Gap regeneration patterns in relationship to light heterogeneity in two old-growth beech–fir forest reserves in South East Europe

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Summary

Gap regeneration in two old-growth forest reserves in Slovenia (Rajhenavski Rog) and Croatia (Čorkova Uvala) was analysed in relation to within gap light heterogeneity. Both reserves were located in the Dinaric mountain range in south-central Europe and were dominated by beech (Fagus sylvatica L.) – silver fir (Abies alba Mill.) forest communities with similar growing conditions. In total, the two largest gaps (700–2000 m²) in each reserve were included in the study (n = 4), plus a further four gaps in Rajhenavski Rog and three in Čorkova Uvala (200–500 m²). All the gaps were ~10 years old and originated from one or two successive events, mostly due to a combination of fungi attack and windthrow. Consequently, all gaps had complex geometry and were covered by a well-developed regeneration layer. Each gap was mapped, followed by establishment of a N–S oriented 5 × 5 m grid within and around the area of the canopy opening. At the grid intersections 773, 1.5 × 1.5 m plots were established. On each plot, the coverage of tree regeneration and ground vegetation, seedling density in different height classes and browsing damage were recorded. In addition, the total stretched length and last growing season increment of the leading stem was measured on selected seedlings in each plot. Relative diffuse and direct radiation were estimated using digital hemispherical photographs. All plots were classified into four microsites according to direct and diffuse radiation levels, and microsites were tested for differences in regeneration height and density. While there was more woody regeneration and an almost fivefold higher (6.2 vs 1.3 m⁻²) average total regeneration density in Rajhenavski Rog, mainly due to a high (5.5 vs 0.6 m⁻²) density of beech, there was more ground vegetation and a higher density of silver fir seedlings in Čorkova Uvala. The within-gap regeneration patterns proved to be similar in both forest reserves and showed that 1-year-old seedlings of beech and silver fir and small beech seedlings preferably recruit on microsites under closed canopy or close to gap edges with lower levels of direct and diffuse radiation. There was no significant difference in density of large-beech seedlings among the microsites, yet height and height increment were higher on microsites receiving the highest levels of direct and diffuse radiation. Within-gap heterogeneity in light conditions appears to significantly
Introduction

The importance of tree-fall gap disturbances for forest regeneration processes has long been recognized (Watt, 1925; Platt and Strong, 1989). One of the important characteristics of gaps that affects the establishment and growth of tree seedlings is within- and around-gap environmental heterogeneity (Beatty, 1984; Lawton and Putz, 1988; Veblen, 1989; Gray and Spies, 1996). Within-gap heterogeneity may result from many factors, such as variation in microtopography or microsites (i.e. nurse logs and root pits and mounds). Another important factor includes heterogeneity in light regimes, especially if we partition light into direct and diffuse components. For example, the amount of diffuse and direct radiation varies within gaps, from the centre to the edges and along N–S and E–W gradients (Poulson and Platt, 1989; Canham et al., 1990; Wayne and Bazzaz, 1993; Ritter et al., 2005). There is a substantial difference in photon flux density between the direct and diffuse components of radiation and reaction of different plant species to certain combinations of both components vary significantly (Larcher, 1983). Abiotic factors like incidence to frost, soil and air temperature humidity as well as biotic factors such as insect abundance and crown and root competition are related to the distribution radiation components (Krcmer, 1966; Ausslenac, 2000; Schütz, 2004; Brang et al., 2005). Knowledge about the distribution of both components can therefore be useful for explaining environmental heterogeneity within canopy gaps (Poulson and Platt, 1989; Diaci and Thommann, 2002), which may have important consequences for patterns of tree regeneration (Galhidy et al., 2006; Mountford et al., 2006).

In the beech–fir dominated forests in south-central Europe, small- to intermediate-scale canopy gaps are the dominant disturbance process driving forest dynamics (Diaci et al., 2003; Zeibig et al., 2003; Nagel and Diaci, 2006; Nagel et al., 2006). Natural regeneration and tree species composition of these ecosystems has been well studied in the past (Mlinšek, 1967; Prpić, 1972; Mayer and Neumann, 1981; Boncina, 2000; Bončina et al., 2003), but there is a lack of knowledge concerning the regeneration response to different regimes of direct and diffuse light in beech–fir forests in the Dinaric region (Matić, 1983). While seedlings of beech and fir can establish and grow in the relatively low light levels beneath the forest canopy (Madsen, 1995; Szwagrzyk et al., 2001; Stanciu and O’Hara, 2006b), the increased light levels in canopy gaps may be important for the recruitment of saplings for both species (Collet and Chenost, 2006). However, little is known about how light asymmetry within gaps influences the density and height growth of regeneration of these two species.

