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Gap regeneration in near-natural European beech forest stands in Central Bohemia – the role of heterogeneity and micro-habitat factors

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Abstract: Gap regeneration in a European beech (*Fagus sylvatica* L.) forest reserve was analyzed in relation to within-gap resource heterogeneity and ground vegetation competition. The study was carried out in two one-hectare permanent research plots (PRP) which included five smaller research plots (RP) encompassing two large gaps (500–700 m^2), two small gaps (300–400 m^2), and location under canopy. The coverage of woody regeneration, ground vegetation, dead wood, seedling density in eight height classes, characteristics of dominant trees of the beech regeneration, and the total thickness of holorganic horizons were measured. Soil moisture and light conditions were also assessed in selected sample plots. The relative direct and diffuse light was estimated by hemispherical photography. Small gaps showed both the highest cover of tree regeneration and the highest density of individuals per hectare. Slightly less regeneration was recorded in large gaps, while under closed canopy, regeneration densities were 5–10 times lower than in small gaps. Beech regeneration cover and the size (diameter and height) of dominant beech seedlings were positively related to relative diffuse light and negatively related to ground vegetation cover. The latter was positively related to diffuse light and soil moisture content. A pronounced statistically significant contrast in the cover and size of beech regeneration in relation to micro-site conditions (diffuse light, cover of graminoids) was only confirmed between sample plots located below canopy cover and those within gaps. Graminoids, in particular *Calamagrostis epigejos* L., occurred mainly in the large gap centre and along the southernmost edge of the large gap, increasing competition for resources here. The cumulative cover of ground vegetation and regeneration was relatively low (9–56%) compared with more mesic natural beech forests. The indicated negative influence of direct light at the northern gap edge suggests that extension of gaps on comparable sites in managed forest should not proceed in this direction.

Additional key words: *Fagus sylvatica*, natural regeneration, ground vegetation, resource heterogeneity, competition

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Introduction

Today, forests in nature reserves, national parks, and protected landscape areas comprise approximately 25% of the forest cover in the Czech Republic. In these areas, ecological, protective, and social functions receive more emphasis than timber production. Nature reserves and other protected areas provide an important reference for managed production forests and a basis for evaluating new methods for near-natural silviculture based on principles of sustainability (Průša 1985). Since the 1970s, the remnants of natural (beech) forests in nature reserves in the Czech Republic have been subjected to increasing research and monitoring efforts in order to understand their structure and natural dynamics (Průša 1985, Vrška et al. 2001). However, little information has been gathered about natural gap dynamics and gap regeneration in these forests. Such knowledge is important for application of near natural silvicultural system, especially irregular shelterwood.

In natural forests dominated by shade-tolerant tree species, regeneration is dependent on several factors such as seed production and dispersal (Wagner 1999), germination and survival (Szwagrzyk et al. 2001), abiotic site factors (Madsen 1995; Madsen and Larsen 1997), canopy openings (Emborg 1998), the competition of under-storey herbal vegetation (Dolling 1996), browsing, individual species performance (Modrý et al. 2003) and seed predation (Birkedal et al. 2009, Löf et al. 2004). In European beech forests, windstorms often create canopy gaps that result in changes in incidental light, soil moisture, and the availability of nutrients on the forest floor (Gálhidy et al. 2006). In general, tree seedlings react positively to increased light levels (Minotta and Pinzauti 1996; Szwagrzyk et al. 2001), which are often initiated by tree fall gaps. Since light is a key growth factor along with water and nutrients (Madsen 1995), the regeneration success in (near) natural forests is often related to structural dynamics and gap formation (Emborg 1998). Furthermore, uprooted trees, which are associated with the absence of a thick hologranic layer, lower herbal competition, crumbled compacted loamy soil, and decreased soil acidity, may create favourable germination sites. In Belgium Muys et al. (1988) recorded the presence of higher seedling densities and seedling height (for both beech and other species) in uprooted zones. Rapid closure of gaps was due to the lateral expansion of existing tree crowns. At the same time, Koop and Hilgen (1987) found that gap-edge trees in France are more subject to decline and tree fall than other trees, presumably due to increased insolation and asymmetric crowns, thus enlarging the gap area. Nonetheless, within the forest cycle of particular forest development stages (Korpel' 1995; Leibundgut 1982), gaps trigger regeneration and thus initiate the next turn of the cycle.

Although substantial research has been done on gap regeneration in beech forests, it has mainly been confined to Atlantic and Baltic Europe (e.g. Collet and Chenost 2006; Koop and Hilgen 1987; Ritter et al. 2005; Madsen and Hahn 2008). In those regions beech is close to the border of its natural distribution, which is manifested in difficulties in natural regeneration (Topoliantz and Ponge 2000). It is likely that in East-Central Europe, with more continental climate the regeneration patterns are different (e.g. gap partitioning), therefore direct transfer of knowledge may be limited. In addition, few studies have investigated within-gap resource heterogeneity, which plays an important role in regeneration processes (Gálhidy et al. 2006; Mountford et al. 2006; Rozenbergar et al. 2007). These studies also indicate that within-gap micro site patterns are variable among site and stand combinations.

The aim of the current study was to investigate the effects of the parent stand on the growth of beech regeneration in conditions characterized by sub-continental climate with low annual precipitation. The research questions this study addresses are as follows: (1) What are the main micro-habitat factors which influence successful natural beech regeneration in the studied conditions? (2) How does gap size and within-gap heterogeneity influence natural beech regeneration in conditions with limited annual precipitation?

Materials and Methods

Study Area

The Voděradské bučiny National Nature Reserve (NNR) (49°58' N, 14°48' E) is situated in Central Bohemia (Czech Republic), 345–501 m a.s.l. The parent rock is granite, and Cambisols of low humus content predominate within the forest stands. According to the nearest climate and precipitation station located at Říčany (401 m a.s.l., 9 km distance from the study area), mean annual temperature is 7.8°C and annual precipitation is 623 mm. In the period from April to September mean temperature is 14.0°C and precipitation totals 415 mm. The duration of the vegetation period with mean daily temperature above 10.0°C is more than 158 days.

