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The spatial pattern and microsites requirements of *Abies alba* natural regeneration in the Karkonosze Mountains

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Abstract: Progeny of four adult silver firs, which were an admixture in Norway spruce (*Picea abies*) stand was, analyzed. The study was done in lower mountain zone of the Karkonosze (Giant Mts.) National Park (SW Poland). The seedlings occurred in two clumps related to the position of adult trees, whereas spatial pattern of the seedlings inside each clump was random. The seedlings were spaced mainly in distances 5–25 from the nearest adult tree. The maximal distance was up to 50 m. Most seedlings were established in accordance with main wind directions. Also, in these directions seedlings were more distant from adult trees than in other directions. The seedlings grew in better light environment (12% of PPFD) than average (9,6% PPFD). This effect was statistically significant. The height increment of the seedlings was low and was not correlated with light conditions. Similarly, there was not any correlation between the apical dominance ratio and light. The lack of this correspondence we attributed to browsing. The silver fir seedlings were significantly underrepresented in patches of *Vaccinium myrtillus*, on raw needles, under crown of adult trees and in concave micro-relief form. The underrepresentation in the places covered by canopy and in patches of bilberry we related to the indirect effect of continuous browsing, which leads to higher seedlings mortality in more shaded places and sites of stronger competition between forest floor vegetation and silver fir seedlings.

Additional key words: age structure, browsing, K-Ripleys function, safe sites, seedlings dispersal.

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Introduction

The actual number of silver fir in the Karkonosze Mts. (Giant Mts.) as well as in the whole Sudety massif, is extraordinary low. It is a consequence of past forest management and high level of air pollution in the 20-th century. The process of silver fir natural regeneration in the Sudety Mts. is also very poor (Dobrowolska 2000; Filipiak 2002; Filipiak and Barzdajn 2004). Natural regeneration in the Sudety Mts. is intensively studied, as a source of information about ecological requirements which lead to successful establishment of new fir generations (Dobrowolska 2000; Filipiak 2002; Robakowski and Wyka 2003). However, there are still questions concerning (a) the spatial pattern of regenerations, (b) seedlings microhabitats preferences, (c) influence of continuous browsing by red deers and deers.

The main reason of scarce silver fir regeneration in the Sudety Mts. at a landscape level is an extremely low number of parent's trees and their clumped distribution. Most of the sparsely distributed trees clumps consist of very low number of adult trees – more than half of them was composed of up to ten adult individuals (Filipiak and Barzdajn 2004). At the stand level, new individuals of silver fir are limited to the area of several square meters, in the vicinity of adult trees (Filipiak 2002). Thus, the natural regeneration is constrained by seeds supply, occurring only in sparse clumps of adult trees. However, detailed data about spatial distribution of silver fir regeneration and seeds dispersion is scarce. It is known that silver fir seedlings are readily browsed by large herbivores (e.g. Jaworski i Zarzycki 1983; Senn and Suter 2003), which can substantially affect the pattern of silver fir regeneration (Ammer 1996; Heuzea et al. 2005).

The aim of the study was to explore the habitat preference of fir regeneration, derived from detailed spatial analysis of seedlings distribution.

Materials and methods

Study site

The research was conducted in the compartment 47g of the Karkonosze National Park (50°46'04"N; 15°43'13"E). It is located in lower mountain zone (850 m a.s.l.), on a steep south slope (north exposition) of Pląsawa river valley. The soil was dystric cambisol. The stand was composed of Norway spruce with an admixture of common pine, larch and silver fir. The average trees density was 600 N/ha, with basal area 52.9 m^2/ha, trees diameter varied from 7 up to 63 cm (average 29 cm). In the analysed stand the silver fir was represented by four adult individuals only.

Forest floor vegetation covered 65% of the ground in average and was consisted predominantly of *Vaccinium myrtillus* (L.), less abundant *Deschampsia flexuosa* (L.) Trin. and mosses (mainly *Polytrichum formosum* Hedw., *Dicranum scoparium* Hedw.). Within the investigated area some stumps and fallen logs were present.

Methods

The location of all seedlings and adult silver fir trees was mapped by azimuth, slope and distance measurement to the previously established groundwork points, using forest surveying compass Tracon LS–25. The map of seedlings and adult silver firs location was prepared using WinKalk and MikroMap software. This map was used to measure the distance of each seedling to its nearest adult tree and the azimuthal angle between the seedling and the adult tree. Furthermore, the pattern of spatial distribution of seedlings was verified on the basis of the completely spatial random distributions concept (*CSR*) and the computed *L(t)* functions (Ripley 1981, Diggle 1983). It was done using PASSAGE software.

