

# Thirty years of gap dynamics in a central european beech forest reserve

KATA KENDERES, BARBARA MIHÓK AND TIBOR STANDOVÁR\*

Department of Plant Taxonomy and Ecology, Loránd Eötvös University, H-1117 Budapest, Pázmány Péter sétány 1/C, Hungary

\*Corresponding author. E-mail: standy@ludens.elte.hu

## Summary

Investigation of gap characteristics and tree regeneration patterns is central for our understanding of forest dynamics. By integrating aerial photograph analyses and ground surveys, we provide a study of long-term canopy gap dynamics and tree regeneration patterns in a Hungarian beech forest reserve. We found (1) that in spite of the overall increase of gap area during the investigated 30-years (from 2.5 to 7.7 per cent), total gap area and average gap size (40–93 m<sup>2</sup>) were remarkably similar to those found in other temperate and tropical forests, (2) if the fate of individual gaps was followed, two to three times more intensive canopy dynamics (gap creation, closure and expansion) could be recognized than simple change of gap area indicated, and (3) average seedling density was considered to be sufficient for natural regeneration. However, it was apparent that recent increased deer browsing had prevented establishment of younger trees of 1–2 m in height, as taller saplings were recorded only in old gaps. Our results not only provide useful information on forest dynamics but can also contribute to understanding the potential roles that small forest reserves can play in providing essential reference data for nature-based forest management of this forest type.

## Introduction

European beech (*Fagus sylvatica* L.) is one of the major tree species of temperate Europe. It is a vigorous, long-lived, shade-tolerant tree that has a wide climatic and edaphic tolerance and a strong ability to compete with other tree species (Jahn, 1991). Forests dominated by or containing European beech as a major species are one of the most widespread and abundant vegetation types in Europe (Rübel, 1932; Mayer, 1984; Polunin and Walters, 1985; Ellenberg, 1988; Jahn, 1991; Peters, 1997). According to the data derived from the map of potential natural vegetation of Europe (Bohn *et al.*, 2004), beech and mixed beech

forests could have covered >92 million hectares in Europe during the last 1000 years. Based on national forest inventory data on contemporary distributions, beech-dominated forests still cover >14 million hectares.

Where beech forests had not been destroyed or converted to coniferous plantation, for the past 200 years they have mostly been managed in line with the paradigm of Central European forestry. It is based on very intensive treatment of forest stands organized by age classes, on very strict and prescriptive planning and on sophisticated management techniques. To keep this timber production system under control in a closed management system, natural processes in forests

have been largely ruled out (Hahn and Fanta, 2001). This approach to forestry prevailed from the beginning of the nineteenth century to the mid-twentieth century. The forests created and maintained under this system are—among other things—characterized by the creation of large, homogeneous (often pure, even-aged) stands. A number of criticisms have been formulated in the past few decades in relation to the ecological and economic risks, the difficulties of regeneration and the loss of biodiversity caused by the uniformity and simple structure of these forests. Because of these criticisms and the increasing demand for the social and protective functions of forests, there has been a growing interest for nature-based silviculture.

The implementation of nature-based silviculture should be based on knowledge about natural processes and structures. However, in Europe, where forest utilization has a very long history, it is hard to find appropriate reference forests to study the characteristics of natural forests for most forest types. Because of this, strict forest reserves play an essential role. They are areas left for free development, therefore they have the potential to provide essential reference data for nature-based silviculture (Parviainen *et al.*, 2000a). Their importance was recognized in the early nineteenth century when the first forest reserves were designated in Central Europe. A new era of this approach to forest reserves started after the works of Leibundgut (1959, 1966, 1978, 1982). Nowadays, it is generally accepted that natural forests are a good model for the realization of nature-based silviculture (for detailed information on research in European forest reserves cf. Diaci, 1999; Parviainen *et al.*, 1999, 2000b). However, to gain the necessary information, long-term investigations on forest dynamics are required.

Fine-scale gap-phase dynamics is a characteristic feature of natural beech-dominated forests of Central Europe (Peterken, 1996; Splechna *et al.*, 2005). The gap phase is important in forest regeneration by providing opportunities for tree recruitment, establishment and development (Watt, 1947; Canham, 1989; Runkle, 1989; Peterken, 1996; Brokaw and Busing, 2000; McCarthy, 2001; Mountford *et al.*, 2006; Page and Cameron, 2006; Baier *et al.*, 2007). Gaps are also important in maintaining plant species diver-

sity (Poulson and Platt, 1989; Busing and White, 1997; Brokaw and Busing, 2000; Schumann *et al.*, 2003; Degen *et al.*, 2005). The size, shape, age and temporal changes of gaps influence the regeneration patterns of the tree species, due to the different ecological traits of the particular tree species and to the effects on the herbaceous layer (e.g. Collins *et al.*, 1985; Canham, 1989; Poulson and Platt, 1989; Whitmore, 1989; Denslow and Spies, 1990; Peterken, 1996; Diaci, 2002; Gálhidy *et al.*, 2006).