The Voděradské bučiny NNR was established in 1955 on a total area of 658 ha in a former managed forest, including both homogeneous, even-aged beech stands and beech stands of near-natural forest structure. In the same year the reserve was divided into two parts, one with limited forest management and the other with active forest management aimed at the enhancement of diversified forest structure.

The research was conducted in forest stand located in the first part with continuous protection status ensuring the lowest direct human impact since the establishment of the reserve (only damaged or uprooted trees and snags were to some extend removed till 1991).

Data Collection

Two permanent research plots (PRP) were established in 2006 to study stand and regeneration dynamics, both 100 × 100 m (1 ha) in size; the location of both PRPs was selected in the most differentiated parts of the stand with minimal management interventions in the area (forest stand 417A16a/8a). The site type was classified as forest type complex 4B *Fagetum eutrophicum* – Nutrient-rich Beech forest (according to the Czech typological system of forest management planning). The age of the over story and under story was 160 and 90 years, respectively. The plots are 470 m a.s.l. and have a northern exposition and a slope inclination of 10%. Beech comprised 96.0% and 69.4% of the total timber volume on PRP 01 and PRP 02, respectively. Total timber volume (dbh ≥ 7 cm over bark) amounted to 707.21 $m^3\ ha^{-1}$ (PRP 01) and 505.60 $m^3\ ha^{-1}$ (PRP 02). For detailed description of both plots see Bílek et al. (2011). Within PRP 01 and 02, smaller research plots (RP) were established. In each PRP only one large gap was present, consequently, in each PRP we selected a smaller gap. RP C (canopy) was placed under closed forest stand without gaps in its direct proximity. Within the RPs we established a 5 × 5 m grid aligned N-S. At each grid intersection, one 1.5 × 1.5 m sample plot (SP) was placed. The expanded gap area was measured as a polygon with the vertices represented by the stem basis of the gap border trees (Table 1).

Furthermore, we evaluated gap resource heterogeneity by dividing the gaps into gap centers (sample plots with all four neighboring plots in direction N, S, E, W) and gap boundaries (sample plots having from 1 to 3 neighbours in the regular grid). The canopy (RP C) was considered as a separate category. Additionally, the large gap (D) boundary was divided into north and south edges.

Table 1. Basic data for research plots (RP) within PRP 01 and 02 (SP – sample plot)

RP	PRP	Location	No. of SPs	Expanded gap area (ha)	Exposure
A	01	Small gap	23	0.04	N
C	01	Canopy	34	0.06*	N
D	01	Large gap	44	0.07	N
E	02	Large gap	30	0.05	N
F	02	Small gap	20	0.03	N

*area of the sample plot.

Light was measured on 54 sampling plots only within PRP 01 using hemispherical photography. For this we used a Nikon F50 camera equipped with a Sigma 8 mm, f/4 fisheye lens which was calibrated to establish the degree of lens distortion (Diaci and Kolar 2000). Light measurements were performed at breast height in completely overcast sky conditions to avoid direct radiation. Photographs were taken with the top of the camera oriented to the north. The film was scanned and the images processed on a computer with Corel PHOTO-PAINT 9 software to acquire quadratic binary images in GIF format. The images were then analyzed by hemIMAGE software (Bruner 2002).

Soil moisture (on 80 sampling plots within PRP 01) measurements were performed using the frequency domain probe (IMAG) that simultaneously measures soil temperature. Sensor was calibrated using soil moisture content values obtained for each soil type by the gravimetric method (Hilhorst 1998; Dirksen 1999). The probe length was 10 cm and the probe was stuck into the soil surface vertically after removal of the top litter layer. On average, soil moisture was measured three times at each sampling plot. Average values were then used in the final analysis. Measurements were taken in June 2002 after an extended period without heavy rain, to more precisely capture the difference among micro-sites within gaps under stress conditions.

The total thickness of holorganic horizons was measured in opposite corners of the SPs. If unrepresentative features such as stones and stumps were present, measurement was relocated towards the centre of the sample plot. Cover in per cent was visually estimated from above for tree regeneration, total ground vegetation, coarse woody debris (CWD), litter, bare soil, stones, and surface roots. Layering was ignored and the interval for the total cover estimation was 1–100%. In addition, on every SP, cover was visually estimated for each species separately (tree, shrub, and ground vegetation). In this case, layering was included, meaning that the sum for each SP could be well over 100%.

All seedlings and saplings were counted and categorized according to height classes (one-year old seedling, ≤ 20 cm, 21–50 cm, 51–90 cm, 91–130 cm, 131–200 cm, 201–300 cm, ≥ 300 cm). In one quadrate of the SP, seedlings and saplings were checked for browsing damage and categorized into one of three damage classes (minor damage = less than 10% of the shoots browsed, terminal shoot not damaged; moderate damage = 10–50% of the shoots browsed and/or terminal shoot damaged; severe damage = more than 50% of shoots browsed including terminal shoot). On each SP the five dominant trees of the beech regeneration (if present) were selected and several parameters for each tree were measured or estimated: browsing damage, total stretched length of the stem, previous year's growth, diameter of root collar, stem form (one, two, or multiple stems), and whole plant branching (upright, stem deviation, or plagiotropic). Relative height increment was estimated as the ratio of the previous year's growth to total length.

