

Effects of gap size and associated changes in light and soil moisture on the understorey vegetation of a Hungarian beech forest

László Gálhidy¹, Barbara Mihók², Andrea Hagyó³, Kálmán Rajkai³ and Tibor Standovár^{2,*}

¹Production Biology Research Group, Hungarian Academy of Science-University of West Hungary, H-9400, Sopron, Bajcsy-Zsilinszky u. 4., Hungary; ²Department of Plant Taxonomy & Ecology, L. Eötvös University, H-1117, Budapest, Pázmány P. st. 1/c, Hungary; ³Research Institute for Soil Sciences and Agricultural Chemistry of the Hungarian Academy of Sciences, H-1022, Budapest, Herman Ottó u. 15., Hungary; * Author for correspondence (e-mail: standy@ludens.elte.hu)

Received 12 January 2005; accepted in revised form 23 June 2005

Key words: Beech, Gap partitioning, Herbs

Abstract

In European beech forests windstorms often create canopy gaps and change the level of incident light, soil moisture and nutrient availability on the forest floor. Understanding the interrelations between gap size and environmental change, and the effects these have on regeneration processes is a prerequisite for developing techniques of nature-based forestry. The aims of this study were to investigate the effects of gap size on the resulting spatial distributions of key abiotic environmental variables (light and soil moisture) in gaps, and to study how light and soil moisture affect the abundance and distribution of herb layer species. To do this we used eight artificially created gaps – three large (diameter: 35–40 m) and five small (diameter: 10–15 m) – in a mesotrophic submontane beech forest. Data on species' importance and substrate types were collected in systematically distributed 1 m×1 m quadrats before gap creation and on four occasions during the next two growing seasons. Hemispherical photographs were taken and analysed to estimate relative light intensity. Soil moisture was measured by frequency domain and capacitance probes. It was found that gap size had a profound effect on the environmental variables measured. While relative light intensity values in small gaps did not reach those in large gaps, soil moisture levels did reach similar maximum values in gap centres regardless of gap size. Richness, composition and total cover of herbaceous vegetation were different in small versus large gaps. Much of this difference was attributed to the presence of specific relative light intensities and also to the increased amount of available soil moisture in gaps. Species were differently affected by the combined effects of light and soil moisture, as well as by differences in available substrates. All this resulted in species-specific distribution patterns within gaps.

Introduction

Gap formation by wind is a characteristic disturbance event in temperate deciduous forests (Runkle 1989). Gap size varies greatly from the size of

only a single crown to vast open fields with diameters of many tree lengths. The fall of canopy trees results in increased total incident light levels at the ground and in some cases also in increased nutrient and moisture availability (Denslow and

Spies 1990). Gap microclimates may enhance seed germination and increase growth rates of herbs and woody species in comparison with rates in the forest understory (Schaetzel et al. 1989; Denslow and Spies 1990; Goldblum 1997). However, changes in abiotic and biotic conditions depend both on gap size and within-gap position (Nakashizuka 1985; Vitousek and Denslow 1986; Collins and Pickett 1987; Collins and Pickett 1988; Canham 1989; Platt and Strong 1989; Poulson and Platt 1989; Runkle 1989; Holeksa 2003; Kwit and Platt 2003). Different explanations and concepts have been published on how woody and herbaceous species establish and survive in gaps of different forest types. Most of these studies focus on the dynamics of woody regeneration, and only a few concentrate on herbaceous species (Collins and Pickett 1987; Hughes and Fahey 1991; Schumann et al. 2003). Many studies focused on the role of resource gradients (e.g. light) from beneath intact canopy to the centre of the gap, which are too broad to be dominated by one species (Gray and Spies 1996). Establishment and growth of different tree species are therefore correlated with gap size and within-gap position (Busing and White 1997; Brokaw and Busing 2000). In consequence, a zonation of regeneration sometimes develops, especially in large gaps (Poulson and Platt 1989). A few papers have discussed the distribution of specific herbaceous species along abiotic (mainly light) gradients (Ricard and Messier 1996, Schmidt et al. 1996). Some papers have included soil moisture as another important resource gradient that should be observed more widely (Collins and Pickett 1987, 1988; Schumann et al. 2003). Other studies stressed the importance of specific substrates (e.g., logs, pits and mounds), which can be important as regeneration niches. Heterogeneity observed at the seedling scale (< 10 cm) often overrides larger-scale environmental gradients (> 2 m) associated with gap size and within-gap position (Gray and Spies 1997). Spatial distribution of both tree seedlings and herb layer species depends upon the abundance of specific substrates available for colonization (Beatty 1984; Goldblum 1997 and references therein, Lawton and Putz 1988; Schaetzel et al. 1989; Peterson and Campbell 1993).

Studying dynamic responses of herbaceous species to gap formation in artificially created gaps can help to understand tree regeneration processes,

since herbs can affect abiotic variables, compete with seedlings and consequently influence the success of tree regeneration in gaps (Maguire and Forman 1983; Gilliam and Turrill 1993; Abe et al. 1995). Thus, establishment and survival of herbaceous species in canopy gaps of different sizes should be observed more widely (Collins and Pickett 1987; Goldblum 1997; Schumann et al. 2003).

The aim of our study was to investigate the effect of gap-size on the spatial distribution of abiotic environmental variables and on the distribution and abundance of herb layer species. For this purpose fieldwork was carried out in artificially created gaps representing two size classes.

Our questions are: (1) How does gap size influence the environmental gradients of direct, diffuse and total relative light intensity, and soil moisture within gaps? (2) Are there any differences in the composition and dynamics of herbaceous and woody vegetation in small versus large gaps and in zones of different light availability? (3) How do environmental factors (light intensity, soil moisture, substrate features) influence the occurrence and the abundance of herbaceous and tree species?

Methods

Study area

The study site is located in the Börzsöny Mountains, northern Hungary (47,9° N, 18,9° E). Out of the 34,000 ha forest in the Börzsöny, approximately 5000 ha are covered by beech woods. In selecting the location of the experimental gaps several conditions were taken into consideration. To minimize the effects of site differences, we concentrated our experiment in two subcompartments that cover only 12.5 ha, have similar elevation (540–610 m), slope and aspect (east-northeast). Mean annual temperature is 8 °C, mean monthly temperature is –3.5 and 18 °C in January and in July, respectively. Annual precipitation is 700–800 mm. Bedrock is andesite, on which medium deep brown forest soil has developed. In the mesotrophic submontane beech forest covering these subcompartments, European beech (*Fagus sylvatica* L.) is monodominant, common ash (*Fraxinus excelsior* L.), Norway maple (*Acer*

platanoides L.), sycamore (*Acer pseudoplatanus* L.), field maple (*Acer campestre* L.), lime (*Tilia cordata* Mill., *Tilia platyphyllos* Scop.), and hornbeam (*Carpinus betulus* L.) are present in small amounts. The beech stands of these subcompartments are old enough (86 years old) to produce seeds. Average tree height is 25 m, mean diameter at breast height is 30 cm. These subcompartments were chosen because they were the least affected by recent natural disturbance events (ice-break in 1996, windstorm in 1999) providing a typical dense homogeneous monodominant stand for this experiment.