The following morphological features of seedlings were measured: height (*H*), length of the last height increment (*Increment*) and a mean length of the lateral shoots in the uppermost whorl (*MLLS*). The apical dominance ratio (*ADR*) was calculated as the *Increment* to *MLLS* ratio. The seedlings age was assessed by counting the number of nodes of yearly increment or traces of the nodes.

The microhabitat characteristics of each seedling was defined by recording the microrelief form (convex or concave), forest floor plant species, substrate type (raw needles, bare soil, stumps, fallen logs) and the influence of adult trees (covered with the canopy).

The light environment just above seedlings was derived from hemispherical photographs using WinScanopy 2003b software. Results were expressed as a relative photosynthetic photon flux density under canopies (%PPFD). Unfortunately, during the study the canopy structure was disturbed by clear – cuttings in southern part of the research area. Light conditions were evaluated only in the undisturbed northern part of the research area, above 37 randomly chosen seedlings.

A set of regular sampling points, nested in the net 5×10 m, was established to derive the characteristic of the study site. A total number of 130 regular points were established. On each point the microhabitat parameters were described. Additionally, on every second point the light conditions were evaluated, at height of 40 cm above ground layer, using hemispherical photographs. Due to the above mentioned clear – cutting the light measurements also were conducted only in the northern part of the study area, all together in 35 points.

We assume that the data set obtained from regular points reflects the conditions variability within the study site. Habitat requirements or "preferences" of silver fir seedlings were evaluated, by comparison of the habitat conditions where seedlings are located with conditions in the regular net of points. The statistical significance of disproportion between the frequency of appearance of seedlings in given microhabitats type versus frequency of this type in regular points was checked by χ^2 tests. When the number of habitat units occurrences was lower than five, the χ^2 test was rectified by Yates' corrections. The significance of differences in light conditions between the seedlings and the regular points was done by U Mann – Whitney test.

Results

In the investigated site 4 adult individuals occurred (Fig. 1). One, a single tree (A) grew in the upper part of the valley, while the three other (B, C, D) were located along the river with 20 m interval, about 60 m away from the tree A. Such distribution of the adult trees results in a clumped distribution of seedlings – into two groups, referred further as to group I (around the tree A) and group II (in vicinity of the trees B, C, D).

On the study site 292 seedlings of silver fir were found. 154 in group I, whereas 138 in the northern part of the study site in group II (Fig. 1). The density of seedlings was 2200 N/ha (area 0.07 ha) and 511 N/ha (area 0.26 ha) in group I and group II, respectively. The average ratio of seedlings number per adult tree was 73, while for two groups individually this value was 154 for group I and 51 for group II.

The general description of seedlings morphology was presented in Table 1. The seedlings age (accounts for 224 individuals) was shown in Figure 2.

Seedlings in group I were established mostly in NE and E directions, in relation to tree A, whereas in group II in E and SE from trees B, C, D (Fig. 3). Up to 60% of seedlings within each group were established in the above mentioned directions. These main directions of seedlings dispersal are in agreement with prevailing wind directions in the Karkonosze Mts., as well as with the local wind direction, constrained by valley's W-E orientation. The seedlings were established mainly (above 70%) in distance 5–25 m to the nearest adult tree. However, the distance is clearly greater along the directions where seedlings are most abundant (Fig. 3), whereas much smaller in directions less favored by seedlings. Seedlings in group I were distributed closer to adult trees, with considerable amount of seedlings occuring closer than 5 m (16% of seedlings) and the maximal distance from adult tree of up to 30 m. Seedlings in the group II were more widely distributed, with maximum distance of up to 50 m from adult trees and generally avoided the nearest vicinity of adult trees. The mean value of seedlings dispersal distance was 11.5 m and 16.9 m for group I and II respectively. The overall mean distance from adult tree was 14.1 m.

Table 1. The morphological traits of silver fir (*Abies alba* Mill) seedlings

Traits	Mean	S.D.
H [cm]	11.5	5.3
Increment [cm]	2.3	2.0
MLLS [cm]	3.7	3.2
ADR	0.8	1.6

The spatial distribution within each group of seedlings does not differ significantly from random distribution. However, some tendencies to clustering (*L(t)* empirical value exceeds the *CSR* line) up to distance of 4 m in group I and up to 9 m in group II can be observed (Fig. 4).