Co-dominant and dominant mature gap border trees were cored at breast height using an increment borer for the dating of releases and estimation of the age of particular gaps. Cores were mounted and polished and the ring width was then measured to the nearest 0.01 mm using the measuring device LINTAB™ and the software TSAP-Win™. Cores were aged using a statistical cross-dating technique (Yamaguchi 1991). We analyzed three cores per gap, except RP-F, for which only one spruce core could be analyzed. We used the running means method for release identification by comparing ten-year growth segments and using 50% increases in growth rates to identify major release events (Nowacki and Abrams 1997; Lorimer and Frelich 1989).

Statistical Analyses

Data normality was tested using the Shapiro-Wilk normality test. Not all data within groups were normal, therefore the non-parametric Kruskal-Wallis test was used to compare recorded vegetation and environmental variables between research plots, and to compare gap heterogeneity. Post-hoc comparisons of the mean ranks of all pairs of groups were performed. To determine the correlation among particular abiotic factors (direct light, diffuse light, soil moisture, total thickness of holorganic horizons), ground vegetation and regeneration characteristics the Spearman non-parametric correlation coefficient was used. Multiple comparisons for proportions of direct and upright stems among RPs were carried out by using test statistics

$$T = \frac{|p_i - p_j|}{\sqrt{\frac{1}{8}\left(\frac{1}{n_i} - \frac{1}{n_j}\right)}} \sim q_{k,\infty}, \quad i = 1, 2, \ldots, k-1, \quad j > i,$$

(Anděl 1998), where k is number of RPs, p_i is proportion of upright stems at i-th RP, n_i is total number of stems at i-th RP and $q_{k,\infty}$ is critical value of Studentized range.

The effects of ecological factors (direct light, diffuse light, soil moisture, total thickness of humus horizons, and ground vegetation cover) on the size and growth of beech regeneration and beech regeneration cover were analysed with linear mixed-effects models (LMMs) (Pinheiro et al. 2013). The models were built with the "nlme" package. RP was considered random factor. Only SPs with complete data were included in the calculation (both light and moisture measurements were performed only on particular plots). In order to check for multicolinearity between independent variables, the values of variance inflation factors (VIF) were calculated. For all independent variables the VIF value was below 1.846. Data were analysed in Statistica 9, Microsoft Excel Version 2003 and R 2.15.0 (R Development Core Team, 2012).

Results

Within-Gap Resource Heterogeneity

Values of direct and diffuse light were expressed as the percentage of above-canopy light PACL (Table 2). There was a significant difference in PACL among research plots (Kruskal-Wallis test: $P < 0.001$) under the canopy (C) and in the small gap (A) and the large gap (D). The large gap (D) clearly showed the highest light input regarding both diffuse and direct components. Light conditions under the closed canopy (C) and the small gap (A) differed mainly with respect to diffuse light and were more similar with respect to direct light, with higher light variability inside the small gap. There was a positive correlation ($R_s = 0.428$, $P = 0.002$) between both light components. Contrary to our expectations, measurements did not show significant differences in soil moisture conditions among large and small gap and below the canopy (Kruskal-Wallis test: d.f. = 2, H = 1.11, $P = 0.575$). The average value of volumetric moisture content (%) was highest within the small gap (A – 16.14%) and the lowest under closed canopy (C – 14.98%). Within the large gap (D), the average value was 15.58%. Total light input and the thickness of holorganic horizons were significantly negatively correlated ($R_s = -0.300$, $P = 0.030$). The total thickness of the holorganic horizon significantly differed between gaps and canopy and ranged from 0 to 10 cm. The average thickness ranged from 2.6 cm in large gap (D) to 3.3 cm under canopy (C) and 3.4 cm in small gap (A).

Our approach to the division of SPs within gaps on PRP 01 produced six-staged zoning across the gradient from large gap centre to closed canopy. A marked contrast was observed between factors below canopy and within gaps, with the exception of soil moisture content and ground vegetation cover. Conditions in the centre and in the edges of the small gap were very similar and did not differ in any of the selected variables mentioned in Table 3. Within the large gap (D) there were significant differences in the height of dominant beeches, these being higher

Table 2. Percentage of above-canopy light for direct and diffuse light in small gap (A) and large gap (D) and under canopy (C)

RP	N	Average ± SD	Median	Variance	Q25	Q75	Min	Max
Direct solar radiation %								
A – small gap	20	3.57 ± 3.23	2.28	10.45	1.05	6.15	0.42	9.76
C – canopy	11	4.98 ± 2.15	5.44	5.11	3.12	6.46	1.32	8.54
D – large gap	23	15.48 ± 8.44	16.91	71.30	5.84	23.28	2.37	28.00
Diffuse solar radiation %								
A – small gap	20	10.51 ± 2.36	10.58	5.5492	8.52	11.69	6.74	16.20
C – canopy	11	5.61 ± 1.09	5.82	1.3029	4.464	6.31	4.07	7.88
D – large gap	23	16.06 ± 4.35	15.30	18.943	12.45	20.27	9.35	24.10

Note: N – number of SPs, where measurement was performed, SD – standard deviation, Q25 – lower quartile, Q75 – upper quartile, Min – Minimal value, Max – Maximal value

in the gap centre, and in relative height increment, which was greater along the north boundary. Values of direct light in the centre of the large gap and in the north edge of the large gap (D) were significantly different from both, values in the small gap edges and the small gap centre (A). Between the south and the north edge of the large gap (D), no significant differences were determined. The north edge of the large gap (D) was characterized by high levels of direct PACL (they were comparable to those of the gap centre), and to lower rates of diffuse PACL. The lowest moisture levels were measured here, as well as low levels of ground vegetation coverage, but these differences were not statistically significant. Regeneration cover and the number of beech trees were somewhat higher in the large gap centre. In contrast, in the south position the cover of graminoids was highest among the positions within gap and number of beeches under 50 cm was the lowest there (with the exception of full canopy). Regarding the characteristics of dominant beech individuals, significant differences were confirmed between heights and relative height increment. The height of beech regeneration was the highest in the gap centres and the lowest in the north edge of the large gap. Conversely, relative height increment was lowest in the gap centres and highest along the north-oriented gap boundary of the large gap.

