Gap Regeneration Patterns in a Semi-natural Beech Forest Stand in Hungary

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Abstract – The authors studied the effects of canopy openness, substrate features and herbaceous species cover on regeneration in eight natural canopy gaps and the surrounding stands in a semi-natural beech forest stand. Canopy openness was estimated by spherical densitometer, with relative light intensity being calculated using hemispherical photographs along gap-canopy transects. The high variance of relative light intensity and canopy openness values reflects the heterogeneity of canopy structure. Total cover of herbaceous species in and around gaps also reflected fine-scale canopy heterogeneity. Herbaceous species composition varied with total coverage, e.g. *Urtica dioica* dominated the dense herb layer found in the gaps. Tree individuals of various species and size classes showed different spatial patterns. Substrate features, canopy openness and also understorey herb density, all affected these patterns as consequence of the different ecological preferences of tree species in establishment and development, and their different sensitivity to browsing.

fine-scale disturbance / herbaceous layer / browsing / canopy openness / substrate features

Kivonat – Lék-felújulási mintázat vizsgálata egy magyarországi természetközeli bükkösben. A cikk egy természetközeli bükkös nyolc lékjében elvégzett vizsgálatot mutat be, amely a lék felújulása és a lombkorona-záródáshány, aljzati tényezők illetve a lágyszárú borítás közti kapcsolatot kutatja. A lombkorona-záródáshiány becsléséhez szférikus denziométert használtunk, illetve három lék fénymintázatát halszemoptikás képekkel is jellemeztük. A záródáshiány és a megvilágítottság értékei tükrözték a heterogén lombkorona-szerkezet sajátságait. A lágyszárúak borítása a finomléptékű fénymintázatra reagált. A lágyszárúak összborításának függvényében más-más lágyszárú fajok kaptak domináns szerepet a gyepszintben. A különböző méretosztályba és fajhoz tartozó csemeték változó térbeli megoszlást mutattak. A vizsgált változók együttesen komplex módon befolyásolták a fafajok megtelepedési és fejlődési feltételeit.

finomléptékű dinamika / lágyszárú szint / vadrágás / záródáshiány / aljzati tényezők

1 INTRODUCTION

Disturbance is a permanent feature of forest ecosystems, determining species composition, structure and process (Attiwill 1994, McCarthy 2001). Disturbance events range from the small-scale disturbance of single tree-falls or crown-breaks to the large-scale disturbance caused by e.g. catastrophic windstorms. Depending on the intensity and area of disturbance,

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gaps of different sizes are formed in forest stands at different points of time identifying the "gap-phase" in the forest developmental cycle, and creating different mosaic patterns in forest stands (Watt 1947, Runkle 1985, Busing – White 1997, McCarthy 2001). The importance of gap dynamics in forest ecosystems was discovered in the early 20th century, and intensive investigation of gap dynamic features are dated from the late 1970s (McCarthy 2001).

Gap formation changes the amount of total incident light reaching the ground level and influences nutrient and moisture availability (Collins et al. 1985, Denslow – Spies 1990, McCarthy 2001, Ritter et al. 2005, Mihók et al. 2005, Gálhidy et al. 2006), providing potential establishment sites for regeneration. Microclimate of gaps may accelerate seed germination and increase growth rates of herbs and woody species compared to below-canopy (Collins – Pickett 1988, Denslow – Spies 1990, Goldblum 1997, Brokaw – Busing 2000, Schumann et al. 2003, Holeksa 2003). Abiotic and biotic conditions can be very different both within individual gaps and among different sites (Nakashizuka 1985, Vitousek – Denslow 1986, Collins – Pickett 1987, Runkle 1989, Platt – Strong 1989, Kwit – Platt 2003). Different concepts have been formulated describing the relationship between resource heterogeneity and tree recruitment. According to the *gap partitioning* hypothesis, resource gradients (e.g. incident light) display a continuum in flux and concentration along the gap – canopy gradient – determined by, among others, the surrounding stand or gap size (Ricklefs 1977, McCarthy 2001). Species show different habitat preferences along this continuum, and in consequence, partition the gap environment (Poulson – Platt 1989, Sipe – Bazzaz 1994, Busing – White 1997). Other studies show that the effects of *micro sites* often override the gradual resource continuum, highlighting the role of specific substrates (e.g. logs, pits and mounds) in tree regeneration processes (Beatty 1984, Schaetzl et al. 1989, Peterson – Campbell 1993, McCarthy 2001). Although gaps have become an important focus of interest in the last few decades, "generalizations about the role of gap processes in the determination of forest composition and structure are less clear and likely to vary among different forest ecosystems" (Denslow – Spies 1990). Although there are examples from European temperate deciduous forests (Schmidt et al. 1996, Schumann et al. 2003, Holeksa 2003, Mihók et al. 2005, Ritter – Vesterdal 2006, Gálhidy et al. 2006, Naaf – Wulf 2007) the vast majority of gap-studies have been conducted in the temperate (deciduous and coniferous) forests of the United States and Japan and also in tropical forests (see McCarthy (2001) and references therein) focusing mainly on tree regeneration processes. Only a few studies concentrate on herbaceous species and the effect of herbaceous species on tree regeneration (Maguire – Forman 1983, Collins et al. 1985, Hughes – Fahey 1991, Collins 2003, Schumann et al. 2003, Galhidy et al. 2006, Naaf – Wulf 2007). However, herbs can affect abiotic variables, compete with seedlings, and consequently influence the success of tree regeneration in gaps (Maguire – Forman 1983, Abe et al. 1995, Castleberry et al. 2000, Collins 2003).