Under the homogenous beech canopy, the herb layer is rather poor. The most abundant vascular species include *Mycelis muralis* (L.) Dum., *Luzula luzuloides* (Lam.) Dandy, *Carex pilosa* Scop., *Epilobium montanum* L., *Mercurialis perennis* L., *Hieracium* spp., *Athyrium filix-femina* (L.) Roth and *Dryopteris filix-mas* (L.) Schott. Spring geophytes are sparse. Tree seedlings and saplings are greatly affected by intensive browsing. Advance regeneration (> 1 m) is poor. The area has been under organised forestry management using a uniform shelterwood system for a long time. Nowadays it is managed by a state owned forest enterprise (Ipoly Erdő Ltd.).

Data collection

Gaps of two sizes were created: (i) in the three large gaps the proportion of tree height of surrounding stand (H) to gap diameter (D) was 1:1.5 allowing direct light to reach the ground in the gap; (ii) in the five small gaps H:D was 1:0.5 gaps allowing much less light – mostly diffuse light – to reach the ground. Diameters of large gaps are about 36–40 m, diameters of small gaps are about 12–14 m respectively. Gaps were located in a restricted random way within the 12.5 ha, so that minimum distance (50 m) between two neighbouring gap margins approximates to twice the average tree height. Gaps were created by sawing trees, in February 2001. Fallen trees were removed.

For recording environmental and vegetation data we used a systematic sampling design, which extended beyond the gap boundaries with 5-meter grid resolution and 1 × 1 m quadrats. As Figure 1 shows, each large gap contained 123 quadrats,

whereas small gaps contained 64 quadrats each. Altogether we sampled 689 quadrats.

Vegetation data were recorded on five occasions (in September 2000 – before gap creation – May/September 2001, and May/September 2002). On each occasion we determined the cover of each herbaceous species using visual estimation in each quadrat. In addition, abundance (number of individuals) of young trees was counted for all tree species using 4 height classes (0–10, 10–20, 20–50, > 50 cm).

In each quadrat, coverage of five different substrate types (intact surface, bare surface, coarse woody debris–CWD, living tree, stone) was recorded in May 2001 and 2002.

Hemispherical photographs were taken at 70 cm height above ground in the sample quadrats along N–S, E–W transects in 2002 to calculate relative light intensity as percent of above canopy light (PACL). Seventeen photos were taken in small gap No. 1., and eight in the other four small gaps, and 37 were taken in large gap No. 2., and 15 in the other two large gaps, both in 2001 and 2002.

The study of soil water content required an even finer spatial resolution; hence a non-regular grid design (Figure 1) was implemented in small gap No. 1 and large gap No. 2. These measurements were supplemented by cover estimates of herbaceous and woody species in circular plots of 20 cm diameter around each measurement point. The presence of CWD, litter and stones was recorded as a binary variable in these circular plots.

Two instruments were used in July 2002: a Frequency Domain device (MCM102, IMAG, Hilhorst 1998; Dirksen 1999) and a capacitance probe (BR-30, Várallyay and Rajkai 1987). Further soil water content measurements (2002 July–October, once in each month in both gaps) were made with the capacitance probe because it proved to be more enduring in the stony soil. Both probes were stuck vertically to the soil surface after clearing away the litter. The measured soil volume by the MCM102 and the capacitance probe were about 125 and 100 cm³, respectively. They measure volumetric water content.

Data analyses

Hemispherical photos were analysed using a Windows-based software, hemIMAGE (Brunner

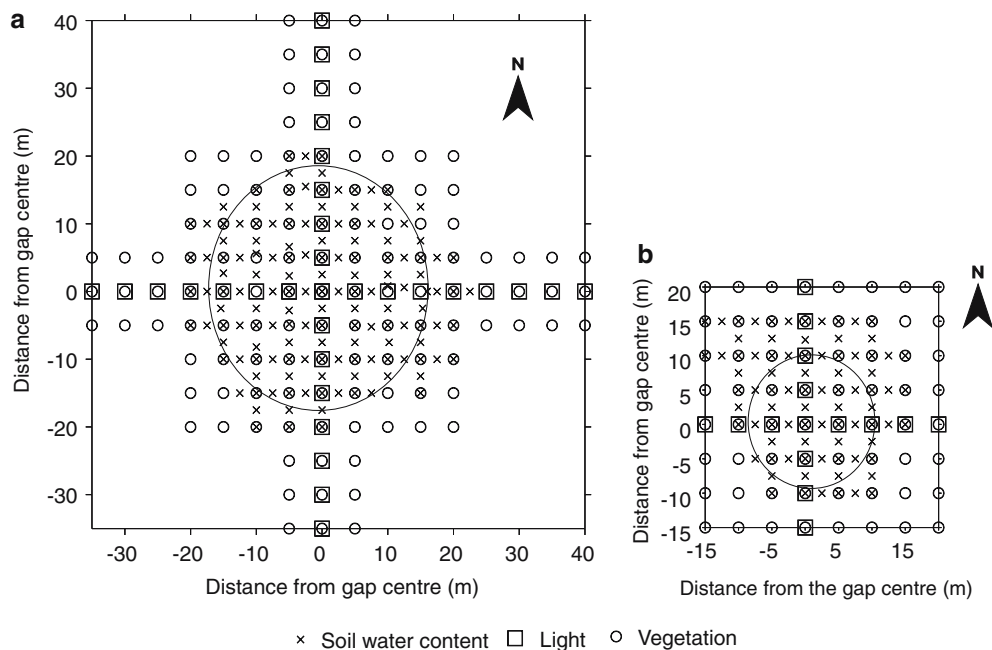


Figure 1. Sampling design in the (a) large and (b) small gaps. Crosses: plots where measurement of soil-moisture was carried out; Rectangles: plots where fish-eye photographs were taken; Circles: plots where sampling of herb layer was carried out. Large ellipses represent the approx. margin of the artificial gap.