Cover of SPs

In general, the regeneration cover was the highest in small gaps, decreased in large gaps, and was the lowest below canopy. A substantial percentage of litter cover on all RPs was reported, while an almost complete cover of litter occurred under the canopy. Bare soil, stones, and roots were scarce. A general overview with average and median values is given in Table 4.

On PRP 01, a total of 30 plant species were found (5 tree species: beech, hornbeam, sycamore maple, spruce, larch; 1 shrub; 3 ferns; 11 grasses; 1 moss; and 9 herbs). More plant species were present in gaps (RP A – 21 sp.; RP D – 23 sp.) than under closed canopy (RP C – 17 sp.). Total ground vegetation cover was higher inside gaps (RP A – 64.7%; RP D – 48.3%) than below canopy (RP C – 9.3%). RP A (small gap) and D (large gap) were dominated by beech (46.4% and 17.5%, respectively). Below canopy, beech was present on 44.1% of SPs, but average cover was only 2.6%. Within the large gap, hornbeam represented a substantial contribution to tree regeneration (29.0%). The regeneration was clearly dominated by beech, representing 75.8% of all individuals. Hornbeam was the second most abundant species, representing 15.5% of all individuals. Table 5 shows data on tree species regeneration for individual RPs. In large gap (D) the per cent ratio of grass species was considerable – 21.9% (compared to 4.4% on RP C and 4.2% on RP A). *Calamagrostis epigejos* L. covered 12.4% and *Calamagrostis arundinacea* L. covered 4.9%. *Carpinus betulus* L. and *Athyrium filix-femina* L. each covered more than 1.0%. Large gap (D) was also characterized by the highest cover of grass species. In contrast, RP C – canopy was marked by the highest number of herbs but had the lowest total ground vegetation cover.

On PRP 02, the average total ground vegetation cover was 26.1% in large gap (E) (17 plant species: 1 tree species, 5 herbs, 8 grasses, 2 ferns, 1 moss) and 28.8% in small gap (F) (14 plant species: 1 tree species, 5 herbs, 6 grasses, 1 fern, 1 moss). Beech was the only tree species which dominated tree regeneration (average cover RP E – 18.9%, RP F – 26.4%; present on 86.2% and 90.0% of sample plots respectively). In large gap (E) mosses nearly reached an average cover of 2.0%, followed by *Calamagrostis epigejos* L., covering 1.8%.

Total ground vegetation cover was positively correlated with soil moisture content (R_s = 0.381, P = 0.005) and diffuse light (R_s = 0.309, P = 0.026). Graminoids were positively correlated with diffuse

Table 3. Within gap heterogeneity: comparison of mean values (± standard deviation) of within-gap and canopy levels of selected variables (different indices indicate significant differences among groups)

Variable*	Large gap centre (n=9)	Large gap N-edge (n=6)	Large gap S-edge (n=6)	Small gap centre (n=8)	Small gap edge (n=12)	Canopy c (n=11)	Kruskal-Wallis test: H	P-value
PACL direct (%)	18.91 ± 7.30a	19.84 ± 3.99a	7.56 ± 7.11ab	2.33 ± 2.10b	4.39 ± 3.45b	4.98 ± 2.15ab	29.95	0.000
PACL diffuse (%)	18.38 ± 3.65a	11.69 ± 2.24abc	17.66 ± 3.39ab	10.52 ± 1.48abc	10.50 ± 2.71bc	5.61 ± 1.09c	40.23	0.000
Moisture (%)	15.23 ± 4.47	11.43 ± 6.64	20.16 ± 5.96	18.49 ± 4.08	15.57 ± 3.04	15.89 ± 5.41	8.13	0.150
LFH (mm)***	2.11 ± 0.81a	3.25 ± 1.73ab	2.71 ± 1.31ab	2.83 ± 0.66ab	3.70 ± 1.15b	3.27 ± 1.35ab	10.70	0.058
Ground vegetation (%)	20.11 ± 12.17	9.85 ± 9.48	23.33 ± 12.47	14.63 ± 12.12	12.17 ± 11.49	10.10 ± 14.46	8.00	0.156
Graminoids (%)	21.00 ± 14.37a	8.30 ± 11.72ab	21.27 ± 16.49ab	5.26 ± 4.88ab	4.31 ± 6.07ab	3.41 ± 6.60b	16.64	0.005
Regeneration (%)	30.89 ± 23.38a	13.33 ± 8.99ab	11.75 ± 6.73ab	41.25 ± 20.27a	44.25 ± 31.84a	3.41 ± 4.23b	26.87	0.000
Beech cover (%)	28.11 ± 22.87a	15.00 ± 9.76ab	11.58 ± 8.51ab	41.25 ± 18.52a	47.93 ± 33.84a	3.45 ± 4.37b	26.89	0.000
Hornbeam cover (%)	4.28 ± 4.44a	0.52 ± 0.70ab	2.17 ± 2.78ab	2.43 ± 4.66ab	0.95 ± 1.96ab	0.05 ± 0.14b	16.35	0.006
No. of beeches ≤ 50 cm per SP	10.11 ± 8.24a	9.67 ± 4.19a	5.50 ± 5.06ab	10.5 ± 6.76a	12.91 ± 10.23a	1.36 ± 1.61b	21.15	0.001
No. of beeches ≥ 50 cm per SP	10.33 ± 14.19	0.83 ± 1.07	1.50 ± 1.50	5.25 ± 5.76	3.92 ± 4.55	0.10 ± 0.29	14.11	0.015
Dominant beech characteristics**	Large gap centre (n =42)	Large gap N-edge (n=29)	Large gap S-edge (n=22)	Small gap centre (n=38)	Small gap boundary (n=54)	Canopy (n=12)	Kruskal-Wallis test: H	P-value
Height (cm)	70.33 ± 29.88ad	37.31 ± 19.37bc	54.00 ± 24.69abd	68.24 ± 35.89d	68.80 ± 40.19d	25.17 ± 19.11c	38.25	0.000
Diameter (mm)	8.98 ± 3.61a	9.17 ± 5.75ab	9.50 ± 3.33a	9.68 ± 4.51a	10.26 ± 4.78a	5.33 ± 3.37b	15.29	0.009
Height increment (cm)	16.29 ± 8.56ac	12.83 ± 5.70ab	16.57 ± 6.93ac	19.23 ± 8.46c	19.22 ± 8.53c	7.75 ± 5.52b	29.19	0.000
Rel. height increment (cm.cm^{-1})	0.25 ± 0.12a	0.39 ± 0.17b	0.33 ± 0.15ab	0.33 ± 0.15ab	0.32 ± 0.12ab	0.32 ± 0.11ab	15.34	0.009