Several Hungarian authors have studied different aspect of beech regeneration. Márkus (1959) studied the number of beech seeds in a 100 year old beech stand in the Bakony Mts, Hungary. He showed that at edges seed numbers per unit area were higher than within the stand. Mendlik (1989) found similar patterns, while he compared stand centre with edge. Márkus and Mátyás (1966) carried out a country-wide survey of seed production in Hungary. They collected data from 611 forest ranges from all over the country representing all forest regions where beech occurs. They found large variation within each forest region, but the average differences in the amount of beech seeds produced in different forest regions could be explained by the climatic differences of previous year. Májer (1982) published historical data on beech seed crops in the Bakony Mts., covering 242 years. A heavy crop can be expected (on average) once every 14 years, an average crop every 7 years, and a poor crop every 3-4 years. However, heavy crops can occur at short intervals (1948, 1951). Török (2000, 2006) developed a new method of beech regeneration in the Bakony Mts. He took into account the dynamic nature of forest types and the different courses of change following canopy opening depending on slope aspect and steepness. In order to provide optimal conditions for beech regeneration, he applied uneven cutting regimes taking into account both the original forest type and the direction of shade that old trees shed.

The aim of our study was to investigate how the presence of gaps affects regeneration processes in a semi-natural European beech forest stand. More specifically, our aims are:

1) To test if there are differences in canopy openness and incident light intensity between gap plots and below-canopy plots.
2) To test if there are differences in herbaceous species cover between gap plots and below-canopy plots.
3) To test if the amount and species composition of regeneration are different in gap plots and below-canopy plots.
4) To show any correlations between regeneration and the studied potential explanatory variables (canopy openness, substrate features and herbaceous species cover).

2 METHODS

The study was conducted in the Őserdő Forest Reserve, Northern Hungary. Őserdő is a small (25 ha) stand situated on the plateau of the Bükk Mountains (48° 03'N, 20° 27'E). Elevation ranges from 830 to 900 m. Mean annual temperature is 6.1°C (January: -4.1°C, July: 15.5°C), the annual precipitation is 896 mm. The bedrock is limestone, the soil is characterized as shallow to medium brown forest soil, but on steeper slopes, rendzina soils occur. In the southern part of the reserve the terrain is rather flat with typical karstic topography. The stand is dominated by European beech *(Fagus sylvatica* L.*)*, with small proportion of other species, e.g. European ash (*Fraxinus excelsior* L.), sycamore (*Acer pseudoplatanus* L.) and wych elm (*Ulmus glabra* Huds.). The age of the dominant beech trees varies between 150-200 years. The stand was managed and cut in the past, but it has developed undisturbed during the last 60 years. The stand structure is heterogeneous with trees of different size-classes, canopy gaps, and regeneration patches. The shrub layer is nearly absent, but the forest floor is covered with a dense herb-layer. Most frequent species are *Galium odoratum* (Scop.), *Glechoma hederacea* L., *Hordelymus europaeus* (L.) Jessen, and *Sanicula europaea* L. The Reserve has been protected since 1942.

According to the analysis of an aerial photograph taken in 2000, the total gap area was 9191 m^2, which is 4.3% of the reserve area. Average gap size was 61 m^2 (standard deviation: 71.33). The smallest gap was 4 $m^{2,}$ while the maximum gap size was 378 m^2 (see also Kenderes et al. in press).

Eight canopy gaps (two large, where the maximum diameter = 1-1.5 x tree height and 6 small, where the maximum diameter = 0.5 x tree height) were selected in winter 2001/2002. *Table 1* shows the size attributes of the chosen gaps. We defined a "gap" as a canopy opening created by the death of at least one canopy tree. The shapes of the selected gaps were close to regular circles in cases of small gaps, but the two large gaps were irregular.

Table 1. Area and perimeter of the studied gaps (S: small, L: large)

Gap ID	S3	S8	S11	S1	S2	S12	L10	L5
Area (m^2)	39	24	27	36	40	60	178	203
Perimeter (m)	28	19	20	28	24	39	55	103

The age of the gaps were determined using aerial photographs from 1975, 1980, 1993 and 2000. Five gaps were identified in the 1975 photo, and one in the 1980, 1993 and 2000. We used the date of the aerial photographs, where the gaps first appeared, to refer to the age of the gaps (i.e. 28 years in the case of the 1975 photos).

