

Factors controlling the regeneration process in unevenly aged silver fir forests: inferences from the spatial pattern of trees

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ABSTRACT: The main objective of this study was to prove the relationship between the spatial pattern of trees and distribution of advanced regeneration in structured *Abies alba* Mill. forests in the Western Carpathians (of southern Poland). In 13 sample plots (0.45–1.00 ha in size), the locations of all live trees above 15 cm in $d_{1.3}$ and all stumps of canopy trees (above 50 cm in $d_{1.3}$) were determined. In addition, in all plots the coordinates of all live and dead pole-stage trees (5–15 cm in $d_{1.3}$), in seven plots the coordinates of all live and dead younger saplings (0.5–1.3 m in height), and in eight plots the coordinates of all live and dead older saplings (above 1.3 m in height and below 5 cm in $d_{1.3}$) were registered. The univariate and bivariate Ripley's K -function was applied to test spatial independence of the patterns of trees representing different size categories. In each of the stands, younger and older saplings and pole-stage trees showed an aggregated pattern. The strongest attraction between trees of these size categories was detected at the scale 6, 5 and 10 m, respectively. At the scale below 10 m, a positive spatial correlation was frequently found between large firs and pole-stage trees and saplings. A spatial repulsion between advanced fir regeneration and trees of the middle stand layer was negligible or observable only in a relatively large scale above 15 m. The patterns of saplings and trees of the lower stand layer appeared to be spatially independent in most of the stands being studied. These results suggest that in unevenly aged fir forests, a stable mechanism is generating the aggregated patterns of regeneration functions and the factors involved are spatially linked with the distribution of large firs. Therefore, a hypothesis is advanced that the spatial pattern of regeneration in such forests is controlled by edaphic factors – in particular, the humus form – and that light conditions play only a secondary role.

Keywords: *Abies alba*; selection forest; regeneration; microhabitat

The silver fir (*Abies alba* Mill.), as a long-living and one of the most shade-tolerant European arborescent species (ŠAFAR 1954; SCHÜTZ 2001; JAWORSKI 1979), is known to spontaneously form unevenly aged stands of complex structure (FRÖLICH 1954). The replacement of tree generations in such forests is spatially linked with the formation of gaps, which enhances the successful recruitment of regeneration. However, some shade-tolerant species, including silver fir, are able to establish a permanent bank of regeneration before a canopy opening is created (DOBROWOLSKA 1998a; SZWAGRZYK et al. 2001; PALUCH 2005a). This adaptation facilitates the durable occupation of a given microhabitat and ensures an initial height advance in relation to more light-

demanding tree species and forest floor vegetation (AMMER 1996; PIROŹNIKOW 1998; McCLURE et al. 2000).

Young trees forming the bank of regeneration exhibit uniform distribution over the whole forest area rather exceptionally. As reported by DUC (1991), in the fir selection forests, saplings occur in irregularly distributed clumps 100–300 square m in size. The formation of aggregated patterns gives evidence that factors crucial for the establishment of regeneration show significant spatial variability.

Recent studies provide convincing arguments that the spatial distribution of regeneration does not always correspond directly with the spatial variability of light conditions. Rather, regeneration occurrence

can also be controlled by more temporarily stable factors such as seedbed features (CHRISTY, MACK 1984; CACCIA, BALLARÉ 1998; SIMARD et al. 1998), competition of forest floor vegetation (JAWORSKI 1973; MAGUIRE, FORMAN 1983; BURSCHEL et al. 1985; SHELTON 1995), understory (BECKAGE et al. 2000), post-dispersal seed predation (SCHREINER et al. 2000), or microtopography (HÖRNBERG et al. 1997; HOLEKSA 1998; COLLINS, BATAGLIA 2002). Therefore, young trees do not always occur in the forest patches that actually give the best opportunity for growth up into the canopy.