The frequencies of habitat units for seedlings and regular points and the results of χ^2 tests are presented in Table 2. The seedlings grow less frequently than expected in synusiae of *Vaccinium myrtillus*, on raw needles. They also "avoid" concave relief and trees canopy cover (Table 2).

There was a statistically significant difference in light conditions between the points with seedlings and the regular sampling points ($Z = 2.57$, $p = 0.01$). Seedlings usually grow in better light conditions (mean 12% of PPFD) than "average" conditions estimated from regular samplings points (mean 9.6%) (Fig. 5). The morphology of 37 randomly chosen seedlings was not correlated with light conditions estimated just above it.

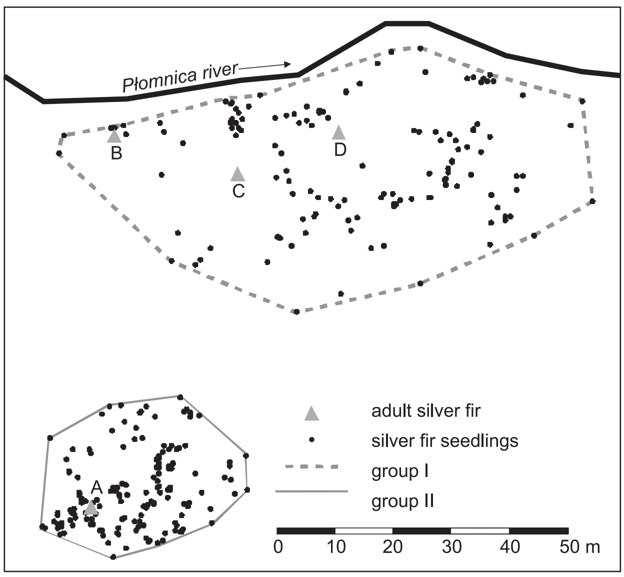

Fig. 1. The map of study site

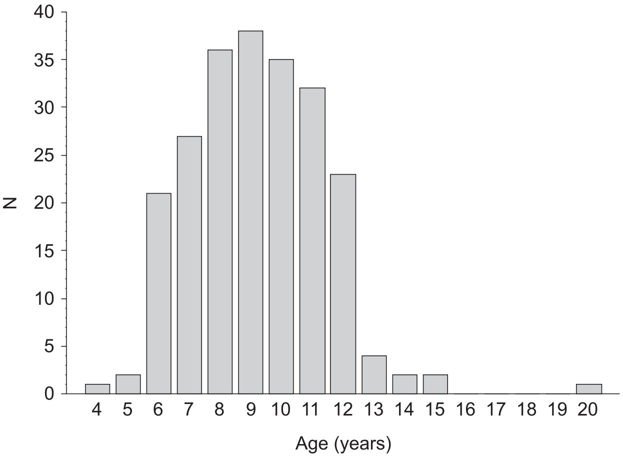

Fig. 2. Age distributions of silver fir seedlings

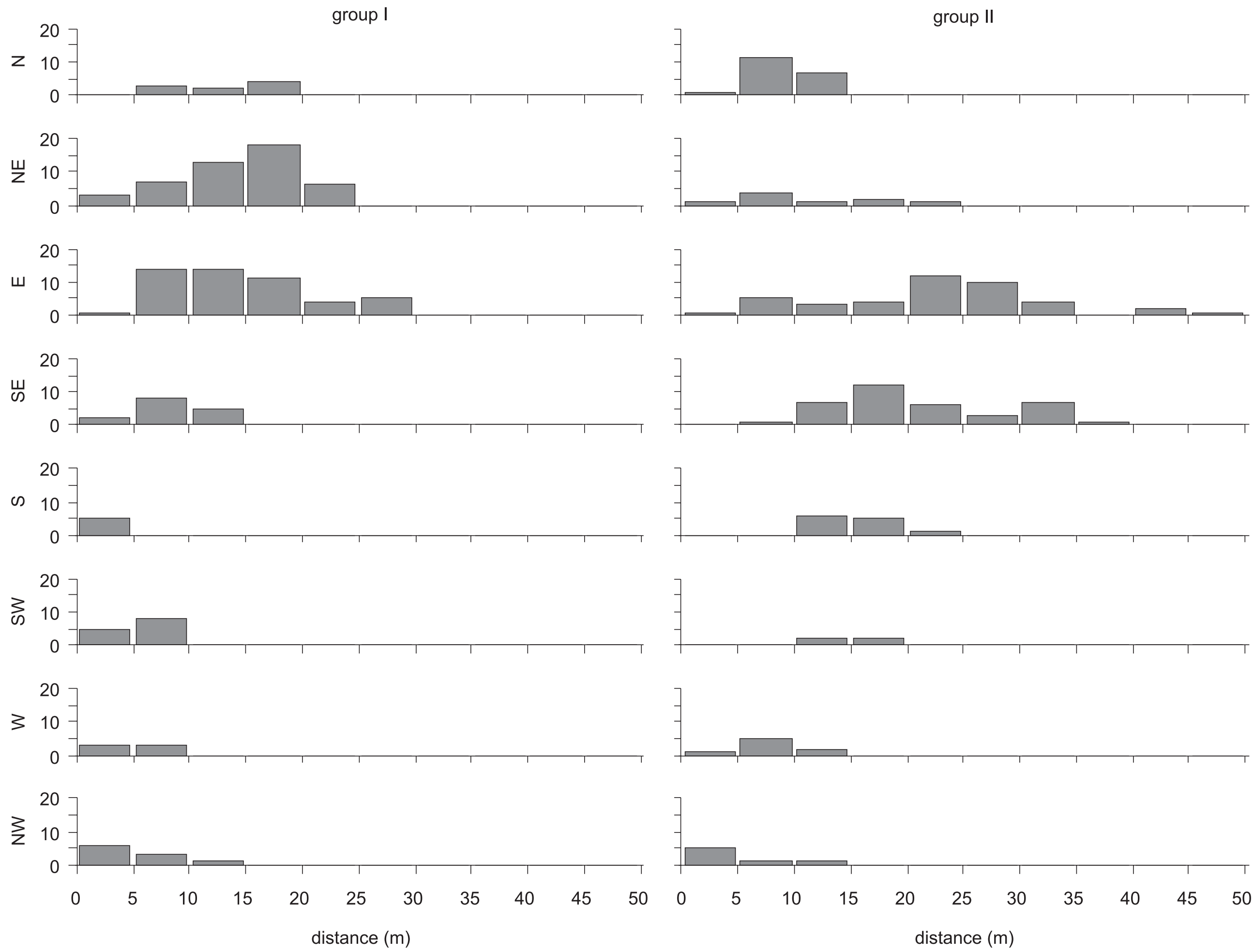

