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Regeneration Dynamics Following the Formation of Understory Gaps in a Slovakian Beech Virgin Forest

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Abstract: The frequency and size of canopy gaps largely determine light transmission to lower canopy strata, controlling structuring processes in the understory. However, quantitative data from temperate virgin forests on the structure of regeneration in gaps and its dynamics over time are scarce. We studied the structure and height growth of tree regeneration by means of sapling density, shoot length growth and cumulative biomass in 17 understory gaps (29 to 931 m^2 in size) in a Slovakian beech (*Fagus sylvatica* L.) virgin forest, and compared the gaps with the regeneration under closed-canopy conditions. Spatial differences in regeneration structure and growth rate within a gap and in the gap periphery were analyzed for their dependence on the relative intensities of direct and diffuse radiation (high vs. low). We tested the hypotheses that (i) the density and cumulative biomass of saplings are higher in gaps than in closed-canopy patches, (ii) the position in a gap influences the density and height growth of saplings, and (iii) height growth of saplings increases with gap size. Sapling density and biomass were significantly higher in understory gaps than under closed canopy. Density of saplings was positively affected by comparatively high direct, but low diffuse radiation, resulting in pronounced spatial differences. In contrast, sapling shoot length growth was positively affected by higher levels of diffuse radiation and also depended on sapling size, while direct radiation intensity was not influential. Conclusively, in this forest, regeneration likely becomes suppressed after a short period by lateral canopy expansion in small gaps (<100 m^2), resulting in a heterogeneous understory structure. In larger gaps (≥ 100 m^2) saplings may be capable even at low plant densities to fill the gap, often forming a cohort-like regeneration layer. Thus, gaps of different sizes imprint on the resulting canopy structure in different ways, enhancing spatial heterogeneity.

Keywords: regeneration dynamics; direct light; diffuse light; *Fagus sylvatica*; gap age; gap size; sapling biomass; sapling density; sapling growth rate

1. Introduction

Understanding the natural dynamics of forests and the resulting structural change is a major focus of forest ecological research, since forest structure has a large influence on the energy and matter fluxes in the stand. Knowledge about forest dynamics processes may also serve as guidance for the development of close-to-nature forest management strategies, forest conservation and restoration efforts [1].

Tree regeneration is a fundamental process which drives forest dynamics. Except for very dry and nutrient-poor soils, seedling establishment and sapling growth in the forest interior are largely controlled by light availability [2]. The structural attribute which largely controls radiation transmission to the understory is the degree of canopy closure in the upper tree layer. Due to species differences in light requirement for regeneration and in the canopy structure of adult trees [3], the relation between canopy closure, light transmission and regeneration success is highly variable among forest types and also depends on the disturbance regime [4]. A more general picture for temperate forests has not yet emerged.

Large parts of Central Europe would be covered by European beech (*Fagus sylvatica* L.) if man had not extensively altered vegetation cover in this region over the last millennia. This species often forms monospecific stands, or it is co-dominant together with a few other tree species [5]. Beech forest ecosystems are therefore of special interest to forest ecology, conservation and management in Europe.

Even though a variety of factors influencing the regeneration process of beech have been identified [6,7], a strong dependence on light availability has been documented for both, seedling establishment and sapling growth [8–12]. As a highly shade-tolerant tree species, seedlings, saplings and understory trees of beech can endure long periods of low light and suppression by the upper canopy, during which ontogenetic development is greatly retarded [5]. As a consequence, the presence of beech regeneration may be uncoupled from the actual light regime, rather reflecting the growing conditions of the past. This may be the reason why beech saplings have been found to be nearly omnipresent in beech virgin forests (sensu Hunter [13]), even though stem density and canopy cover vary largely in space [14–20]. When the suppressed saplings (which often are termed "advanced regeneration") are released by disturbance events from the competitive pressure of the overstory and light levels increase, they benefit from a developed root system and advanced height growth in the understory, overtopping lower seedling layers and leading to competitive superiority over newly recruited seedlings.

The disturbance regime of natural beech forests in central and southern Europe is characterized by local biotic and abiotic events, which typically create only small canopy gaps [21], while medium and large-scale disturbances are rare and most often related to windthrow [21,22]. Quite a number of detailed studies on gap formation in beech-dominated virgin forests have been published since the late 1990s [23–33]. From these studies, it is visible that the gap size frequency distribution in beech old-growth forests is generally best described by exponential decay functions, i.e., the frequency of gaps decreases with increasing size, and small gaps caused by the mortality of single or a few trees occur most often. Similar canopy disturbance patterns have been reported from many other forest types [34]. However, gap area, which largely determines the ground area to be colonized by tree offspring, is disproportionate to the frequency of gaps of a given size [25,27,29,30,33].

The importance of the different gap size categories for forest dynamics does not only depend on their share in total gap area, but also on their specific effect on the dynamics of the understory vegetation. Gap size and gap geometry are main determinants of the quantity of light reaching the understory and how light intensity varies across the gap and its immediate vicinity in the stand [34–40]. Furthermore, direct and diffuse radiation that might act differently on regeneration success show a pronounced difference in their spatial distribution [38]. The great variability of light intensities encountered by seedlings and saplings in gaps of different sizes influences seedling establishment success and sapling growth, determining the future development of the considered forest patch and, in mixed stands, the competitive interaction of different tree species [41,42].

It has been argued that the physiology of beech offspring and beech regeneration dynamics fit well with the light regime, which is created by canopy gaps in beech-dominated natural forests [7]. Yet, the regeneration layer has been studied only rarely in the gaps of beech-dominated virgin forests. The existing studies document a generally high spatial heterogeneity in the regeneration layer, i.e. sapling density and sapling height differ largely across a single gap and also between gaps of different sizes, and they suggest that gaps in most cases release already established advanced regeneration [17,33,43,44].

This seems to be different from the majority of 'natural' forests with management history, where gaps generally do not release advanced regeneration or, if so, only a relatively homogeneous cohort-like regeneration layer is released [43,45].

An extensive gap survey in a mixed beech-Silver fir (*Abies alba*)-Norway spruce (*Picea abies*) virgin forest in Bosnia revealed for the beech-dominated regeneration layer no differences in structure between gaps differing in size [17]. Even more surprising, the authors found no differences in regeneration density in different height classes between gaps and average stand conditions, suggesting that no direct link between gap creation and the regeneration process exists in this primeval forest. This would further imply that gap-induced structural patterns have only a small influence on stand structure, if human influence is absent. In contrast to these findings, studies in European beech and beech-Silver fir virgin forests reported that gap formation had a significant influence on seedling and sapling density and sapling growth, as well as that growth rate increased with the size of the gap [33,43,44]. Rozenbergar et al. [44] observed that seedling establishment after gap formation was generally more successful in the periphery of the gap, while seedling and sapling height growth was greater in the gap interior.

To summarize, rather discrete canopy disturbances control radiation transmission to the understory in beech virgin forests, where they cause a heterogeneous light regime. Even though the development of beech regeneration depends on light availability, the simple presence of beech regeneration is not necessarily an indicator of the actual light regime or current regeneration development, due to the species high shade-tolerance. Furthermore, canopy gaps often release already established and heterogeneously structured advanced regeneration which complicate the identification of patterns in regeneration establishment and development. Yet, there is no consistent evidence on the role of canopy gaps for the regeneration process in beech virgin forests.