Data from previous inventories (Hartman, 1987; Prpić and Seletković, 1996; Roženbergar, 2000) in old-growth Dinaric beech–fir forest show an alternation in the dominance of silver fir and beech. Once silver fir-dominated forests are, especially in the last three decades, turning into forests dominated by beech in the total living volume and regeneration. This trend has been much more emphasized in Slovenia, where a low level of recruitment success for silver fir has been documented (Debeljak, 1997; Bončina et al., 2003). In contrast, no problems with silver fir regeneration were reported in similar forest communities on comparable site conditions in Croatia (Prpić and Seletković, 1996). Therefore, one of the aims of this study was to understand if this difference can be explained with differences in light conditions and to discuss other factors which could also be involved.

In this research, we examined regeneration of beech and silver fir in relation to light regimes
in and around a range of different-sized canopy gaps in two old-growth forest stands in the Dinaric mountain range. Other less abundant species are also present in both forest stands, including sycomore maple (Acer pseudoplatanus L.), wych elm (Ulmus glabra Huds.), spruce [Picea abies (L.) Karsten], common ash (Fraxinus excelsior L.) and large-leaved lime (Tilia platyphyllos Scop.). Previous research has documented a 10 per cent decrease of silver fir living volume between 1976 and 1995 in Rajhenavski Rog. In Čorkova Uvala, silver fir volume has also declined, but only by 2 per cent from 1970 to 1987. The volume of beech, in contrast, has increased by >10 per cent in both reserves during the same periods (Figure 2). According to the latest inventory, these trends are continuing in the same direction in both regions (Ficko and Boncina, 2006).

Both study sites occur on a typical karst landscape with limestone parent material and free draining and patchy rendzina soils. Soil depth and macro- and microtopography are highly variable, changing the site conditions significantly over very small spatial scales. In addition, karst phenomena such as sinkholes and rock outcrops at or close to the surface are common on both sites.

Materials and methods

Research sites

The research was performed in two natural old-growth forest reserves, Rajhenavski Rog in Slovenia and Čorkova Uvala in Croatia (Figure 1). The site conditions are similar in both forest reserves, except the elevation is a bit higher in Čorkova Uvala (Table 1). Both forests are dominated by beech–fir communities, which are typically located between 700 and 1200 m in the Dinaric mountain range. Other less abundant species are also present in both forest stands, including sycomore maple (Acer pseudoplatanus L.), wych elm (Ulmus glabra Huds.), spruce [Picea abies (L.) Karsten], common ash (Fraxinus excelsior L.) and large-leaved lime (Tilia platyphyllos Scop.). Previous research has documented a 10 per cent decrease of silver fir living volume between 1976 and 1995 in Rajhenavski Rog. In Čorkova Uvala, silver fir volume has also declined, but only by 2 per cent from 1970 to 1987. The volume of beech, in contrast, has increased by >10 per cent in both reserves during the same periods (Figure 2). According to the latest inventory, these trends are continuing in the same direction in both regions (Ficko and Boncina, 2006).

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Field methods

Field surveys of both forest reserves were carried out to find the largest existing canopy gaps with a regeneration layer of approximately the same age. The latter was defined by the presence of seedlings and saplings generally not exceeding 2 m in height. Thus, all the gaps chosen in this study were relatively young (around 10 years old). Except for very recently created gaps less than a few years old, where the regeneration response was still poor, most gaps in both reserves had a well-developed regeneration layer in different developmental stages depending on the gap age. Gaps were only chosen if the adjacent canopy in the neighbourhood of the gap was closed in order to avoid the influence of gaps in close surroundings. The canopy around the gaps was composed of beech and silver fir in approximately equal proportion and was ~40 m high. The two largest gaps (700–2000 m²) found in each reserve were included (n=4), plus an additional four gaps in Rajhenavski Rog and three in Čorkova Uvala (200–500 m²) with site conditions (slope, exposition, soil) and gap age similar to those in

Figure 1. The location of the old-growth forest reserves Rajhenavski Rog, Slovenia and Čorkova Uvala, Croatia.
the large gaps. All selected gaps were diverse in shape, around 10 years old and created in one or two successive events mostly due to a combination of fungi attack and windthrow.

