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Regular research paper

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THE INFLUENCE OF GAPS ON TREE REGENERATION: A CASE STUDY OF THE MIXED LIME-HORNBEAM (*TILIO-CARPINETUM* TRACZ. 1962) COMMUNITIES IN THE BIAŁOWIEŻA PRIMEVAL FOREST

ABSTRACT: Tree stand regeneration in ten natural gaps, ranging in size from 250 to 1610 m², and three artificial clearings of 650–1150 m² was compared to the undergrowth in the adjacent stands representing mesic lime-hornbeam (*Tilio-Carpinetum* Tracz. 1962) assemblages of the Białowieża Primeval Forest. The purpose of the study was to find how gaps influence the tree regeneration in such forests, regarding sapling density and composition. Most of the gaps were formed by the decline of groups of spruce (*Picea abies* (L.) Karst.) trees. In the largest openings spruce logs contributed to more than 80% of the volume of fallen trees.

Having four times higher all saplings density and eight times higher tall saplings (h > 1.3 m) density, comparing to the canopy-sheltered undergrowth, gaps play an important role of successful tree regeneration centres. Pioneering, intolerant species such as birch (*Betula pendula* Roth), aspen (*Populus tremula* L.), goat willow (*Salix caprea* L.), rowan (*Sorbus aucuparia* L.), and alder (*Alnus glutinosa* L.), regenerate almost solely in gaps. The gap size had no influence on the gap-filler composition. The most successful gap-fillers, both in small and large gaps were tolerant species: hornbeam (*Carpinus betulus* L.) and lime (*Tilia cordata* Mill.). Spruce, the third dominant canopy species of the neighbouring stands was absent in the gap-filling regeneration.

The study showed that under the current environmental conditions only hornbeam reveals a

continuous mode of regeneration giving it a big competitive advantage both under canopy and in gaps. Other species, including lime, oak (*Quercus robur* L.) as well as pioneering birch and aspen seem to regenerate in a discrete and irregular manner. It was hypothesised that their regeneration depends on ephemeral opportune circumstances occurring at the initial phase of gap filling, such as presence of layering fresh logs, sprouting stumps and roots, spots of exposed mineral material, as well as inaccessibility to browsers.

Artificial openings, created by forestry operations, considerably differ from natural gaps, mimicking a 'catastrophic mode' of dynamics, quite uncommon in the observed forest assemblages, favouring abundant regeneration of pioneering species.

Further research necessary to explain important structural and dynamic characteristics of natural stands should address the following questions:

- overall gap size structure;
- mechanisms determining successful regeneration of less competitive and intolerant species;
- history of the gap dynamics (dendrochronology) and its future development (modelling);
- average rate of disturbance and turnover time in *Tilio-Carpinetum*;
- minimal conservation area.

KEY WORDS: artificial gaps, Białowieża, developmental gaps, mesic deciduous forest, regeneration mode, spruce decline

1. INTRODUCTION

Gap dynamics is one of the key issues in contemporary forest ecology. Gaps are studied from various perspectives: stand dynamics and structure, species composition, nature conservation, and forestry practice.

A gap is defined as “the ground area under a canopy opening extending to the bases of canopy trees surrounding the canopy opening” (Runkle 1981). It is a concept wide enough to contain different ecological categories, i.e. edaphic canopy gaps (specific site conditions preventing from canopy closure) and developmental gaps (caused by tree mortality) Lertzman *et al.* (1996). Qinghong and Hytteborn (1991) proposed to distinguish “crown openings,” natural discontinuities of the canopy layer, from actual gaps, caused by disturbances. Gaps are substantial spatial and functional elements of natural forest ecosystems. They may cover from several to more than forty percent of the area of a forest surface (Kneeshaw and Bergeron 1998). A very exhaustive review of the topical literature was presented by McCarthy (2001). Here only the few aspects are to be addressed by the following study.

The indices commonly used to describe gaps are: single gap area, gap diameter(s), the number of gap makers, and the D/H ratio (gap diameter-to-tree height at the gap border). The area of the gaps studied has varied from 5 m² (central Japan, Abe *et al.* 1995) to 2.5 ha (SE Pennsylvania, Castelli *et al.* 1999). However, most of the gaps reported in the reviewed literature range between 50 and 500 m².

Discussing the influence of gaps on species composition in temperate forests, Runkle (1985) pointed at the severity of disturbances as a major discriminating factor. Although the author clearly discriminates between “gap dynamics” and “ecological succession” (involving massive regeneration of pioneering species), other researchers show that even small gaps (50–450 m²) may secure successful regeneration of intolerant species such as tuliptree, *Liriodendron tulipifera* L. (Runkle 1985, and the authors cited therein).

Analysis of tree regeneration in relatively large experimental gaps (from 1600 to 2400

m²) in northern hardwoods (New Hampshire, USA) demonstrated the dominance of advanced regeneration of shade-tolerant species (established up to 30 yr before the gap formed). The majority of yellow birch trees (*Betula alleghanensis* Britton, moderately tolerant) became established during the first four years after gap formation (McClure *et al.* 2000). Similarly, many other reviewed studies carried out in North America and Japan report that gaps ranging from forty to several hundred square metres mainly enhance the regeneration of shade tolerant species, contributing to a steady decrease in abundance of light-loving species (e.g. Cho and Boerner 1991, Leemans 1991, Nakashizuka *et al.* 1992, Abe *et al.* 1995, Gray and Spies 1996, Masaki *et al.* 1999, Cook 2000). On the other hand, Busing (1994) observed some positive reaction from intolerant species in the larger gaps (>400 m²). Similarly, Dahir and Lorimer (1996), studying hardwood stands in Porcupine Mts (MI, USA) discovered that in gaps larger than 80 m², mid-tolerant species (yellow birch, green ash *Fraxinus pennsylvanica* Marshall and basswood *Tilia americana* L.) had a competitive advantage over typical shade tolerant species. Runkle (1982) suggested that although most of gaps in mesic forests in the eastern US boost the growth of tolerant species, opportunists can persist at low densities. Interestingly, even in very large gaps created by windblow in southern Pennsylvania deciduous forest (2.5 ha), caused a mere structural “reorganisation of existing vegetation” instead of the expected development of a pioneering stand (Castelli *et al.* 1999).