An essential part of microsite heterogeneity in a stand is linked to the spatial pattern of trees. Trees directly modify microclimatic conditions on the forest floor (PUKKALA et al. 1993; CANHAM et al. 1994; PARKER 1997; GRAY et al. 2002), exert influence on characteristics of the soil through root systems and litter-fall (HIRABUKI 1991; LISKI 1995; DIEFFENBACH, MATZNER 2000; HINSINGER et al. 2003), change physical and chemical properties of precipitation (JANEK 2002), and form habitats for animals and forest floor vegetation (PALUCH 2005b). Therefore, it seems likely that the spatial pattern of trees also affects the spatial pattern of regeneration.

The main objective of this study was, firstly, to test whether any spatial dependence (attraction, repulsion) exists between regeneration and the trees in the stand layer in multilayered, uneven-aged fir forests, secondly, to determine what is the spatial range of the possible interactions, and thirdly, to discuss which ecological factors may potentially be responsible for such a spatial pattern.

Study area and sample plots

In the Polish part of the Western Carpathians, fir stands (*Abies alba* Mill.) account for 26% of the total forested area (TRAMPLER 1990). Because in the past a considerable part of these stands was managed using either single-tree cuttings or partial cuttings lasting more than 40–50 years, many fir forests of today show diversified vertical structure.

Fir forests, occurring in the lower montane belt on leached brown and acid brown soils (*Eutric* and *Dystric Cambisols* according to WRB 1998) developed on Flysch rocks, represent the fir subassociation of eutrophic Carpathian beech forest (*Dentario glandulosae-Fagetum* Klika 1927 em. Mat. 1964). In this zone, the vegetation period is 210 days, the average annual temperature is 6–8°C, and the annual precipitation is 850–950 mm, 550–600 mm of which occurs between April and September (TRAMPLER 1990).

In the Pieniny Mountains, Sadecki and Wyspowy Beskid (the central part of the Western Beskid), 13 representative stands were selected and in each of them a rectangular sample plot 0.45–1.00 ha in size was established. Spatial analyses showed that the pattern of trees in the selected stands, in spite of a wide tree diameter range, did not significantly violate a hypothesis of random labelling. This finding indicates that the stands are characterised by a homogeneous selection structure with barely distinguishable groups of trees of similar dimensions (i.e. size categories are not spatially segregated). Some characteristics of the stands in the sample plots are summarised in Table 1.

METHODS

Stem coordinates (to the nearest 0.1 m), species, and diameters at the breast height ($d_{1.3}$) of all live trees above 15 cm in $d_{1.3}$, as well as the coordinates and diameters at 30 cm in height of all stumps and dead trees above 50 cm in $d_{1.3}$ (approximation see below) were recorded in 13 sample plots. The coordinates were determined using a compass and an ultrasonic distance-meter. During the fieldwork, the stumps were divided into two categories: recently harvested stumps with slightly decomposing but still compact wood, probably not older than 15 years; and old stumps or their remnants in advanced decay, recognisable up to about 30 years after the respective tree was cut down. In addition, in all plots the coordinates of all live and dead pole-stage trees (5–15 cm in $d_{1.3}$), in seven (representative) plots (I–VII) the coordinates of all live and dead younger saplings (0.5–1.3 m in height), and in eight plots (I–VIII) the coordinates of all live and dead older saplings (above 1.3 m in height and below 5 cm in $d_{1.3}$) were registered. Comparison of the decay rate of fir logs (OTTO 1994; KORPEL 1995) and the height growth rate of fir saplings in Carpathian selection forests (GAZDA 1988) allow to assume that the saplings registered had become established before the cuttings assessed by the recorded stumps were carried out. All recorded trees were grouped into the categories given in Table 2. The diameters at breast height of the stumps were extrapolated according to the formula given in BRUCHWALD et al. (2002).