An approach that might help to better understand the complex regeneration process in beech forests is to combine data on the regeneration structure and performance with spatially explicit information on the recent history of canopy conditions. The present study utilizes a detailed regeneration survey in 17 understory gaps of variable size and in 32 plots under closed canopy in the beech virgin forest reserve "Kyjov" in the Carpathians of eastern Slovakia. The time of gap formation could be assigned either to the period 2003–2013 (= "new gaps") or to prior to 2003 (= "old gaps"). To analyze the effect of spatial differences in light availability, the area of a gap and its direct neighborhood was divided into different light categories in terms of direct and diffuse radiation intensity according to a concept proposed by Diaci [38].

Main study goals were (i) to search for differences in the structure of the regeneration layer between gaps and forest patches with closed canopy, testing the observation that gaps do not affect regeneration structure [17] for broader validity, (ii) to investigate differences in sapling density and height structure in gaps differing in age, and (iii) to analyze the spatial distribution of saplings and sapling growth in gaps in relation to gap size and the position within a gap.

We explicitly tested three hypotheses:

H1: *Gaps stimulate the height growth of beech seedlings and saplings through higher radiation intensities with the consequence that the density and cumulative biomass of saplings of* $\geq$ *0.5 m in height is higher in gaps than in closed-canopy patches of the stand.*

H2: *The position in the gap and the related variation in light intensity influence both, the establishment success of beech seedlings after gap formation and the height growth of seedlings and saplings. The older the gap, the more heterogeneous is the spatial distribution of sapling density and biomass in a gap.*

H3: *Since gap size has a positive effect on average radiation intensity in the gap, average sapling growth rate increases with gap size.*

2. Material and Methods

2.1. Study Site

The study was conducted in the virgin forest reserve Kyjov in the Vihorlat Mountains in eastern Slovakia (48°53´ N, 22°06´ E) at 700–820 m a.s.l.. This strict forest reserve covers an area of 53 ha on a north- to north-east-facing slope of moderate steepness (11–24%). The mean annual temperature is 5.2–5.7 °C and the mean annual precipitation is 950–1000 mm along the elevation range [46]. Dystric Cambisols with good water-holding capacity have developed from andesite as bedrock [15,16]. The dominant plant community is a *Fagetum dentarietosum glandulosae* association. European beech (*Fagus sylvatica* L.) is the dominating tree species which forms almost pure stands (99% of stems) with little admixture of sycamore maple (*Acer pseudoplatanus* L.), Norway maple (*Acer platanoides* L.), common ash (*Fraxinus excelsior* L.) and wych elm (*Ulmus glabra* L.). The height of the dominant trees is approximately 30 m, which seems typical for the Vihorlat Mountains but is lower than in other regions of the Carpathians [15]. At the scale of a few m to tens of meters, the stand structure is highly heterogeneous in vertical and horizontal directions [47,48].

2.2. Study Design

In the Kyjov forest, canopy gaps were sampled by the line-intercept method in 2003 [24] and 2013 [33]. Using the same transect lines in both surveys allowed for assigning gap formation either to the time before 2003 (old gaps) or to the period 2003–2013 (new gaps). In the second inventory, the cover of sub-canopy tree layers (<20 m in height) was visually estimated on the expanded gap area, i.e., the area enclosed by the stems bordering the gap, for all 34 canopy gaps mapped in this survey. Many of the gaps had a complex vertical structure of different layers of tree regeneration and understory trees. In order to study the response of tree regeneration to gap formation in the upper canopy, we selected a subset of gaps that guaranteed relatively comparable initial conditions in terms of tree understory structure and allowed us to conduct the measurements described below. In the chosen gaps tree regeneration had not exceeded an approximate maximum height of 3 m at the time of release, i.e., vertical gap closure was in a relatively early stage. This criterion broadly meets the definition of an understory gap given by Brokaw [49], i.e., "a 'hole' extending through all levels down to an average height of two m above ground". We further excluded gaps where the light regime at the gap edge was obviously influenced by a neighboring gap. These selection criteria were fulfilled by 17 gaps (i.e. half of the number of mapped canopy gaps), which were located in the entire study area of Kyjov forest with gap size ranging from 29 to 931 m^2. Eleven of the gaps were formed prior to 2003 (old gaps) and six in the period between 2003 and 2013 (new gaps). The decay stage of tree trunks in the new gaps that once led to the creation of the gaps (gapmakers; data not shown), indicates that at least five of the six disturbance events must have happened more than five years before 2013.

The study is completed by data on sapling density (height ≥ 0.5 m and dbh < 7 cm) in plots in sections of Kyjov forest with closed canopy that were collected during a systematic forest structure inventory conducted by Glatthorn et al. [50].

2.3. Field Methods

In all 17 gaps, a transect of 2 m width was placed from North to South passing through the approximate gap center and extending by 10 m beyond the projected gap edge in both directions in order to cover the full range of light intensities encountered by tree regeneration in the gaps (Figure 1). The belt transect was divided into adjacent squares of 4 m^2 size. In each square, the density of tree saplings was determined in four height classes (50–149 cm, 150–299 cm, 300–699 cm and ≥700 cm, if dbh was <7 cm). Squares with ingrowing leaf layers from trees growing outside the plot or groups of larger pole-sized trees within the plot were excluded from the analysis (17% of the 276 squares), as the light regime of these plots differed largely from that of plots with small-sized regeneration.

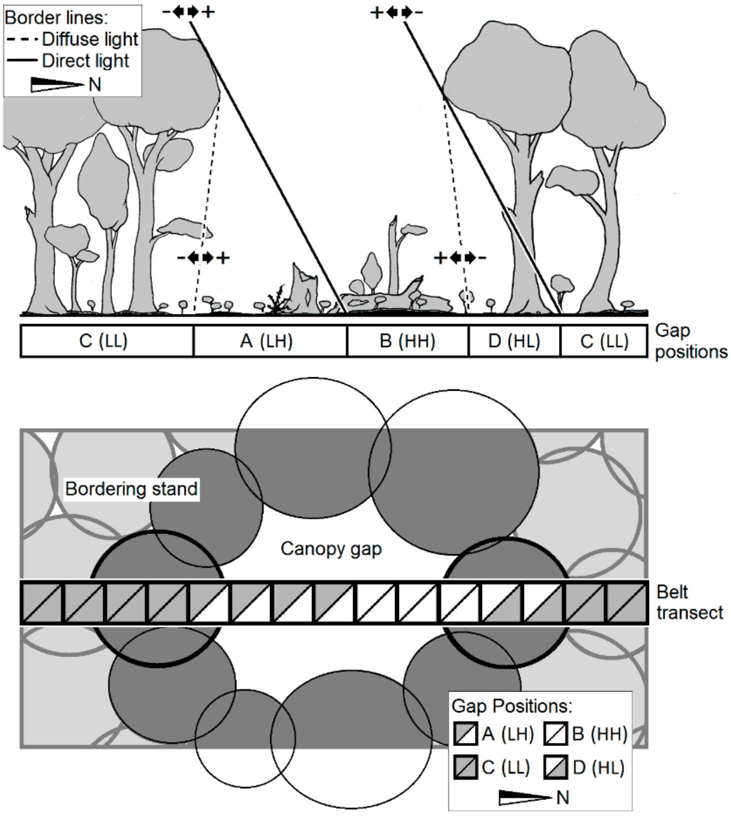

Figure 1. Cross-section in north-south direction and horizontal projection of a schematic canopy gap. The sketches illustrate the categorical zonation of the relative intensities of direct and diffuse radiation along a south-north-directed belt transect and the location of four classes of radiation input on the forest floor (C = low direct and low diffuse radiation (*LL*), A = low direct and high diffuse radiation (*LH*), B = high direct and high diffuse radiation (*HH*), D = high direct and low diffuse radiation (*HL*)) according to the conceptual model of Diaci [38] (labelling modified).

