence of advance regeneration (Naaf and Wulf 2007). It seems likely that the main factor influencing the magnitude of change is the contrast between gap and stand environments (Fahey and Puettmann 2007, Fahey and Puettmann 2008). This contrast is greater for gaps occurring in the kind of dense, homogeneous stands created by current shelterwood practices.

Tree species composition can also be a factor in herbaceous diversity because of the diverse effects on light regime and soil properties of multi-species stands. Mölder et al. (2008) for example found greater herb diversity in mixed forests, than in pure beech stands under closed canopies. In our study, the number of herbaceous species was very low before gap formation and its increase with the resulting greater availability of resources was expected. Disturbances could also lead to a temporal reduction or extirpation of some species (Davison and Forman 1982). However, since the gaps in our study were created in winter when the soil was frozen, the substrate was not greatly impacted as would have been the case in a gap created by a fire or by tree uprooting.

The number of species that disappeared from the gaps increased over time and in contrast to other studies (e.g. Goldblum 1997, Schumann et al. 2003, Fahey and Puettmann 2008), substantial turnover of species was observed. Most transient species occurred in low frequencies (less than 2 occurrences on average for those present in only one survey) and less detailed investigations could easily miss such species.

In most temperate deciduous forests, gap size affects species composition (Degen et al. 2005, Naaf and Wulf 2007). As Fig. 6 shows, different sets of species are associated with the centres of large and small gaps. The centres of large gaps are characteristically dominated by a few light demanding species (e.g. *Rubus fruticosus* L., *Clematis vitalba* L.) with a limited number of associated species (e.g. *Cirsium arvense* (L.) Scop.) that can also occur in other disturbed habitats. The centres of small gaps are also usually dominated by a small number of dominant species (e.g. *Athyrium filix-femina* and *Rubus idaeus* L.). Since *Athyrium filix-femina* is a shade-tolerant and water demanding species, it is understandable that it occurs in small gaps, where soil moisture levels are higher (Ritter et al. 2005, Gálhidy et al. 2006). On the other hand, *Rubus idaeus* is light demanding and competition could explain why it is almost absent from the centre of large gaps. However, in a study involving this species Gaudio et al. (2008) showed that competition was unlikely to influence the partitioning of the gaps.

In summary, both large and small gaps were successful in maintaining herbaceous species

richness. Although composition continuously changed in the different zones within the gaps, species present before cutting (e.g. *Viola sylvestris* Lam., *Mercurialis perennis*) survived. Light conditions seemed to be the most important factor in determining the direction and speed of dynamic change, but soil properties and competition cannot be ruled out as factors.

4.3 Colonization of Gaps

It has been shown previously that species can colonize forest gaps both from an in situ soil seed bank and through long distance seed dispersal (Naaf and Wulf 2007). Most plant species seem to have either good dispersal abilities or persistent seed banks, though some possess both (Eriksson 2000). Our data suggest that new colonization is facilitated by both long-term seed bank and long distance dispersal (including wind, mammals and birds); therefore species with a successful dispersal strategy in both space and time are by far the fastest to arrive. Species with continued presence and dominance in the centre of gaps (most importantly *Rubus fruticosus*) belonged to this group pointing to the importance of early colonization. This could be an important characteristic of “gap species”, forest herbs reacting positively to openings (Anderson and Leopold 2002). We also found that species with long-term persistent (LP) seed banks, but which lacked mechanisms to disperse long distances (e.g. autochorous species) occurred in greater number early on after gap creation compared to species with a non-LP seed bank. This indicates that the soil seed bank is more important than dispersal in determining species composition early after gap creation.