McClure *et al.* (1993) comparing gaps of different sizes (324–2400 m²) in New Hampshire hardwood forests, came to the conclusion that gap size and light condition were not significant factors favouring shade-tolerant or intolerant species. They pointed to changes in soil conditions following forestry management in artificial gaps (through exposed mineral soil). A similar conclusion came from the study of semi-deciduous tropical forest in Mexico, where regeneration of shade-intolerant species was attributed to soil disturbance caused by the logging activity, while the natural gaps were dominated by shade-tolerant species (Dickinson *et*

al. 2000). Also Battles and Fahey (2000) suggested that appropriate rate of mineral seedbed is a factor controlling regeneration of intolerant, opportunistic species.

Most of the literature reviewed concerns relatively small gaps which are considered to be temporary canopy openings, usually filled by a single or only few successor trees. While continuous formation and closure of small gaps is ascribed to the old-growth 'biostatic' stage of stands (e.g. Lertzman *et al.* 1996), larger gaps (usually from several hundreds of m² on) evolve into a new developmental phase of a stand, following their own developmental trajectories (e.g. Oldeman 1990, Valverde and Silvertown 1997, Bobiec *et al.* 2000). Lewis and Lindgren (2000) proposed an interesting approach to incorporate the phenomena occurring on different spatial scales into a universal model of the forest dynamics. They discriminated between "matrix disturbances" (operating over a long time period, modifying the matrix), "patch disturbances" (caused by short lasting, usually exogeneous agents, initiating sudden changes on the landscape level), and "patch-modifying disturbances" (changing patches, until the patches blend into the matrix). Such a "nested," non-linear concept seems to correspond with the model suggested for the mesic deciduous stands in the Białowieża Primeval Forest (Bobiec *et al.* 2000).

In Europe most of the canopy gap studies refer either to boreal (e.g. Qinghong and Hytteborn 1991, McCarthy 2001), mountane (e.g. Diaci 2002, Grassi *et al.* 2004) or beech forests (NAT-MAN 2005). As the hemiboreal deciduous ecosystems have been severely re-shaped and dismembered the Białowieża Forest is one of the few places where the original gap dynamics specific to European mesic lime-hornbeam forests can still be observed (Falinski 1986, Koop 1989).

The goal of the present study was to compare the composition of the natural tree regeneration in canopy gaps to the neighbouring undergrowth in mesic lime-hornbeam forest (*Tilio-Carpinetum*, Falinski 1986, Sokołowski 1993). This could reveal how the existing theories referring to the gap influence on tree regeneration apply to the processes observed in the lowland forest of

Białowieża. Does the gap size determine the species composition of the future tree layer? Does regeneration in gaps differ significantly from canopy sheltered regeneration?

2. STUDY AREA

The Białowieża Primeval Forest (BPF, 52°43'N, 23°50'E), split by the Polish-Belarusian border, is the most preserved lowland forest in the European temperate zone. Abiotic conditions are primarily determined by the continental climate (mean annual precipitation 641 mm, ranging from 426 to 940 mm, 85% in rain; mean annual temperature 6.8 °C, ranging from 5.1 to 8.8 °C, with the mean temperature in July ranging from 15.2 to 21.6 °C, and in January from -13.4 to 1.8 °C; Olszewski 1986), the post-glacial geological formation (vast plains with small altitude differences; altitude ranging from 134 to 202 m a.s.l.), and its location on the continental watershed making the system dependant on precipitation (Falinski 1986).

The natural gaps described in the paper are located in the strict reserve of the Białowieża National Park (BNP), covering 4747 hectares, ca. 8% of the Polish part of the forest. Details concerning the BPF administrative division, zones of different management/protection regimes, and its history are provided by Bobiec (2003). The lime-hornbeam community was characterised by Falinski (1986) and Sokołowski (1993).

3. MATERIAL AND METHODS

The selected gaps should have resulted from "patch disturbance" (according to the definition by Lewis and Lindgren 2000) leading to the development of new stand units. Small, usually single-tree gaps, considered as the components of the biostatic phase of stand development (Bobiec *et al.* 2000) were deliberately omitted. Neither very recent gaps (younger than 5 years) were included. All but one (R10) of the selected openings in the BNP (L1-9) had sharp edges making it possible to discriminate between the gap and non-gap (under canopy) area (Fig. 1, Table 1). One exceptional area did not display "typical" gap characteristics. Instead it was a fine-grained