Univariate (trees of the same category) or bivariate (trees of two different categories) Ripley's *K*-function was applied to test the spatial independence of the tree locations (DIGGLE 1983). A distance of 20 m and an interval of 1 m were assumed as a maximal distance and a minimal interval of analysis, respectively. To estimate confidence intervals (at the

Table 1. Characteristics of the stands

Sample plot	Size (ha)	Percentage in G			N (ha)	G (m ² /ha)	V (m ³ /ha)	$d_{1.3}$			h mean (m)
		fir (%)	spruce (%)	beech and others (%)				mean (cm)	max (cm)	coeff. of var. (%)	
I	0.75	81	14	5	569	27.6	362.1	20.1	92.0	72.4	16.3
II	1.00	98	–	2	630	37.3	532.6	21.8	86.0	76.5	16.5
III	0.50	96	–	4	754	35.3	468.4	20.1	76.0	69.0	16.3
IV	0.65	92	1	7	665	36.4	477.7	20.1	87.0	76.4	16.3
V	0.50	95	3	2	526	36.4	510.8	23.7	93.0	75.4	17.3
VI	0.50	94	–	5	580	33.0	452.3	21.9	120.0	71.1	16.9
VII	0.90	93	1	6	383	37.2	525.4	29.0	93.0	62.8	19.4
VIII	0.65	93	–	7	489	34.3	502.3	22.9	102.0	83.4	17.2
IX	1.00	94	4	2	686	39.5	559.9	21.0	92.0	81.8	16.2
X	0.50	93	–	7	716	37.2	351.2	19.4	90.0	86.5	14.4
XI	0.45	89	–	11	731	34.7	428.5	19.3	90.0	79.0	14.7
XII	0.65	95	2	3	758	37.8	496.7	19.8	95.0	78.7	15.8
XIII	0.55	94	4	2	744	38.1	522.4	20.5	98.5	74.3	16.5

N – number of trees (above 6.9 cm in $d_{1.3}$), G – basal area, V – volume, $d_{1.3}$ – diameter at breast height, h – height

conventional 95% level) for the computed empirical distribution functions, Monte Carlo procedures (120 simulations) were adopted, and simulations under the hypothesis of complete spatial randomness (for univariate patterns) or of independent components (for bivariate patterns) were carried out (DIGGLE 1983; GOREAUD, PÉLISSIER 2003). The method of random toroidal shifts used in simulations of bivariate patterns preserved the empirical spatial patterns of each of the components (i.e. the independence was tested conditionally on the observed component structure).

In the theory of spatial point processes the K -function is defined as

$$K(r) = E/\lambda$$

$$K_{kl}(r) = E_l \lambda_l$$

where: E – number of events within distance r of an arbitrary event,

E_l – number of type l events within distance r of an arbitrary type k event,

λ – intensity (mean number of events per unit area),

λ_l – intensity (mean number of type l events per unit area).

As proposed by Ripley, unbiased estimators for $K(r)$ and $K_{kl}(r)$ can be obtained in the following way (DIGGLE 1983):

$$\underline{K}(r) = n^{-2} |A| \sum_{i \neq j} w_{ij}^{-1} I_r(u_{ij})$$

$$\underline{K}_{kl}(r) = (n_l n_k)^{-1} |A| \sum_{i=1}^{n_l} \sum_{j=1}^{n_k} w_{ij}^{-1} I_r(u_{ij})$$

$$\underline{K}_{lk}(r) = (n_l n_k)^{-1} |A| \sum_{i=1}^{n_l} \sum_{j=1}^{n_k} w_{ji}^{-1} I_r(u_{ij})$$

$$I_r(u_{ij}) = \begin{cases} 1 & \text{if } u_{ij} \leq r \\ 0 & \text{otherwise} \end{cases}$$

$$\underline{K}_{kl}(r) = \underline{K}_{lk}(r) = (n_l + n_k)^{-1} \{ n_l \underline{K}_{kl}(r) + n_k \underline{K}_{lk}(r) \}$$

where: n – number of events,
 $n_k(n_l)$ – number of type $k(l)$ events,
 $|A|$ – area of study region,
 $u(i,j)$ – distance between i -th and j -th events,
 w_{ij} – proportion of the circumference of the circle with centre i and radius u_{ij} which lies within the study region A (formulae according to DIGGLE 1983).