Several investigations of gap characteristics have been carried out in different forests in the temperate regions. Most of them provide information on gap size distribution and total gap area (e.g. Runkle, 1982; Yamamoto, 1992; Pontauiller *et al.*, 1997; McCarthy, 2001; Fujita *et al.*, 2003a; Zeibig *et al.*, 2005). However, many of them describe a static picture and there is still limited information on the detailed pattern and dynamics of canopy gaps based on repeated observations of the individual stands, especially in *Fagus* forests. Such data on the temporal changes in gap size distribution and total gap area were given by several authors (Runkle, 1990; Tanaka and Nakashizuka, 1997; Miura *et al.*, 2001; Fujita *et al.*, 2003b; Henbo *et al.*, 2004; Mountford, 2004). More detailed quantitative information on turnover rate (Runkle 1982, 1990), on changes in canopy status, i.e. gap—closed canopy (Fujita *et al.*, 2003b; Henbo *et al.*, 2004; Itaya *et al.*, 2004), and on spatial pattern (Tanaka and Nakashizuka, 1997) are much scarcer. Retrospective studies of canopy gap dynamics using series of aerial photograph can provide useful supplementary information to labour-intensive field surveys.

The purposes of our analyses were (1) to use a time series of aerial photographs to define descriptive gap characteristics of the Óserdő Forest Reserve, Northern Hungary in four years (1975, 1980, 2000, 2005); (2) to analyse gap dynamics over 30 years by following the fate of individual gaps, i.e. to quantify the rate of creation of new gaps, of gap closure by lateral expansion versus by infilling of young undergrowth; (3) to study the amount, composition and survival of tree regeneration in gaps in relation to gap age, the height of potentially competing herbaceous vegetation and browsing damage caused by ungulate herbivores.

## Materials and methods

### Study area

Őserdő Forest Reserve is a small (25 ha) beech-dominated stand situated on the plateau of the Bükk Mountains (48° 03' N, 20°27' E) in Northern Hungary (cf. Figure 1). Elevation ranges from 830 to 900 m. The topography is varying with flat plateaus, karstic sink-holes (dolinas) and slopes of different steepness (for more details, cf. Table 2). Mean annual temperature is 6.1 °C (January: -4.1 °C, July: 15.5 °C) and the annual precipitation is 896 mm.

Soils reflect the high spatial variation in topography. In the lower part of the study plot, where topography is flat, limestone is covered by loess deposits, on which relatively deep illuviated brown forest soils developed, with signs of temporary gleying. On steeper south facing slopes without loess deposits, limestone serves as bedrock, on which skeletal soil and shallow black rendzina soil developed. The transition is continuous between these two extreme soil types. Colluvial soils of increasing depth occur downhill (G. Kovács, personal communication).

The forest is dominated by beech (*Fagus sylvatica* L.); the most important associated tree species are common ash (*Fraxinus excelsior* L.), sycamore (*Acer pseudoplatanus* L.) and wych elm (*Ulmus glabra* Huds.). The age of the dominant beech trees varies between 150 and 200 years.

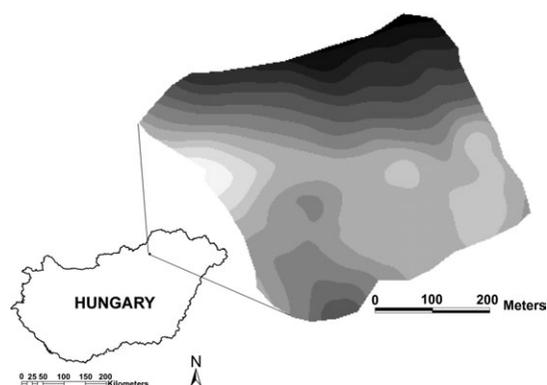


Figure 1. Location (within Hungary) and topographic map of the Őserdő Forest Reserve. Elevation ranges from 830 to 900 m and darker colours indicate higher elevation.

Dominant beech trees reach 41–47 m maximum height with diameter at 1.3 m height (d.b.h.) up to 100 cm. Stand structure is heterogeneous with trees of different sizes, canopy gaps and regeneration patches. The reserve can be divided into two distinct parts in terms of stand structure and composition. In the Northern and North-Western part, where topography is steeper and soil is shallower (cf. Figure 1), the proportion of the associated species is higher, and tree dimensions (tree-height, d.b.h., crown width) are smaller. In the Southern and South-Eastern part of the reserve, the stand comprises mainly huge beech trees. In both parts most of the highest canopy trees are more or less even-sized, but trees of smaller height classes form sub-canopy layers. The amount of dead wood is 175 m<sup>3</sup> ha<sup>-1</sup>, from which the proportion of logs is almost 87 per cent (Christensen *et al.*, 2005). All these make this stand a good representative of beech-dominated forest reserves in East-Central Europe (cf. Table 1 in Standovár and Kenderes 2003).