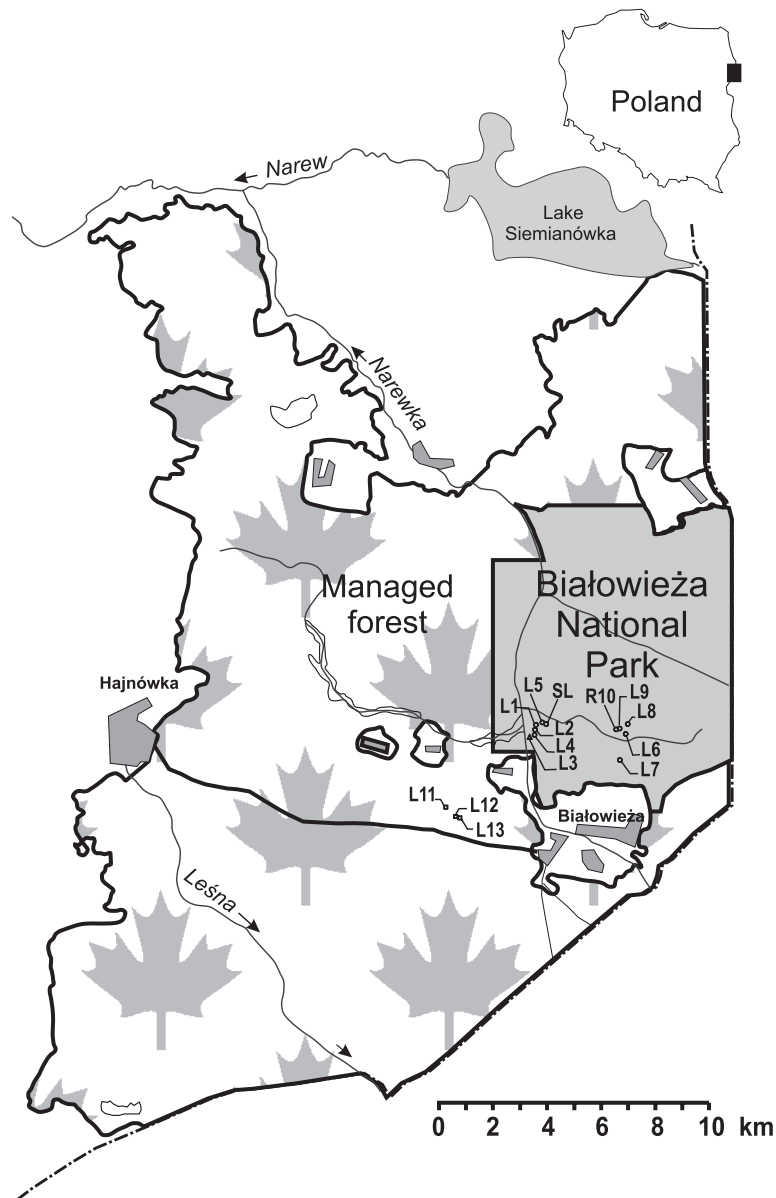


Fig. 1. Białowieża Primeval Forest; L1–9 – natural gaps, SL – old, fully recovered gap, R10 – regeneration phase (following Bobiec *et al.* 2000), L11–13 – artificial openings.

combination of the declining old stand and small, single-tree regenerating gaps with no clear edge line, as described as a regeneration phase (Bobiec *et al.* 2000). Therefore, it was represented by the arbitrarily established 2500-m² sampling plot R10. Three artificial gaps (L11–13) were selected in the managed zone of the forest, representing the same type of community – *Tilio-Carpinetum*. Development of the gap-filling young trees and the degree of decay of fallen gap-

making canopy trees indicate that the gaps were created between 1985 and 1992. Additionally, one former gap SL, fully recovered by the 25 year-old hornbeam-dominated stand, was subject to trees and dead wood measurement (Table 1).

Gaps have been defined by the edge of the crown of the canopy trees around the border of the open area. Each gap was delineated by segments 8–50 m long (on average 21 m), creating 5–7-side polygons. The

“starting” point position of every polygon was adjusted to match the permanent grid of the BPF division.

All the trees, which used to grow within the present gaps, were considered the gap makers (including the trees which fell into the canopy zone, but not the debris from trees in the canopy zone). The gap makers volumes were assessed with the geometric formulae (cylinder and cone).

Ten percent of the area of each gap was sampled using 4-m² circular plots (from 6 to 40 plots per gap and 60 plots in the 0.25-ha arbitrarily designated square R10, Table 1). The central points of circles were located at random. Within each circle all saplings taller than 30 cm (1–2 yr old seedlings were not considered) and thinner than 11 cm (DBH) were recorded and attributed to the following height classes: 0.3–1.3 m, 1.3–2.5 m, taller than 2.5 m.

For comparison, an equal number of samples were collected under the canopy in the zone immediately adjacent to each gap, about 20 m away from the edge – sampling plots from D1 to D9, referring to L1–L9, and D11 to D13, referring to L11–L13. Because R10 represented mixed conditions of gap and canopy shelter and did not have any clear border, it was not assisted with an adequate set of circular plots representing the canopy-sheltered regeneration. The only exception was the artificial opening L11 (Table 1) which was almost completely surrounded by young plantations. Therefore, only 10 canopy-sheltered samples in D11 were recorded in the limited area of the adjacent mature stand (Table 1). Additionally, the canopy layer composition, based on four nearest trees around the centres of canopy-sheltered circular plots (each species was scored from 0 to 4) was assessed for every canopy edge sample.

Table 1. General characteristics of gap (L1–9) and regeneration phase (R10) areas in the Białowieża National Park (BNP) and artificial openings L11–13 in the managed part of the Białowieża Primeval Forest (BPF); SL – old fully recovered gap in BNP; CS – number of 4-m² circle samples; %Pa – per cent of spruce wood in GM volume; numbers with “D” indices refer to the number of saplings and % hornbeam (Cb) in the canopy-sheltered immediate vicinities of particular gaps; h – height, d – stem diameter.

Gap	Area (m ²)	CS	Gap-makers (GM)					Saplings			
			No.	d (cm)	SD	GM volume		h> 0.3 m, d=<0.1 m			
						(m ³)	%Pa	Number per 100 m ²		%Cb	
L1	1250	31	24	40	11	29	85	234	50 _{D1}	94	48 _{D1}
L2	1400	35	26	36	13	20	86	134	80 _{D2}	80	64 _{D2}
L3	1400	35	29	40	15	34	90	104	26 _{D3}	54	28 _{D3}
L4	1600	40	27	36	15	25	93	72	21 _{D4}	64	15 _{D4}
L5	650	16	11	40	16	10	11	498	33 _{D5}	96	52 _{D5}
L6	700	18	32	31	12	22	88	100	51 _{D6}	19	16 _{D6}
L7	400	10	9	35	9	4	4	208	68 _{D7}	46	37 _{D7}
L8	700	17	10	40	9	9	45	171	28 _{D8}	41	37 _{D8}
L9	250	6	6	46	5	8	24	67	42 _{D9}	0	60 _{D9}
R10	2500	60	23	36	16	20	55	84		46	
L11	1150	28	56	39*	nd	nd	3–8	163	30 _{D11}	22	33 _{D11}
L12	650	16	17	49*	nd	nd	1–10	178	94 _{D12}	11	72 _{D12}
L13	800	19	31	41*	nd	nd	2–9	108	21 _{D13}	5	31 _{D13}
SL	1750		34	30	10	19	80				

*stumps of the cut trees, nd – not determined

The regression of the gap area (dependent variable) and the percentage of spruce in the gap maker volume (independent variable) was calculated as a possible indicator of the dependence of gap pattern on canopy composition. The hierarchical agglomerative clustering, complete linkage method, was applied to group the areas revealing similarities in vertical structure and species composition of tree regeneration. The differences between the areas were tested with the χ^2 test.