The results of this study cannot be held as representative for the whole area of both reserves, since they do not include information on highly shaded areas under closed canopy. However, in both forest reserves, the research plots were created in open and partly shaded parts of the forest stands and were therefore representative for the areas where intensive regeneration processes were taking place, which was the main focus of this study.

All gaps were mapped to analyse gap shape and area. The gap edge was defined as the vertical projection of the crowns of the canopy trees surrounding the gap. Between 2001 and 2004, under each gap and a short distance (5–15 m) under the adjacent canopy, a N–S oriented 5×5 m grid was established and 773, 1.5×1.5 m plots were established on the grid intersections (see Table 1). For each plot, we measured the light conditions and tree regeneration. The per cent cover of tree regeneration and ground vegetation was visually estimated to the nearest 1 per cent. All seedlings of each tree species were counted, scored for browsing damage (seedlings were categorized as browsed when the leading stem was damaged) and categorized within several height classes, which include 1-year-old seedlings, small seedlings (<20 cm tall) and large seedlings (>20 cm tall and <5 cm d.b.h.). Thus, the large seedling category also includes individuals >1.3 m in height (generally termed saplings). In addition, the total stretched length and increment of the leading stem in the last growing season were recorded to the nearest 1 cm for the five tallest dominant beech seedlings in each plot.

Relative per cent diffuse (FDIF) and per cent direct (FDIR) radiation were estimated from digital hemispherical photographs taken in completely overcast sky conditions at 1.3 m height with a Nikon 995 digital camera and calibrated...
fish-eye lens from Regent WinScanopy accessories. Light intensity parameters were processed with WinScanopy pro-d software (Regent, 2003).

Data analyses

Gap geometry was analysed by examining gap area–perimeter relationships. An index was calculated to show how much the perimeter of the gap deviates from that predicted for a circle at a certain gap size. An increasing index value indicates an increase in the irregularity of gap shape (Lertzman and Krebs, 1991). A comparison of light conditions among gaps was only performed for plots located inside the gaps without any coverage of the upper canopy.

Due to non-normal data, non-parametric Mann–Whitney U tests were used to test for differences in density and browsing damage for both main tree species between the two sites (Zar, 1999). Binary logistic regression procedures were used to test the relationship between direct and diffuse light and the appearance of 1-year-old, small and large beech and silver fir seedlings per square metre, where the presence of silver fir and beech was used as a dependent variable. For this analysis, all plots were classified according to the occurrence of silver fir or beech seedlings (0, no silver fir or beech seedlings and 1, one or more silver fir or beech seedlings). The analysis was performed in each forest reserve separately for FDIR and FDIF as predictor variables. The odds ratio and associated 95 per cent confidence interval were used for interpretation. The odds ratio represents the change in odds when the independent variable increases by 1 unit. In our case, an odds ratio >1 indicates that a seedling has a higher predicted probability of being present with increasing radiation values, while an odds ratio <1 indicates a lower predicted probability of being present with increasing radiation values (Hosmer and Lemeshow, 2000).

To examine the influence of direct and diffuse relative radiation on certain measured parameters, the plots were classified into four microsite types (A, B, C and D) according to the prevailing combinations of both radiation components (Diaci, 2002). The median radiation values were used as thresholds for the four types as follows: A, high FDIF and low FDIR; B, high FDIF and high FDIR; C, low FDIF and low FDIR, and D, low FDIF and high FDIR. Regardless of irregular gap shape, the plot types are typically located in certain areas of the gaps (Figure 3). The locations of the plot types indicate that there is a connection between groups defined by radiation and other ecological factors, such as precipitation, temperature, humus decomposition rate and soil moisture, as they all partly follow gap geometry (Diaci, 2002; Diaci et al., 2003). Kruskall–Wallis tests (Zar, 1999) were then performed separately for both forest reserves to examine differences in several variables between the four microsites. Significant differences between pairs of microsites were tested using Nemenyi and Dunn post-hoc tests (Zar, 1999). The variables tested were woody regeneration coverage, ground vegetation coverage, density of 1-year-old beech and fir seedlings per square metre, density of small and large beech and fir seedlings per square metre and average length and length increment of five dominant beech seedlings per plot.