The shrub layer is extremely sparse, but the forest floor is covered with a dense herb layer. Most frequent species are *Mercurialis perennis* L., *Galium odoratum* (L.) Scop., *Sanicula europaea* L., *Glechoma hederacea* L., *Urtica dioica* L., *Euphorbia amygdaloides* L., *Viola reichenbachiana* Jord. ex Boreau, *Hordelymus europaeus* (L.) Jessen, *Alliaria petiolata* (M. B.) Cavara et Grande, *Aegopodium podagraria* L., *Melica uniflora* Retz., *Mycelis muralis* (L.) Dum, *Stachys sylvatica* L., *Geranium robertianum* L., *Dentaria bulbifera* L. and *Oxalis acetosella* L.

The forest was managed and cut in the past, but it has been developed freely during the last 80 years. The Reserve has been protected since 1942.

### Data collection

We collected available archive aerial photographs from different sources. Some were taken for forest management planning, whereas others for military and general land survey purposes. As a result, their quality varied depending on different factors: time of the year when the photos were taken, the flying height of the airplane, the position of our study site in the photo, etc. After excluding inappropriate photos (e.g. taken from

extreme height, in winter), for this study we used photographs taken in the growing season of 1975, 1980, 2000 and 2005.

We built a GIS database that contained the georeferenced and orthorectified photographs and the digital elevation model of the area. We analysed 21.3 ha of the reserve to avoid edge effects. Canopy gaps were mapped on-screen using aerial photographs. For each study year, the border lines of each gap were digitized into a polygon layer of our GIS database. To resolve ambiguities and uncertainties caused by differences in shade and tilt in each photograph, we also used 3D images generated from pairs of photographs. Canopy openings were considered as gaps with a minimum area of 4 m<sup>2</sup>. To improve our understanding of stand dynamics, we used an ArcView extension (Patch Structure) developed for the purposes of this study. This calculated not only the gap characteristics for each time step but also the fate of the individual gaps. We thereby quantified the rate of overall canopy dynamics and the importance of certain dynamic processes: creation of new gaps, gap closure, dissection of gaps and merger of neighbouring gaps.

To check the reliability of our maps, we carried out a ground survey during the summer of 2005. The existence and the borders of individual gaps were checked.

In addition, a field study of tree regeneration was conducted in 27 gaps. The gaps were selected by age and size criteria. The selected gaps were small (30–200 m<sup>2</sup>) with a roughly circular shape. They were divided into two groups according to their age: ‘old gaps’ were created before 1980 and ‘young gaps’ appeared later.

In each gap, we counted seedlings and saplings in a 25-m<sup>2</sup> quadrat, and recorded the species, height class and browsing damage for each individual. Six height classes were determined: seedling (with cotyledons or with maximum of two leaves), <0.5 m, 0.5 to <1 m, 1 to <2 m, 2 to <8 m and ≥8 m. Browsing level was categorized as follows: B0—no sign of browsing; B1—plant damaged only in last year; B2—viable plant with shoots damaged for several years; B3—same as B2, but with thick trunk base indicating that the plant could have grown to higher height class; B4—non-viable plant with shoots damaged for several years.

### Data analyses

For each study year, gap characteristics of the study area were described in terms of number of gaps, size distribution (mean, standard deviation, minimum, maximum) of gaps, proportion of the whole area in gaps and topographic position (altitude, slope steepness and aspect) of gaps. Kruskal–Wallis tests with post-hoc comparisons of mean ranks were used to test the significance of differences between average gap sizes in each of the study years (Zar, 1999).

The significance of the effects of gap age (old *vs* young), canopy openness (gap *vs* non-gap) and height of herbaceous vegetation (low *vs* high) on regeneration density was tested by *t* test or by Welch test after testing the normality of variance by *F* test. Independence of browsing damage, height class and species was tested by Pearson’s  $\chi^2$  (Zar, 1999).

The fate of the gaps was determined by using the ArcView extension ‘Patch Structure’. The number, proportion and area of opened, closed and surviving gaps were compared for the two 5-year long study periods (1975–1980 and 2000–2005).