Additionally, the shoot length growth during the last three years of one sapling per quadrant with a height of the dominant or co-dominant saplings was determined by measuring the distances between consecutive bud scars (internodes) along the leading shoot.

For comparing the regeneration in the 17 gaps with that under closed canopy conditions, we also investigated the regeneration layers on plots located under closed canopy, using the data collected by Glatthorn et al. [50]. The criteria for defining closed canopy conditions were that (i) the stem volume of dead canopy trees was < 3 m^3 in the 500 m^2-study plots (which corresponds to the volume of one beech tree with a dbh of approximately 50 cm) and (ii) the surrounding stand area was only slightly or not affected by canopy tree mortality. Tree seedlings and saplings were assigned to four height classes (<50 cm, 50–149 cm, 150–299 cm, >300 cm) and counted along 32 transects under closed canopy with a total area of 13 m^2 each (2 m × 6.5 m).

2.4. Data Analysis

The structure of the tree regeneration along the transects was analyzed for sapling density and estimated cumulative sapling biomass per ground area using the allometric equation proposed for beech saplings by Annighöfer et al. [51]. Sapling biomass per ground area was used as a proxy for estimating the space filling by beech regeneration in the quadrants, combining information on plant density and height in a single biomass number. Clearly, this parameter is only a rough measure of biomass, which should only be used for relative comparisons, as calculations solely base on the mean height of the sapling size classes.

Addressing hypothesis 1, we first investigated differences in the regeneration structure in gaps and under closed stand by comparing the density and the cumulative biomass of saplings ≥ 0.5 m tall on the "closed stand" plots ($n = 32$) to that on the gap plots ($n = 17$). To conduct the comparison for similar plot areas, we contrasted the closed-canopy transects (13 m^2 size) with the gap transects by considering only the three squares closest to the approximate gap center (total area $4\ m^2 \times 3 = 12\ m^2$). Since the data were not normally distributed according to visual inspection of the residuals and a K-S test, we applied the non-parametric Wilcoxon rank-sum test to test for significantly different means of gap and closed-canopy plots.

Second, we tested for differences in the regeneration structure at different light microsites within a gap and in the immediate gap surroundings ("gap periphery"). As equipment to adequately quantify light intensities was not available when the study was conducted, we used a conceptual scheme proposed by Diaci [38] that was modified to subsequently obtain rough estimates of light intensity levels in different gap positions. This scheme subdivides the area of a gap and its direct neighborhood into the four light intensity and quality classes A to D according to the relative intensity (high vs. low) of direct and diffuse radiation that reaches the ground as a consequence of gap structure and its exposition to the sun (see Figure 1 and Table 1).

Table 1. Definition of four light regime classes in a gap (A–D) according to the relative availability of direct and diffuse radiation after Diaci [38].

Gap Position	Direct Radiation	Diffuse Radiation	Symbol
A	low	high	(*LH*)
B	high	high	(*HH*)
C	low	low	(*LL*)
D	high	low	(*HL*)

To evaluate the assignment of the light categories, we used a basic geometric estimation: A dominant tree of 30 m in height casts a shadow of 14 m length in summer (incident angle of sunlight at noon = 65°). The canopy gap begins where the lateral extension of the tree crown ends. A dominant trees crown radius is approximately 8 m in the Kyjov forest [16], which results in a 6 m long shadow into the canopy gap at the southern gap edge. On average the tree crowns begin at a height of 11 m, which allows direct sunlight to reach about 5–6 m under the canopy at the northern gap edge. Diffuse radiation is expected to decrease rapidly with increasing distance from the gap area. Thus, it was considered to be comparatively high in the gap interior and comparatively low in the gap periphery. As trees bordering a gap might be different in height and the shape of their crowns, the basic geometric estimation is a very static perspective. Nevertheless, we found high conformity with other studies that have adopted the conceptual scheme by Diaci [38,40,44,52]. We concluded that comparatively high intensities of diffuse radiation reach 1–2 m beyond the gap edge and comparatively high direct radiation has an offset of 5–6 m in northern direction from the gap edge.

We re-labeled the four classes of Diaci [38] into *LH* (A), *HH* (B), *LL* (C) and *HL* (D) to indicate the relative intensity of direct radiation (first letter) and diffuse radiation (second letter) with *H* for high and *L* for low (for example, *HH* stands for comparatively high direct and diffuse radiation). The four light classes cannot be aligned with different light intensity levels on the ground, but rather characterize microsite differences in the diurnal illumination regime and in light quality on the ground that are caused by the different paths of direct and diffuse sun light toward the ground. The term "relative intensity" refers to the specific light gradients within a gap of certain size. The light intensity levels in the light classes differ between gaps of different size. These microsites with contrasting light regimes may be linked to spatial variation in other ecological factors such as precipitation, soil moisture, temperature, humus decomposition rate and seed dispersal, which are partly dependent on gap geometry and size [38,52].

The effects of the log gap size, gap age (old: formed prior to 2003; new: formed between 2003 and 2013) and position in the gap and the associated light regime (relatively high or low levels of direct and diffuse radiation) on seedling and sapling numbers were analyzed with a zero-inflated generalized linear mixed-effects model (GLMM). We used the logarithm of gap size in the model calculations to reduce the influence of rare large gaps and to account for an assumed asymptotic effect of gap size on light availability on the ground. Residuals were assumed to follow a negative binomial distribution with a quadratic parameterization and we used the log link function. Gap id was used to specify a random effect of individual gaps on the intercept of the model. The zero-inflation component of the model was specified using the same covariables and using gap id as random effect identical to the conditional model. A spatial exponential covariance structure was assumed to account for spatial auto-correlation.

Before analyzing the relationship between seedling and sapling biomass and gap variables, we log transformed the biomass estimates as they were heavily right skewed. As a log transformation is only possible for biomass values larger than zero, this analysis was restricted to the subset of subplots with regeneration present (179 of 229). A GLMM was fitted using the same covariables, random effect and spatial covariance structure as for the stem number data. A gaussian distribution of residuals with an identity link was assumed.

To explore the effects of sapling size, competition intensity (i.e. density of co-dominant saplings on a quadrant divided by 4, 2 and 1 for height classes <1.5 m, <3 m and ≥3 m, respectively) and gap position (as a proxy for the relative availability of direct and diffuse radiation) on sapling shoot length growth in gaps of variable size, we further modeled mean annual shoot length growth during three years (2012 to 2014) in dependence on these five variables with a linear mixed effects model. Apart from different covariables, shoot length growth was modelled with identical model specifications as the biomass data.