4.4 Single Species Preferences – Gap Size and Within-gap Position

Where significant relationships were detected, species were more abundant in large gaps with only one exception. No species grew better beneath the dense canopy than in gaps. This seems to be a general pattern in gap studies (Goldblum 1997, Schumann et al. 2003, Fahey and Puettmann 2008). Better growth within gaps can partly be

related to the fact that even shade-tolerant species grow faster under better light conditions (Valladares and Niinemets 2008). However, there were species that occurred only under the canopy and never in gaps (e.g. *Gymnocarpium dryopteris* (L.) Newman, *Epipactis helleborine* (L.) Crantz), but because these occurred infrequently, the relationship was not statistically significant. In other words, the preferences of such species were difficult to assess. The only species that preferred small gaps, *Galium odoratum*, was also found to reach higher abundance in shady plots in a study comprising various forest types (Tinya et al. 2009b) underlining the importance of light levels for individual species.

4.5 Implications for Forest Management

We assessed the effects of gaps on herbaceous vegetation in a beech stand under conversion from a shelterwood system to continuous cover forestry. During this conversion, decisions about gap size and number of gaps/hectare need to be taken. Relatively small (<0.1 ha) gaps were used, and taken that the goal is to produce an uneven-aged stand structure, our previous studies indicate that such gaps are large enough to facilitate regeneration (Mihók et al. 2005, Gálhidy et al. 2006). Beech seemed to be able to regenerate naturally in both gap sizes, although a longer time-frame will be needed for certainty. Our study revealed several important aspects of the response of the herbaceous layer to gap opening providing practitioners a tool to decide on gap sizes.

The composition of the herbaceous vegetation depends largely on gap size and within-gap position. The centres of gaps are usually dominated by a few species. If the gaps are too large, common competitive weeds (such as *Rubus fruticosus* or *Calamagrostis epigejos* (L.) Roth) will likely be dominant and hamper regeneration. Although this indicates that larger gap cutting might be undesirable, *Rubus fruticosus* can also protect tree seedlings from browsing where herbivore pressure is high (Naaf and Wulf 2007). In a recent study on the relationship of *Rubus fruticosus* and seedling establishment and growth Harmer et al. (2010) conclude that the protective effect of *Rubus fruticosus* is species specific. Although

there is generally a positive correlation between *Rubus fruticosus* cover and seedling height, seedling numbers can decrease hampering natural regeneration.

Herbaceous cover can increase to 100% even in small gaps and tree seedlings compete with herbs for light and water. It has been recorded at our site that small saplings are more abundant at gap edges. Older saplings show positive correlation with herbaceous cover (Mihók et al. 2005), which can be the effect of the advance regeneration growing above the herbaceous layer and thus being released from competition. However, *Rubus fruticosus* often limits growth of such individuals by overtopping them (Mountford et al. 2006). Herbaceous vegetation might also have a protective effect where herbivore pressure is high (Naaf and Wulf 2007).

We conclude that small gaps are better suited for the regeneration of beech, because of less competition in the herbaceous layer and the absence of common forestry weeds. Although it is possible that small gaps are closed by lateral extension of neighbouring trees, saplings can be further aided by selective cutting of individuals bordering the gap at a later stage. On the contrary, if regeneration is hampered in large gaps, costly measures need to be taken to enable the filling of the gaps. The creation of a few large gaps could be beneficial at the landscape scale: they favour admixing tree species. Large herbivores highly influence the success of natural regeneration in gaps because of their preference for admixing species (such as *Fraxinus excelsior* L., *Acer platanoides* L.) and herbaceous species. Therefore the large-scale use of artificial gaps as means for transitional silvicultural system must be accompanied by strict game management.

Acknowledgements

Thanks are due to János Ruff forest manager of the site for permission and assistance; Sándor Bartha, Péter Ódor and János Podani for their comments on the manuscript. Part of the research was carried out under the NAT-MAN project – Nature-Based Management of Beech in Europe – funded by the European Community Fifth Framework Programme.