Note: *Sample plots only with complete data included (both light and moisture measurement), **data from all sample plots analysed, *** total thickness of above ground horizons in mm.

Table 4. Average and median cover on research plots

	Nr. of SPs	%	Regeneration	Ground vegetation	CWD	Litter	Other
A – small gap	23	average	43.96	11.96	1.31	41.75	1.09
		median	40.00	8.00	0.30	40.00	0.00
C – canopy	33	average	2.50	6.32	4.92	84.74	1.52
		median	0.00	2.00	4.00	89.00	0.00
D – large gap	44	average	17.85	23.57	2.00	52.95	3.63
		median	10.00	20.00	0.10	52.95	0.00
E – large gap	29	average	18.91	6.11	12.76	54.46	7.76
		median	10.00	2.00	5.00	51.00	0.00
F – small gap	20	average	26.35	1.58	4.35	62.04	5.68
		median	20.00	0.50	2.50	71.00	0.00

Note: CWD – Coarse woody debris, Other – bare soil, stones and surface roots.

light (R_s = 0.483, P = 0.000), ferns were negatively correlated with direct light (R_s = – 0.362, P = 0.008) and positively correlated with soil moisture (R_s = 0.442, P = 0.001). There was a significant correlation of graminoids cover with the diameter, height, and absolute height increment of dominant beeches (R_s = – 0.180, P = 0.011; R_s = – 0.217, P = 0.002; R_s = – 0.279, P = 0.000), whereas herbs cover was significantly correlated only with the diameter of beeches (R_s = – 0.159, P = 0.026).

Characteristics of Beech Regeneration

The highest density of beech regeneration was found in small gaps (RP A and RP F), with the highest tree density in the 3rd height class (21–50 cm). Similar height development with lower densities was recorded within large gaps (RP D and RP E). The lowest density of beech regeneration was under closed canopy (the majority of individuals in 2nd height class) – (Fig. 1). We did not record any one-year-old seedlings in a given year.

In the large gaps (D and E) and small gap (A) a considerable percentage of beech regeneration reached the 4th height class. In small gap (F) a considerable number of plants in the 7th and 8th height classes were found (667 and 222 individuals per ha resp.). More advanced beech regeneration seemed to be clustered within small gaps (A and F), indicating that the gap was older (A) or that the regeneration had already been established before the gap creation (F). However, the presence of taller plants did not lower the density of younger beech regeneration within the small gaps.

The most important factors influencing the cover of beech regeneration and the performance of dominant beech trees were diffuse and direct light and the presence of ground vegetation (Table 6). Descriptive characteristics of the dominant individuals of the beech regeneration on RPs are given in Table 7.

Table 5. Average density of tree regeneration per 1 ha on research plots (RP)

Species	RP A	RP C	RP D	RP E	RP F
	Average ± SD (ind.)	Average ± SD (ind.)	Average ± SD (ind.)	Average ± SD (ind.)	Average ± SD (ind.)
Fagus sylvatica	71,111 ± 44,771	9,020 ± 16,541	51,414 ± 56,253	54,713 ± 68,675	75,778 ± 75,181
	78.63%	95.85%	69.34	100.00%	100.00%
Carpinus betulus	5,411 ± 9,263	130 ± 750	21,414 ± 29,439	0	0
	5.98%	1.38%	28.88	0.00%	0.00%
Picea abies	8,117 ± 8,659	261 ± 1,045	909 ± 2,238	0	0
	8.98%	2.77%	1.23%	0.00%	0.00%
Larix decidua	773 ± 2,134	0	404 ± 1,277	0	0
	0.85%	0%	0.54%	0.00%	0.00%
Acer pseudoplatanus	5,024 ± 9,047	0	0	0	0
	5.55%	0.00%	0.00%	0.00%	0.00%
Total	90,436	9,411	74,141	54,713	75,778
	100.00%	100.00%	100.00%	100.00%	100.00%

Note: SD – standard deviation; ind. – individuals.