We used a systematic sampling design, with 5-meter grid resolution and 1m x 1m quadrats (*Figure 1*). In cases of small gaps, the grid went 5-15 m below the closed canopy. In cases of large gaps, the distance was 15-25 m respectively. Altogether, 657 quadrats were recorded: 64 in and around small gaps, 136 and 137 in and around large gaps. In each quadrat, *relative cover of substrate types* (intact soil, mineral soil, coarse woody debris (CWD), stem of a living tree and stone), *relative cover of herbaceous species*, *number of individuals belonging to each tree species* in 4 size classes below 1.3 m (0-10 cm, 10-20 cm, 20-50 cm, 50cm<) and seedlings with cotyledons separately were recorded in July 2002.

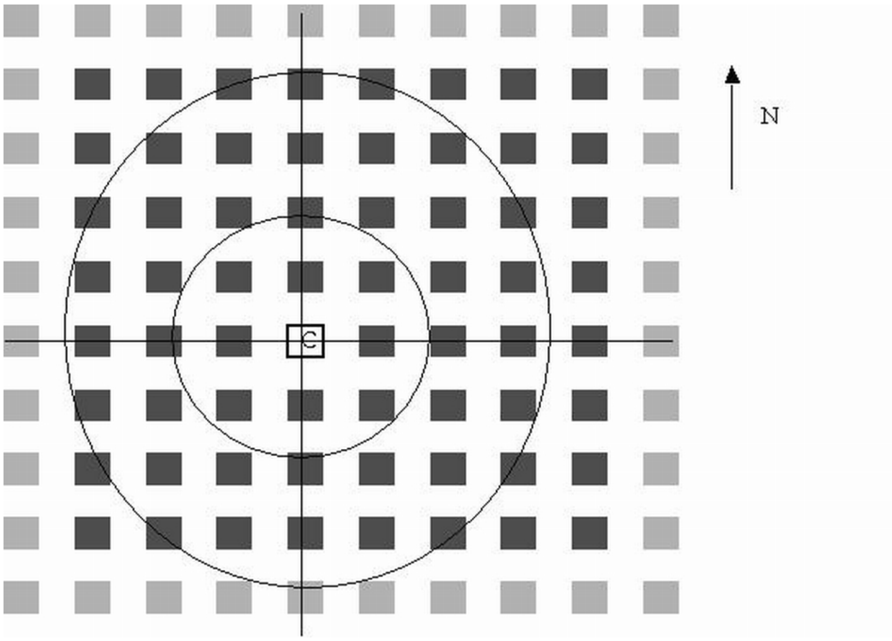

Figure 1. Sampling design in small (dark cells) and large gaps (light cells). 1 m x 1 m quadrats are signed by filled cells, gaps are signed by circles. Straight lines show the transects along which estimation of canopy openness was made and hemispherical photographs were taken.

C*anopy openness* was estimated by spherical densiometer (Lemmon 1956) in every gap along the N-S and E-W transects running along gaps – below-canopy gradients in 2003 (see *Fig. 1*). The spherical densiometer is a simple instrument for estimating canopy cover. It consists of a convex or concave mirror with a grid of 24 squares, within each of which the observer scores canopy cover at four equally spaced points. In order to characterize relative light intensity (in Percent of Above Canopy Light, PACL) in small and in large gaps, hemispherical photographs with Sigma-adapter fisheye lens on a Canon AE1 camera were taken at 70 cm in height, above the ground. The photographs were taken in three gaps – one large, one small with high advance regeneration (5-7 m) and one small with no advance regeneration above 0.5 m. This was along the N-S and E-W transect running along gaps – below-canopy gradients in 2003 (*see Fig. 1*). Altogether, 28 photos were taken (9 and 6 in small gaps, 13 in a large gap, 17 in below-canopy plots, 11 within in-gap plots). We used a crown mirror to group the quadrats as “in-gap” or “below-canopy” quadrats. If the canopy was not visible in the crown mirror, we considered the quadrat as a gap-quadrat. At the edge, we identified the quadrats as "below-canopy" if more than half of the mirror area reflected the canopy.

Hemispherical photographs were analysed using a Windows-based software, hemIMAGE (Brunner 2002). Relative light intensity (in Percent of Above Canopy Light, PACL) was calculated in a certain location for a given period of time: 1st March to 31st October. With hemIMAGE, the direct and the diffuse site factor can be calculated separately for a given location.