## Results

### *The gap characteristics in the four study years*

Figure 2 shows maps of the canopy gaps in the four study years. These covered 2.5–7.7 per cent of the total area (Table 1.). Both mean gap size and total gap area increased during the 30 years of the study period (from 40 to 93 m<sup>2</sup> and from 5319 to 16477 m<sup>2</sup>, respectively). Significant change took place between 1980 and 2000 and 2005, especially in the south-eastern part of the area (cf. Figure 2). By 2000, relatively large new gaps had been created in this part of the reserve. This process continued after 2000. In 2004 and 2005, several trees were blown down by strong wind. The number of gaps varied between 132 and 178 in the different years. Gaps down to the minimum recording size (4 m<sup>2</sup>) were recorded in every year, whereas maximum gap size was greatest in 1980 and 2005.

The spatial distribution of gaps among different topographic positions changed slightly during the 30 years (Table 2.). Though in 1975, gaps were spread across the area, in the following

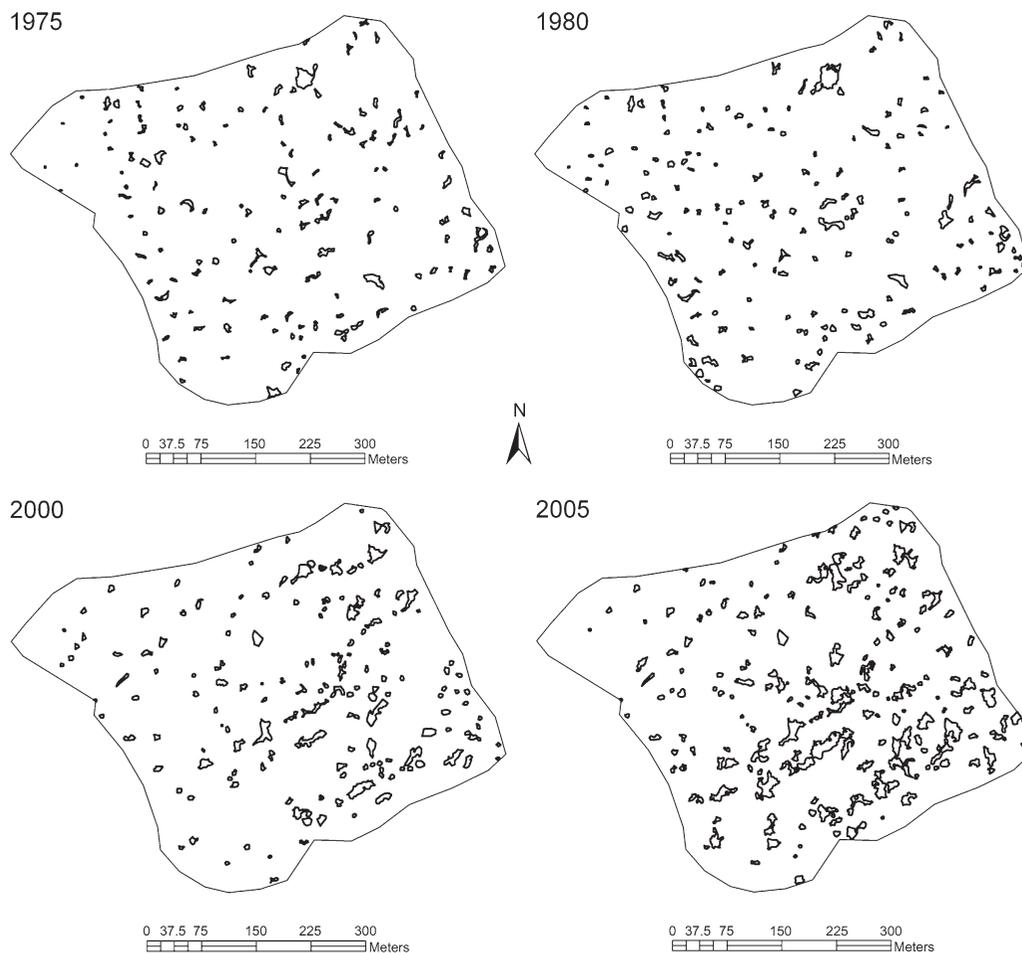


Figure 2. Distribution of canopy gaps in the study area as measured off aerial photographs from 1975 to 2005. See Table 1 for descriptive statistics.

30 years, mean elevation and slope steepness of the whole gap area decreased. Gaps on S-facing slopes fell markedly while on NE-E-facing slopes it increased. This was a consequence of increased gap creation taking place by 2000 and 2005 in the rather flat south-eastern part of the reserve (cf. Figure 2).

#### *Processes of canopy dynamics*

Because of the lack of appropriate aerial photographs, the time steps are rather uneven in our dataset. For this reason, we compared the dy-

namical characteristics of the two 5-year periods (1975–1980, 2000–2005).