To stabilise the variance, the functions $\underline{K}(r)$ and $\underline{K}_{kl}(r)$ were transformed:

$$L(r) = \underline{K}(r)^{0.5} \pi^{-0.5} - r$$

$$L_{kl}(r) = \underline{K}_{kl}(r)^{0.5} \pi^{-0.5} - r$$

In the case of complete spatial randomness, an expected value of the transformed function $L(r)$ is 0. The components of a bivariate pattern are inde-

Table 2. Number of trees in size categories (per ha)

Sample plot	Regeneration						Stand			Stumps ($d_{1.3} > 50$)	
	live	dead	live	dead	live	dead					
	$0.5 > h < 1.3$		$d_{1.3} < 5$		$5 > d_{1.3} < 15$		$15 > d_{1.3} < 25$	$25 > d_{1.3} < 50$	$d_{1.3} > 50$	not older than 15 years	15–30 years-old
I	105	152	308	473	411	544	63	95	35	–	–
II	83	88	171	70	343	133	131	114	65	53	57
III	78	100	176	190	434	282	200	128	50	50	56
IV	103	237	200	257	375	282	109	120	54	–	45
V	48	98	58	54	234	134	94	118	52	–	58
VI	34	70	86	92	280	268	128	150	32	–	18
VII	37	46	56	72	128	121	74	99	64	14	48
VIII	×	×	74	49	212	86	82	72	58	15	43
IX	×	×	×	×	349	71	116	111	64	41	50
X	×	×	×	×	644	318	96	68	72	38	–
XI	×	×	×	×	602	287	120	76	60	22	–
XII	×	×	×	×	398	95	192	97	46	–	105
XIII	×	×	×	×	362	–	193	125	45	–	100

pendent (i.e. spatially uncorrelated) if they satisfy $K_{kl}(r) = 0$, and they are positively/negatively correlated at a range r if the derivative of $L_{kl}(r)$ with respect to r is positive/negative.

To facilitate the analyses, the scale of maximal attraction/repulsion (AS/RS) and the intensity of attraction/repulsion (AI/RI) were also determined. For each stand, the intensity of attraction/repulsion (AI/RI) was evaluated as an average positive/negative departure of the empirical function $L(r)$ (univariate pattern) or $L_{kl}(r)$ (bivariate pattern) from the value expected for a complete random pattern (univariate case) or for a pattern with independent components (bivariate case). To make the respective results comparable for stands differing in tree number, the departure from the expected value was weighted with the width of the confidence interval:

$$AI = r_{\max}^{-1} = \sum_{r=1}^{r_{\max}} \{2 I_A(r) [UL(r) - LL(r)]^{-1}\}$$

$$I_A(r) = \begin{cases} L(r) - EL(r) & \text{if } L(r) > EL(r) \\ 0 & \text{otherwise} \end{cases}$$

$$RI = r_{\max}^{-1} = \sum_{r=1}^{r_{\max}} \{2 I_R(r) [UL(r) - LL(r)]^{-1}\}$$

$$I_R(r) = \begin{cases} L(r) - EL(r) & \text{if } L(r) > EL(r) \\ 0 & \text{otherwise} \end{cases}$$

- where: $L(r)$ – value of the function $L(r)$ or $L_{kl}(r)$,
- $UL(r), LL(r)$ – upper and lower limits of the confidence interval (obtained from the simulations),
- $EL(r)$ – expected value of the function $L(r)$ or $L_{kl}(r)$,
- r_{\max} – maximal distance analysed.

The greater the intensity of attraction/repulsion (AI/RI), the greater the tendency to form aggregated/regular univariate patterns or spatially positively/negatively correlated bivariate patterns. Because all the plots were regarded as random samples from a general population, the total intensity of attraction/repulsion (i.e., for all the stands) was evaluated as an average of the intensities computed for each of the stands.

The scale of maximal attraction/repulsion determines a scale on which the empirical distribution function summed over all the plots shows the greatest/smallest departure from the expected distribution function for a pattern with independent components:

$$AS = \max \left\{ \sum_{i=1}^N 2 [L(r) - EL(r)] [UL(r) - LL(r)]^{-1} \right\}$$

$$RS = \min \left\{ \sum_{i=1}^N 2 [L(r) - EL(r)] [UL(r) - LL(r)]^{-1} \right\}$$

where: N – denotes the number of sample plots.