Fig. 3. Spatial distributions of silver fir seedlings in relation to location of nearest adult individuals. X axis shows the 5 m distance class, Y axis the number of observations. Left column shows the distribution of seedlings in group I; right column shows seedlings in group II. In each row results are present for 45 degree directions units (the N direction includes seedlings which grow in azimuths from 337.5° to 22.5°, the NE direction includes azimuths > 22.5° to 67.5° – and so forth)

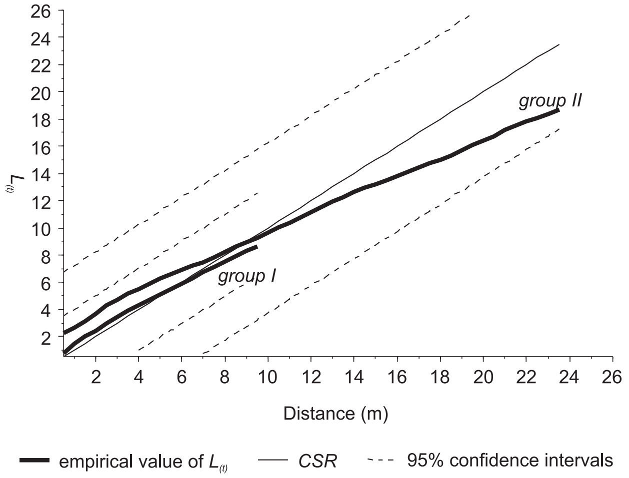

Fig. 4. Spatial distribution of silver fir seedlings. Solid bold line shows the empirical value of *L(t)* function (short line seedlings in group I, long line seedlings in group II). Thin solid line shows value of *L(t)* function for complete spatial randomness (*CSR*), dashed lines present 95% confidence intervals – short for group I, long for group II