As Table 3 shows, total gap area increased in both periods, though at different annual rates (0.13 and 0.68 per cent, respectively), indicating more intensive canopy dynamics in the second period. In addition to this information derived from comparing maps of different years, we obtained a better understanding of the dynamic process by applying the ArcView extension Patch Structure. Figure 3 shows two subsets of the output that Patch Structure created. In the figure, study year is shown at the beginning of each line, while dots mark individual gaps. Lines connecting

Table 1: Descriptive statistics of canopy gaps in the four study years

	1975 <sup>a</sup>	1980 <sup>a</sup>	2000 <sup>b</sup>	2005 <sup>c</sup>
Number of gaps	132	155	151	178
Mean gap size (m <sup>2</sup> )	40	43	61	93
Standard deviation of gap size	52	67	71	117
Maximum gap size (m <sup>2</sup> )	487	731	378	870
Minimum gap size (m <sup>2</sup> )	4	4	4	4
Total gap area (m <sup>2</sup> )	5319	6675	9191	16477
Percent of total area covered by gaps (%)	2.5	3.1	4.3	7.7

Significant differences between gap size distributions of individual years (based on Kruskal–Wallis test;  $H=46.98$ ;  $P < 0.0001$  and post-hoc comparisons of mean ranks) are indicated by superscripted letters (a, b, c).

Table 2: Topographical characteristics of the whole study area and separately for the area under canopy gaps in each of four study years

	Whole study area	Gap area in			
		1975	1980	2000	2005
Mean altitude (m)	848	848	845	844	843
Mean slope (°)	13	11	12	10	10
N-facing (%)	9	9	6	6	7
NE-facing (%)	9	12	12	12	16
E-facing (%)	6	6	5	15	15
SE-facing (%)	9	10	9	10	9
S-facing (%)	49	42	37	36	34
SW-facing (%)	8	8	12	9	8
W-facing (%)	4	7	10	6	5
NW-facing (%)	6	6	9	6	6

gaps indicate relationships ('is the same' or 'created from'). Based on these results, mean annual rate of change could be calculated for each period. As Table 3 shows, the number of new gaps (46 and 67) was higher than the number of closed gaps (29 and 36) in both periods. The same held when gap area was considered (1565 m<sup>2</sup> created and 730 m<sup>2</sup> closed between 1975 and 1980; 3645 m<sup>2</sup> created and 1045 m<sup>2</sup> closed between 2000 and 2005). During the two study periods, the annual rate of gap creation was 0.15 and 0.34 per cent, respectively, whereas that of gap closure was 0.07 and 0.1 per cent, respectively. The area of gaps that remained also increased by 520 and 4685 m<sup>2</sup>, resulting in a mean annual increase in gap area of 0.05 and 0.44 per cent, respectively. If all types of changes are considered, the average annual proportion of area

experiencing some kind of canopy change was 0.27 per cent (of total study area) between 1975 and 1980 and 0.88 per cent between 2000 and 2005.

### Regeneration

As Table 4 shows, seedling density (given in number per hectare) was significantly (Welch  $t=2.27$ ;  $df=17.01$ ;  $P<0.05$ ) higher in old gaps ( $36494 \pm 51326$ ) than in young ones ( $7733 \pm 6702$ ). Young trees belonging to height classes 2 to <8 m and  $\geq 8$  m were only found in old gaps ( $212 \pm 450$  vs  $141 \pm 242$ ). However, because of the small sample size, the  $t$  test was significant (Welch  $t=2.4$ ;  $df=16$ ;  $P < 0.05$ ) only for height class  $\geq 8$  m.

Based on data from all the 27 sampled gaps, the average number of saplings of <1 m height was  $45541 \pm 41093$  ha<sup>-1</sup>. Saplings higher than 1 m but smaller than 2 m did not occur in our samples.

Browsing pressure on the regeneration was considerable (see Table 5): only 15 per cent of the individuals in height class <0.5 m were not affected by browsing, with most individuals (84.5 per cent) having been damaged for >1 year. In the 0.5 to <1 m height class, 95.4 per cent of individuals had been damaged for >1 year. According to the chi-square test, degree of browsing damage was not independent from height class (Pearson  $\chi^2=40.1$ ;  $df=4$ ;  $P < 0.001$ ). In the lower height class (<0.5 m), the observed number of individuals belonging to B0 and B3 browsing category was higher, whereas the number in category B2 was less than expected. For higher saplings (0.5 to <1 m), the opposite was observed (cf. Table 5).