2000). Relative light intensity (Percent of Above Canopy Light, PACL) was calculated for a given period of time in a certain location. With hem-IMAGE, the direct and the diffuse site factor can be calculated separately for a given point, assuming (based on meteorological data) that 0.5 of the Above Canopy Light (ACL) is the diffuse light component. We calculated the PACL for the period from 1st March to 31st October. Different light intensity zones were distinguished within each gap based on diffuse PACL as follows: Z1 – 0–10% diffuse PACL (under canopy); Z2 – 10–20% diffuse PACL (in centre of small gaps and at the edge of large gaps); Z3 – > 20% diffuse PACL (in centre of large gaps). These zones were used for analysing species responses.

Soil water content contour maps and light post maps were made with Surfer 8 software (Golden Software 2002) to visualize the spatial patterns of these abiotic factors. Radial Basis Function (Multiquadric function) was used for interpolation: $B(h) = \text{SQRT}(h^2 + R^2)$, where: h is the anisotropically rescaled, relative distance from the point to the node; and R^2 is the smoothing factor specified by the user. R^2 is calculated as follows: $(\text{length of diagonal of the data extent})^2 /$

$(25 \times \text{number of data points})$ (Carlson and Foley 1991).

Nonparametric statistical analyses – Mann–Whitney U test and Kruskal–Wallis ANOVA – were used to compare the recorded vegetation and environmental variables between small and large gaps. The same method was used to compare the soil water content between gaps and below canopy.

Interactions between pairs of different abiotic factors (volumetric water content measured in July 30–31, and PACL for July) and between abiotic factors and species abundances recorded in 2002, were tested by calculating Spearman Rank correlations.

A hierarchical classification of species was carried out based on their average cover per quadrat in different light zones. For the analysis – carried out by the SYNTAX software package – we used chord distance as the resemblance function and the group average clustering algorithm (Podani 2000, 2001).

Nomenclature

Nomenclature is based on Simon (2000)

Results

Relative total light intensity under the homogeneous beech canopy was 5–10% (Table 1, Figure 2). Depending on gap size, it increased up to 10–36% towards the centre of the gap. On average, a larger proportion of diffuse light reached the ground than direct sunlight from the sunbeams in most of the sample plots. This pattern may not refer consequently to the energy flux coming from incident light, since more energy might arrive in direct light than in diffuse light, even if the direct light was a lower proportion of the above canopy light. However, the above-mentioned pattern can also vary in certain parts of the gaps.

The pattern of diffuse PACL reflected gap geometry and was also influenced by the structure of the surrounding stand. In the centre of small gaps diffuse PACL was ca.15%, it was ca.10% at the edges, and it decreased below 10% under the canopy. In large gaps diffuse PACL values varied between 30–36% near the gap centre, were ca. 20–25% at the edges, and they decreased below 10% in the 10–15 m, i.e. 0.5 tree length into the forest from the edge.

The pattern of the direct PACL is influenced by the sun path (i.e., time of the year), aspect, and also the topography of neighbouring slopes. Direct sunlight reaches the ground for longer periods in the N, and N-W part of the gaps during the whole

Table 1. Relative light intensity (in Percent of Above Canopy Light, PACL) in small and in large gaps (Mean \pm std. dev., (min–max)).

	Small gaps under-canopy values ($N=30$)	Small gaps under-opening values ($N=22$)	Large gaps under-canopy values ($N=23$)	Large gaps under-opening values ($N=27$)
Direct	7.01 ± 5.13 (1.37–19.78)	6.39 ± 4.77 (2.08–17.09)	9.276 ± 8.415 (0.926–30.306)	18.42 ± 13.28 (0.71–39.29)
Diffuse	8.19 ± 2.02 (4.54–13.66)	12.93 ± 1.95 (9.76–6.24)	9.363 ± 4.327 (4.982–24.755)	27.63 ± 6.59 (15.45–36.42)
Total	7.60 ± 2.74 (3.92–14.65)	9.66 ± 2.17 (6.35–14.85)	9.320 ± 5.610 (3.779–25.594)	23.03 ± 7.77 (8.36–34.61)

Direct: Relative direct light intensity, Diffuse: Relative diffuse light intensity, Total: Relative total light intensity (all in PACL, Percent of Above Canopy Light).

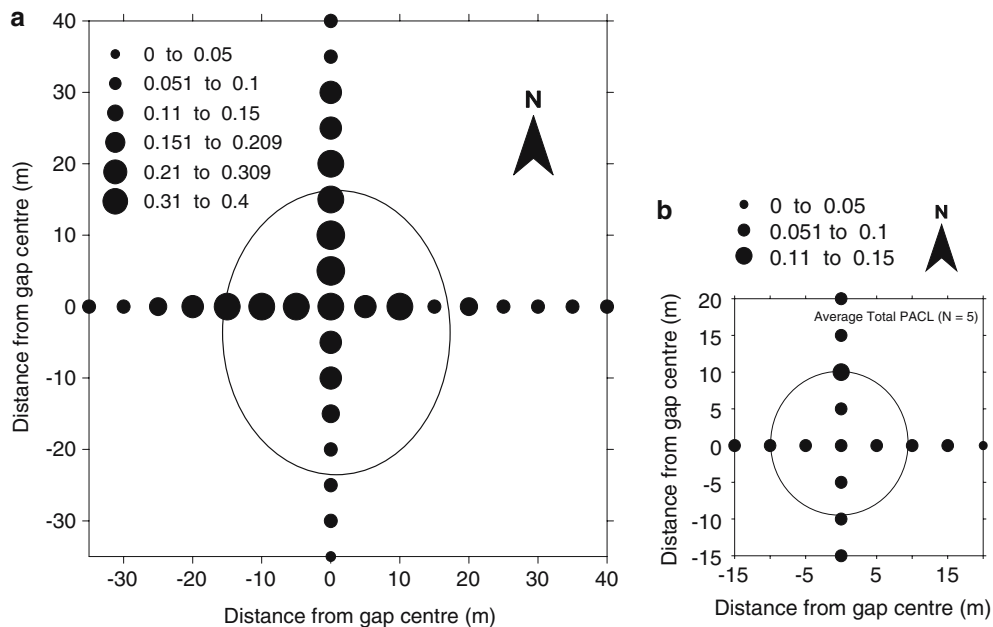


Figure 2. Average of total PACL (Percent of Above Canopy Light) in the (a) large, and (b) small gaps. Circles represent the locations where fish-eye photographs were taken from. The larger the size of the circles, the larger amount of total PACL was calculated by hemIMAGE.

growing season. In small gaps direct PACL reached 19% in the N parts of the gap, whereas in large gaps it reached 39%.

Both in small and large gaps the northern and the western direction had the highest direct and diffuse PACL values. The spatial variation of relative light intensity was also the highest in these parts. The eastern part received the lowest irradiance.