The data were collected in 1998–1999, with the hand-held computer. They were stored and arranged with MS Office 97. STATISTICA 5.1 (StatSoft, Inc. 1997) was used for statistical analysis.

4. RESULTS

4.1. Gap size, gap maker trees, and surrounding canopy shelter

The average area of the gaps studied was 1010 m². The size of the gaps ranged from 250 to 1750 m² (Table 1). Although the gaps L1–4 first appeared in the early 1980s, the process of their formation extended in time due to expansion of fungal infection and consecutive bark beetle attacks on neighbouring spruce trees *Picea abies* (L.) Karst. (Gutowski, personal comm.). Also the regeneration in these gaps does not represent

a single cohort of saplings, but ranges from very young, five-year-old to twenty-year-old individuals (usually of hornbeam, *Carpinus betulus* L.). Ten-to-fifteen-year-old saplings were the most abundant there. In other, smaller gaps (L6–9), emerged in 1985–1988, numerous lime saplings represent a vegetative cohort of root and layering sprouts. The youngest natural gap L5 (approximately 10-yr old) differed from the previous ones due to the densest and least variable regeneration of hornbeam (Table 1). In the artificial (felling) gaps L11–13, established between 1990 and 1992, pedunculate oak *Quercus robur* L. (with addition of Norway maple *Acer platanoides* L., wych elm *Ulmus glabra* L. and ash *Fraxinus excelsior* L.) were planted.

The number of fallen trees ranged from 6 in the smallest L9 gap, to 34 trees in the largest, old gap SL. However, in the felling gap L11 fifty-six stumps were found. The relative quantity by volume of gap maker coarse woody debris (CWD) ranged from 270 in L8 to 629 m³ ha⁻¹ in L9. In the old gap SL as much as 183 m³ per hectare was still detectable and in R10 as much as 168 m³ ha⁻¹. The average CWD volume per gap area (R10 excluded) amounted to 380 m³ ha⁻¹. The contribution by volume of spruce CWD to gap makers ranged from 4 to 93%. There is a strong correlation between spruce as a gap maker and the area of gaps

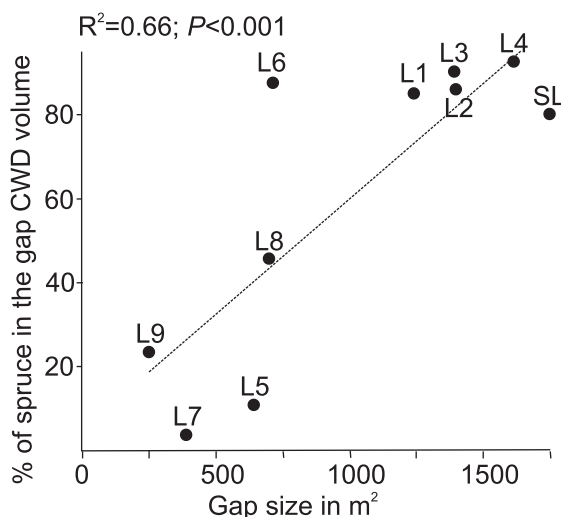


Fig. 2. The spruce (*Picea abies*) % contribution to the volume of fallen trees (gap makers) vs size of gaps

(Fig. 2). A visible threshold divides larger gaps from the smaller ones. In gaps from 700 to 1750 m² spruce CWD contributed to 80–93% of the gap-maker trees volume, while smaller gaps emerged in consequence of a more diverse canopy decline, in which spruce contributed the gap maker volume to 4–45% (Table 1, Fig. 2).

The relative canopy composition of stands around particular gaps was compared (Table 2). The non-parametric χ^2 test revealed high variability between the areas with few exceptions. Lack of significant differences occurs only between L1 and L5 (very similar proportions of four most frequent deciduous species), L3 and L5 (very similar proportions of two deciduous species and spruce), L4 and L7–9 (similar proportions of three deciduous species and relatively weak representation of spruce). A high number of stumps (56) found in the gap L11 together with the disproportionately high percentage of birch in the canopy

layer around that gap, indicates that it was created through removal of a secondary, pioneer stand (Tables 1 and 2).

4.2. Species composition of sapling layer in gaps and under the canopy shelter

In 588 circular samples 2404 saplings were recorded (on average one sapling per 1 m²). The density of all recorded saplings ($h > 0.3$ m) was higher in gaps than in their canopy-sheltered neighbourhood by a factor of 4 on average, ranging from 1.5 (L9/D9) to 15 (L5/D5) (Table 1). If only taller than 1.3 m saplings were considered, the gaps appeared even more favourable environment for tree regeneration, with the average sapling density eight times higher, than under the canopy shelter (Fig. 3A).

Twelve different species in sapling layer were found: hornbeam, small leaved lime (*Tilia cordata* MILL), pedunculate oak, Norway maple, wych elm, rowan (*Sorbus aucu-*

Table 2. Relative (%) stand composition in the neighbourhood of twelve gaps; Cb – *Carpinus betulus*, Tc – *Tilia cordata*, Qr – *Quercus robur*, Ap – *Acer platanoides*, Pa – *Picea abies*, Ag – *Alnus glutinosa*, Fe – *Fraxinus excelsior*, Ug – *Ulmus glabra*, Sa – *Sorbus aucuparia*, Bp – *Betula pendula*; for gap names see Table 1.; (LX,...) indicates lack of significant difference at $P < 0.05$ between a given gap and LX gap(s), according to χ^2 test.