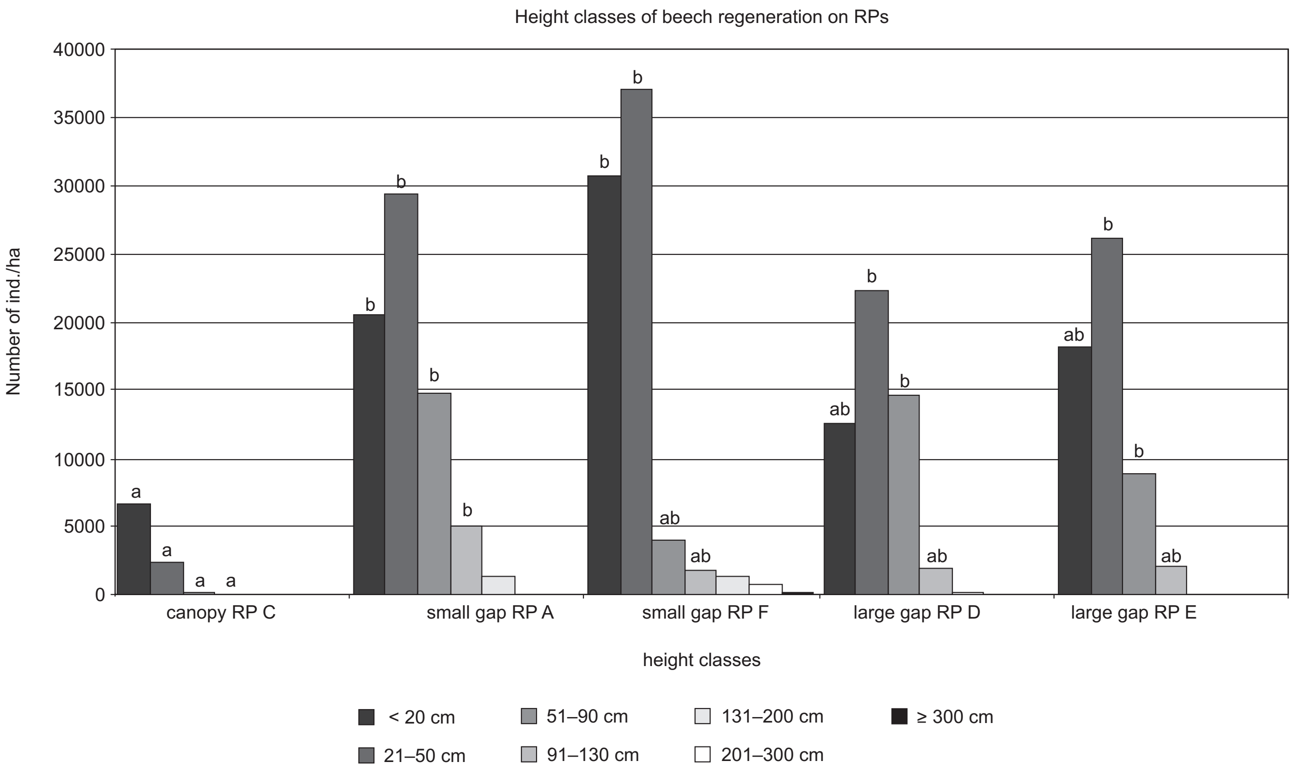

Fig. 1. Height classes of beech regeneration on research plots (RP) (one-year-old seedlings are not displayed)

An ungulate browsing inventory was performed in June and September. In general, the damage caused by browsing increased during the vegetation period, but the differences were not significant (only the 2nd inventory is presented). Greater damage on beech saplings was recorded within gaps (for moderate damage ranging from 13.3% to 21.0% of the number of plants). Beech was browsed heavily only in large gap D (0.9%) and small gap F (4.1%). Under canopy only 7.7% of beech showed moderate damage; the rest were not browsed or showed only minor damage. In general, the browsing pressure on hornbeam was higher (7.1% heavy damage and 28.6% moderate damage). Little browsing was recorded on spruce.

The ratio of beech individuals of direct stem ranged from 44.9% to 50.6% with the exception of PRP E with distinctly above-average proportion of plants without stem branching (68.0%). Nevertheless statistically significant differences were recorded only between RP_S A end E, and RP_S D and E (T = 0.231, Q = 0.178 and T = 0.235, Q = 0.160 resp.). More expressed differences among RPs were recorded with respect to the overall plant branching (Table 8). Beech regeneration of poor quality was recorded mainly under canopy (C), where there was an absence of upright individuals, and the majority of individuals had stem deviations (knee-shaped growth) and plagiotropic growth. In gaps the ratio of upright individuals ranged from 31.1% to 58.0%.

Gap Age

On PRP 01, a major release event was dated at the end of the 1940s and at the beginning of the 1950s. This release event probably contributed to the development of the complex forest structure on PRP 01; nevertheless, moderate release events after 1984 were crucial for the development of beech regeneration (originating mostly from the mast year in 1993). On PRP 02, the release events of particular trees did not coincide and we therefore assumed that the large gap originated from the last release event in the late 1980s and early 1990s. Spruce border trees (RP F small gap) indicate a release event in 1982. In general we can assume that canopy gaps on PRP 01 and PRP 02 originated from the period between 1982 and 1992.

Discussion

Under small gaps the combination of moderate levels of diffuse light and relatively low levels of direct light created more favourable conditions for the establishment and growth of shade-tolerant forest regeneration (Wagner et al. 2011; Diaci 2002). In our study diffuse light availability influenced the beech seedling height and diameter positively; ground vegetation influenced these dependent variables negatively. Small gaps (RPs A and F) showed both the highest

Table 6. Regression statistics for selected dependent variables: Diameter = diameters of root collar of dominant beeches on sample plots (SP), Height = heights of dominant beeches on SPs, Height increment = absolute height increment of dominant beeches on SPs, Relative height increment = relative height increment of dominant beeches on SPs, Cover of beech = ratio of beech regeneration on SPs. In several cases less than five dominant beeches were present on SP. Missing data were casewise deleted.