As the sample size was small and did not show normal distribution, a nonparametric Mann-Whitney U test was used to compare the recorded vegetation and environmental variables between gaps, versus below canopy and small versus large gaps. Ordination analysis was employed by Canoco for Windows 4.5 software (Ter Braak - Smilauer 2002). Since in the exploratory detrented correspondence analysis the maximum length of gradient exceeded 4SD, and the data showed a strong unimodal response, a canonical correspondence analysis was carried out. Abundance of tree species and abiotic variables (intact soil, mineral soil, coarse woody debris (CWD), stem of a living tree, stone and coverage of herbaceous plant species and canopy openness) recorded in the quadrats were included in the analysis. Interactions between abiotic factors and species' abundances were tested by calculating the Spearman Rank Order correlation.

3 RESULTS

3.1 Light conditions

Light conditions differed considerably depending on gap size, however, the relative light intensity under the canopy showed high variability and high mean and maximum values. Under the canopy, mean total relative light intensity (PACL) was between 4-5%, around the gaps. In small gaps, it reached 4-5% as a maximum with a 2-3% average, whereas in large gaps, the total PACL mean values reached 8% and maximum values reached 12%.

Canopy openness estimates obtained by the spherical densiometer were consistently higher than the relative light intensity estimates obtained by analysing hemispherical photographs. However, canopy openness values showed strong significant positive correlation with diffuse light values (Spearman Rank Order Correlation, $R=0.45$, $p<0.01$, $N=28$). Canopy openness values reflected gap geometry, they showed a clear gradient from below-canopy position to gap centre. Maximum values were approximately 25% in the centre of small, and 37% in that of large gaps. Below canopy variance of canopy openness was very high (mean = 12.26, variance = 20.65), and the maximum values were similar to those in the gap plots in small gaps - reflecting the structural heterogeneity of the canopy. Canopy openness was significantly (Mann Whitney U Test $p<0.001$, $N=84$) higher in large gaps than in small gaps, and also showed significant difference between in-gap and below-canopy plots, both in small and in large gaps (Mann Whitney U Test, $p<0.05$, $N=84$), which was in favour of in-gap position.

3.2 Herbaceous vegetation

Altogether, 57 herbaceous species were found. Most frequent species were (in descending order): *Viola reichenbachiana, Mercurialis perennis, Galium odoratum, Sanicula europaea, Hordelymus europaeus, Glechoma hederacea, Aegopodium podagraria, Oxalis acetosella*, and *Mycelis muralis*. Species with the highest total coverage were (in descending order): *Galium odoratum, Mercurialis perennis, Sanicula europaea, Glechoma hederacea, Urtica dioica, Euphorbia amygdaloides, Viola reichenbachiana,* and *Hordelymus europaeus.*

Table 2. Mean of total cover (as the result of the addition of individual species cover) of herbaceous species from grids in the gaps (S: small, L: large, number indicates the gap no.)

Gap ID	Valid N	Mean	Minimum	Maximum	Standard Error
S1	64	27.53	0.00	99.02	3.04
S2	64	14.44	0.00	67.20	2.18
S3	64	17.74	0.00	100.00	2.49
S8	64	42.51	8.20	104.10	2.62
S11	64	45.48	3.00	104.00	2.45
S12	64	43.98	3.02	88.00	2.43
L5	137	16.52	0.00	89.10	1.98
Ll0	136	34.66	0.00	131.10	2.52

Total cover of herbaceous species varied greatly both within and between gaps, and around them (*Table 2*). Total cover was significantly (Mann Whitney U test, $p<0.01$) higher in the in-gap plots of large gaps than below canopy. There was no significant difference in small gaps between in-gap and below-canopy quadrats in terms of herbaceous cover if all plots were pooled. However, if individual gaps were treated separately, significant differences were found in the case of three small gaps between in-gap and below canopy plots. In one gap, herbaceous vegetation was more abundant in plots under the canopy, because tall regeneration was present in the gap. Canopy openness showed a strong significant positive correlation (Spearman Rank Order Correlation, $R=0.53$, $p<0.01$, $N=84$) with total cover of herbaceous species.

The relative cover of individual herbaceous species varied greatly among plots with different total coverage (data not shown). Existence of some species, *e.g. Urtica dioica* and *Geranium robertianum* is characteristic in plots with high (>60%) total cover, whereas others (e.g. *Oxalis acetosella, Galium odoratum*) showed preference for plots with lower cover or did not show any preference.

3.3 Regeneration

The percentage of the saplings/seedlings with visible browsing damage can be seen in *Table 3*. Tree regeneration is under high browsing pressure, according to the observations, and nearly 50% of the higher saplings of each species were affected by browsing. The high game pressure can also be concluded from the fact that saplings with a height between 50 cm and 2 m are extremely rare.

Table 4 shows the mean number of individuals per quadrat for each tree species in *a* – the whole grid; *b* – in the in-gap quadrats; *c* – in below-canopy quadrats. When plots of all gaps were pooled, total number of tree seedlings and saplings did not differ significantly between in-gap and below-canopy quadrats. Beech and ash saplings, taller than 50 cm, were more abundant in gaps than under canopy (Mann Whitney U Test, $p<0.1$). Although, this result was greatly affected by the patterns found in one small and one large gap. Spatial pattern of tree regeneration was rather gap-specific, when in-gap and below-canopy plots were compared.