Gaps	Cb	Tc	Qr	Ap	Pa	Ag	Fe	Ug	Sa	Bp
L1 (L5)	33	25	10	5.5	24		1.5	1		
L2	20	35	11	1	32			1		
L3 (L5)	36	10	5	5	35	4	3	1	1	
L4 (L7,8,9)	46.5	24.5	4	4	17	1		1		2
L5	28	21	8	5.5	37.5					
L6	15	27		4	38	6	10			
L7(L9)	41	32	7	7	11	2				
L8	44	16	6	4	20	3	7			
L9	42	33		8	13		4			
L11	34	17		2	10	10	5			22
L12(L13)	45	3		23.5	28.5					
L13	51	7	2.5	15	21		2.5	1		

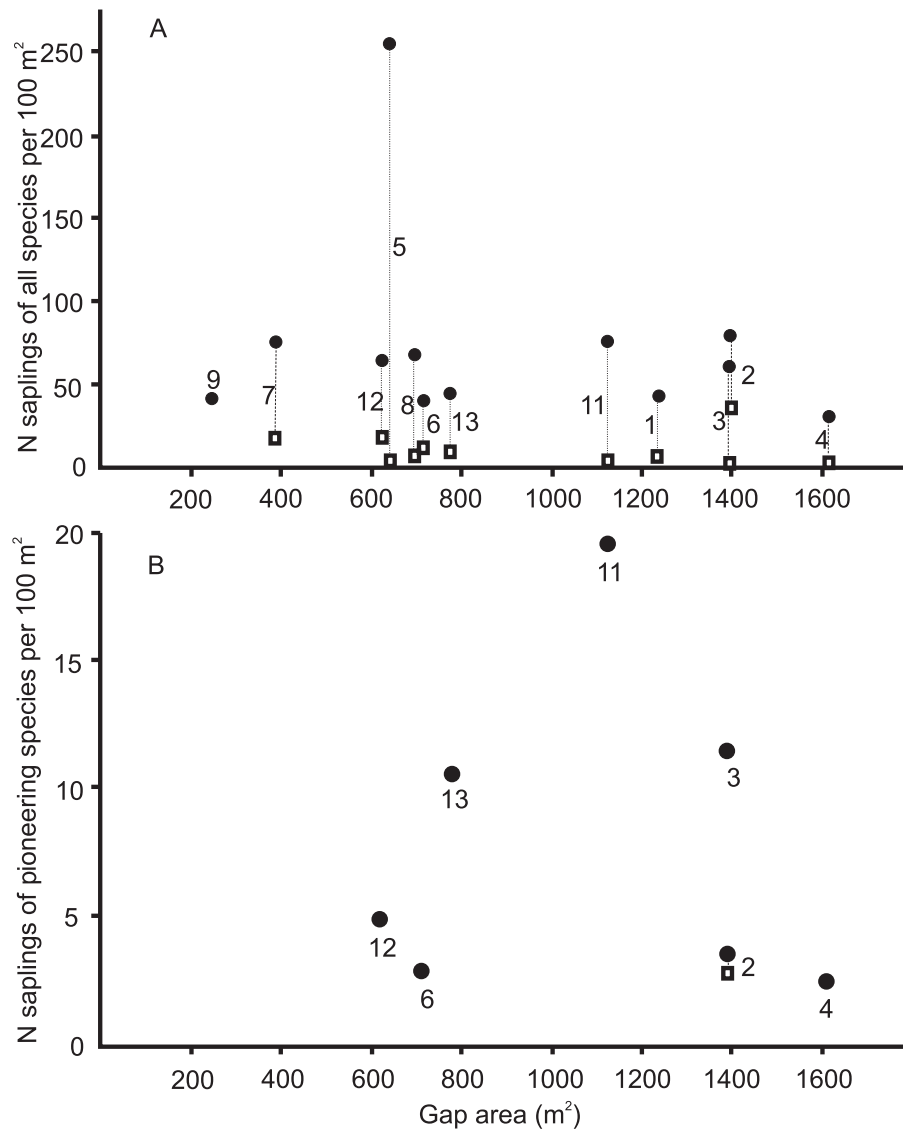


Fig. 3. (A) All saplings ($h > 1.30$ m) densities in gaps (dots) and their canopy-sheltered neighbourhood (squares) vs gap size; (B) Densities of saplings ($h > 1.30$ m) of pioneering species (*Betula pendula* + *Populus tremula* + *Sorbus aucuparia* + *Salix caprea* + *Alnus glutinosa*) in gaps (dots) and their canopy-sheltered neighbourhood (squares) vs gap size; numbers 1–9 and 11–13 refer to gaps L1–9, L11–13, and their canopy sheltered neighbourhood D1–9, D11–13.

paria L.), ash, birch (*Betula pendula* ROTH), aspen (*Populus tremula* L.), goat willow (*Salix caprea* L.), alder (*Alnus glutinosa* L.), and Norway spruce. The great majority of saplings recorded in all plots were represented by hornbeam (55%) and lime (27%), while other ten species contributed to 0.1–3% of the overall number of regenerated trees (see Table 3 for details).