In the computations original programs developed in Statistica Visual Basic were used.

RESULTS

In all plots, both younger and older saplings, as well as pole-stage firs, showed an aggregated distribution pattern (AI = 1.96, 3.27 and 2.85, respectively) (Table 3). The strongest attraction was detected at the scale of 6, 5 and 10 m, respectively (Table 3). It should be noted that these values may be

interpreted as an average radius of clumps formed by saplings and pole-stage firs.

The patterns of live and dead saplings (younger and older) were positively correlated (AI = 2.51 and 2.49) in all stands, with a maximal attraction scale of 3 and 2 m, respectively (Table 3). The null hypothesis assuming the spatial independence of the patterns of younger and older saplings and pole-stage firs had to be rejected in favour of the hypothesis assuming a positive correlation in 57% and 100% of the stands, respectively (Table 3).

The spatial distributions of younger and older saplings and large firs were positively correlated in 14% (AI = 0.36, AS = 3 m) and 50% (AI = 0.50, AS = 4 m) of the stands, respectively (Table 3). A significant spatial correlation between dead younger and older saplings and live large firs occurred in 57% (AI = 0.57, AS = 3 m) and 50% (AI = 0.51, AS = 3 m) of the stands, respectively. In 33% and 50% of the stands,

Table 3. Positive spatial correlation between trees in the investigated stands

Size category	Characteristics	Regeneration			Stand			Stumps ($d_{1.3} > 50$)	
		$0.5 > h < 1.3$	$d_{1.3} < 5$	$5 > d_{1.3} < 15$	$15 > d_{1.3} < 25$	$25 > d_{1.3} < 50$	$d_{1.3} > 50$	not older than 15 years	15–30-years-old
Firs $0.5 > h < 1.3$	AI	1.96	1.89	0.75	0.18	0.12	0.36	1.03	0.65
	AS	6	2	5	8	15	3	6	10
	departures (in %)	100(7)	100(7)	57(7)	0(7)	14(7)	14(7)	33(3)	50(6)
Firs $d_{1.3} < 5$	AI	×	3.27	1.23	0.31	0.11	0.50	0.52	0.22
	AS		5	3	9	–	4	4	12
	departures (in %)		100(8)	100(8)	0(8)	0(8)	50(8)	25(4)	0(7)
Firs $5 > d_{1.3} < 15$	AI	×	×	2.85	0.34	0.11	0.31	0.43	0.37
	AS			10	13	1	4	4	8
	departures (in %)			100(13)	46(13)	15(13)	53(13)	42(7)	60(10)
Dead firs $0.5 > h < 1.3$	AI	2.51	2.21	1.27	0.23	0.20	0.57	1.02	0.23
	AS	3	2	4	1	1	3	3	6
	departures (in %)	100(7)	100(7)	100(7)	14(7)	14(7)	57(7)	33(3)	16(6)
Dead firs $d_{1.3} < 5$	AI	1.66	2.49	1.78	0.70	0.22	0.51	0.53	0.23
	AS	3	2	3	12	2	3	3	3
	departures (in %)	42(7)	100(8)	100(8)	37(8)	0(8)	50(8)	25(4)	14(7)
Dead firs $5 > d_{1.3} < 15$	AI	0.07	0.57	0.45	0.49	0.18	0.26	0.30	0.21
	AS	2	2	3	9	14	5	7	1
	departures (in %)	0(7)	62(8)	91(12)	66(12)	25(12)	41(12)	28(7)	11(9)

AI – intensity of attraction, AS – scale of maximal attraction, departures – frequency of significant departures from spatial independence (in the parentheses is given the number of plots in which the analysis was carried out)