References

- Anderson, K. L. & Leopold, D. J. 2002. The role of canopy gaps in maintaining vascular plant diversity at a forested wetland in New York State. *Journal of the Torrey Botanical Society* 129: 238–250.
- Bradshaw, R., Gemmel, P. & Björkman, L. 1994. Development of nature-based silvicultural models in Southern Sweden: the scientific background. *Forest and Landscape Research* 1: 95–110.
- Brunet, J., Fritz, Ö. & Richnau, G. 2010. Biodiversity in European beech forests – a review with recommendations for sustainable forest management. *Ecological Bulletins* 53: 77–94.
- Busing, R. & White, P. 1997. Species diversity and small-scale disturbance in an old-growth temperate forest: a consideration of gap-partitioning concepts. *Oikos* 78: 562–568.
- Canham, C.D., Denslow, J.S., Platt, W.J., Runkle, J.R., Spies, T.A. & White, P.S. 1990. Light regimes beneath closed canopies and tree-fall gaps in temperate and tropical forests. *Canadian Journal of Forest Research* 20: 620–631.
- Collins, B.S. & Pickett, S.T.A. 1988. Response of herb layer cover to experimental canopy gaps. *American Midland Naturalist* 119: 282–290.
- Csontos, P., Tamás, J. & Tobisch, T. 2002. A magyar flóra magterjesztési-mód adatbázisának bemutatása, elemzési példák: a szociális magatartási típusok értékelése. [Description of the seed dispersal database of the Hungarian flora with examples]. PTE, Pécs. (In Hungarian).
- Davison, S.A. & Forman, R.T.T. 1982. Herb and shrub dynamics in a mature oak forest: a thirty-year study. *Bulletin of the Torrey Botanical Club* 109: 64–73.
- Degen, T., Devillez, F. & Jacquemart, A. 2005. Gaps promote plant diversity in beech forests (Luzulo-Fagetum), North Vosges, France. *Annals of Forest Science* 62: 429–440.
- Doornik, J.A. & Hansen, H. 2008. An omnibus test for univariate and multivariate normality. *Oxford Bulletin of Economics and Statistics* 70: 927–939.
- Dufrene, M. & Legendre, P. 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. *Ecological Monographs* 67: 345–366.
- Ellenberg, H. 1988. *Vegetation ecology of Central Europe*. Cambridge University Press, Cambridge.