Figure 3. Typical spatial distribution of plot types (A, B, C and D) according to received diffuse (FDIF) and direct (FDIR) radiation values in a gap in an old-growth beech–fir forest (A, high FDIF and low FDIR; B, high FDIF and high FDIR; C, low FDIF and low FDIR, and D, low FDIF and high FDIR). One of the research gaps in Rajhenavski Rog with an area of 794 m² and an area–perimeter index of 3.1 is presented. The bold line represents the edge of a gap (e.g. crowns of surrounding trees) and + signs show the locations of sampling plots.
Results

The average gap size in Rajhenavski Rog (N=6) was larger (640 ± 166 m²) compared with Čorkova Uvala (N=5) (487 ± 91 m²), which was due to one larger gap in Rajhenavski Rog (1317 m²). The remaining gaps were comparable in size (Figure 4). In all gaps, the relative radiation values for FDIF and FDIR were relatively low, and they did not exceed 23 and 18 per cent, respectively. Both FDIR and FDIF increased with gap size. When similar-sized gaps were compared, there was less radiation in Čorkova Uvala in all cases (Figure 4). No significant difference was observed in the area–perimeter relationships between gaps in both forest reserves. All gaps had between two and four times larger perimeter compared with that of a circle, indicating complex gap geometry.

The average total density of all regeneration was nearly five times higher (6.2 m⁻²) in gaps in Rajhenavski Rog compared with gaps in the Čorkova Uvala (1.3 m⁻²) forest reserve (U=17 482, P < 0.0001). This was mostly due to the higher (5.5 vs 0.6 m⁻²) density of beech in Rajhenavski Rog (see Figure 5, right). However, the average density per plot of silver fir seedlings was greater in Čorkova Uvala (0.6 vs 0.3 m⁻², U=62 720, P=0.0004) and there were no silver fir seedlings taller than 50 cm in Rajhenavski Rog (see Figure 5, left). The distribution curves for beech and silver fir (Figure 5) indicate that in Rajhenavski Rog there had been a recent, vigorous flush of beech establishment, whereas in Čorkova Uvala this had been more limited. Silver fir seedlings established in both reserves, but only recruited into taller seedling height classes in Čorkova Uvala.

On average, the proportion of heavily browsed beech seedlings was 26.3 and 13.9 per cent in Rajhenavski Rog and Čorkova Uvala, respectively (U=22 774, P < 0.0001). There were more heavily

\[Figure 4.\] Mean values and ±95% confidence interval for relative (%) direct (FDIR) and diffuse (FDIF) radiation according to gap size separately for the Rajhenavski Rog and Čorkova Uvala old-growth forest reserves. Only plots with no upper canopy were analysed.

\[Figure 5.\] Density (number per square metre) of fir (left) and beech (right) 1 year old (oy) and older seedlings in different height classes (cm) based on all recorded seedlings in the Rajhenavski Rog and Čorkova Uvala old-growth forest reserves.
browsed silver fir seedlings in Rajhenavski Rog (31.8 per cent) compared with Čorkova Uvala (11.3 per cent, \( U = 9424, P < 0.0001 \)). In general, the damage was more severe compared with beech due to the successive occurrence of browsing on the leading and first two lateral stems.

A significant, but weak relationship between FDIR and FDIF and the presence of silver fir and beech seedlings was confirmed in both forest reserves (Table 2). This was especially the case for 1 year old and small seedlings of beech and silver fir in Rajhenavski Rog. In Čorkova Uvala, there was a significant relationship between radiation and occurrence of silver fir seedlings in almost all height classes, which was not the case for beech. In all significant cases, except for small silver fir seedlings and FDIF, the odds ratio was <1, meaning that the probability of seedling occurrence decreased with an increase of FDIF and FDIR (Figure 6).