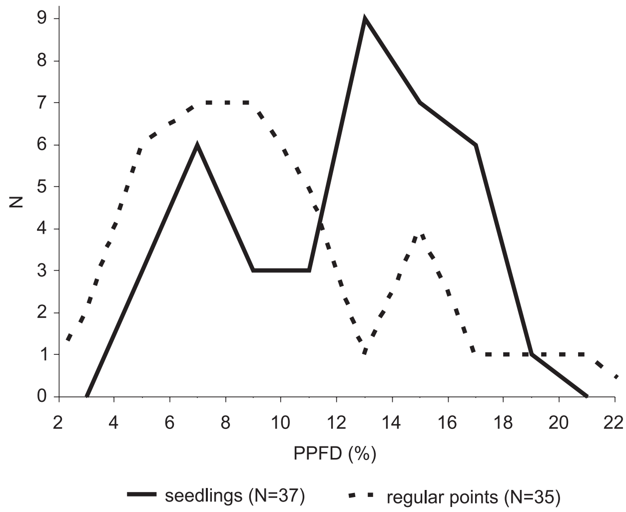

Fig. 5. The distributions of PPFD above silver fir seedlings and regular sampling points

Table 2. The frequency of occurrence of given habitats units in silver fir (*Abies alba* Mill) seedlings, regular sampling points and results of comparison of χ^2 test. The significant differences are distinguished in bold

Habitats units	Frequency		*Chi*²	*p*
	Seedlings	Regular points		
	N=292	N=130		
Calamagrostis villosa	0.04	0.06	0.32[a]	*0.569*
Deschampsia flexuosa	0.14	0.10	0.92	*0.338*
Polytrychum sp	0.08	0.10	0.18	*0.668*
Sphagnum sp	0.00	0.02	0.50[a]	*0.478*
Vaccinium myrtillus	0.16	0.44	**23.74**	***0.000***
needles	0.23	0.44	**12.59**	***0.000***
bare soil	0.02	0.01	0.25[a]	*0.614*
fallen logs	0.02	0.02	0.00[a]	*1.000*
stumps	0.04	0.08	1.13[a]	*0.287*
convex relief	0.13	0.22	3.25	*0.071*
concave relief	0.00	0.12	**14.98**[a]	***0.000***
canopy overlap	0.31	0.84	**74.84**	***0.000***

[a] – test with Yates' corrections

Discussion

The persistence of adult silver fir in the study area is an effect of local land relief. Deep stream valley, with steep slopes, created microclimate favorable for silver fir (Matuszkiewicz and Matuszkiewicz 1974) and is not easly accessible, thus the past forest management was less intensive there.

The silver fir regeneration in the Sudety Mts. is very poor – the seedlings densities varied from 108 to 9794 N/ha, average 1761 N/ha (Filipiak 2002). Other results from the Karkonosze National Park also confirm the low seedlings density, changing in range from 491 to 1832 N/ha (Dobrowolska 2000). The seedlings density in the investigated site is very similar. If the regeneration is expressed as a number of progeny per one adult silver fir individual, the value reported in this paper is higher than in case of Sudety Mt., where only 1.39–37.9 seedlings per adult fir were found (Filipiak 2002).

The observed spatial pattern of seedlings occurrence seems to be dependent on seed dispersal. Seedlings dispersion pattern corresponds generally with Gaussian plume model, which is commonly applied to a description of wind spore dispersal (Okubo and Levin 1989); namely, the seedlings were most abundant at certain distance from the parent trees and their density increases along prevailing wind directions. Some study reveals that seedlings distribution not necessarily reflects the seeds rain (Duchesneau and Morin 1999). Nevertheless, the seedlings distribution was used to assess seeds diffusion in forests (Ribbens et all 1994), as well as seedlings density pattern was reported to be correlated with seeds rain (Dovčiak et all 2003). The distance of seedlings dispersion observed in this study was generally consistent with the reported silver fir seed dispersal distance in stands, defined as 20–30 m (Korpel and Vinš 1965). The maximum distance of seedling to an adult tree reaches 30 m in group I, while in group II only 10% of seedlings exceeds this threshold. The average dispersal distance (14.1 m) is comparable to other species with similar seeds, reported from forests of Northern America (Ribbens et al. 1994).

The process of seedlings establishment is long-lasting. The analysis of the age structure shows that most of the analysed seedlings were established in the period 1994 – 2000. The mast-year effect is not revealed, however most numerous were 8–10 years old seedlings, what corresponds with abundant cone crops in 1996 and 1998 observed over the Sudety Mts. (Filipiak 2002).