Table 3: Characteristics describing different aspects of gap dynamics during two 5-year periods in Öserdö Forest Reserve

Dynamic process	1975–1980	2000–2005
Change in total gap area (m <sup>2</sup> )	2820	9375
Change in total gap area (%/year)	0.13	0.68
Number of new gaps created during the period	46	67
Total area of newly created gaps (m <sup>2</sup> )	1565	3645
Percent of total area covered by new gaps (%/year)	0.15	0.34
Number of gaps that closed during the period	29	36
Total area of gaps that closed (m <sup>2</sup> )	730	1045
Percent of total area covered by gaps that closed (%/year)	0.07	0.10
Proportion of area where canopy dynamics occurred (%/year)	0.27	0.88

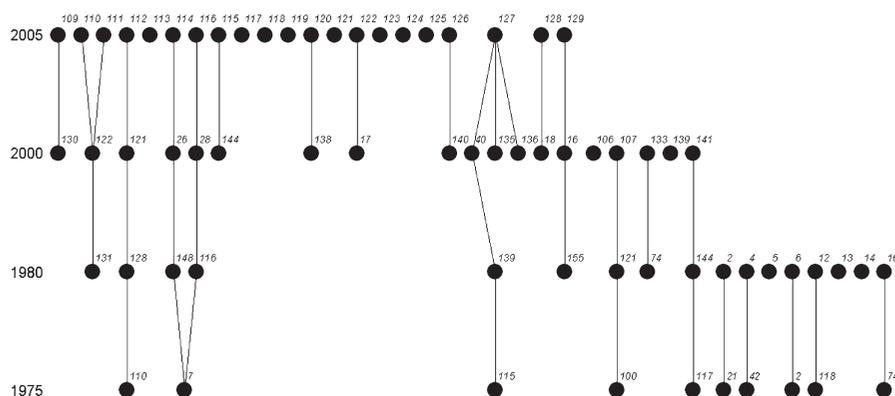


Figure 3. Example pathways of canopy gaps recorded in the study area during 1975–2005. Numbers to the left of each line show the year of recording. Each dot is an individual gap. The connecting lines indicate pathways and relationships. Possible events are gap closure (e.g. gaps No. 107 or 141 in 2000), gap creation (e.g. gaps 131 and 155 in 1980), merger of neighbouring gaps (e.g. gaps Nos. 40, 135 and 136 in 2000 merge to gap 127 in 2005) and dissection of gaps by infilling trees creating several sister gaps (e.g. No. 7 in 1975). Gaps can be traced back in the map and the database by their identification numbers.

The data presented in Table 6 demonstrate that browsing was significantly (Pearson  $\chi^2 = 387.7$ ;  $df = 16$ ;  $P < 0.001$ ) influenced by species. Browsers showed clear preference for ash (93 per cent damaged for several years (B2–B3–B4); only 6.5 per cent not damaged) and Norway maple (86.6 per cent in B2–B3–B4 classes; 13.4 per cent not damaged). Sycamore (67.9 per cent in B2–B3–B4 classes; 31.8 per cent not damaged) and beech (66.7 per cent in B2–B3–B4 classes; 33.2 per cent not damaged) were less affected.

As Table 7 shows, there was a significant (Pearson  $\chi^2 = 139.7$ ;  $df = 4$ ;  $P < 0.001$ ) decrease in the frequency of associated tree species: the observed

numbers of ash, Norway maple, sycamore and wych elm individuals were higher than expected in height class  $<0.5$  m, and lower than expected in the higher height class. Individuals  $>2$  m were all beeches.

## Discussion

### Canopy dynamics

Our results show that both the percentage coverage of gaps and average gap size in the Öserdö Forest Reserve are within the lower part of the

range found in different natural temperate and tropical forests (collected data in McCarthy, 2001; Ott and Juday, 2002; Fujita *et al.*, 2003a, b; Henbo *et al.*, 2004; Piovesan *et al.*, 2005). Gap diameter in this reserve was typically smaller than 1 tree-height. Data from Central European, beech-dominated reserves lacking recent, large-scale disturbance are relatively close to our results. For example, Zeibig *et al.* (2005) found a 5.6 per cent gap proportion and 137 m<sup>2</sup> average gap size in Krokár (Slovenia), while K. Kenderes and T. Standovár (unpublished data) found gap proportion and average gap size to be 10.8 per cent and 95 m<sup>2</sup> in Zofin (Czech Republic) and 7 per cent and 76 m<sup>2</sup> in Kékes (Hungary). At the other end, many forest reserves in NW-Europe are characterized by less natural processes and by the occurrence of recent, large-scale, wind disturbance; hence, gap proportion and mean gap area are much higher (e.g. data in Mountford 2004).