Based on the composition of saplings taller than 1.3 m, the sampling areas were agglomerated in six distinct clusters at the Euclidean distance threshold of 30. The biggest of them, including all the canopy-sheltered samples, is composed of 13 areas. Gaps created one 5-component, two 2-component and two single-component clusters. Apart from the number of saplings (the case of L5),

Table 3. Differences in % species composition between three regeneration layers A, B, C, detected by χ^2 test within particular gaps; A – 0.3–1.3 m, B – 1.3–2.5 m, C – taller than 2.5 m; two asterisks in one column within the same area indicate significant difference at $P < 0.05$; [Cb/Tb] – hornbeam/linden dominance coefficient $[Cb/Tb] = (+/-)(n_{Cb}^2 + n_{Tc}^2)/(n_{Cb} + n_{Tc})^2$, where n_{Cb} and n_{Tc} are % participation of hornbeam and lime saplings in the regeneration layers; it is positive when hornbeam and negative when lime dominates; for area names see Table 1; Sa – *Sorbus aucuparia*, Sc – *Salix caprea*, Pt – *Populus tremula*, Ms – *Malus silvestris*, for other names see Table 2.

Area	Layer	Difference		Gap filler species													
		A/B	B/C	Cb	Tc	[Cb/Tc]	Bp	Qr	Fe	Sa	Ap	Sc	Ug	Pt	Ag	Pa	Ms
L1	A			96	2	1.0	0	0	0.5	1	0.5	0	0	0	0	0	0
	B		*	97	3	0.9	0	0	0	0	0	0	0	0	0	0	0
	C		*	61	39	0.5	0	0	0	0	0	0	0	0	0	0	0
L2	A			67	9	0.8	0	5.5	0	5.5	13	0	0	0	0	0	0
	B			92	8	0.9	0	0	0	0	0	0	0	0	0	0	0
	C			85	5	0.9	3	0	2	0	0	0	0	0	5	0	0
L3	A	*		47.5	16	0.6	5	6.5	0	23	0	2	0	0	0	0	0
	B	*		69	22	0.6	6	0	0	3	0	0	0	0	0	0	0
	C			54	19	0.6	21	2	0	0	0	0	0	2	2	0	0
L4	A			71	6	0.9	2	3	0	12	0	0	0	1.5	0	1.5	3
	B			55	24	0.6	0	3	0	12	0	0	0	0	0	0	6
	C			59	41	0.5	0	0	0	0	0	0	0	0	0	0	0
L5	A			95	4	0.9	0	0	0	0	0	0	0	0	0	1	0
	B			97	3	0.9	0	0	0	0	0	0	0	0	0	0	0
	C			97	3	0.9	0	0	0	0	0	0	0	0	0	0	0
L6	A	*		28	5	0.8	0	0	60	0	0	0	0	0	0	7	0
	B	*		33	50	-0.5	0	0	17	0	0	0	0	0	0	0	0
	C			0	69.5	-1.0	0	0	22	0	0	0	0	0	8.5	0	0
L7	A	*		66	28	0.6	0	0	0	4	0	0	0	2	0	0	0
	B	*		17	83	-0.7	0	0	0	0	0	0	0	0	0	0	0
	C			8	92	-0.8	0	0	0	0	0	0	0	0	0	0	0
L8	A	*		61	20	0.6	0	0	16	0	3	0	0	0	0	0	0
	B	*		25	75	0.6	0	0	0	0	0	0	0	0	0	0	0
	C			0	100	-1.0	0	0	0	0	0	0	0	0	0	0	0
L9	A			0	100	-1.0	0	0	0	0	0	0	0	0	0	0	0
	B			0	100	-1.0	0	0	0	0	0	0	0	0	0	0	0
	C			0	100	-1.0	0	0	0	0	0	0	0	0	0	0	0
R10	A	*		56.5	39	0.5	0	0	2.5	0	2	0	0	0	0	0	0
	B	*		10	90	-0.8	0	0	0	0	0	0	0	0	0	0	0
	C			6	94	-0.9	0	0	0	0	0	0	0	0	0	0	0
L11	A	*		26	8	0.6	0	39	0	0	19	2	2	4	0	0	0
	B	*	*	18	46	-0.6	1.5	16	0	0	1	7	0	9.5	0	1	0
	C		*	18.5	0	1.0	45.5	0	0	0	0	18	0	18	0	0	0
L12	A	*		14	19	-0.5	3	15	16	0	1	0	32	0	0	0	0
	B	*	*	5.5	66.5	-0.9	0	16.5	3	0	0	3	5.5	0	0	0	0
	C		*	20	0	1.0	40	40	0	0	0	0	0	0	0	0	0
L13	A			8.5	60.5	-0.8	0	23	2	0	0	6	0	0	0	0	0
	B		*	0	80	-1.0	0	12	0	0	4	4	0	0	0	0	0
	C		*	0	0	-	78	22	0	0	0	0	0	0	0	0	0