Small and large gaps were significantly (Mann-Whitney, $p < 0.001$) different in terms of total, diffuse and direct PACL values. As Table 1 shows, their minimum values, characterising dense beech canopy, were similar, but maximum PACL values were different. About 20% more direct and diffuse light reached the ground in the centre of large gaps than that of small gaps. The light environment near the edges of large gaps was similar to the brightest part of small gaps.

In small gap No. 1 and in large gap No. 2 the measured soil water contents were similar at gap centres, at the edges of the gaps, and below the adjacent closed canopy forest. However, the spatial pattern of soil water content was different in the two gaps (Figure 3). It had a more heterogeneous pattern in the large gap, but in the small one it decreased continuously from the gap centre toward the stand. This occurred at all the measurement dates from July to October.

The average soil water content was 22.4 and 21.8% in small gap No.1. and large gap No.2. (in July 30–31), respectively. There was no significant difference between them (Mann-Whitney, $p < 0.1$, $N_{\text{total}}=228$, $N_{\text{small gap}}=81$, $N_{\text{large gap}}=147$). Soil water content was different below the closed canopy (10–20%) and in the gaps ($>20\%$), and was independent of the gap size at all measurement dates. (Mann-Whitney, $p < 0.001$, $N_{\text{small}}=62$, $N_{\text{large}}=120$, Figure 4).

Mean cover of herb layer vegetation increased almost continuously in all gaps. Initially, it was higher in small gaps, but in the second year it reached higher values in large gaps (Table 2). Mean species richness of quadrats has changed similarly to that of cover, although the differences between small and large gaps were less pronounced.

Mean cover and mean species richness of quadrats were also different in different light zones (Figs 5–6). After two years mean cover in understorey plots (Z1) was significantly lower than in plots receiving 10–20% PACL (Z2) in both gap size classes (Mann-Whitney U-test $p < 0.01$ for both $N_{Z1}=352$, $N_{Z2}=196$), and in large gaps it was higher in gap centres (Z3) than in Z2 (Mann-Whitney U-test $p < 0.01$, $N_{Z3}=141$). Although the same zones had the same light intensity in both gap size classes, the mean cover of quadrats was

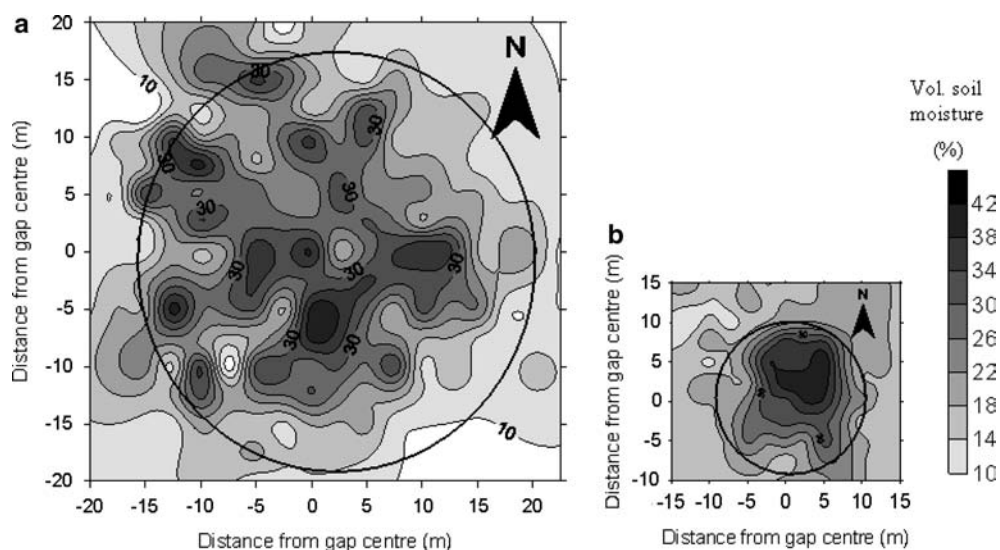


Figure 3. Spatial pattern of soil water content in large gap No. 2. and in small gap No. 1. Grey-scale represents the zones of interpolated amount of soil water content around the measurement points.

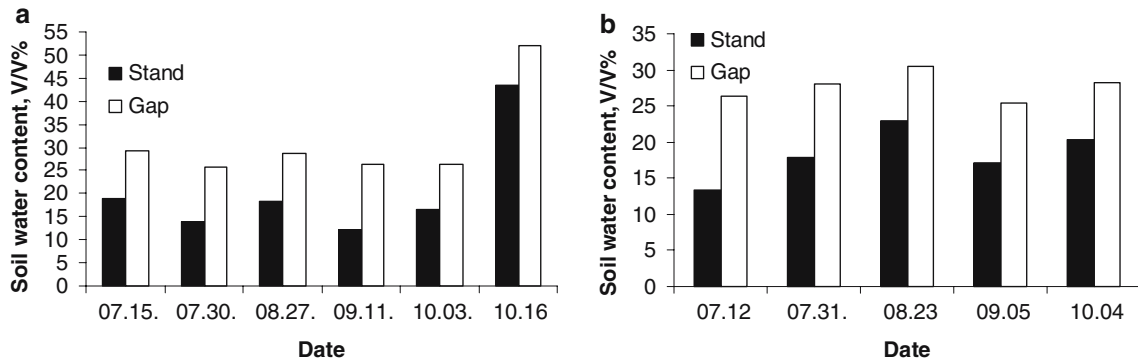


Figure 4. Average soil water content values in (a) large gap No. 2., (b) small gap No. 1. Dark columns represent measurement points under canopy; light columns represent measurement points in gap.

Table 2. Mean cover (%) and mean species richness per quadrat in small ($N=320$) and large ($N=369$) gap quadrats. In case of significant differences (Mann–Whitney U-test) results are marked with indices a and b, otherwise marked with a and a.

	No. of samples	Small gap 320 mean \pm std. err.	Large gap 369 mean \pm std. err.
Mean cover (%)	2000 autumn	0.23 \pm 0.09a	0.02 \pm 0.01b
	2001 spring	0.87 \pm 0.19a	0.08 \pm 0.02b
	2001 autumn	1.89 \pm 0.40a	3.55 \pm 0.53b
	2002 spring	3.66 \pm 0.73a	3.41 \pm 0.57a
	2002 autumn	8.06 \pm 1.23a	18.45 \pm 1.63b
Mean species richness	2000 autumn	0.23 \pm 0.04a	0.04 \pm 0.01b
	2001 spring	0.68 \pm 0.06a	0.26 \pm 0.03b
	2001 autumn	1.11 \pm 0.11a	2.00 \pm 0.16b
	2002 spring	1.15 \pm 0.10a	1.08 \pm 0.11a
	2002 autumn	2.04 \pm 0.15a	3.10 \pm 0.21b

higher in small gaps than in large ones after the first year both in Z1 ($N_{Z1,S}=239$, $N_{Z1,L}=113$) and Z2 ($N_{Z2,S}=81$, $N_{Z2,L}=115$), and cover increased more during the investigation period in small gaps than in large ones. These results suggest that higher values of mean cover and species richness in large gaps (Figures 5–6) are due to the higher values of Z3 light zone in large gaps. Both in the case of cover and species richness the mean values were similar in Z2 light zones of small gaps and Z3 light zones of large ones till 2002 spring, but in the last inventory these values were higher in the Z3 zones of large gaps.