Table 3. The percentage of tree individuals in different height classes with visible browsing damage

Tree regeneration	Height classes (cm)	Percentage of individuals with visible browsing damage
*Acer campestre **		3.7
Acer campestre	0-10	0.0
Acer campestre	10-20	50.0
Acer platanoides	0-10	22.2
Acer platanoides	10-20	35.5
Acer platanoides	20-50	33.3
*Acer pseudoplatanus **		0.0
Acer pseudoplatanus	0-10	27.1
Acer pseudoplatanus	10-20	50.9
*Fagus sylvatica**		0.0
Fagus sylvatica	0-10	23.9
Fagus sylvatica	10-20	31.4
Fagus sylvatica	20-50	40.0
Fagus sylvatica	>50	0.0
*Fraxinus excelsior**		0.7
Fraxinus excelsior	0-10	30.8
Fraxinus excelsior	10-20	46.7
Fraxinus excelsior	20-50	60.4
Ulmus glabra	0-10	25.0
Ulmus glabra	10-20	42.8
Ulmus glabra	20-50	55.5

*: seedlings with cotyledons

Table 4.a Mean number of saplings per quadrat in the whole grid in each gap.

GAP ID	*Acer platanoides*	*Acer pseudoplatanus*	*Fagus sylvatica*	*Fraxinus excelsior*	*Ulmus glabra*	*All saplings*
S1	1.36	0.22	0.53	2.19	0.09	4.48
S2	0.20	0.06	1.23	0.92	0.03	2.45
S3	0.13	0.02	0.58	0.64	0.00	1.36
S8	0.89	0.53	0.47	0.63	0.00	2.53
S11	0.86	0.38	0.42	5.17	0.06	6.91
S12	2.09	0.16	0.89	3.22	0.08	6.45
L5	0.18	0.04	1.92	0.67	0.00	2.85
L10	0.37	0.51	0.58	3.07	0.04	4.60

Table 4.b Mean number of saplings in the in-gap quadrats in each gap

GAP ID	*Acer platanoides*	*Acer pseudoplatanus*	*Fagus sylvatica*	*Fraxinus excelsior*	*Ulmus glabra*	*All saplings*
S1	1.00	0.44	0.67	2.78	0.11	5.33
S2	0.22	0.00	1.11	0.56	0.00	1.89
S3	0.00	0.00	0.75	0.25	0.00	1.00
S8	1.00	0.00	0.33	0.67	0.00	2.00
S11	1.33	0.00	0.00	3.67	0.00	5.00
S12	1.50	0.00	1.83	3.50	0.00	6.83
L5	0.18	0.12	3.94	0.71	0.00	5.06
L10	0.15	0.38	0.77	1.92	0.00	3.23

Table 4.c Mean number of saplings in the below-canopy quadrats in each gap

GAP ID	*Acer platanoides*	*Acer pseudoplatanus*	*Fagus sylvatica*	*Fraxinus excelsior*	*Ulmus glabra*	*All saplings*
S1	1.42	0.18	0.51	2.09	0.09	4.35
S2	0.20	0.07	1.25	0.98	0.04	2.55
S3	0.13	0.02	0.57	0.67	0.00	1.38
S8	0.89	0.56	0.48	0.62	0.00	2.56
S11	0.84	0.39	0.44	5.25	0.07	7.00
S12	2.11	0.16	0.75	3.21	0.08	6.34
L5	0.18	0.03	1.63	0.67	0.00	2.54
L10	0.39	0.53	0.56	3.20	0.05	4.75

According to the results of canonical correspondence analysis (CCA) the first two canonical axes explained a 12.3% variance of species data and a 77.6% of species-environment relation (*Figure 2*).

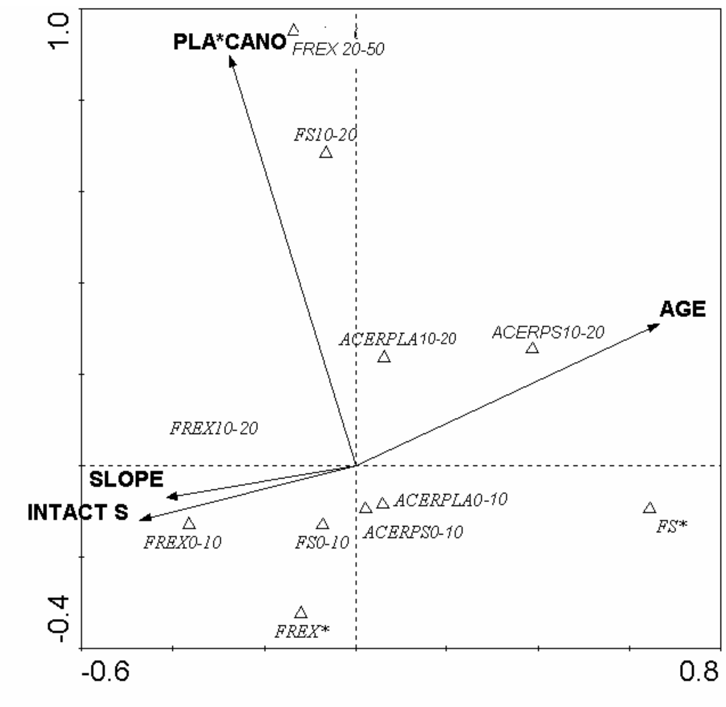

Figure 2. Species and environmental variables biplot of the canonical correspondance analysis.