An assessment of differences in stem density, biomass and shoot length growth between the four light regime categories (*LL*, *LH*, *HH*, *HL*, Table 1) in gaps of different size (<100 m^2 and ≥100 m^2) and age (new and old) was done with generalized linear hypothesis tests. We also assessed differences between the same light regime categories in small and medium gaps of the same age, and in new and old gaps of the same size category. A scheme of the testing procedure is given in Figure S1 in the supplement.

To test for the significance of influencing factors in the different models, analyses of variance (ANOVA) were performed. A significance level of $p < 0.05$ was applied throughout all analyses. All GLMMs were fitted using the glmmTMB package [53] of the R statistical software [54]. Generalized linear hypothesis testing was done using the multcomp package [55] in R.

3. Results

The tree regeneration on the gap plots and the plots in the closed-canopy stand consisted nearly exclusively of beech seedlings and saplings. Since other species occurring in the forest (sycamore maple, Norway maple, common ash and wych elm) were present in only negligible numbers, they were not counted separately. A dense cover of herbal vegetation was rarely present. Thus, herbal vegetation was not addressed as a factor influencing regeneration dynamics in the Kyjov forest. Browsing by ungulates in winter was surveyed in spring 2014 on the inventory plots (data not shown). Only 4% of the seedlings <0.5 m height and 9% of the beech saplings <1.5 m height were found to be browsed. We assumed that browsing is not an important factor for beech sapling vitality and survival in this forest.

3.1. Comparison of Gaps with Closed-Canopy Conditions

The density of saplings (≥0.5 m height) was about five times higher in gaps (mean: 10147 ha^{-1}) than in the closed stand (mean: 1923 ha^{-1}, p <0.001) (Figure 2). The difference was even greater when considering the estimated cumulative sapling biomass per ground area (means: 513 g m^{-2} in gaps vs. 79 g m^{-2} in the closed stand, p <0.001).

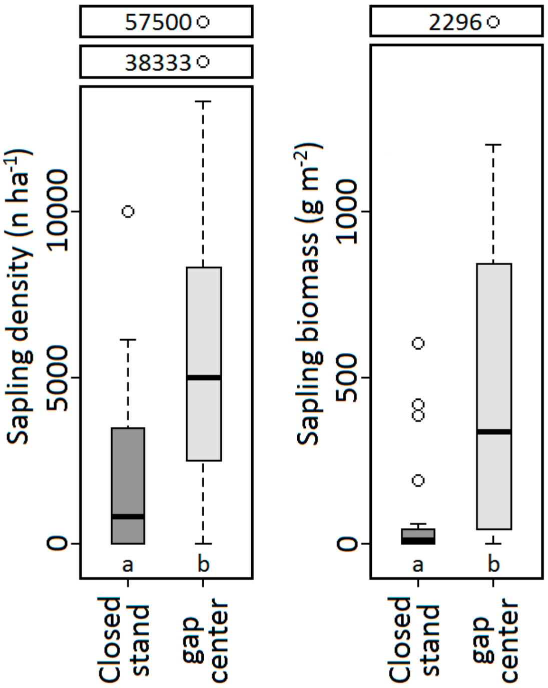

Figure 2. Density of saplings (≥0.5 m) and estimated cumulative sapling biomass in closed-canopy plots and gap plots (only gaps with regeneration layer <3 m height at the time of gap formation). Box-whisker plots with median (thick black line), 25-and 75-percentiles (box) and extremes not exceeding the 1.5fold of the interquartile range (whiskers). Dots mark extreme data points beyond 1.5 times the IQR. $N = 17$ plots in gaps and 32 plots under closed canopy. The dashed grey line marks the median values of samples containing 48 plots á 13 m^2 selected by random in the forest (including gap and closed-canopy plots). Different letters below the boxes indicate significant differences between the groups (Wilcoxon rank-sum test).

3.2. Spatial Differences in Regeneration Structure

3.2.1. Sapling Presence or Absence

According to the zero-inflation component of the GLMM of the sapling density data, only direct light was indicated to be related to the presence or absence of saplings (Table 1). The influence of the factors diffuse light, gap size and gap age was not statistically significant. Microsites in the light regime classes *HH* and *HL*, which receive relatively high intensities of direct radiation, contained saplings more frequently (91% of all squares) than squares receiving relatively low direct radiation (classes *LH* and *LL*; 71%).

3.2.2. Sapling Density

The GLMM indicates that sapling density in canopy gaps and their immediate surroundings was promoted by comparatively higher intensities of direct radiation. The other factors had no significant effects on sapling density in the models. However, a positive effect of increasing gap size on *LL* microsites is indicated, as they had significantly higher densities in medium old gaps than in small old gaps (Table S1).

Compared to closed-canopy conditions, sapling density was generally found to be higher in all gap positions (Figure 3). In accordance with the model results, in new small gaps (<100 m^2) formed between 2003 and 2013, sapling density was low in class *LH* and *LL* squares (low direct radiation) and highest in class *HL* squares (high direct but low diffuse radiation), i.e. at the northern gap edge. However, significant differences were only found between *HL* squares and *LL* squares. In old small gaps, which had formed prior to 2003, maximum sapling density was similarly high as in younger gaps, but it was reached instead in class *HH* squares and again, it was significantly higher than in *LL* squares. While young gaps were characterized by a high variation of sapling density in patches with comparatively high direct radiation (*HH* and *HL*), density variation was much lower in these positions in old gaps.