Table 4. Negative spatial correlation between trees in the investigated stands

Size category	Characteristics	Regeneration			Stand		Stumps ($d_{1.3} > 50$)		
		$0.5 > h < 1.3$	$d_{1.3} < 5$	$5 > d_{1.3} < 15$	$15 > d_{1.3} < 25$	$25 > d_{1.3} < 50$	$d_{1.3} > 50$	not older than 15 years	15–30-years-old
Firs $0.5 > h < 1.3$	RI	0.04	0.06	0.05	0.01	0.40	0.49	0.05	0.35
	RS	1	18	19	2	4	1	1	1
	departures (in %)	0(7)	0(7)	0(7)	14(7)	57(7)	14(7)	0(3)	66(6)
Firs $d_{1.3} < 5$	RI	×	0.01	0.01	0.13	0.50	0.16	0.31	0.48
	RS		20	20	2	16	1	1	2
	departures (in %)		0(8)	0(8)	12(8)	62(8)	12(8)	0(4)	57(7)
Firs $5 > d_{1.3} < 15$	RI	×	×	0.02	0.04	0.18	0.05	0.19	0.15
	RS			1	1	15	11	1	4
	departures (in %)			15(13)	23(13)	23(13)	7(13)	0(7)	20(10)
Dead firs $0.5 > h < 1.3$	RI	0.03	0.04	0.01	0.41	0.47	0.18	0.32	0.60
	RS	18	20	20.0	6	5	18	1	1
	departures (in %)	0(7)	14(7)	0(7)	28(7)	28(7)	0(7)	33(3)	33(6)
Dead firs $d_{1.3} < 5$	RI	0.14	0.01	0.01	0.06	0.47	0.27	0.33	0.54
	RS	20	20	20	1	6	15	17	1
	departures (in %)	0(7)	0(8)	0(8)	0(8)	37(8)	12(8)	25(4)	42(7)
Dead firs $5 > d_{1.3} < 15$	RI	0.15	0.03	0.02	0.06	0.08	0.15	0.25	0.10
	RS	19	20	20	1	9	14	7	1
	departures (in %)	0(7)	0(8)	0(12)	16(12)	0(12)	8(12)	28(7)	11(9)

RI – intensity of repulsion, RS – scale of maximal repulsion, departures – frequency of significant departures from spatial independence (in the parentheses is given the number of plots in which the analysis was carried out)

the patterns of younger saplings were positively correlated with the patterns of recently harvested stumps (AI = 1.03, AS = 6 m) and old stumps of large firs (AI = 0.65, AS = 10 m) (Table 3). Repulsion between large trees and saplings was found only sporadically (Table 4).

A positive spatial correlation between large firs (> 50 cm in $d_{1.3}$) and pole-stage firs was detected in 53% (live large firs, AI = 0.31), 42% (recently harvested stumps of large firs, AI = 0.43) and 60% (old stumps of large firs, AI = 0.37) of the stands, respectively (Table 3). The greatest departures from independence occurred up to a distance of 8 m.

In 57, 62 and 23% of the stands, respectively, a significant, negative spatial correlation was found between firs 25–50 cm in $d_{1.3}$ and younger saplings, older saplings, and pole-stage trees (RI = 0.40, 0.50, and 0.18, respectively) (Table 4). The maximal repulsion occurred at a relatively large scale of 4, 16,

and 15 m, respectively (Table 4). In the case of live saplings and trees 25–50 cm in $d_{1.3}$, the proportion of positive departures was insignificant.

The patterns of saplings and the trees 15–25 cm in $d_{1.3}$ appeared to be spatially independent in most of the stands being studied (Table 3). The intensity of attraction between pole-stage firs and firs 15–25 cm in $d_{1.3}$ was significantly greater than the intensity of repulsion between them (AI = 0.34 vs. RI = 0.04) (Tables 3 and 4). In 46% of the stands, the distribution patterns of pole-stage trees and trees 15–25 cm in $d_{1.3}$ were positively correlated. The maximal attraction between trees of these categories was detected at the scale of 13 m (Table 3).

DISCUSSION

As reflected by the diameter structure, the process of regeneration lasted in the stands studied for

at least a few decades. Nonetheless, the aggregated patterns of saplings and pole-stage trees indicate that the conditions for the establishment or survival of regeneration were more favourable in some stand patches than in others.