Both the mean of total cover/quadrat and the relative importance of the 11 most abundant species (see Table 3) increased with time in both gap size classes. In 2002 these species contributed almost 85% of total cover in the herb layer of both small and large gaps.

The total species richness of gaps also increased during the investigation (Table 4). Differences in species richness among gaps were considerable. The process was similar to what we observed at finer scale: initially species number was lower in large gaps, and then finally it increased to higher values compared to small gaps.

Classification of species and correlation between abiotic factors and species

Based on hierarchical classification species were classified into six species groups. In Table 5 the mean cover of twenty selected species representing the six groups is shown.

Group 1 (1–7): species that are most abundant in Z3 of large gaps. Generally, they showed significant positive correlation with diffuse light

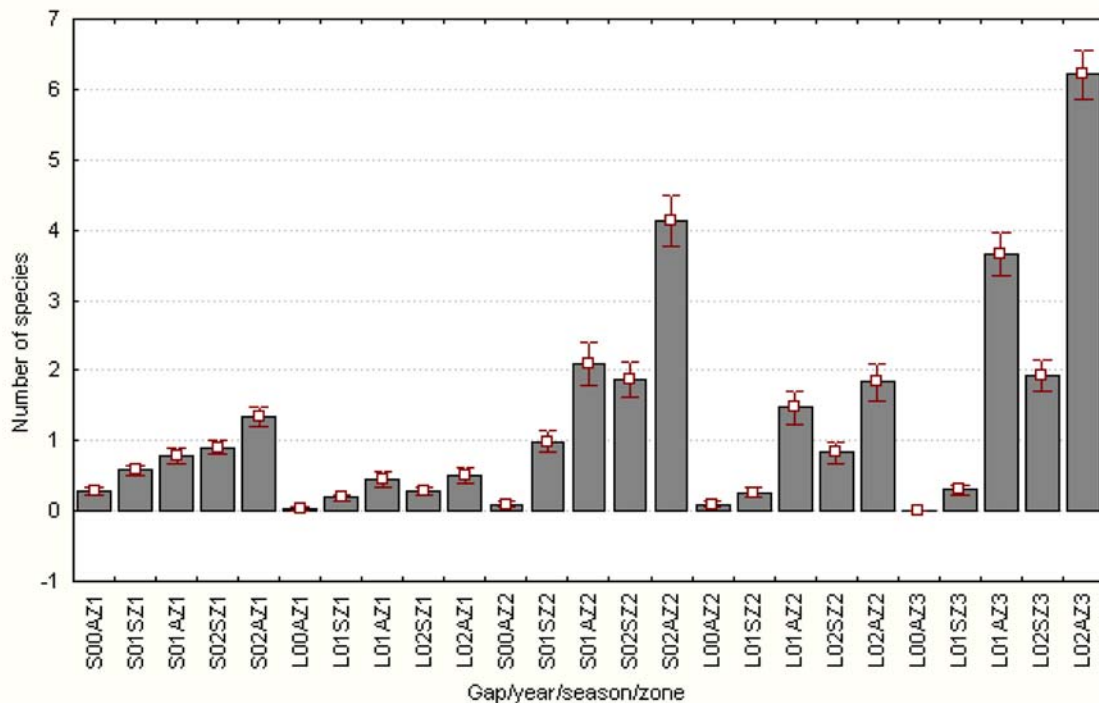


Figure 5. Mean species richness of quadrats in small and large gaps in different light zones (Columns and whiskers indicate mean and standard error of mean). Light zones were defined as: Z1 – 0–10% diffuse PACL; Z2 – 10–20% diffuse PACL; Z3 – >20% diffuse PACL. (S00SZ1 stands for small gap in 2000 spring light zone 1, L02AZ3 stands for large gap in 2002 autumn light zone 3).

and the proportion of bare surface (Spearman Rank Order Correlation, $N=102$, 689 , $p < 0.1$). Both ecological variables reached their maxima in the Z3 zone (middle) of large gaps. Some weeds (species usually occurring on disturbed sites; e.g. *Erigeron canadensis* L., *Cirsium arvense* (L.) Scop), and some so-called “clear-cut” species (species which usually occur on forestry clear-cuts; e.g. *Scrophularia nodosa* L., *Rubus idaeus* L.) belong to this group.

Group 2 (8–12): species that were abundant either in Z2 of small gaps, or in Z3 of large gaps (e.g. *Atropa bella-donna* L., *Urtica dioica* L., *Epilobium montanum* L.). Some of them (*Hypericum perforatum* L., Spearman Rank Order Correlation, $N=81$, $p < 0.05$) were also positively correlated with diffuse light and most of them were positively correlated with bare surface as species of Group 1 were (Spearman Rank Order Correlation, $N=689$, $p < 0.05$); however they were also positively correlated with soil water content, which was not a significant factor for Group 1 (Spearman Rank Order Correlation, $N=81$, $p < 0.05$)

Group 3 (13): The species of this group, like *Rubus fruticosus* L., can be abundant in different light zones (as Z1 of small gaps and Z3 of large gaps), but it is the only species that was positively correlated with diffuse light only (Spearman Rank Order Correlation, $N=102$, $p < 0.05$). Because of the intensive horizontal clonal growth of this species, its clones can survive for long and allocate spatially the resources well.

Group 4 (14): It contains light demanding plant species that were most abundant in Z2 and Z3 of large gaps (e.g. *Poa nemoralis* L.).

Group 5 and 6 (15–17 and 18–20): These groups contain characteristic species of Central European beech forests that are more abundant under canopy or in small gaps (such as *Mycelis muralis* (L.) Dum. and *Geranium robertianum* L. from Group 5 and *Carex pilosa* Scop., *Viola reichenbachiana* Jord. and *Mercurialis perennis* L. from Group 6). According to results of the Spearman Rank Order Correlation analysis, their abundance was not correlated with light intensity and bare surface.