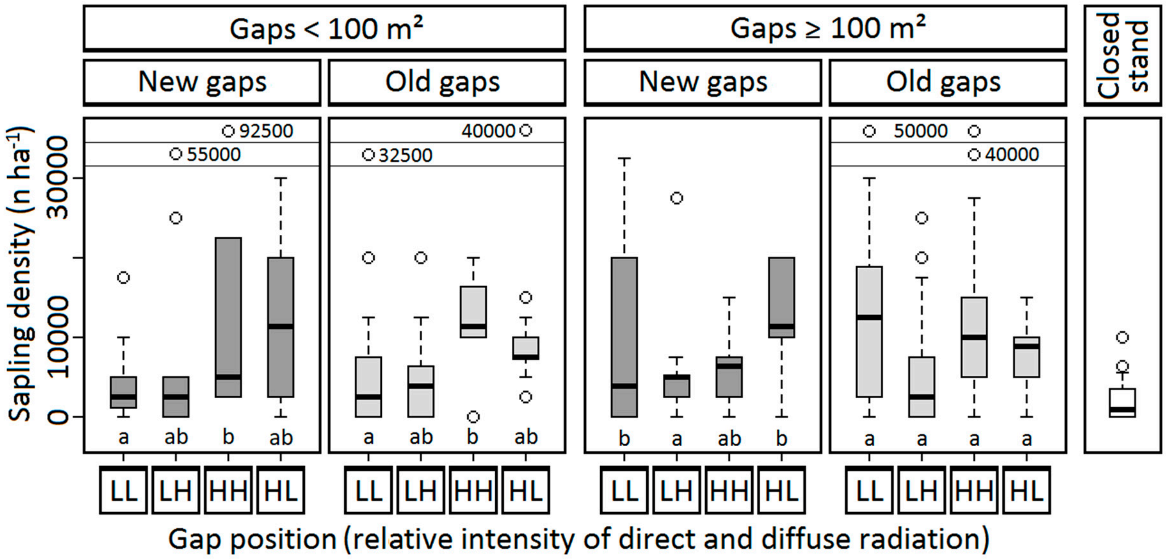

Figure 3. Sapling density in squares at different position in a gap that formed between 2003 and 2013 (new gaps; dark grey) or prior to 2003 (old gaps; light grey) presented for small (<100 m^2) and medium-sized gaps (≥100 m^2). The four gap positions are characterized by the availability of different relative intensities of direct and diffuse radiation (high = H, low = L; first letter for direct and second for diffuse radiation; see Table 1 and Figure 1) following Diaci [38]. The density values of closed-canopy plots are displayed at the right for comparison (32 belt transects á 13 m^2 size). Box-whisker plots with median (thick line), 25-and 75-percentiles (box) and extremes not exceeding the 1.5fold of the interquartile range (whiskers). Dots indicate extreme data points beyond 1.5 times the IQR. Different letters below the boxes indicate significant differences between the gap positions within gaps of a certain size and age class (linear hypothesis testing).

Regarding the median values a similar sapling density pattern as in small gaps was found in new medium-sized gaps (≥100 m^2). Here, the sapling density in *LL* and *HL* squares was significantly higher than in *LH* positions, which indicates a positive effect of positions in the gap periphery in this gap size class. However, this gap size class contained deviating sapling densities when the gaps were formed before 2003. Particularly high densities were recorded in *LL* squares, exceeding classes with high direct radiation (*HH* and *HL*). *LH* squares contained lowest sapling densities in medium-sized old gaps. All gap positions show rather high variation in sapling density and there were no significant differences between them.

No significance was found, when testing the effect of gap age on the individual gap positions (e.g. *HH* in new gaps <100 m^2 compared to *HH* in old gaps <100 m^2; Table S1 in the supplemental materials). Nevertheless, the differences between the gap age classes described above indicate that this factor also influenced the sapling density pattern. Gap size had a significant positive effect on *LL* squares in old gaps. Regarding the other gap positions the pattern is similar in both gap size classes.

3.2.3. Shoot Length Growth and Sapling Height

The measured shoot length growth of saplings (recorded in 151 plants) was largely determined by the initial size of the plants and the availability of diffuse radiation (Table 1), but also by gap size. In contrast, the relative intensity of direct radiation did not influence sapling growth. The presence of competitors in a square was found to have neither a positive nor a negative effect on shoot length growth of (co-) dominant saplings. The positive influence of plant size is displayed by the generally accelerating height growth of saplings with increasing plant height (Figure 4). The generally higher growth rate in the patches receiving high diffuse light intensities (classes *LH* and *HH*) and the generally higher growth rate in medium- than in small-sized gaps indicate a positive effect of increasing diffuse radiation. However, significant differences between the diffuse light classes were only found for large saplings (≥3 m), and between gap size classes only for the medium-sized saplings (<3 m) (Table S2). While we either found no change or even a decrease in height growth rate with increasing sapling size from <1.5 to 3 m in small gaps (<100 m^2), growth rate increased with plant size more continuously in medium-sized gaps (≥100 m^2).

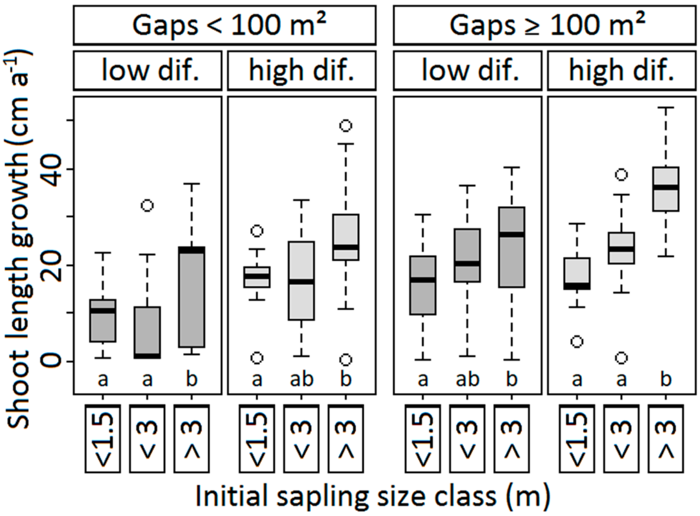

Figure 4. Shoot length growth of saplings in squares exposed to different levels of diffuse radiation (relatively low: dark grey; relatively high: light grey) in gaps of two size categories (<100 m^2 and ≥100 m^2). Box-whisker plots with median (thick line), 25-and 75-percentiles (box) and extremes not exceeding the 1.5fold of the interquartile range (whiskers). Dots indicate extreme data points beyond 1.5 times the IQR.

3.2.4. Sapling Biomass

In the model calculations sapling biomass per square meter increased significantly with gap size and gap age. It is indicated that the level of direct light (comparatively high or low) also had a positive effect on sapling biomass ($p = 0.069$), while the level of diffuse light had no influence (see Table 1).

The estimated cumulative sapling biomass in small new gaps was at a low level. It did hardly differ from that under closed-canopy, irrespective of the square's position in the gap (Figure 5). The higher sapling density found in squares receiving high intensities of direct radiation (Figure 3) (classes *HH* and *HL*) led to only small differences in sapling biomass. The vast majority of saplings were still small (Figure S2) and accordingly contributed with only little biomass. In old small gaps, however, median sapling biomass showed a distinct peak in class *HH* (high direct and diffuse radiation), where a large proportion of the comparably high number of saplings already grew into larger height classes. In *HL* with high direct but low diffuse radiation, median biomass was much smaller. It remained close to zero in *LH* and *LL* with only diffuse radiation. These positions contained significantly less biomass than *HH* squares.