- Englund, S.R., O'Brien, J.J. & Clark, D.B. 2000. Evaluation of digital and film hemispherical photography and spherical densiometry for measuring forest light environments. *Canadian Journal of Forest Research* 30: 1999–2005.
- Eriksson, O. 2000. Seed dispersal and colonization ability of plants – assessment and implications for conservation. *Folia Geobotanica* 35: 115–123.
- Euskirchen, E.S., Chen, J.Q. & Bi, R.C. 2001. Effects of edges on plant communities in a managed landscape in northern Wisconsin. *Forest Ecology and Management* 148: 93–108.
- Fahey, R.T. & Puettmann, K.J. 2007. Ground-layer disturbance and initial conditions influence gap partitioning of understorey vegetation. *Journal of Ecology* 95: 1098–1109.
- & Puettmann, K.J. 2008. Patterns in spatial extent of gap influence on understorey plant communities. *Forest Ecology and Management* 255: 2801–2810.
- Falk, K.J., Burke, D.A., Elliott, K.A. & Holmes, S.B. 2008. Effects of single-tree and group selection harvesting on the diversity and abundance of spring forest herbs in deciduous forests in southwestern Ontario. *Forest Ecology and Management* 255: 2486–2494.
- Gaudio, N., Balandier, P. & Marquier, A. 2008. Light-dependent development of two competitive species (*Rubus idaeus*, *Cytisus scoparius*) colonizing gaps in temperate forest. *Annals of Forest Science* 65: 104.
- Goldblum, D. 1997. The effect of treefall gaps on understorey vegetation in New York State. *Journal of Vegetation Science* 8: 125–132.
- Gálhidy, L., Mihók, B., Hagyó, A., Rajkai, K. & Standovár, T. 2006. Effects of gap size and associated changes in light and soil moisture on the understorey vegetation of a Hungarian beech forest. *Plant Ecology* 183: 133–145.
- Hammer, Ø., Harper, D. & Ryan, P. 2001. PAST: Paleontological statistics software package for education and data analysis. *Palaeontologia Electronica* 4.
- Harmer, R., Kiewitt, A., Morgan, G. & Gill, R. 2010. Does the development of bramble (*Rubus fruticosus* L. agg.) facilitate the growth and establishment of tree seedlings in woodlands by reducing deer browsing damage? *Forestry* 83: 93–102.
- Kenderes, K. & Standovár, T. 2003. A review on natural stand dynamics in beechwoods of East Central Europe. *Applied Ecology and Environmental Research* 1: 19–46.
- Klotz, S., Kühn, I. & Durka, W. 2002. [online database] BIOLFLORE – Eine Datenbank zu biologisch-ökologischen Merkmalen der Gefäßpflanzen in Deutschland, Bundesamt für Naturschutz, Bonn. Available at: <http://www.ufz.de/biolflor>. [Cited 2 May 2011].
- Laska, G. 2001. The disturbance and vegetation dynamics: a review and an alternative framework. *Plant Ecology* 157: 77–99.
- Lemmon, P. 1956. A spherical densiometer for estimating forest overstorey density. *Forest Science* 2: 314–320.
- Liu, K., Eastwood, R., Flynn, S., Turner, R. & Stuppy, W. 2008. Seed information database. (Release 7.1, May 2008), Royal Botanic Gardens, Kew. Available at: <http://www.kew.org/data/sid>. [Cited 2 March 2010].
- Lysik, M. 2008. Ten years of change in ground-layer vegetation of European beech forest in the protected area (Ojców National Park, South Poland). *Polish Journal of Ecology* 56: 17–31.
- McIntyre, S., Diaz, S., Lavorel, S. & Cramer, W. 1999. Plant functional types and disturbance dynamics – introduction. *Journal of Vegetation Science* 10: 604–608.
- Metzger, F. & Schultz, J. 1981. Spring ground layer vegetation 50 years after harvesting in northern hardwood forests. *American Midland Naturalist* 105: 44–50.
- Mihók, B., Gálhidy, L., Kelemen, K. & Standovár, T. 2005. Study of gap-phase regeneration in a managed beech forest: relations between tree regeneration and light, substrate features and cover of ground vegetation. *Acta Silvatica et Lignaria Hungarica* 1: 25–38.
- Mölder, A., Bernhardt-Romermann, M. & Schmidt, W. 2008. Herb-layer diversity in deciduous forests: Raised by tree richness or beaten by beech? *Forest Ecology and Management* 256: 272–281.
- Moore, M.R. & Vankat, J.L. 1986. Responses of the herb layer to the gap dynamics of a mature beech-maple forest. *American Midland Naturalist* 115: 336–347.
- Mountford, E.P., Savill, P.S. & Bebbler, D.P. 2006. Patterns of regeneration and ground vegetation associated with canopy gaps in a managed beechwood in southern England. *Forestry* 79: 389–408.
- Naaf, T. & Wulf, M. 2007. Effects of gap size, light and