We tested the differences among the four microsites (A, B, C and D) for the selected parameters separately for the Rajhenavski Rog and Čorkova Uvala forest reserves. The average regeneration and ground vegetation cover per plot differed significantly between the four plot types in both reserves (Table 3). Regeneration cover was highest in plot type B, while ground vegetation cover was highest in plot type A. The results for 1 year old and small beech seedlings were consistent with both methods of analysis (Kruskal–Wallis test and logistic regression) and in both reserves, and showed that microsite A had the lowest density of these seedlings. Larger seedlings, which were the most numerous in both reserves, did not show any significant difference in density across the microsites. However, they were significantly taller and had larger height increments within gaps (microsites A and B) in both reserves and thus occupied larger areas compared with smaller seedlings.

A similar pattern was also observed for 1-year-old silver fir seedlings, yet seedling success was lowest in microsite B. Here, the results were significant only for Rajhenavski Rog. The results of the Kruskal–Wallis test were not significant for small seedlings, whereas the logistic regression showed a negative relationship with FDIR in both reserves. Taller silver fir seedlings were only present in Čorkova Uvala and again negatively related to direct light, while the post-hoc comparison of Kruskal–Wallis pairs was not significant (Table 3).

**Discussion**

This study provides useful information about natural regeneration processes in two old-growth, fir-beech forest reserves in the Dinaric Mountains. Major differences in the regeneration density and height distribution of both dominant species growing in gaps were detected between Rajhenavski Rog and Čorkova Uvala. We found an almost five times higher density of beech regeneration in Rajhenavski Rog, where the densities of beech seedlings were higher on the whole range of height classes. There are several possible explanations for this flush of beech regeneration in Rajhenavski Rog. One possible cause could be related to the lower relative radiation found in Čorkova Uvala, even though gap area–perimeter relationships and the height of trees surrounding the gaps were similar in Rajhenavski Rog. Other studies have reported a more diverse stand structure, larger gap fraction and lower levels of total living volume in Rajhenavski Rog (Mayer and Neumann, 1981; Hartman, 1987; Pričić and Seletković, 1996; Boncina, 2000). The more open canopy in Rajhenavski Rog may be partly related

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<tr>
<th>Table 2: Odds ratio estimates for logistic regression models predicting the probability of occurrence of silver fir and beech seedlings according to FDIF and FDIR</th>
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<tr>
<td>Rajhenavski Rog</td>
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<tr>
<td>Beech 1 year old 0.8384** 0.9806</td>
</tr>
<tr>
<td>Beech small seedlings 0.8898** 0.9688*</td>
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<tr>
<td>Beech large seedlings 0.9740 1.0128</td>
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<tr>
<td>Fir 1 year old 0.9303** 0.9727*</td>
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<tr>
<td>Fir small seedlings 1.0733** 0.9640*</td>
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<tr>
<td>Čorkova Uvala</td>
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<tr>
<td>Beech 1 year old 0.9427 1.0178</td>
</tr>
<tr>
<td>Beech small seedlings 0.9397 0.9074*</td>
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<tr>
<td>Beech large seedlings 1.0609 1.0016</td>
</tr>
<tr>
<td>Fir 1 year old 0.9128* 1.0086</td>
</tr>
<tr>
<td>Fir small seedlings 1.1091* 0.9154*</td>
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<tr>
<td>Fir large seedlings 0.9792 0.9132**</td>
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* \( P < 0.05 \), ** \( P < 0.01 \).
to the decline of silver fir in the reserve (Boncina et al., 2002), which likely increased the radiation levels beneath the canopy throughout the entire stand. In Rajhenavski Rog, there were twofold less silver fir, amounting to a density of ~0.3 m$^{-2}$. This number is reported to be insufficient for normal development and recruitment of this tree species in the upper canopy (Perko, 1977; Veselić, 1991; Jarni et al., 2005). Moreover, there were no silver fir seedlings taller than 50 cm, which may have important implications on the future tree species composition and natural development of this forest.

Beech, which can tolerate a broad range of understory light levels, manages to recruit in a variety of light conditions in young stages of growth, as it is capable of decurrent and polycyclic growth (Nicolini, 2000; Collet et al., 2001; Stanciociu and O’Hara, 2006a). In our study, the results of the comparison among microsites indicate differences
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in beech establishment and further recruitment niches. Beech 1 year old and small seedlings successfully establish on microsites under canopies as advance regeneration (Szwagrzyk et al., 2001), sustaining low light and precipitation levels and higher root competition from mature trees. These suppressed individuals can wait for long periods before experiencing a release event.