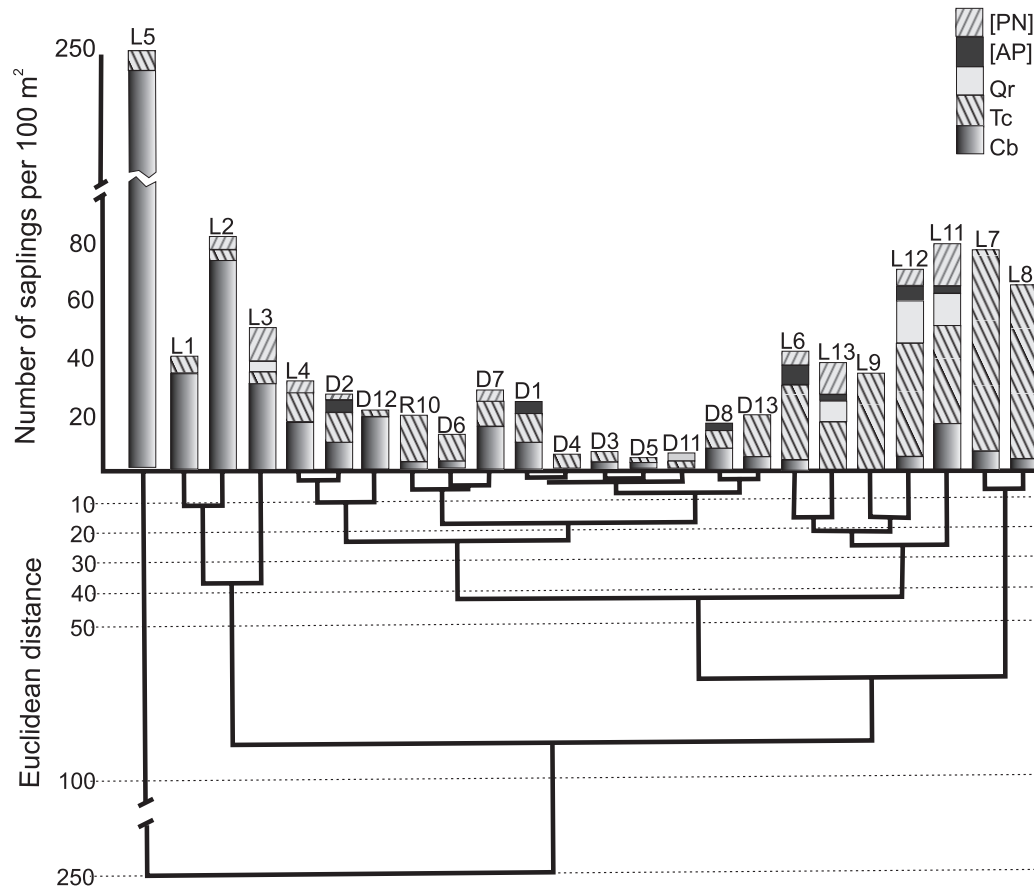


Fig. 4. The density and composition of tree regeneration inside gaps (L1–9, L11–13) and in surrounding stand (D1–9, D11–13); Cb – *Carpinus betulus*, Tc – *Tilia cordata*, Qr – *Quercus robur*, [AP] – *Acer platanoides* + *Fraxinus excelsior* + *Ulmus glabra*, [PN] – *Alnus glutinosa* + *Betula pendula* + *Populus tremula* + *Sorbus aucuparia* + *Salix caprea*; (only saplings taller than 1.30 m and thinner than 11 cm were considered); complete linkage method of clustering.

dominance of either hornbeam or lime was an important discriminating factor: while the clusters on the left side of the chart are clearly dominated by hornbeam, on the right side lime is a leading gap-filler (Fig. 4).

The χ^2 test was applied to check the compositional differences between three height classes of saplings, shorter than 1.3 m (A), 1.3–2.5 m (B), and taller than 2.5 m (C), within particular areas. The results exhibited in Table 3 indicate that most of differences occur between layer A and B except for L1 and three artificial gaps L11–13. The major differentiating factor was the dominance of the most common species, expressed by the dominance coefficient

$$[Cb/Tc] = (+/-)(n_{Cb}^2 + n_{Tc}^2) / (n_{Cb} + n_{Tc})^2$$

where n_{Cb} and n_{Tc} are % participation of hornbeam and lime saplings in the regeneration layers; it is positive when Cb and negative when Tc dominates. Unlike in other natural gaps, oak and rowan sapling densities caused significant difference between layers A and B in L3. In artificial gaps L11–13 the major changes in hornbeam-lime ratio were accompanied with sharp differences in oak, birch, elm and goat willow densities (Table 3). It was shown that gap size had no influence on the regeneration of pioneering species, namely birch, aspen, goat willow, rowan and alder. Saplings of these species representing layers B and C were found in seven gaps and only one canopy-sheltered area (Fig. 3B).

5. DISCUSSION

The gaps studied in the Białowieża Primeval Forest were larger than the average gaps reported throughout the reviewed literature. It results from the assumption made by Bobiec *et al.* (2000) and follows the concept of 'eco-units'. According to this idea, the functional gap should efficiently initiate a certain spatial unit following its own developmental trajectory (Oldeman 1990). Therefore, the arbitrary selection of sampling areas in the BPF has deliberately avoided small canopy openings, which are assumed to be inherent structures of the matrix of the biostatic developmental phase (Bobiec *et al.* 2000). On the other hand, objective factors, such as species composition, latitude, slope, average tree height, may have caused substantially finer grains of the mosaic, evolved from much smaller functional gaps, as reported from the US Tennessee (e.g. Busing 1994), New York (Ziegler 2000), Wisconsin (Cook 2000), Michigan (Dahir and Lorimer 1996), Japan (e.g. Abe *et al.* 1995), in Europe from France (Wijdeven 2003) and Slovenia (Diaci 2002). However, the studies carried out in Rothwald (Austria) revealed that the gaps from 0.04 to 0.5 hectare are common in Central European natural spruce-fir-beech forests (Splechtina and Gratzner 2005).

The most important gap maker in the study area was spruce. Large sized gaps emerged in the forest fragments where stand was dominated by this species. According to Falinski (1986) and Bernadzki *et al.* (1998), spruce reached a dominant position at the turn of the 19th and 20th centuries and has since gradually declined in *Tilio-Carpinetum* assemblages. Further spruce recession could probably result in the disappearance of distinct spatial units of clearly defined developmental phases (Bobiec *et al.* 2000) and lead to a shift from a coarse-scale to a fine-scale mosaic pattern (Qinghong and Hytteborn 1991), typical to the West European beech forests (Mountford 2001).

Revealing substantially higher densities of all recorded saplings and even higher densities of successful grown-up saplings ($h > 1.3$ m) than under the neighbouring shelter, gaps proved efficient regeneration centres.

Most of the gaps studied match the concept of a "gap-phase mode". Even though the shade-tolerant ('climax') species tend to dominate the initial phase of stands, certain gaps secure suitable conditions for a successful regeneration of intermediate and intolerant species, such as oak, birch, aspen and rowan. Three first species are likely to participate in the future canopy layer established in the place of the former spruce-dominated stand prior the establishment of L3. The regeneration success of pioneering species does not depend on the gap size. The artificial openings, seem to follow an alternative "catastrophic mode" of regeneration leading to the emergence of the pioneering stand, dominated by intolerant species (Veblen 1992). The third way of regeneration – "a continuous mode" (Veblen 1992) was demonstrated in R10, representing natural regeneration phase (Bobiec *et al.* 2000). It comprises a complex of small openings with fuzzy edges caused by a decimated canopy and is characterised by a lower sapling density than "typical" regenerating gaps. The continuous mode of regeneration is also represented by the canopy-sheltered area, where scarce undergrowth strives to fill small scattered canopy openings and single-tree gaps.