Dependent Variable	Independent Variables	Regression coefficient	P-value	Regression Statistics
Diameter	Intercept A	9.094	0.000	
	Intercept C	6.930	0.000	$F = 6.224$
	Intercept D	7.963	0.000	$DF_R = 189$
	PACL Direct	–0.062	0.285	$DF_M = 7$
	PACL Diffuse	0.295	0.001	p-value = $1.4.10^{-6}$
	Moisture	–0.057	0.409	$R^2 = 0.187$
	LFH (mm)	0.099	0.683	
	Ground vegetation	–0.117	0.000	
Height	Intercept A	63.984	0.001	
	Intercept C	33.727	0.001	$F = 10.757$
	Intercept D	45.939	0.001	$DF_R = 189$
	PACL Direct	0.009	0.983	$DF_M = 7$
	PACL Diffuse	1.694	0.010	p-value = $2.2.10^{-11}$
	Moisture	0.742	0.134	$R^2 = 0.285$
	LFH (mm)	–3.032	0.087	
	Ground vegetation	–1.236	0.000	
Height increment	Intercept A	19.558	0.000	
	Intercept C	9.979	0.000	$F = 10.129$
	Intercept D	16.660	0.000	$DF_R = 189$
	PACL Direct	–0.073	0.502	$DF_M = 7$
	PACL Diffuse	0.162	0.310	p-value = $9.6.10^{-11}$
	Moisture	0.214	0.075	$R^2 = 0.273$
	LFH (mm)	–0.526	0.220	
	Ground vegetation	–0.283	0.000	
Relative height increment	Intercept A	0.312	0.000	
	Intercept C	0.312	0.000	$F = 2.809$
	Intercept D	0.312	0.000	$DF_R = 189$
	PACL Direct	0.001	0.408	$DF_M = 7$
	PACL Diffuse	0.006	0.031	p-value = 0.008
	Moisture	0.000	0.966	$R^2 = 0.094$
	LFH (mm)	0.014	0.079	
	Ground vegetation	0.002	0.048	
Cover of beech	Intercept A	53.195	0.076	
	Intercept C	17.494	0.076	$F = 7.400$
	Intercept D	31.311	0.076	$DF_R = 44$
	PACL Direct	–0.205	0.728	$DF_M = 7$
	PACL Diffuse	0.732	0.435	p-value = $7.2.10^{-6}$
	Moisture	–0.522	0.415	$R^2 = 0.541$
	LFH (mm)	0.171	0.942	
	Ground vegetation	–0.682	0.012	

Note: PACL – percentage of above-canopy light, LFH (mm) – total thickness of above ground horizons in mm.

cover of beech regeneration and the highest density of individuals per ha. The superiority of small gaps was further confirmed with respect to the growth characteristics of dominant individual beech trees and height growth. Results of this study are similar to results of Mountford et al. (2006) and Gálhidy et al. (2006) who found more prolific beech regeneration in small and medium gaps and are in accordance with conclusions of Bolte et al. (2007), who stressed the importance of soil water resource management through adequate beech regeneration in small gap openings. On the contrary Madsen and Hahn (2008) didn't confirm gap partitioning of regeneration and stressed the importance beech advance regeneration.

In the larger gaps, the N–S asymmetry was of particular importance. The northern margin of the large gap (D) received the highest direct light levels, whereas soil moisture values were the lowest. The latter was probably a result of high temperatures, high evaporation, and root competition from gap edge trees. This unfavourable combination of ecological factors can explain the small regeneration size and the poor absolute height increment of beech regeneration (see Diaci 2002) as well as the limited cover of ground vegetation here. The main reason for the rather homogenous conditions in small gaps was probably the limited area of the canopy opening, the limited number of soil and moisture measurements,

Table 7. Descriptive characteristics of the dominant individuals of the beech regeneration on research plots (RP)

Heights of dominant trees of beech regeneration						
RP	N	Average ± SD(cm)	Median (cm)	Variance	Min	Max
A – small gap	106	72.13 ± 41.26	70.00	1702.76	12.00	180.00
C – canopy	39	21.85 ± 11.55	20.00	133.31	8.00	85.00
D – large gap	176	53.98 ± 27.42	48.50	752.12	12.00	140.00
E – large gap	103	60.94 ± 31.82	57.00	1012.25	18.00	174.00
F – small gap	81	68.52 ± 52.81	50.00	2788.92	14.00	247.00
Last year growth of dominant trees of beech regeneration						
RP	N	Average ± SD (cm)	Median (cm)	Variance	Min	Max
A – small gap	106	19.81 ± 8.54	20.00	72.89	3.00	38.00
C – canopy	39	6.96 ± 4.09	6.00	16.75	0.50	23.00
D – large gap	176	14.59 ± 7.18	15.00	51.55	0.00	32.00
E – large gap	103	16.35 ± 8.27	17.00	68.32	0.00	36.00
F – small gap	81	15.02 ± 12.61	12.00	158.91	0.00	53.00
Diameter of root collar of dominant trees of beech regeneration						
RP	N	Average ± SD (mm)	Median (mm)	Variance	Min	Max
A – small gap	106	10.12 ± 4.62	10.00	21.34	2.00	25.00
C – canopy	39	4.89 ± 2.38	5.00	5.67	1.00	15.00
D – large gap	176	8.74 ± 4.40	8.00	19.37	0.50	25.00
E – large gap	103	8.70 ± 4.34	7.60	18.83	2.70	24.10
F – small gap	81	9.36 ± 4.99	8.00	24.92	2.10	24.60

Note: N – Number of measured individuals, SD – standard deviation, Min – Minimal value, Max – Maximal value.

and the presence of advanced beech regeneration in the area of the whole canopy opening.

Despite the fact that multiple regression of the selected variables accounted for less than 30% of the variation in the size of dominant trees of the beech regeneration, the high relative contribution of ground vegetation cover in the prediction of dominant beech size indicated that even established beech regeneration was considerably influenced by the presence of ground vegetation cover (i.e. competition for resources), whereas moisture and the thickness of above ground horizons may play a crucial role in the establishment and early development of beech regeneration. In particular, *Calamagrostis epigejos* represented a major competitor (Wagner et al. 2011) which negatively impacted beech regeneration development. Therefore, under the given conditions, the control of competitors should be directed primarily at this species.