Since in each of the stands numerous seed-trees should ensure relatively uniform cover with fir seeds (presumably all trees in the upper and middle stand layer are fructifying every 3–8 years), the spatial distribution of regeneration did not appear to be controlled by seed-fall. Owing to limited vegetation cover in the stands studied (only sporadically exceeding 70%, PALUCH 2005b), the influence of post-dispersal seed predation, although a significant factor in patches with lush vegetation (SCHREINER et al. 2000), seems to be improbable. By the same token, nor could a competitive impact of forest floor plants play an important role.

Consequently, the detected aggregated pattern of the saplings and pole-stage trees seems to be caused by spatially varying seedling mortality. A real contrast between the mortality rates in patches favourable and unfavourable for regeneration is revealed by the positive spatial correlation detected between the patterns of live and dead saplings. Such patterns are to be interpreted as follows: Whereas in some parts of the stand, excessive density causes self-thinning of regeneration; in other parts, regeneration is missing completely.

In multilayered stands, the variability of light conditions at the forest floor is controlled by trees of the lower stand layer with low-based crowns (MARTENS et al. 2000). The irradiance pattern under the canopy of tall trees, with crown bases far from the ground, is rather uniform (KUULUVAINEN, PUKKALA 1987). Therefore, it follows that the least favourable light conditions occurred in the neighbourhood of trees of the lower stand layer, particularly because they are distributed in clumps. Moreover, the clumps of trees in the understory frequently grew close to large firs; hence, in their locations, light conditions were particularly unfavourable. Yet, according to the results from the spatial analyses, fir regeneration frequently appeared in such patches. This finding leads to the hypothesis that the light regime was not the most important factor controlling the survival of regeneration, a conclusion also supported by the results obtained by BURSHEL et al. (1985), CESCATTI (1996 after SCHÜTZ 2001), and DOBROWOLSKA (1998b).

This positive spatial correlation between large firs (live and dead) and pole-stage trees and saplings suggests that the factor controlling regeneration survival was linked in the past to the spatial pattern of large trees. Furthermore, the small scale of the ob-

served attraction points to interactions via edaphic factors. Taking into account that the large firs produce a considerable needle mass (BURGER 1942), provide an ample fall of decomposition-resistant litter (OTTO 1994) in their neighbourhood (HIRABUKI 1991), intercept precipitation and modify its chemical properties (JANEK 2002), and influence the soil through their roots, it is likely that they could considerably affect the humus form and characteristics of the upper soil horizons (BOETTCHER, KALISZ 1990; RUARK, ZARNOCH 1992; LISKI 1995). This assumption was confirmed by findings of PALUCH (2005b), who in stand patches characterised by higher local basal area found more frequent occurrence of forest floor plant species associated with mesic sites, and in gaps and canopy openings more abundant occurrence of species associated with fertile sites. Moreover, in gaps and canopy openings, despite moderate forest floor vegetation coverage, seedlings of silver fir were usually absent.

Frequently reported in the literature is the better germination of fir seeds and higher survival rate of fir seedlings on moder(-mor) humus than on mull humus (DUCHAFOUR, MILISCHER 1954; MAYER 1960; ROUSSEAU 1960; GRUNDA 1972; JAWORSKI 1973; SCHREMPF 1978). A possible explanation for this finding, as proved by KOWALSKI (1980a,b), is a more frequent occurrence of the parasitic fungus *Cylindrocarpon destructans* (Zins.) Scholt, which infects roots of young seedlings in the mull humus, together with the rare occurrence of the preventive fungus *Mycelium radialis atrovirens* Mel. In fact, in the moder-mor humus, *Cylindrocarpon destructans* was isolated only sporadically. Additionally, the lower pH of the upper soil horizons contributes to the neutralisation of toxins reaching the soil through precipitation and inhibiting the growth of seedling roots (BECKER, DRAPIER 1984, 1985). As reported by ROUSSEAU (1960), the higher pH also favours accumulation of manganese, which can toxically affect fir seedlings on soils with a low availability of base cations.