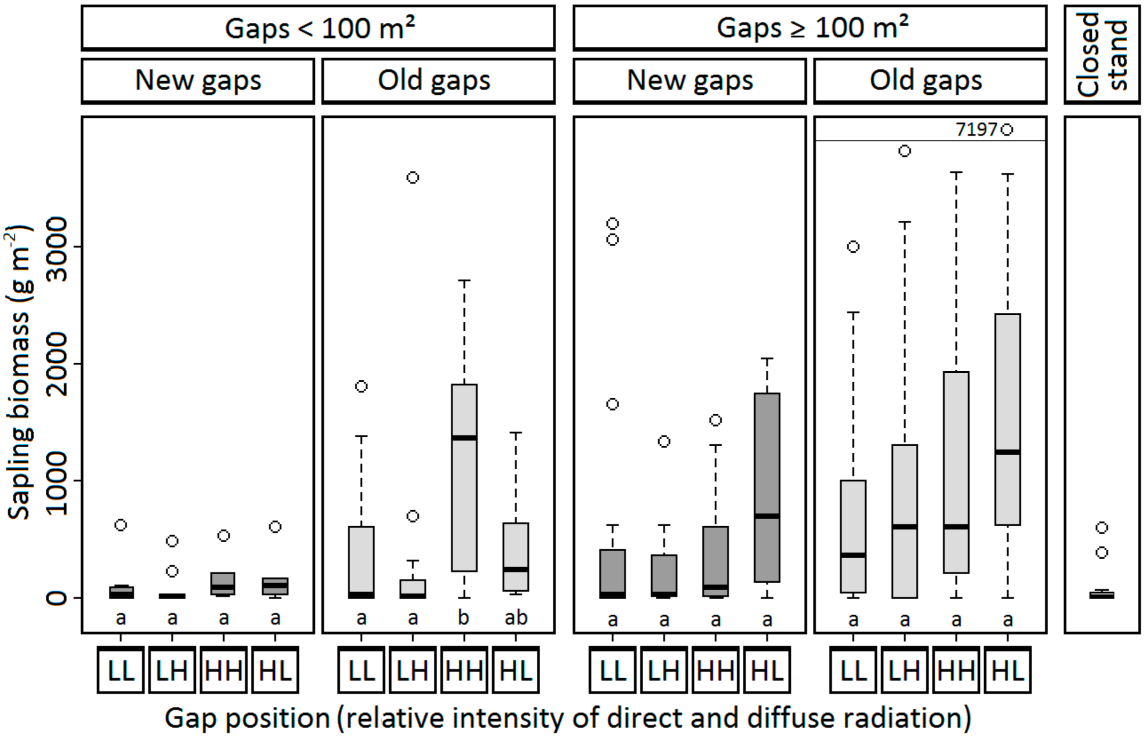

Figure 5. Estimated sapling biomass in squares at different position in a gap that formed between 2003 and 2013 (new gaps; dark grey) or prior to 2003 (old gaps; light grey) presented for small (<100 m^2) and medium-sized gaps (≥100 m^2). The four gap positions are characterized by the availability of different relative intensities of direct and diffuse radiation (high = H, low = L; first letter for direct and second for diffuse radiation; see Table 1 and Figure 1) following Diaci [38]. The density values of closed-canopy plots are displayed at the right for comparison (32 belt transects á 13 m^2 area). Box-whisker plots with median (thick line), 25-and 75-percentiles (box) and extremes not exceeding the 1.5fold of the interquartile range (whiskers). Dots indicate extreme data points beyond 1.5 times the IQR. Different letters below the boxes indicate significant differences between the gap positions within gaps of a certain size and age class (linear hypothesis testing).

In medium-sized new gaps, median biomass values were very low in classes *LL* and *LH*. They increased slightly toward *HH* and peaked at a much higher level in class *HL*. As the relative proportions of saplings in different height classes were relatively similar across gap positions (Figure S2), the pattern largely reflects that for sapling density. In old gaps of medium size, *LH* and *HL* comprised relatively large proportions of saplings in larger size classes. Consequently, the pattern for cumulative sapling biomass differed considerably from that for sapling density. Sapling biomass was at a comparably high level already in low-light conditions (*LL*). It reached a somewhat higher median in squares receiving high diffuse radiation (*LH* and *HH*), and peaked at twice this value in squares receiving high direct, but low diffuse radiation (*HL*). Especially in the medium-sized gaps, variation of sapling biomass among squares was generally high in all four light classes.

When testing the effect of gap age on the individual gap positions (Table S1), sapling biomass in *HH* squares of old gaps was found to be significantly higher than that in *HH* squares of new gaps for both gap size classes (small and medium). Gap size had no significant effect. However, the differences between the gap size and gap age classes described above visually reflect the influences of both factors on the sapling biomass that were found to be significant in our model calculations (Table 2).

Table 2. Summary of ANOVA results (p-values) of generalized linear mixed effects models (GLMM) on the influence of higher levels of direct or diffuse radiation, gap size and gap age, and sapling height and competition intensity on sapling abundance or performance. Sapling density and presence or absence were modelled together in a zero-inflated GLMM using a negative binomial distribution in the complete sample of 229 plots (squares of 4 m^2 size). Influence on the log biomass per ground area in the subsample of 179 plots with regeneration was modeled with a GLMM with a Gaussian distribution. Shoot length growth was modeled for 151 plants as well with a GLMM with a Gaussian distribution. Significant results ($p \leq 0.05$) are printed in bold. Factors that were not considered in the respective model are marked by -.

Response Variables	**Influencing Factors**					
	High Dir.	**High Diff.**	**Gap Size**	**Gap Age**	**Sapling Height**	**Comp. Intensity**
Sapling presence	**0.001**	0.605	0.212	0.889	—	—
Sapling density	**0.031**	0.382	0.077	0.860	—	—
Shoot length growth	0.971	**<0.001**	**<0.001**	—	**<0.001**	0.472
Sapling biomass	0.069	0.634	**<0.001**	**0.004**	—	—

4. Discussion

4.1. Comparing Beech Regeneration in Gaps and Closed-Canopy Patches

In this beech virgin forest, the density and estimated cumulative biomass of saplings ≥0.5 m height were significantly higher in "understory gaps", i.e., gaps allowing radiation penetration to at least 3 m above ground, than in closed-canopy patches ($p < 0.001$, Wilcoxon rank-sum test). This clearly demonstrates that gap formation has a large influence on the regeneration structure, in support of our first hypothesis. Positive gap effects on regeneration have been observed in many forest types from the boreal zone to the tropics [41,42], and they should be especially strong in light-demanding tree species. One would expect that highly shade-tolerant late-successional species such as beech are less dependent on gap formation, and very large gaps might even inhibit the development of shade-tolerant tree saplings, which thrive best in semi-shade [5,56]. The evidence from beech-dominated virgin forests on the role of canopy gaps for the regeneration process is indeed contradictory. While some authors found, similar to our study, gaps to have a positive effect on the establishment and growth of beech offspring [33,43,44], others detected no explicit gap influence on the structure of the regeneration [17]. The latter finding suggests that beech saplings are capable of tolerating the shade cast by the nearly closed canopy in natural beech forests, which is characteristic for large parts of the stand. This may not only be caused by the well-known high physiological shade tolerance of *Fagus sylvatica* seedlings and saplings [5,9,11], but may also reflect the fact that canopy gaps increase the light levels on the ground on a much larger area than just in the projected gap area [57]. The cumulative expanded canopy gap area, i.e. the area of the stand approximately influenced by gap formation, comprises more than a quarter to half (29–55%) of the total area in beech-dominated virgin forests, even though cumulative gap area itself covers only about 13–16% [24,27,31].

However, there may be other reasons related to methodology, why Nagel et al. [17] did not detect a significant gap effect on the structure of the regeneration. These authors used a relatively broad gap definition in terms of the regeneration layer, including also gaps that are filled by larger saplings and young trees (up to 15 m in height). If a broader gap definition is used which considers both understory gaps and canopy gaps, the average gap becomes more similar in its light regime to the closed-canopy stand. The presence of larger saplings and understory trees decreases light transmission to the ground and thereby effectively reduces the number of surviving saplings in lower strata. If we had included canopy gaps with such tall saplings and understory trees, it is likely that the statistical difference of tree density in gaps compared to that in closed-canopy plots would have been weakened or even lost. Actually, Nagel et al. [17] did not compare gaps with the closed-canopy stand, but with average stand conditions, which also may have included plots that were affected by gaps. The difference between gaps and average stand conditions diminishes with a growing proportion of gaps in total stand area.