The study showed that tree regeneration in gaps differs significantly from that under the canopy not only quantitatively (by higher sapling densities in gaps), but also qualitatively. There are much more similarities among gaps in their relative species composition than between particular gaps and their immediate canopy-sheltered vicinities. In spite of a high variability of tree layer around gaps the canopy-sheltered undergrowth revealed a high degree of quantitative and compositional uniformity, what may indicate that disturbances creating larger gaps contribute to most of the spatial diversity of stand regeneration.

Another finding relates to the differences between the distinguished gap-filler layers in their species composition. In all gaps, except for the smallest one L9 and two artificial openings L12 and L13, hornbeam dominated in the lowest (and youngest) sapling layer 0.3–1.3 m. The shift in the proportion of species that occurred either at the transition from 0.3–1.3 m to 1.3–2.5 m

layer (in most instances) or from 1.3–2.5 m to the highest layer might have resulted from a discontinuous character of regeneration in the studied gaps. While hornbeam tends to regenerate continuously due to the abundant annual seed rain, other species exhibit more opportunistic strategies. Their regeneration success may depend on certain favourable instant and local conditions such as layering logs or sprouting stumps (lime – Pawlaczyk 1991), root sucker supply (aspen), disclosed mineral seedbeds (birch – Battles and Fahey 2000) or inaccessible to ungulates moss cushions (oak – Paczoski 1930). A very high number of maple seedlings at the ground vegetation layer (<0.30 m), averaging 520 individuals vs. 570 of hornbeam seedlings per 1000 m² (A. Bobiec, unpublished data) indicates a similar pattern of the abundant annual seed supply of both species. The recruitment of sparse maple regeneration may depend on the substantial suppression of competitive hornbeam saplings by browsing ungulates, following the “intermediate disturbance” rule (Connel 1978).

The described observations lead to the hypothesis saying that under current environmental circumstances the tree regeneration in the BPF mesic deciduous communities has a complex and asynchronous character. The spatially uniform, continuous and extensive regeneration occurring under the the matrix of canopy shelter is locally affected by large gaps, intensifying and boosting the most prolific species, hornbeam. However, the ultimate dominance of this most stress-tolerant competitor, is prevented by ephemeral features and processes, occurring in certain gaps at the initial phase of their recover, favourable to less tolerant species. As a result, the patches of intensive regeneration embedded in the surrounding canopy matrix can develop either a single regeneration trajectory (the initial dominant becomes the ultimate gap-filler) or undergo a more complex development, consisting of regeneration waves of opportunistic species (lime, oak, pioneers) followed by younger hornbeam cohorts.

Strong dissimilarities between regeneration layers in artificial openings result from deliberate efforts aimed to model the future

canopy species composition. Older saplings of planted “target species” (such as oak and elm), accompanied by cohorts of pioneers emerged after soil preparation, are followed by spontaneous regeneration of slower growing hornbeam and/or lime stump sprouts.

The suggested hypothesis might be used to reconcile the contradictory findings concerning the impact of gaps on intolerant species regeneration, as reported in the reviewed literature. As the most tolerant species tend to be the best competitors also in gaps, the other ones (less prolific or/and less competitive), including intolerant species depend on discrete and stochastic processes, and do not follow the assumed rules related to the gap size.

Although the study shows the evidence of the quantitative and qualitative influence of gaps on tree regeneration in mesic deciduous BPF assemblages, further important questions arise. Will the regeneration variability develop and persist in the future canopy layer, as suggested by Runkle and Yetter (1987)? Is the spatial variability of the present canopy a foot-print of a similar regeneration model in the past? To what extent the stand variability determines location and type of the future gaps, as suggested by Abe *et al.* (1995)? Is, therefore, the spatial and dynamic pattern involving gap regeneration regionally specific, depending on local species composition (Brokaw and Busing 2000)?

An appropriate programme of the long-term monitoring of gap development supplemented by detailed analysis of spatial tree age variability is necessary to answer these questions. Special attention should be paid to the specific role of spruce in the gap formation process in view of its recession observed in the mesic lime-hornbeam assemblages (Bernadzki *et al.* 1998).

6. CONCLUSIONS

1. Tree regeneration in gaps is substantially more abundant and efficient than under the canopy shelter. Intolerant species regenerate almost solely in gaps.

2. Most of the gaps observed in the protected forest of the BPF were formed by the decline of spruce stands. The gaps studied

were larger in size than the average gaps reported from other forests. The greater the local density of spruce in the former stand, the larger the gaps that resulted.

3. Gap size had no influence on the gap-filler composition. The most successful gap-fillers were hornbeam and lime. Spruce, the third dominant species in the gap surrounding stands was absent in the gap-filling regeneration.

4. While hornbeam tends to regenerate continuously and extensively throughout the canopy matrix or intensively in gaps, regeneration of other species, including lime, oak and pioneers has a spatially and temporarily discrete character, following ephemeral opportunistic circumstances.

5. Forestry activity, though operating at the scale of average natural gap size, considerably modifies the processes of regeneration, mimicking 'catastrophic mode' of dynamics, uncommon in natural mesic deciduous forests.

6. Better understanding of the dynamics of mesic lime-hornbeam forests requires a concerted research program aimed at quantitative assessment of the important community parameters. The problems to be investigated are, in particular:

- overall gap size structure;
- mechanisms determining successful regeneration of less competitive and intolerant species;
- history of the gap dynamics (dendrochronology) and its future development (modelling);
- average rate of disturbance and turnover time in *Tilio-Carpinetum*;
- minimal conservation area.

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