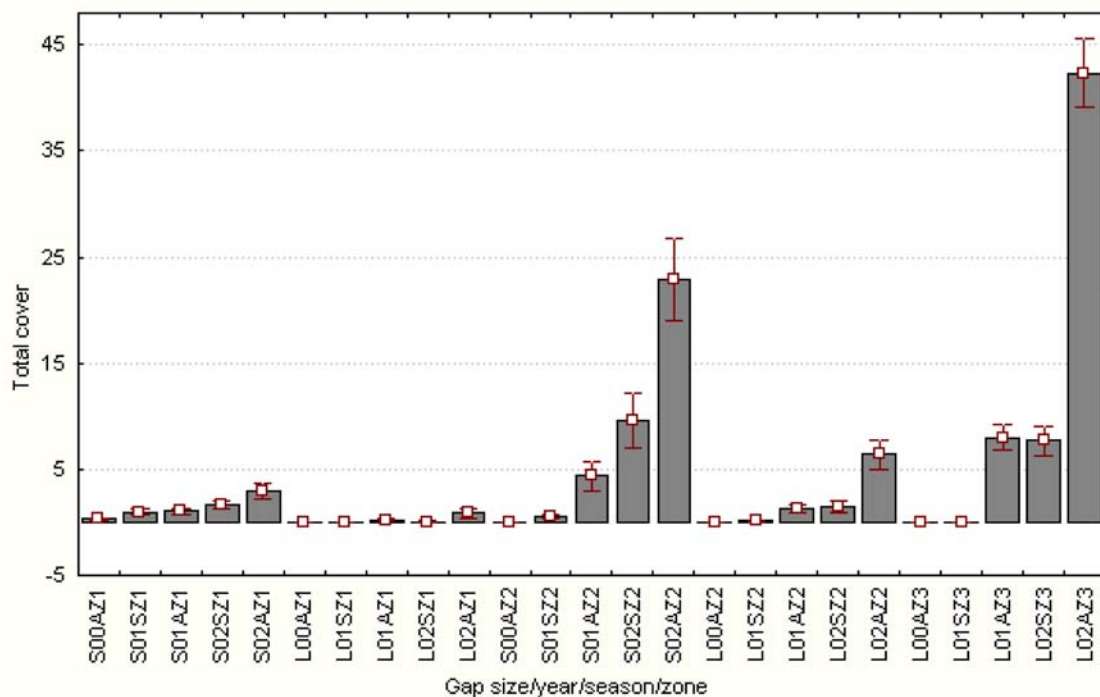


Figure 6. Mean cover of quadrats in small and large gaps in different light zones (Columns and whiskers indicate mean and standard error of mean) Light zones were defined as: $0\% < Z1 \leq 10\%$; $10\% < Z2 \leq 20\%$; $20\% < Z3$ diffuse PACL. (S00SZ1 stands for small gap in 2000 spring light zone 1, L02AZ3 stands for large gap in 2002 autumn light zone 3).

The regeneration was very sparse in 2000 before gap creation, with little difference among gaps. The next year there was only a small increase in number, but by autumn 2002 we found somewhat more seedlings as a result of beech mast in 2001. There were more seedlings in small gaps than in large ones, but the total number of seedlings was insufficient for statistical tests.

Many herbaceous species were positively correlated with relative light intensity (Spearman Rank Order Correlation, $N=102$, $p < 0.05$) (Table 5). Most of them were correlated with the diffuse light component; *Atropa bella-donna* and *Rubus idaeus* were the only species that showed correlation with direct light. Many species were positively correlated with bare surface (Spearman Rank Order Correlation, $N=689$, $p < 0.05$). Results showed significant positive correlation between volumetric water content (vwc) and cover of *Atropa bella-donna*, *Epilobium montanum*, *Fragaria vesca* L. and *Urtica dioica* (Spearman Rank Order Correlation, $N=70$, $p < 0.05$).

Discussion

Previous studies in temperate forests found that on the whole gap scale light quantity increases with opening size, whereas the pattern of soil moisture is less straightforward: it does not always increase in gaps, but it is generally more spatially variable than light (Canham et al. 1990 and references therein; Collins and Pickett 1987, 1988). Our results supported these findings, e.g. overall light levels were increased considerably in gaps. However, whilst relative light intensity values in small gaps could not reach those in large gaps, maxima of soil moisture was the same in small and large gaps. This indicates that even centres of small gaps (radius < 10 m) are beyond the reach of the root system of surrounding trees. Soil moisture and temperature patterns are also affected by local variations in soil depth and stoniness.

The combined effect of gap formation on light and soil moisture had profound effects on the herbaceous vegetation. Total cover and species

Table 3 Mean cover (%) per quadrat of selected species in different light zones of small and large gaps in 2002, autumn. The most abundant species are marked with bold letters. Group is based on numerical classification of species based on their occurrences.

Species	Group	Small Z1	Small Z2	Large Z1	Large Z2	Large Z3
<i>Scrophularia nodosa</i>	1	0.28	1.22	0.20	1.76	4.76
<i>Rubus idaeus</i>	1	0	0.54	0	0.23	2.97
<i>Calamagrostis arundinacea</i>	1	0	0.06	0.03	0	0.28
<i>Carex remota</i>	1	0.04	0.40	0.04	0.10	1.35
<i>Cirsium arvense</i>	1	0	0.12	0	0.03	1.75
<i>Erigeron canadensis</i>	1	0	0	0	0	0.33
<i>Fragaria vesca</i>	1	0.08	0.05	0	0.05	1.37
<i>Epilobium montanum</i>	2	0.15	1.09	0.04	0.43	1.31
<i>Atropa bella-donna</i>	2	0.28	6.47	0.37	1.32	11.43
<i>Hypericum perforatum</i>	2	0	0.79	0	0.14	1.5
<i>Stachys sylvatica</i>	2	0.21	0.61	0	0	0.88
<i>Urtica dioica</i>	2	0.44	9.24	0	0.53	7.74
<i>Rubus fruticosus</i>	3	0.78	0.19	0	0.35	0.92
<i>Poa nemoralis</i>	4	0.07	0.06	0.08	0.23	0.12
<i>Mycelis muralis</i>	5	0.06	0.43	0	0.1	0.21
<i>Geranium robertianum</i>	5	0.03	0.4	0	0.07	0.04
<i>Carex pilosa</i>	5	0.26	0.3	0	0	0.11
<i>Viola reichenbachiana</i>	6	0.03	0.03	0.01	0	0
<i>Galium odoratum</i>	6	0.03	0	0	0	0
<i>Mercurialis perennis</i>	6	0.04	0	0	0	0

richness were increased, as was the average species richness per quadrat. The colonization dynamics of the forest floor below gap openings was a continual process, but in some cases we observed temporary setback during the spring. The observed phenomenon was attributed to the late arrival of annual species, which were only recorded in autumn. Initial differences in the total cover between individual gaps were still detectable three years after their creation. These were observed especially in quadrats under the surrounding canopy or close to the gap edge, whereas the vegetation located closer to gap centre responded more

to the changes in light and soil moisture and overrode any previous vegetation patterns.