4.2. The Role of Gaps for Beech Regeneration

Openings in the forest canopy do not only affect the light availability on the projected gap area but cause a range of light conditions in the gap and the surrounding forest area, from deep shade to full sunlight [58]. By analyzing beech regeneration along belt transects that reached well beyond the projected area of differently sized gaps, and on plots under closed-canopy conditions, our study covers the existing gradient in light availability.

We hypothesized that the position in the gap influences the establishment success of beech seedlings and the height growth of seedlings and saplings, and thus causes heterogeneity in the spatial distribution of sapling density and biomass in the course of time (H2). When an understory gap is created and light levels become more favorable for beech offspring, newly established seedlings usually meet an already existing seedling and sapling population that managed to persist at low densities under closed-canopy conditions. According to the shoot length growth data from Kyjov forest, small seedlings that established prior to gap formation, and many younger saplings from post-disturbance colonization events must have reached or exceeded the height threshold (≥0.5 m) used here to count them as saplings even in new gaps. In newly formed understory gaps, we found an equally low median sapling biomass in most gap positions (Figure 5) which differed only slightly from that of closed-stand conditions. This finding suggests that there were no differences in pre-disturbance regeneration structure.

Changes over time in sapling density largely depend on the availability of seeds and the conditions for germination and survival. While seed germination seems not to depend on light availability in European beech [6,9], radiation intensity has frequently been reported to be a key factor determining the survival and development of seedlings and saplings [9,11,12,59–62]. Small saplings of 0.5–1.5 m height showed a median shoot length growth rate of 10–18 cm a^{-1} in the gaps in Kyjov, which is in the range of growth rates recorded for beech saplings under 9–15% relative light intensity [11]. At such light intensities, beech is capable of forming stable seedling banks, as observed in a mixed beech-fir-spruce forest in Poland [9], which implies that mortality rate generally did not exceed the rate of establishment. In accordance, median sapling density was higher in all gap positions than in the closed stand in Kyjov.

The GLMM revealed a significant effect of direct radiation intensity on sapling density, but no effect of diffuse radiation intensity. Generally higher sapling densities were observed in the light regime classes *HH* and *HL* with comparatively high direct radiation as compared to class *LH* with high diffuse radiation, suggesting a dominant effect of direct light intensity on sapling density in support of the first part of our second hypothesis (H2). In contrast, high amounts of diffuse radiation seem to promote sapling growth but not seedling establishment. This view is supported by the observation that sapling shoot length growth was higher in gap positions with high diffuse radiation than in positions with low diffuse light, while there was no positive effect of elevated levels of diffuse radiation on sapling density (Table 2). Thus, the rate of seedling establishment and early survival seems to depend largely on the intensity of direct radiation.

Even though the availability of direct light is comparatively low in the *LL* microsites, in old medium gaps they showed the highest median sapling density of all gap positions. Sapling density in these gap positions (*LL*) was significantly higher in old medium gaps than in old small gaps. Thus, there must be other factors that positively influenced establishment and survival in the *LL* microsites of medium gaps. We suggest that a combination of seed dispersal effects and higher diffuse radiation (due to increasing gap size) likely is responsible for the high sapling density. Beech seeds are dispersed only within small distance to the source tree through barochory and zoochory. Therefore, seed density is typically by far higher below fruiting trees (*LL* and *HL* microsites) than at more distant locations, e.g. in gaps with higher light intensity [7,63,64]. Even if the rate of establishment is comparably low, the higher density of seeds might lead to a higher absolute number of seedlings. The spatial effect of seed availability imprinting on the spatial pattern of tree regeneration in gaps was shown in several studies in previously managed beech forests [40,65,66]. Even though not significant, gap size tended to be an important factor for sapling density in the model calculations ($p = 0.077$). Assuming similar seed densities in positions below the canopy, the higher sapling density in *LL* microsites of medium gaps indicates that the rate of establishment is higher in medium than in small gaps. As saplings in the gap periphery showed considerably higher shoot length growth rates in medium than in small gaps (Figure 4), it seems likely that seedling and sapling survival also profit from a larger gap size.

Seedling survival and the associated sapling density could also depend on competition for light in dense sapling populations. However, our sapling density data suggest that plant densities were in most cases <1 m^{-2} and thus too low to result in significant competition between saplings. Only in gap position *HL*, median sapling density exceeded 1 m^{-2} already in new gaps and competition may have resulted in self-thinning processes. Median sapling density and variability in these positions were lower in old gaps compared to new gaps.

Several studies reported negative effects on regeneration establishment and development by root competition from the bordering stand [67–69]. Thresholds for categorizing relative intensity of root competition would approximate those for diffuse radiation. The categories of intensity would be inversely arranged, i.e. root competition is relatively high in the gap periphery and low in the gap interior. However, in medium-sized gaps the highest sapling densities and values for biomass were found in the gap periphery (*LL* and *HL*), indicating that establishment and productivity of beech saplings were not fundamentally constrained by root competition.

The significant positive effect of comparatively high direct radiation intensity on sapling density may perhaps relate more to associated thermal effects than to the influence of radiation itself. Notably, air temperature close to the ground and soil surface temperature are typically higher in gap positions which receive high light intensities [70], and these reach maxima when direct sunlight hits the spot [71]. A warmer soil surface could positively affect germination and early seedling development [72], especially at relatively cool sites as in Kyjov forest. Elevated soil surface temperatures could also increase the N mineralization rate in the organic layer [73], which may facilitate seedling survival on acid, relatively nutrient-poor soils. Finally, more rapid decomposition in the warmer gap positions (*HH* and *HL*) could result in thinner organic layers, which represent an improved seedbed and favor early seedling survival [60,74]. A lower thickness of the organic layer along with a higher density of beech regeneration in gap positions receiving relatively high direct sunlight (*HH* and *HL*) was observed in a Slovenian beech-fir forest [40].

Gap age (<10 or >10 years) did not significantly affect regeneration density. However, the higher sapling densities in gaps compared to closed-stand conditions suggest that a considerable number of beech seedlings must have established in the first months or years after gap formation, especially in gap positions *HH* and *HL*. As new gaps were not formed immediately before the survey, this early period of colonization was largely missed in our study. Further, the subsequent temporal development of sapling density was not consistent across gap positions (Figure 3) with either increases, decreases or no changes in density. Therefore, a significant gap age effect did not appear in our data. The observed trends in sapling density between new and old gaps may be interpreted as an expression of interacting effects of seed dispersal (high in *LL* and *HL*), seedling establishment success (high in *HH* and *HL*), and competition (reduced density in *HL* in old gaps).

The main determinants of the shoot length growth of seedlings and saplings were the initial size of the plants and the relative amount of diffuse radiation, which is related to gap size [34,40]. This finding confirms our hypotheses H3 and H2. Positive effects of increased levels of diffuse radiation on shoot length growth of beech regeneration have frequently been observed [10,12,62], but see [75]. In other studies that applied the conceptual model of Diaci [38] for separating light classes, higher growth rates in gap positions receiving relatively high diffuse radiation have been reported as well [44,76]. Thus, our findings are in agreement with the results of experiments and field observations on the light response of tree sapling growth. In accordance, beech sapling height was found to increase progressively from the area under the canopy towards the gap interior [44,77]. However, the positive effects on sapling height development by increasing diffuse radiation are saturating [12], i.e., sapling height development likely benefits from increasing gap size only until a certain size is exceeded [78]. That shoot length growth does not only depend on the abiotic environment but also on plant size supports earlier observations [10] and is an indicator of the competitive advantage for saplings that established prior to gap formation. The growth data indicate that only in the periphery of small gaps, light intensity fell below a certain critical level, which strongly hampered the height growth especially of medium-sized saplings (1.5–2.99 m tall).