As Figure 2 shows, many of the youngest gaps (created by 2000 and especially by 2005) are relatively large, and they occur mostly in the south-

eastern part of the reserve. There are two main reasons behind this observation. First, this part of the reserve is characterized by the deepest soil with the lowest levels of stoniness resulting in rapid growth by the trees once freed up by regular tending cuts before the reserve was designated. As a result, the beech trees in this part of the reserve are widely spaced and have large canopies. In addition, in this part of the reserve there are signs of temporary surface-water gleying, which might have caused beech roots to avoid the deeper soil layers, resulting in increased instability. These large old individuals are rather susceptible to different disturbance agents (e.g. fungi, wind), and when they fall, relatively large gaps are created. Second, field observation confirmed that the relatively large gaps—created in 2004 by strong wind—expanded when strong winds in 2005 uprooted trees at the gap margins. The enlargement of gaps by subsequent storms is a general phenomenon, and it plays an important role in prolonging the time during which extra light and soil nutrients are available to saplings. For example, in 42 per cent of the gaps observed in 1976/1977, at least one surrounding canopy tree had died or was obviously dying by 1983 in the Southern Appalachian (Runkle and Yetter, 1987).

These observations support the findings of a review on East-Central European beech forest dynamics which stated that wind is an important disturbance agent in this region (Standovár and Kenderes, 2003; see also Nagel and Diaci, 2006).

Regarding the rate of canopy dynamics, the average percentage of canopy that was converted to gaps in this reserve is consistent with published data (e.g. Sousa, 1984; Runkle, 1985). We also showed that the canopy dynamics were more intensive in both of the analysed 5-year periods than

Table 4: Comparison of average density per hectare (mean  $\pm$  standard deviation) of tree regeneration belonging to different height classes in old *vs* young gaps

	Old	Young
Seedling*	36 494 $\pm$ 51 326	7733 $\pm$ 6702
<0.5 m	44 424 $\pm$ 45 264	46 444 $\pm$ 31 092
0.5 to <1 m	776 $\pm$ 2282	4489 $\pm$ 5369
1 to <2 m	0	0
2 to <8 m	212 $\pm$ 450	0 $\pm$ 0
$\geq$ 8 m*	141 $\pm$ 242	0 $\pm$ 0

Significant differences (Welch test,  $P < 0.05$ ) are marked with\*.

Table 5: Observed (obs) and expected (exp) number of young trees with different level of browsing in two height classes (<0.5 m, 0.5 to <1 m) in the 27 quadrats (25 m<sup>2</sup> each)

		B0	B1	B2	B3	B4	$\Sigma$
<0.5 m	obs	429	13	1908	499	4	28533
	exp	416	12	1941	480	4	
0.5 to <1 m	obs	6	0	122	3	0	131
	exp	19	1	89	22	0	
$\Sigma$		435	13	2030	502	4	2984

Pearson  $\chi^2 = 40.1$ ;  $df = 4$ ;  $P < 0.001$ .

Table 6: Observed (obs) and expected (exp) number of young individuals (<1 m) with different levels of browsing belonging to different tree species in the 27 quadrats (25 m<sup>2</sup> each)

Species		B0	B1	B2	B3	B4	Σ
<i>Fagus sylvatica</i>	obs	119	2	169	65	3	358
	exp	52	2	244	60	0	
<i>Fraxinus excelsior</i>	obs	109	9	1215	351	1	1685
	exp	246	7	1146	283	2	
<i>Acer platanoides</i>	obs	62	0	336	63	0	461
	exp	67	2	314	78	1	
<i>Acer pseudoplatanus</i>	obs	142	1	292	11	0	446
	exp	65	2	303	75	1	
<i>Ulmus glabra</i>	obs	3	1	18	12	0	34
	exp	5	0	23	6	0	
Σ		435	13	2030	502	4	2984

Pearson  $\chi^2 = 387.7$ ; df= 16;  $P < 0.001$ .

Table 7: Observed (obs) and expected (exp) number of young trees (<1 m) of different species belonging to different height classes (<0.5 m, 0.5 to <1 m) in the 27 quadrats (25 m<sup>2</sup> each)

		<i>Fagus sylvatica</i>	<i>Fraxinus excelsior</i>	<i>Acer platanoides</i>	<i>Acer pseudoplatanus</i>	<i>Ulmus glabra</i>	Σ
<0.5 m	obs	300	1630	448	441	34	2853
	exp	342	1611	441	426	33	
0.5 to <1 m	obs	58	55	13	5	0	131
	exp	16	74	20	20	1	
Σ		358	1685	461	446	34	2984

Pearson  $\chi^2 = 139.7$ ; df= 4;  $P < 0.001$ .

the simple change of total gap area would indicate: the area affected by dynamical processes was two to three times larger than the simple difference (cf. Table 3). This means that intensive gap creation and closure took place simultaneously.