Herbaceous species could be classified based on their preferential distribution in gap zones with different light availabilities. Some seem to prefer well-lit locations (e.g. *Scrophularia nodosa*, *Erigeron canadensis*), i.e. they reach their highest importance in the brightest zone in the centre of large gaps (Z3). Some species (*Atropa bella-donna*, *Epilobium montanum*, *Urtica dioica*) seem to prefer in-gap positions, but were also positively correlated with increasing soil moisture content. The role of soil moisture is also supported by the

Table 4. Total species numbers in small (S) and large (L) gaps.

Gap	Sampling date				
	2000 autumn	2001 spring	2001 autumn	2002 spring	2002 autumn
	<i>Herb species richness</i>				
Small No 1	4	7	17	22	32
Small No 2	2	4	8	0	18
Small No 3	3	12	25	20	27
Small No 4	8	21	27	24	28
Small No 5	13	24	32	37	41
Large No 1	7	8	41	35	61
Large No 2	2	8	33	26	41
Large No 3	5	18	43	18	57

Table 5. Correlation analysis (Spearman Rank Order Correlations) of estimated % cover of ground vegetation and abiotic variables in gaps (VWC: volumetric soil water content, * $p < 0.1$, ** $p < 0.05$, *** $p < 0.01$).

Species	Direct PACL	Diffuse PACL	Bare surface	VWC	Total cover of herbs
<i>Atropa bella-donna</i>	0.23**	0.58***		0.23**	
<i>Carex pairei</i>			0.14***		
<i>Carex remota</i>			0.18***		
<i>Cirsium arvense</i>		0.32***	0.2**		
<i>Epilobium montanum</i>		0.39***	0.2***	0.34***	
<i>Erigeron canadensis</i>			0.17***		
<i>Fragaria vesca</i>			0.14***	0.22**	
<i>Hypericum perforatum</i>		0.3***	0.18***		
<i>Rubus idaeus</i>	0.17*	0.49***	0.19***		
<i>Rubus fruticosus</i>	0.22**				
<i>Scrophularia nodosa</i>		0.47***	0.24***		
<i>Urtica dioica</i>		0.47***		0.36***	
<i>Veronica officinalis</i>		0.24**	0.17***		

fact that in the case of some so-called clear-cut species (*Atropa bella-donna*, *Urtica dioica*, *Stachys sylvatica* L., *Hypericum perforatum*) average cover is higher in the Z2 light zone of small gaps (i.e. gap centre) where the amount of soil moisture is generally higher, than in Z2 zone of large gaps. Some species were restricted to more shady environments, i.e., they grew mainly in small gaps and/or under the closed canopy (e.g. *Viola reichenbachiana*, *Galium odoratum* (L.) Scop.). In a comparable study, Schumann et al. (2003) also distinguished groups of species, including a group that contained species that were relatively insensitive to gap creation. Others have concluded that gap creation has no effect on the herb layer at all (Collins and Pickett 1987, 1988). Both studies were carried out in forests with pre-existent herb layer, and the latter used relatively small gaps that were too small to initiate a pronounced understorey response. The extent to which a canopy gap affects establishment, growth, death and reproduction of understorey species is a function of both the degree to which the opening alters the local physical environment, and the sensitivity of individual species to that environmental change (Collins and Pickett 1988). In our study both gap creation and gap size seem to affect environmental factors and vegetation greatly, as a consequence of the release of resources, e.g. light.

Our results show that the opening of artificial gaps has not (within the three years of study) facilitated a new wave of tree regeneration. Instead, most seedlings and saplings recorded were advance regeneration present before gap creation.

However, there was a mast year for beech in 2001, which had increased the amount of regeneration in two of the gaps by 2002.

The density of *Fagus* seedlings was somewhat higher in small gaps than in large gaps, which is explained by some authors by dispersal limitation (Watt 1925; Peltier et al. 1997). Reactions of different tree species can be analysed when more individuals establish, so we have to use a longer time series (Mihók et al. 2005).

Several authors have stressed that on an undisturbed forest floor spatial patterns may be maintained for many years after gap creation (Collins and Pickett 1987; Hughes and Fahey 1991; Goldblum 1997; Holeksa 2003). Understorey plants already present in the area (including in the seed-bank) increase in number and size in response to changed environmental conditions, in addition to other species that can invade. In our study gaps, we found some persistent patches that had been present beforehand. Nevertheless, in most of the gaps the ground vegetation was sparse or even absent before gap creation. Thus, colonization came predominantly from the seed bank or by immigration. Substrate (bare surface) and soil moisture had a profound effect on the distribution of certain species. Release of nutrients in the soil of gaps may also affect species' distributions (for *Rubus idaeus* see Ricard and Messier 1996). Since both bare surface and soil moisture were patchily distributed it appears that, in addition to the coarse pattern of light, small-scale regeneration microsite niches played an important role in determining the patterns of

colonizing herb species in gaps (Maguire 1983; Beatty 1984).

Since different mixtures of herbaceous species and their patches affect tree seedlings differently, this mechanism could also contribute to maintaining tree species richness, as has been proposed by Maguire (1983) and Gilliam (1993). Although gap formation provides a range of resources that provide for the establishment of a range of species (Łaska 2001), it is clear that its role in regeneration and in maintaining species richness is forest type specific (Canham et al. 1990; Uhl 1988). We hope to get a better understanding of gap regeneration processes by continuing our observations in these new artificial gaps.

Acknowledgments

We would like to thank János Ruff and the Ipoly Erdő Ltd. for supporting the research, Kata Kenderes for helping in data collection and Péter Ódor for his helpful comments on the manuscript. Special thanks to Ed Mountford to improve the English of the manuscript, and also for his useful comments. We would like also to thank two anonymous referees for their helpful corrections and recommendations. The project was financially supported by NAT-MAN: Nature-based management of beech in Europe (Fifth Framework Programme, Contract No.: QLK5-1999-01349). <http://www.flec.kvl.dk/natman/>. Further support was provided by the Hungarian Academy of Sciences.