The fact that there was the highest coverage of ground vegetation on microsites A in both forest reserves suggests that on this locations inside gaps ground vegetation is an important competitor to tree seedlings. These microsites receive full precipitation and less direct radiation, which influences soil and air temperatures. There is also less root competition from older trees. Therefore, microsites A are relatively humid compared with microsites B and have less root competition than microsites C or D. Since ground vegetation is less drought resistant and can sustain less root competition than seedlings, these microsites are more favourable for development of ground vegetation (Helliwell and Harrison, 1979; Welander and Ottoson, 1997; Lof, 2000).

In regard to within gap regeneration of silver fir, the less preferred microsite seems to be B,
where the highest direct and diffuse light levels occur. The highest density of older and taller silver fir seedlings appears to be outside the microsites with higher values of direct light. This pattern was also documented in previous research (Grassi et al., 2004; Paluch, 2005; Stancioiu and O’Hara, 2006b). The difference in silver fir regeneration density between size classes across microsites was not as transparent as with beech. This could be due to additional factors, namely deer browsing (Ammer, 1996; Gill and Beardall, 2001; Kuiters and Slim, 2002; Heuze et al., 2005). Silver fir is far more preferred as forage and much more susceptible to browsing damage than beech (Motta, 1996; Senn and Suter, 2003; Heuze et al., 2005). Moreover, the reported deer density is substantially different between the two areas, amounting to 0.8 and 0.2 per 100 ha for roe deer and red deer, respectively, in the area around Čorkova Uvala (Anonymous, 2007), and 0.9 and 6.6 per 100 ha for roe deer and red deer, respectively, in the area around Rajhenavski Rog (Jerina, 2006, 2007). This was also supported in this study, where a higher level of browsing damage was found in Rajhenavski Rog compared with Čorkova Uvala.

Major differences in gap filling patterns as well as the analysed parameters were observed between the two old-growth forest reserves. This was especially the case for coverage of ground vegetation and regeneration. The former was significantly higher across all microsites in Čorkova Uvala, while the latter was significantly lower. Since the microsite groups were based on the same light data pool and therefore have the same light intervals in both reserves, light cannot explain this difference. Moreover, other ecological factors, such as climate, parent material, soil, exposition, relief and stand conditions were very similar between both reserves. Therefore, the difference in the density of large herbivores seems to be the most likely explanation for the differences in regeneration and ground vegetation abundance and spatial distribution.

Our study focused on middle-aged (around 10 years) gaps filled with seedlings, while younger gaps and relatively closed stands were not included. Therefore, the results presented here are only relevant for gap-phase regeneration in these stands and are not representative of regeneration patterns under the full range of canopy conditions found in these forests. In addition, only a short period of the regeneration cycle was studied, so that future studies should focus on further development of the regeneration including the recruitment of both tree species to the canopy layer.

**Implications for forestry**

This research suggests that the regeneration patterns and tree species composition cannot simply be explained using only light conditions in certain parts of a stand or canopy gap. There are many other factors that influence the regeneration (e.g. browsing, soil moisture, ground vegetation), which should be taken into account when discussing the use of different light conditions as a tool for reaching different silvicultural goals. Nevertheless, we believe that this study demonstrates the importance of partial shading from the upper canopy in regeneration processes in natural beech–fir forests. Two independent analyses used in this study confirmed, that beech and silver fir successfully establish beneath closed canopies. Further recruitment of beech into taller sapling stages seems to profit from both direct and diffuse light, while silver fir seems to avoid direct light. It was demonstrated that the establishment and further regeneration development of both species differs. Taking into account the higher light demand of beech in later regeneration phases and especially the tendency toward plagiotropic growth in low light levels, it seems reasonable to propose a selection system approach in areas with more silver fir, while in areas with prevalent beech regeneration the tending of already established beech stems in gaps seems more appropriate. Foresters in Central Europe have traditionally used the shelterwood system for regeneration of beech forests and partly in beech–silver fir forests (Matthews, 1989). Due to the different development niche of older seedlings between silver fir and beech, a combination of a selection system and irregular shelterwood system appears to be a favourable management solution.

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Conflict of Interest Statement
None declared.

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