In contrast to the situation with diffuse light, we did not find a significant stimulation of sapling growth rate by elevated levels of direct light. This may result from the well-known sensitivity of young beeches to extended periods of excess radiation, which may cause photoinhibition [79] and the formation of small, more xerophytic leaves [12]. Yet, radiation intensity matters: Short episodes of higher direct light intensity, as they occur in sunflecks, can contribute much to the carbon gain of understory plants, as was shown by gas exchange measurements for beech regeneration [80,81]. Beech seedlings and saplings have a remarkable potential to adapt to the elevated light levels, which are found in gap positions receiving direct light [52]. It is not known whether part of the additional carbohydrate gain received through the interception of direct radiation is invested belowground, or in increased diameter growth.

How successful beech regenerates in gaps of different sizes and ages, may best be seen from our data on sapling biomass per ground area. Although we have only biomass estimates and no harvest data, they demonstrate that the regeneration success in small gaps (<100 m^2) is clearly highest in gap position *HH* with comparatively high direct and diffuse radiation. In the other gap positions, either plant establishment (and thus sapling density) or growth rate was limited by low direct light and/or diffuse light.

In medium-sized gaps, sapling biomass reached higher values in most gap positions (except for *HH*) than in small gaps, probably due to higher levels of diffuse radiation that promoted shoot length growth even in the gap periphery. Here, saplings in the smallest recorded size class (<1.5 m) grew in height at relatively similar rates in all gap positions. Consequently, in these larger gaps, the density of seedlings established prior to, or shortly after, gap formation largely determined sapling biomass. In contrast, subsequently colonizing seedlings (which appeared mainly in *HH* and *LL*) contributed only to a minor extent. Thus, early colonizing advanced saplings dominated space filling. The rather low sapling density in gap position *LH* (median density in new medium-sized gaps: $0.5\ m^{-2}$) seems to be sufficient to fill the area without any time lag. The biomass data also suggest that competition between saplings plays a decisive role for sapling survival only in later phases of regeneration development, while seedling densities are generally too low for lateral competitive interaction in the early phase of gap filling. In peripheral gap positions (*LL* and *HL*), lateral canopy closure and increasing sapling heights and leaf areas in the gap interior (*LH* and *HH*) will likely hamper the development of the saplings in the medium term.

5. Conclusions

European beech is one of the most shade-tolerant temperate tree species. It is capable of establishing a vital regeneration layer under the sparse light of a nearly closed canopy with only ca. 5–10% of incident light [5,9]. From complex structured beech virgin forests there is no consistent evidence on the role of canopy gaps for the regeneration process. The comparison of understory gaps and closed-stand conditions clearly indicates that gaps play an important role for the density and growth of beech offspring in the Kyjov forest. However, in many cases gap formation seems to promote the growth of an already existing tree understory rather than facilitating the establishment of new seedlings [33]. This is because beech regeneration might endure long periods of suppression after a gap was closed laterally but also because the gap effect was found to reach well beyond the projected gap area. Furthermore, our study on understory gaps showed marked spatial differences in sapling density and height growth within the gaps and their direct neighborhood and across gaps of different size, which seem to depend on variation in the light regime and seed availability. However, other abiotic factors such as temperature or nitrogen availability could have an additional effect on this pattern. As relevant abiotic factors may differ considerably between different forest stands, the results of our study cannot be generalized without caution. Experimental approaches are needed to disentangle the influence of these often correlating environmental factors on beech regeneration in gaps.

A major result of our regeneration mapping is that gap microsites exposed to different intensities of direct and diffuse light seem to influence sapling density and growth in different ways. It appears that direct light in most cases promotes seedling and sapling density of beech, while growth promotion of existing saplings is generally higher under elevated levels of diffuse light. We interpret these findings as support for the validity of the conceptual model of gap microsites proposed by Diaci [38].

Our approach that combines information on regeneration structure, sapling growth and gap size with information on gap age succeeds in identifying patterns in regeneration development in this complex structured forest. The approach might prove useful for studying the regeneration process in other temperate broadleaved forests, as it seems there are many similarities in forest dynamics processes. However, it must be considered that our study addresses only part of the structural conditions released by canopy disturbances.

We assume that the detected spatial pattern in gap regeneration will change over longer time spans (decades): Small gaps <100 m^2 are often closed by lateral expansion of adjacent beech trees [33] and only very few released understory trees may be able to grow into the canopy within the relatively short period of higher light availability. Thus, the area of former small gaps will usually be associated with quite heterogeneous lower canopy layers. This pattern may increase the resilience of the forest in the face of future disturbances. In medium-sized gaps ≥100 m^2, in contrast, the density of advanced regeneration seems in most cases to be sufficient to completely fill the gap area, even when the rate of post-disturbance colonization is low. This is typically the case in gap position *LH*. A few saplings in the gap interior (gap positions *LH* and *HH*) will likely manage to grow into the canopy, while in the gap periphery (gap positions *LL* and *HL*) sapling growth sooner or later will be suppressed by the cover of trees bordering the gap. Nearly equal current plant sizes and growth rates of the dominant saplings in gap positions *LH* and *HH* suggest that the successful individuals will reach the canopy layer more or less at the same time and form a relatively homogeneous, cohort-like canopy patch that is filling the former gap. However, the high variability in sapling density and growth suggests that other ecological factors might affect regeneration development as well, and understory gaps in beech virgin forests could follow very individual development paths. This may render it difficult to reach at a fully mechanistic understanding of gap dynamics in beech virgin forests.

Looking at our findings from a forest management perspective, the trends for regeneration development in the Kyjov forest suggest that small gaps (<100 m^2) are suitable to initiate regeneration but do not allow for good sapling growth over longer periods. Further, there might be negative effects on growth morphology of saplings [82]. These findings raise doubt on the suitability of small gaps in the management of beech forests for commercial purposes or for a progressive conversion of even aged stands towards a vertically heterogeneous structure, at least under comparable dystric soil conditions. A frequent expansion of gaps to avoid such negative consequences would be costly. In large gaps, that provide good growth conditions for longer time periods, however, the density of saplings might be insufficient to properly recover the area and problems with competing herbaceous plants might occur. A good trade off that accounts for a sufficient density of saplings and good and continuous growth could be archieved by initial irregular shelterwood cutting followed by gap cuttings of 500 to a few thousand m^2. Shelterwood cutting should only cover a part of the later gap or be suspended, if the recruitment of more light-demanding tree species is desired.

Supplementary Materials: The following information is available online at http://www.mdpi.com/1999-4907/11/5/585/s1, Figure S1: Scheme of the testing procedures, Figure S2: Proportion of sapling height classes in different gap positions, Table S1: Report of p-values from testing for differences in sapling density and cumulative sapling biomass, Table S2: Report of p-values from testing for differences in mean shoot length growth.

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