PLA*CANO: variable combined from the interaction of total herbaceous coverage and canopy openness, AGE: age of the gaps, INTACT S: intact soil, SLOPE: slope; FS*: *F. sylvatica* seedling, FS10*:* *F. sylvatica* 0-10 cm, FS20: *F. sylvatica* 10-20 cm, FS50: *F. sylvatica* 20-50 cm, FREX: *Fraxinus excelsior*, ACPLA*:* *Acer platanoides*, ACERPS: *Acer pseudoplatanus*

The most important variables were: *a*, variable combined from the interaction of total herbaceous coverage and canopy openness (PLA*CANO) (p-value 0.0040, F-ratio=3.51; number of permutations=499). *b*, age of the gaps (AGE) (p-value 0.0060, F-ratio=2.91; number of permutations=499). *c*, intact soil (INTACT S) (p-value 0.0080, F-ratio=2.64; number of permutations=499), and *d*, slope (SLOPE) (p-value 0.050, F-ratio=1.82; number of permutations=499). The first axis (x) had the highest correlations with age (0.66), whereas the second axis (y) had the highest correlation with the interaction of total herbaceous coverage and canopy openness (0.9).

According to the CCA, increasing canopy openness and herb cover seemed to enhance the occurrence of larger saplings, whereas smaller seedlings (<10 cm) were situated at the lower values of axis 2. Beech seedlings – unlike other species, most remarkably ash – seemed to prefer plots with relatively low proportion of intact soil as a substrate. Furthermore, the occurrence of beech seedlings was positively correlated with higher age; however, this result can be based upon the high number of seedlings in one older gap.

Results of correlation analyses (Spearman Rank Order Correlation) corresponded well with the results obtained by ordination. Young regeneration (10-20 cm) of all tree species showed significant positive correlation (Spearman Rank Order Correlation, N=657, $p<0.01$) with proportion of intact soil. The number of first year seedlings of ash also showed significant positive correlation with proportion of intact soil, whereas that of beech was positively correlated (Spearman Rank Order Correlation, N=657, $p<0.01$) with proportion of mineral soil. Saplings of all species showed significant positive correlation (Spearman Rank Order Correlation, N=657, $p<0.01$) with total cover of herbaceous species, except for first year beech and ash seedlings. Canopy openness seemed to be in positive relation with the number of higher beech saplings (>10cm, Spearman Rank Order Correlation, N=84, $p<0.1$ and $p<0.05$), whereas ash seedlings showed just the opposite (Spearman Rank Order Correlation, N=84, $p<0.1$).

The relationships between sapling density and herbaceous vegetation cover need more investigation, as the relationship between these variables is not linear, and they can be confounded by the effects of canopy openness on both of these variables. In order to analyse the effects of canopy openness and herb species cover on seedling density, more or less separately, plots were grouped by canopy openness values: <18% and >18%, and by total cover of herb species: <50% and >50% (Table 5).

Table 5. The four groups of quadrats (11, 12, 21, 22) according to the values of the canopy openness and coverage of herb species

	11	12	21	22
Canopy openness (%)	<18	>18	<18	>18
Cover of herb species (%)	<50	<50	>50	>50
Number of quadrats	46	12	15	11

Figure 3 shows how unevenly beech seedlings of different height classes were distributed among the four groups. Other species showed partly similar patterns. The highest beech seedling density was characteristic in quadrats, where herb layer was dense and canopy openness was low; whereas the lowest density was observed in quadrats where herb layer was dense and canopy was opened (*Figure 3*).

Plots with high herbaceous vegetation cover had different species composition, depending on canopy openness. As the results of the Mann-Whitney Test show, the mean cover of *Aegopodium podagraria, Mycelis muralis, Sanicula europaea,* and *Urtica dioica* was significantly ($p<0.05$) different in quadrats belonging to the two compared groups: where total cover of herb species > 50% and canopy openness < 18% or canopy openness > 18%. Cover of *Urtica* was much higher in quadrats under open canopy, whereas cover of the other three species was higher in quadrats with lower canopy openness. The Spearman Rank Order Correlation furthermore showed a very strong negative correlation ($R=-0.61$, $p<0.01$, N=657) between the total number of regeneration and cover of *Urtica dioica.*