The growth of seedlings was weaker, if compared with growth of seedlings from artificial regeneration and protected against browsing. The yearly increment of height of four year old seedlings (previously planted in a nursery at the age of three years) under similar light regime in the area of the Karkonosze Mts. was in average 5.2 cm (Robakowski and Wyka 2003), thus generally two times higher than in this study. Other study of natural regeneration in the Karkonosze Mts. confirms weak growth of seedlings established spontaneously, due to browsing (Dobrowolska 2000). In this study site, a part of the seedlings was actually protected (for one year) against deer and red deer, however most of the seedlings had injuries caused by previous browsing. We also did not find any correlations betweens the seedlings height , height increment, *ADR* value and light conditions. It is known that silver fir young individuals adapt to light conditions on the way of morphological changes (e.g. Grassi and Bagnaresi 2001) and that a positive correlation between the height, height increment, *ADR* value and light conditions exists. (Robakowski et al. 2003; Filipiak et al. 2005). The lack of these correlations in this study we attribute to browsing.

The results also showed the importance of land microrelief, vegetation types, substrate types and canopy trees occurrence for regeneration of silver fir. It should by pointed out that the results of the seedlings preferences should by taken carefully due to a possible impact of spatial autocorrelations. The scant regeneration of silver fir in patches of grasses reported in other studies (Filipiak et al. 2005; Hunziker and Brang 2005) was not statistically significant in our research. Interesting was the underrepresentation of silver fir seedlings in patches of *Vaccinium myrtillus*, which is contrary to results of other studies. This difference could be explained by the site conditions, especially soil fertility, constrained by the competition from forest floor vegetation. The soils in the investigated site are nutrient-poor and acid (Adamczyk et al. 1985, Borkowski et al. 1991). Soils at other reported sites, as it could be stated basing on the plant community structure, are more fertile. In such sites, *Vaccinium myrtillus* indicates microhabitats appropriate for silver fir, while more fertile and wet microhabitats are occupied by other, nutrient demanding plant species. This explanation is satisfactory for the pure uneven-age fir stand from Karpaty Mts. (Paluch 2005), and from in mixed broadleaved forest also (Jaworski 1973). In our study, nutrient-poor soil prevents successful competition of silver fir seedlings with *Vaccinium myrtillus*, which results in low abundance of fir seedlings in its patches.

The absence of silver fir seedlings in depressed places was also found in the analysis of silver fir seedlings establishing in southern Alps (Hunziker and Brang 2005). It can be related to higher seedlings mortality caused by snow associated fungi such as *Gremmeniella abietina* which is known to increase with the duration of snow cover in spring (Gibbs 1984, Senn 1999). The influence of this factor on the silver fir regeneration is only hypothetical and should be studied.

The underrepresentation of firs in sites covered by raw needles could be related with properties of humus which originates from this substrate (Jaworski 1973). This observation was confirmed in other study (Szymura 2007). However, Filipiak (2002) states that fir regeneration was more abundant on litter dominated by spruce needles than by beach leaves. Filipiak (2002) also documented preferences of silver fir for regeneration on mineral soil. This phenomenon was also observed in our study, but it was below the significance threshold.

In the investigated site, seedlings "avoided" shade of crown of adults trees and grew mostly in the open spaces between crowns. Also, the light evaluation results, showed a higher value of PPFD in seedlings grown places compared to the regular net points. Thus, the results of this study are opposite to commonly reported light constrains of silver fir regeneration. Generally, the fir seedlings due to their high shade tolerance can be more numerous under canopy than in the gaps (Grassi et al. 2004), or they prefer the northern margin of gaps (Diaci 2002). Also results of Paluch (2005) do not confirm more abundant fir regeneration in patches with lower impact of neighbouring trees (e.g. gaps or loose stand fragments). Also other studies confirm the negative correlations between seedlings density and percentage of PPFD and that the seedlings were most numerous in places with PPFD below 10% (Filipiak, Iszkuło and Korybo 2005). The environment in the investigated site is strongly or moderately shaded, however generally the PPFD remains higher than the tolerance threshold of silver fir seedlings – 2–3% of PPFD (Diaci 2002). Thus it is not possible to explain the observed pattern of the seedlings distribution in relation to crowns of trees only as a reaction of seedlings to light deficiency. Instead the synergistic effect of low light environment and two other stressors, nutrient-poor soils and browsing, should be considered. It is known that mortality ratio of browsed silver fir seedlings was 50–20% higher under dense canopy (canopy density 83%) than under more open canopy with density 54% (Ammer 1996). Thus, we hypothesize that in worse light environment the combination of continuous stress, lead by nutrient shortage and shading, with frequent disturbances caused by browsing increased mortality of seedlings. Finally, seedlings were more numerous in better light conditions (e.g. beyond areas directly shaded by crown) where the forest floor vegetation was scant at that time.

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