It is surprising that the pattern of saplings, pole-stage trees and large firs was closely correlated, whereas no positive correlation was found between saplings and live trees 15–25 and 25–50 cm in $d_{1.3}$. Thus, it seems likely that the influence of trees of the middle stand layer on the soil properties in their neighbourhood could be too small to produce any effect on the microsite variation. On the other hand, the smaller pole-stage trees, having low-based crowns and frequently growing in clumps close to the large firs, should particularly favour the accumulation of ectohumus and, owing to slow growth,

maintain variation of microhabitats over a considerable period. However, it should be stressed that to gain acceptance this hypothesis must first be proved by means of detailed soil investigations.

Another issue addressed by the research reported here is the question of the extent to which the spatial pattern of trees in the studied forests is a dynamic feature. The lack of spatial dependence between live large firs and younger saplings seems to support the thesis that the observed relationship is dynamic in nature. Worth noting, however, is that the spatial dependence between dead younger saplings and large live firs, and between live younger saplings and large firs already cut down, was comparable or even greater than that between older saplings and large firs. This observation suggests that the prime reason for the less frequent occurrence of younger saplings in the proximity of large trees is competition from older saplings and understory trees that earlier had occupied the favourable microhabitats.

The findings demonstrate that the spatial pattern of trees profoundly influences the distribution of regeneration. This influence is complex, however, and the assumption that regeneration processes are simply promoted by disturbances originating in the canopy zone is a questionable simplification. The spatial pattern of trees affects not only light availability in the subcanopy zone, but also seedbed properties, which in certain conditions may be of crucial and more vital importance than light for the establishment of regeneration. In effect, the spatial pattern of advanced regeneration and trees of lower stand layer may not correspond to the distribution of gaps, in particular in structured stands characterised by heterogeneous canopy of loose closure.

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Faktory ovlivňující proces obnovy v nestejnověkých jedlových lesích: vzájemné působení prostorové struktury stromů

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ABSTRAKT: Hlavním cílem studie bylo prokázat vztah mezi prostorovou strukturou, resp. rozmístěním stromů na ploše, a distribucí přirozené obnovy v bohatě strukturovaných jedlových (*Abies alba* Mill.) lesích v západních Karpatech (jižní Polsko). Na třinácti výzkumných plochách (o velikosti 0,45–1 ha) byly lokalizovány všechny živé stromy nad 15 cm výšky a velké pařezy stromového patra (nad 50 cm ve výčetní výšce). Navíc byly na všech plochách registrovány souřadnice všech živých a odumřelých stromů v růstovém stadiu tyčoviny (5–15 cm v $d_{1,3}$), na sedmi plochách souřadnice všech živých a odumřelých mladých stromů (0,5–1,3 m výšky) a na osmi plochách souřadnice všech živých a odumřelých starších stromů (nad 1,3 m výšky a pod 5 cm v $d_{1,3}$). Pro testování prostorové nezávislosti rozmístění stromů různých velikostních kategorií byla použita unvariantní a bivariantní Ripleyho K -funkce. Ve všech porostech mladší i starší stromy včetně stromů v růstovém stadiu tyčoviny vykazovaly agregované uspořádání. Největší agregovanost stromů těchto velikostních kategorií byla prokázána u rozestupu 6,5 m a 10 m. U stromů s rozstupem pod 10 m byla nalezena pozitivní prostorová korelace častěji mezi většími jedlemi a jedinci tyčoviny i mladých stromů. Negativní vztah mezi prostorovým rozmístěním přirozené obnovy jedle a stromů střední porostní vrstvy byl zanedbatelný nebo byl pozorován pouze v relativně široké škále rozestupů okolo 15 m. Distribuce mladších stromů a stromů nižší porostní vrstvy se ve většině sledovaných porostech jevila prostorově nezávislá. Výsledky naznačují, že v nestejnověkých jedlových lesích stabilní mechanismus vytváří agregovanou strukturu obnovních funkcí, přičemž určujícím faktorem je prostorové rozmístění (horizontální struktura) velkých jedlí. Proto lze vytvořit hypotézu, že prostorové rozmístění obnovy v takových porostech je hlavně určováno edafickými poměry a humusovou formou, světelné podmínky přitom hrají pouze sekundární roli.

Klíčová slova: *Abies alba*; výběrný les; obnova; mikrostanoviště

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