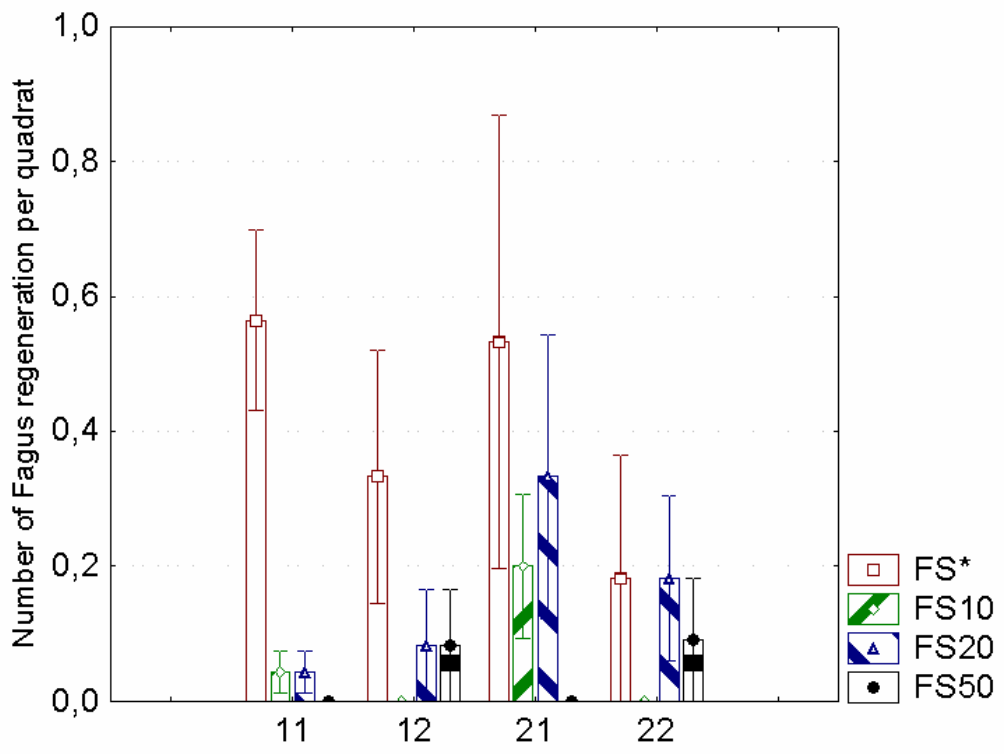

Figure 3. Mean number of Fagus sylvatica seedlings and saplings in the four groups of quadrats.

Canopy openness < 18% and total cover of herb species: < 50% (11),
canopy openness > 18% and total cover of herb species: < 50% (12),
canopy openness < 18% and total cover of herb species: > 50% (21), and
canopy openness > 18% and total cover of herb species: > 50% (22).
FS*: *F. sylvatica* seedling, FS10: *F. sylvatica* 0-10 cm, FS20: *F. sylvatica* 10-20 cm, FS50: *F. sylvatica* 20-50 cm.
Columns represent mean, whiskers represent standard error.

4 DISCUSSION

The high variance of relative light intensity and canopy openness values found both in gaps and below-canopy, reflects the heterogeneity of canopy in this semi-natural beech stand. It was only in larger gaps, where we found more diffuse light reaching the ground than under canopy near the gaps during the vegetation period, however, no significant increase of direct light could be recognized. Results of other gap-studies in temperate forests show increases of incident light depending on gap-size as well (Collins – Pickett 1987, Collins – Pickett 1988, Canham et al. 1990, McCarthy 2001 and references therein). The observed spatial variation in light conditions, however, should focus our attention to the applicability of the gap-partitioning hypothesis. Gap/non-gap situations therefore should not be treated as binary variable, but rather a continuum, which can be characterized by gradients of variables such as canopy openness or relative light intensity. Natural dynamics does create structural heterogeneity, which makes gap-studies – based on sharp dichotomy of gap versus non-gap environment – difficult (Lieberman et al. 1989).

Systematic differences between canopy openness and diffuse light estimations (with higher values of canopy openness) reflect the different view angle of the hemispherical lens and the spherical densiometer. According to the measurements of Englund et al. (2000) the view angle of the spherical densiometer is about 57º, whereas fisheye lenses have a much broader view angle of 167º. As a result, measurements taken by the densiometer overestimate canopy openness.

Variability of total cover of herbaceous species in and around gaps also reflects fine-scale canopy heterogeneity. In general, herbaceous cover correlates positively with canopy openness, with considerable higher values of herbaceous cover in central areas of large gaps. Holeksa (2003) found differences in the abundance of understorey species between gap and under canopy position, if gaps were larger than 50 m^2; other studies are congruent with these findings (Hughes – Fahey 1991, Goldblum 1997). However, in other situations no effect of gap creation could be shown on the total cover of the herb layer (Collins – Pickett 1987, Collins – Pickett 1988), and several groups of species proved to be insensitive to gap (Collins – Pickett 1987, Collins – Pickett 1988, Hughes – Fahey 1991, Schumann et al. 2003).