References

- Abe S., Masaki T. and Nakashizuka T. 1995. Factors influencing sapling composition in canopy gaps of a temperate deciduous forest. *Vegetatio* 120, 21–32.
- Beatty S.W. 1984. Influence of microtopography and canopy species on spatial patterns of forest understory plants. *Ecology* 65(5): 1406–1419.
- Brokaw N. and Busing R.T. 2000. Niche versus chance and tree diversity in forest gaps. *Trends Ecol. Evol.* 15, 183–188.
- Brunner A. 2000. Hemispherical photography and image analysis with hemIMAGE and Adobe® Photoshop® 3.0, (manual).
- Busing R.T. and White P.S. 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. 1989. Different responses to gaps among shade tolerant tree species. *Ecology* 70, 548–550.
- Canham C.D., Denslow J.S., Platt W.J., Runkle J.R., Spies T.A. and White P.S. 1990. Light regimes beneath closed canopies and tree-fall gaps in temperate and tropical forests. *Can. J. Forest Res.* 20, 620–631.
- Carlson, R.E. and Foley, T.A. 1991. Radial Basis Interpolation Methods on Track Data, Lawrence Livermore National Laboratory, UCRL-JC-1074238.
- Collins B.S. and Pickett S.T.A. 1987. Influence of canopy opening on the environment and herb-layer in a northern hardwoods forest. *Vegetatio* 70, 3–10.
- Collins B.S. and Pickett S.T.A. 1988. Demographic responses of herb layer species to experimental canopy gaps in a northern hardwoods forest. *J. Ecol.* 76, 437–450.
- Denslow J.S. and Spies T. 1990. Canopy gaps in forest ecosystems: an introduction. *Can. J. Forest Res.* 20, 619.
- Dirksen C. 1999. Soil Physics Measurements. Catena Verlag GMBH, Reiskirchen, Germany, pp. 39–41.
- Gilliam F.S. and Turrill N.L. 1993. Herbaceous layer cover and biomass in a young versus a mature stand of a central Appalachian hardwood forest. *Bull. Torrey Bot. Club* 120(4): 445–450.
- Goldblum D. 1997. The effect of treefall gaps on understory vegetation in New York State. *J. Veget. Sci.* 8, 125–132.
- Golden Software, Inc. 2002. Surfer 8. User's Guide.
- Gray A.N. and Spies T.A. 1996. Gap size, within gap position and canopy structure effects on conifer seedling establishment. *J. Ecol.* 84, 635–645.
- Gray A.N. and Spies T.A. 1997. Microsite controls on tree seedling establishment in conifer forest canopy gaps. *Ecology* 78(8): 2458–2473.
- Hilhorst, M.A. 1998. Dielectric characterisation of soil. Doctoral Thesis. Wageningen Agric. Univ., pp. 69–71.
- Holeksa J. 2003. Relationship between field-layer vegetation and canopy openings in a carpathian subalpine spruce forest. *Plant Ecol.* 168, 57–67.
- Hughes J. W. and Fahey T.J. 1991. Colonization dynamics of herbs and shrubs in a disturbed northern hardwood forest. *J. Ecol.* 79, 605–616.
- Kwit C. and Platt W.J. 2003. Disturbance history influences regeneration of non-pioneer understory trees. *Ecology* 84(10): 2575–2581.
- Łaska G. 2001. The disturbance and vegetation dynamics: a review and an alternative framework. *Plant Ecol.* 157, 77–99.
- Lawton O. and Putz F.E. 1988. Natural disturbance and gap-phase regeneration in a wind-exposed tropical cloud forest. *Ecology* 69(3): 764–777.
- Maguire D.A. and Formand R.T.T. 1983. Herb cover effects on tree seedling patterns in a mature hemlock-hardwood forest. *Ecology* 64(6): 1367–1380.
- Mihók B., Gálhidy L., Kelemen K. and 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 Silv. Lign. Hung.* 1, 25–38.
- Nakashizuka T. 1985. Diffused light conditions in canopy gaps in a beech (*Fagus crenata* Blume) forest. *Oecologia* 66, 472–474.
- Peterson C.J. and Campbell J.E. 1993. Microsite differences and temporal change in plant communities of treefall pits and mound in an old-growth forest. *Bull. Torrey Bot. Club* 120(4): 451–460.

- Peltier A., Touzand M.-C., Armengaud C. and Ponge J.-F. 1997. Establishment of *Fagus sylvatica* and *Fraxinus excelsior* in an old-growth beech forest. *J. Veget. Sci.* 8, 13–20.
- Platt W.J. and Strong D.R. 1989. Gaps in forest ecology. *Ecology* (70), 535.
- Podani J. 2000. Introduction to the Exploration of Multivariate Biological Data. Backhuys Publishers, Leiden.
- 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.
- Poulson T.L. and Platt W.J. 1989. Gap light regimes influence canopy tree diversity. *Ecology* 70(3): 553–555.
- Ricard J.-P. and Messier Ch. 1996. Abundance, growth and allometry of red raspberry (*Rubus idaeus*, L.) along a natural light gradient in a northern hardwood forest. *Forest Ecol. Manage.* 81, 153–160.
- Runkle J.R. 1989. Synchrony of regeneration, gaps, and latitudinal differences in trespecies diversity. *Ecology* 70, 546–547.
- Schaetzl R.J., Burns S.F., Johnson D.L. and Small T.W. 1989. Tree uprooting: review of impacts on forest ecology. *Vegetatio* 79, 165–176.
- Schumann M.E., White A.S. and Witham J.W. 2003. The effects of harvest-created gaps on plant species diversity, composition and abundance in a maine oak-pine forest. *Forest Ecol. Manage.* 176, 543–561.
- Schmidt W., Weitermeier M. and Holzapfel C. 1996. Vegetation dynamics in canopy gaps of a beech forest on limestone. The influence of the light gradient on species richness. *Verhandlung der Gesellschaft für Ökologie*: 253(-258): 253–258.
- Simon T. 2000. A magyarországi edényes flóra határozója. Harasztok – virágos növények. (In Hungarian) Nemzeti Tankönyvkiadó, Budapest.
- Várallyay Gy. and Rajkai K. 1987. Soil moisture content and moisture potential measuring techniques in Hungarian soil surveys. *Proc. Int. Conf. Measurement Soil Plant Water Status* 1, 183–184.
- Vitousek P.M. and Denslow J.S. 1986. Nitrogen and phosphorus availability in treefall gaps of a lowland tropical rainforest. *J. Ecol.* 74, 1167–1178.
- Uhl C., Clark K., Dezzio N. and Maquirino P. 1988. Vegetation dynamics in Amazonian treefall gaps. *Ecology* 69(3): 751–763.
- Watt A.S. 1925. On the ecology of British beechwoods with special reference to their regeneration. Part II (continued). *J. Ecol.* 13, 27–73.