- herbivory on the herb layer vegetation in European beech forest gaps. *Forest Ecology and Management* 244: 141–149.
- O'Hara, K.L., Hasenauer, H. & Kindermann, G. 2007. Sustainability in multi-aged stands: an analysis of long-term plenter systems. *Forestry* 80: 163–181.
- Pavlovic, N.B., Grundel, R. & Sluis, W. 2006. Ground-layer vegetation gradients across oak woodland canopy gaps. *Journal of the Torrey Botanical Society* 133: 225–239.
- Peterken, G. 1996. *Natural woodland. Ecology and conservation in northern temperate regions.* Cambridge University Press, Cambridge.
- Pinheiro, J. & Bates, D.. 2000. *Mixed effects models in S and S-PLUS.* Springer, New York.
- , Bates, D., DebRoy, S. & Sarkar, D. 2011. R Development Core Team 2011. [software package] nlme: Linear and Nonlinear Mixed Effects Models.
- Podani, J. 2001. SYN-TAX 2000 Computer program for data analysis in ecology and systematics for Windows 95, 98 and NT. User's Manual. Scientia Publishing, Budapest.
- Pommerening, A. & Murphy, S.T. 2004. A review of the history, definitions and methods of continuous cover forestry with special attention to afforestation and restocking. *Forestry* 77: 27–44.
- R Development Core Team 2011. R: A language and environment for statistical computing.
- Ritter, E., Dalsgaard, L. & Einhorn, K. 2005. Light, temperature and soil moisture regimes following gap formation in a semi-natural beech-dominated forest in Denmark. *Forest Ecology and Management* 205: 15–33.
- Roberts, D.W. 2010. [software package] labdsv: Ordination and multivariate analysis for ecology.
- Roberts, M.R. 2004. Response of the herbaceous layer to natural disturbance in North American forests. *Canadian Journal of Botany* 82: 1273–1283.
- Schmidt, W. 1997. Vegetation dynamics in canopy gaps of a beech forest on limestone. *Forstwissenschaftliches Centralblatt* 116: 207–217.
- Schoener, T.W. 1988. On testing the MacArthur-Wilson model with data on rates. *American Naturalist* 131: 847–864.
- Schumann, M., White, A. & Witham, J. 2003. The effects of harvest-created gaps on plant species diversity, composition, and abundance in a Maine oak-pine forest. *Forest Ecology and Management* 176: 543–561.
- Sousa, W. 1984. The role of disturbance in natural communities. *Annual Review of Ecology and Systematics* 15: 353–391.
- Thompson, K., Bakker, J. & Bekker, R. 1997. *The soil seed banks of North West Europe: methodology, density and longevity.* Cambridge University Press, Cambridge.
- Tinya, F., Mihók, B., Márialigeti, S., Mag, Z. & Ódor, P. 2009a. A comparison of three indirect methods for estimating understory light at different spatial scales in temperate mixed forests. *Community Ecology* 10: 81–90.
- , Márialigeti, S., Király, I., Németh, B. & Ódor, P. 2009b. The effect of light conditions on herbs, bryophytes and seedlings of temperate mixed forests in Órség, Western Hungary. *Plant Ecology* 204: 69–81.
- Tutin, T., Heywood, V., Burges, N., Moore, D., Valentine, D., Walters, S. & Webb, D. 1964–1993. *Flora Europea.* Cambridge University Press, Cambridge.
- UN/ECE-FAO 2000. *Forest resources of Europe, CIS, North America, Australia, Japan and New Zealand. Main Report.* Geneva Timber and Forest Study Papers 17. [online report] Available at: <http://www.unece.org/timber/fra/pdf/contents.htm>. [Cited 25 February 2011]
- Valladares, F. & Niinemets, U. 2008. Shade tolerance, a key plant feature of complex nature and consequences. *Annual Review of Ecology, Evolution, and Systematics* 39: 237–257.
- Virola, T., Kaitala, V., Kuitunen, M., Lammi, A., Siikamäki, P., Suhonen, J. & Virolainen, K. 1999. Species immigration, extinction and turnover of vascular plants in boreal lakes. *Ecography* 22: 240–245.
- Watt, A. 1923. On the ecology of British beechwoods with special reference to their regeneration. *Journal of Ecology* XI: 1–47.
- Zeibig, A., Diaci, J. & Wagner, S. 2005. Gap disturbance patterns of a *Fagus sylvatica* virgin forest remnant in the mountain vegetation belt of Slovenia. *Forest Snow and Landscape Research* 79: 69–80.
- Zuur, A., Ieno, E., Walker, N., Saveliev, A. & Smith, G.. 2009. *Mixed effects models and extensions in ecology with R.* Springer, New York.

Total of 61 references