According to our results, the total numbers of tree regeneration did not differ between in-gap and below-canopy plots. Regeneration – as described by e.g. Peterken (1996) – consisted of almost exclusively "tolerant species" found in the canopy layer: beech, ash, maple and elm. Poplar, willow, and birch as pioneer, "intolerant species" usually did not occur in and around gaps. Lack of pioneer, light demanding species can be interpreted as a consequence of fine-scale patterns and low intensity of disturbances, resulting in relatively small gaps which are characteristic of this semi-natural stand and the distant propagule-resources (Poulson – Platt 1989, Peterken 1996, Peterson – Carson 1996). In addition, species composition of regeneration may be also affected by preferential game browsing. According to studies in Germany and Poland for red deer, (*Cervus elaphus*) *Salix* spp. and *Populus tremuloides* are among the most palatable plants, while roe deer (*Capreolus capreolus*) also prefers willow in the summer vegetation period (Gill 1992).

The detected browsing damage affected 25-50% of the individual trees. Higher percentages of damaged saplings were found among the higher size classes. According to our results, individual trees belonging to different size classes show distinct patterns in relation to substrate features, canopy openness and herb cover. Mineral soil seems to be the preferred germination site for beech, whereas larger beech saplings and other species seem to be less abundant in this substrate. According to the observation by Fanta (1995), success of establishment depends more on soil moisture than on light conditions, and thick litter may inhibit seeds to reach the ground surface exposing them to drought. Moreover, larger beech saplings show positive correlation with canopy openness. Some studies (Peltier et al. 1997) indicate that light is a very important factor for the development of beech saplings, enhancing root development. Seedlings are more susceptible to drought in poor light conditions (Topoliantz – Ponge 2000).

We showed that taller saplings are more abundant in plots where cover of herbaceous species is higher. Since game browsing is very intensive in this region and it affects almost all tree species, the sheltering of herbs can be very important in sapling survival. Other studies support this assumption, showing that higher saplings occur in higher and denser understorey vegetation, and they explain this pattern with the same reasoning (Rao et al. 2003). If tree saplings grow on bare ground, smaller individual saplings are more susceptible to browsing, but they are protected from damage in dense herb layers until they grow above the vegetation (Gill 1992).

Moreover, according to some studies, palatable plants can be partially protected from herbivores if they are associated with patches of unpalatable plants (Pietrzykowski et al. 2003 and references therein). These findings emphasize the potential effect of herb species composition on game damage in beech forests. We also found a strong negative correlation between sapling density and the cover of *Urtica dioica,* which shows that a certain height or density of the herb layer can also have negative effects on the regeneration. However, we did not find studies distinctively focusing on the effect of specific plant species e.g. *Urtica dioica* on the distribution of saplings.

In contrast to the above, however, few specific studies in North America focusing on the effects of herbivory and gap size found no effect of herbivory on tree seedling abundance (Castleberry et al. 2000, Collins 2003, Holladay et al. 2006), though short-term results suggested that recruits of some species in smaller gaps are more susceptible to herbivory than those in larger gaps, possibly due to deer preferentially browsing in less open areas (Castleberry et al. 2000). These studies based on exclosure experiments concluded that gap size and herb layer competition are more important factors in tree regeneration patterns than herbivory in the studied areas.

These findings leave several open questions for future research regarding the relationships between tree regeneration, herbaceous vegetation and herbivory, and the direct effect of herbaceous species on saplings survival. Future researches investigating gap regeneration processes in European broadleaved forests should include exclosure-experiments in order to investigate the effect of herbivores and gap size. Since, in Europe, deer numbers in many areas have been increasing during the last 100-200 years (Fuller – Gill 2001), the investigation of natural forest dynamics can be biased because of intense herbivory. Gap size may influence the browsing habits of larger herbivores, and have a profound effect on the herbaceous layer; however, dense herbaceous vegetation can also affect herbivory patterns. The pattern of tree regeneration therefore can be in a complex interaction with gap size, vegetation density, and browsing effect.

5 CONCLUSIONS

Our study focuses on gap regeneration patterns in a semi-natural beech forest stand. Although we only showed a snapshot of a dynamic process, we tried to interpret the findings as an outcome of several important dynamic processes: gap existence, tree regeneration, reaction of herbaceous species, and herbivory. Our findings emphasize the importance of the spatial scale of disturbances, and of the gradual change in abiotic factors (e.g. light) from below canopy to gap centre in gap-studies. Gap regeneration patterns depend not only on the ecological traits of tree species (e.g. light demanding, shade-tolerant etc.), but among others, on the composition and cover of herbaceous vegetation and on game browsing. Therefore, gap studies should focus on these factors as well, in order to get a better understanding of regeneration mechanisms of forest stands.

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