We observed an overall increase of gap area during the 30-year period, because the rate of gap creation exceeded that of gap closure and the size of many surviving gaps (detectable throughout the 30 years) had also increased in many cases. This indicates that after 80 years of non-intervention, this stand has not reached a dynamic equilibrium. The development of a shifting mosaic steady state (S.H. Bormann and G.E. Likens, 1979) requires a much longer time of free development (and the absence of catastrophic disturbances) if the stand has its origin in an age-class silvicultural system. However, even assuming a more natural age and/or size distribution of trees, the outcome of spontaneous stand development is unclear because

of the small size (25 ha) of the study area, and requires continuing investigations. It is definitely smaller than the minimum dynamic area (sensu White and Pickett, 1985) of a Central European beech forest. In this case, therefore, stand size in itself sets limits to drawing general conclusions about the dynamics of this beech forest (Holeksa, 1993). However, we—as many other colleagues in Europe—have to live with the constraint that long and intensive use of our forest has left very little near natural forests for such studies.

### Regeneration

While studying forest dynamics, in-depth knowledge on regeneration has both theoretical and practical importance. Below we discuss sufficiency of regeneration density and the factors that affect the success of established regeneration.

As our data (Table 4) illustrate, average seedling density in the studied natural gaps was in the range (between 40 and 50 thousands per hectare) that is regarded as sufficient for restocking managed beech stands by natural regeneration (Evans, 1984). For example, according to Hungarian forestry regulations, the presence of at least 10 000 individuals per hectare is required for regeneration to be accepted as successful.

Our data are not appropriate to assess the effects of gap size on regeneration success, since we do not have long-term data on regeneration, or on initial size of all studied gaps. This kind of information can be gained from experimental studies (e.g. Mihók *et al.*, 2005; Gálhidy *et al.*, 2006, for Hungarian beech forests). Nevertheless, this study considered the apparent effects of gap age on seedling establishment and survival. More small seedlings were established in old *vs* young gaps, but the density of saplings up to 0.5 m in height was similar, which suggested that seedling survival was less in old gaps, perhaps because of competition from ground vegetation (short herbaceous vegetation was observed widely in old gaps). However, a range of other factors, notably light availability, localized deer browsing and uneven seed fall, may have been involved. Deer browsing was overwhelming in the area. An extremely high proportion of seedlings were damaged (85 and 95 per cent in the <0.5 m and 0.5 to <1 m height classes, respectively, c.f. Table 5). We found no young trees in the 1- to 2-m height class, and trees higher than 2 m were found only in old gaps. Based on data in the National Game Management Database, the estimated population sizes of mouflon (*Ovis musimon* Schreb.), red deer (*Cervus elaphus* L.), roe deer (*Capreolus capreolus* L.) and wild boar (*Sus scrofa* L.) have increased two to five times in the neighbouring two counties since 1980. This suggests that the trees >2 m found in old gaps had grown beyond the reach of browsing game at a time of lower browsing pressure.

Different game species have different food preference; even though to a degree they use the same plant species (e.g. Homolka, 1993; Heroldová, 1996; Gebert and Verheyden-Tixier, 2001). We have no data regarding the site use of the different game species, but in common with many authors (e.g. Ammer, 1996; Čermák and Mrkva, 2003; Modrý *et al.*, 2004), we showed that several of the

associated tree species (ash, Norway maple) were more seriously damaged than beech. Species composition of regeneration varied between different height classes as beech was more frequent in higher height classes. However, this is not a direct proof of preferential browsing, since competition for light in itself or in combination with preferential browsing can also result in the reduced survival of these species (Ammer, 1996; Emborg, 1998; Lei and Lechowicz, 1998; Harmer and Gill, 2000; Modrý *et al.*, 2004; Messaoud and Houle, 2006).

### *Practical implications*

This study in the Öserdő Forest Reserve revealed the spatial and temporal aspects of canopy dynamics in a near-natural Central European beech forest. The findings of this study can support the development of techniques for nature-based silviculture. The observed gap dimensions and rate of canopy dynamics can guide practitioners during the transition process from uniform shelterwood system (Matthews, 1991) towards practices that ensure continuous forest cover. These results also indicated that natural regeneration was possible in naturally occurring gaps. Both the density and species composition of regeneration would enable the development and long-term maintenance of mixed beech-dominated forests. However, the current high game density impeded the recruitment of tree saplings into the canopy layer, and also led to changes in species composition due to selective browsing.

It is necessary to consider that these large herbivores use a much larger area than the Reserve itself. The negative effects of high browsing pressure could be reduced on a landscape scale by the implementation of nature-based forest management techniques in the surrounding landscape. This would improve the quality of game habitat (e.g. by maintaining a viable shrub layer), hence reducing browsing pressure (Reimoser and Gossow, 1996; Reimoser *et al.*, 1999; Mátrai *et al.*, 2004; Szemethy *et al.*, 2004). This is a reasonable alternative to excluding browsers by fences (Szemethy *et al.*, 1994).

In conclusion, we argue that in spite of the limitations set by their small size and the negative effects from the surroundings (e.g. browsing pressure), forest reserves are a useful and indispensable means of studying natural processes in our forests.

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### Conflict of Interest Statement

None declared.

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