Differences between gap and canopy soil moisture conditions may be extremely weather dependent where precipitation plays a major role. Normally, variance of soil moisture content is expressed more during periods of drought which negatively influence the survival rates of beech regeneration. Although the measurement of soil moisture content was performed in a distinctly above average precipitation period (monthly total precipitation in the given year was 112.2 mm, whereas average monthly total precipitation between 1960 and 1995 amounted to 87.2 mm), the precipitation during the 10 preceding days amounted to only 13.8 mm. Moisture conditions were similar in the centres of the gaps (A and D), around the gaps, and below the closed canopy. Also Gálhidy

Table 8. Statistical differences in number of upright individuals of beech regeneration on research plots (RP).

Pairs of RPs/*statistical significance	Difference	Test statistic T	Critical value Q	Significance value
RP A – C*	0.358	0.642	0.241	0.000
RP A – D	–0.124	0.126	0.158	0.240
RP A – E	0.048	0.051	0.178	0.949
RP A – F*	–0.222	0.224	0.180	0.021
RP C – D*	–0.483	0.768	0.228	0.000
RP C – E*	–0.311	0.591	0.242	0.000
RP C – F*	–0.580	0.866	0.251	0.000
RP D – E*	0.172	0.177	0.160	0.035
RP D – F	–0.097	0.098	0.173	0.592
RP E – F*	–0.270	0.275	0.191	0.002

et al. (2006) showed that the maximum soil moisture was the same in small gaps and large gaps. Generally, the pattern of soil moisture is more spatially variable and microrelief-dependent than light (Madsen and Hahn 2008). Moreover, light environment induce changes in soil conditions and the absence of parent trees may both increase soil moisture (Gálhidy et al. 2006). In their companion study in near natural forest of Voděradské bučiny conduced on PRP 01, Podrázský and Remeš (2006, 2007) showed that the amount of dry matter decreased by ca. 25% several years after the canopy opening, especially in the H horizon, the pH, base content and base saturation increased, as well as the content of macronutrients (with the exception of total calcium). The results proved considerable changes in the humus forms during the natural forest development related to gap dynamics. In gaps, moisture and nutrient status may be particularly favourable for drought sensitive European beech seedlings when young individuals compete with surrounding ground vegetation (Bolte et al. 2007). Gessler et al. 2004 showed that not only water shortage has a negative effect on European beech water budget but it also constrains its nitrogen supply.

Light conditions may also positively influence the growth response of beech seedlings to soil fertility. In low light environments, this response is reduced, whereas in non-limiting light conditions, seedling growth is markedly influenced by nutrient availability (Minotta and Pinzauti 1996). Even at 5% relative light intensity (RLI) Madsen (1995) found that light was the main factor in limiting growth, which in this study corresponds to values found below closed canopy with sparse woody regeneration. In these light conditions beech reduced its height growth by a factor of two to three (compared to RPs under gaps), but the density of beech regeneration in RP C was still higher than the recommended afforestation rate of this commercial species (5,000–10,000 ind. ha^{-1} according to Burschel and Huss 1997). Collet et al. (2001) indicated an annual beech seedling height increment of 1.2 cm as the threshold value for seedling growth necessary for survival in shade conditions. Even in the poorest light conditions within our research plots, the average height increment of beech trees dominating the regeneration reached a value of 6.96 cm year^{-1}. The gap environment resulted in higher values of total height and the diameter of the root collar of beech individuals growing under open canopy. A significant shift in the distribution of height classes of beech regeneration (under the canopy the majority of beech individuals were in the 2nd height class, whereas they were in the 3rd height class on all other plots) corresponds with this observation.

On the contrary, increased direct light under gaps leads to higher herbal vegetation cover and thus increased competition for resources (Modrý et al. 2004). However, in this study ground vegetation cover was instead related to diffuse light and soil moisture content. In the large gap (RP D), a noticeably higher cover of total ground vegetation as a possible reaction to higher direct light input was observed.

While heavier ungulate browsing was recorded in gaps with higher densities of beech seedlings, lower plant densities and the absence of other tree species made the RP C below canopy less attractive to ungulate browsers. In the study area, roe deer (*Capreolus capreolus* L.) is the most important browser. Although its densities vary during the year, they normally do not exceed 4.0 ind. 100 ha^{-1} (on average 3.5 ind. 100 ha^{-1}).

No clear difference between beech regeneration quality in small and in big gaps was observed, nevertheless under the closed canopy, the absence of upright individuals and the majority of knee-shaped individuals with a tendency to twin stem underscores the importance of light environment management for the form and quality of beech regeneration. This is mainly relevant for commercial forests. Beech has decurrent growth, and its growing space has a strong influence on the form of the leader. Differences in the allocation of photosynthates lead to differences in tree architecture (Collet et al. 2002). Most stem forking and leaning stems occurred where above-canopy light was below 20% (see Stancioiu and O'Hara 2006).

Conclusions

The performance of tree seedlings was influenced by different light levels as a result of gap formation as described in the forest cycle model. Radiation also has an indirect and often contradictory influence on the establishment and growth of tree regeneration via changes in water and nutrient availability, inducing changes in ground vegetation cover and competition for resources. Besides these factors, an important feature may be the dynamics and local history of gap creation with a direct impact on the establishment and future structure of woody regeneration and the interplay of other factors such as the presence of seed years, biotic and abiotic damage, and macroclimatic conditions. Moreover, the indicated negative effects of direct light at the northern gap margin suggest that the extension of gaps in similar managed forest should proceed in the direction of the southern gap border. The results of this study also suggest that it is important that future research of natural regeneration of beech in low precipitation conditions integrates the continuous soil moisture regime and its role in micro-habitat heterogeneity, where periods of drought may play crucial role both in the survival of beech regeneration and ground vegetation. This case study indicates that for the purposes of close-to-nature forestry, the gap size corresponding to the removal of one to three large beech trees seems to be, in the given conditions (characterized by lower annual precipitation), a minimal measure to ensure natural beech regeneration with a tolerable level of competition of ground vegetation.

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