Growth and development of silver fir (*Abies alba* Mill.) regeneration and restoration of the species in the Karkonosze Mountains

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ABSTRACT: The main task of the study was to investigate the growth conditions of silver fir natural regeneration in the Karkonosze Mts. (Poland). The paper examines the quantity and quality of light reaching the forest floor in stands of different canopies. The aim of the study was also to define the optimal site conditions for silver fir planting under stand canopy. Data on the natural regeneration and stand structure of each investigated stand were collected on circular plots in a grid of 15 × 15 m in 1999 and 2000. Biometric measurements of fir plants planted under various stand canopies were done three times (May 1999, autumn 2000 and 2001). It was found that the fir was not a dominant tree in all size classes from seedlings to saplings. Seedlings (both phases) of spruce, beech, sycamore and rowan occurred in all studied stands. The optimal conditions for fir development were found under larch canopy. That was demonstrated by the highest increment of height, diameter and offshoots. The worst conditions for fir growth were under beech and spruce canopy, which was indicated by the lowest diameter and height. The highest PAR was recorded under pine canopy, whereas the lowest one under beech canopy. Beech stand induced a lower R:FR ratio than the other tree species both on sunny and cloudy days. The highest R:FR ratio was found under the canopy of larch and pine stands.

Keywords: natural regeneration; planting; light; biometric measurements

Silver fir (*Abies alba* Mill.) is one of the most important forest trees in Central Europe, especially in mountain regions (Jaworski 1995). The establishment, growth and survival of fir regeneration are influenced by many environmental factors stemming from the ecological requirements of the species (Bernadzki 1974; Jaworski, Zarzycki 1983) such as site conditions and stand species composition (Jaworski 1995). For instance, fir regenerates well under the canopy of pine (*Pinus sylvestris* L.) and birch (*Betula* spp.) but is less successful under the canopy composed of deciduous species such as ash (*Fraxinus excelsior* L.), alder (*Alnus glutinosa* Gaertn.), aspen (*Populus tremuloides* L.) and lime (*Tilia* spp.) (Dobrowolska 1998a). The lack of fir regeneration can be observed under the mature canopy (Jaworski, Zarzycki 1983). One potential explanation for these differences in fir regeneration under varying canopy conditions may have to do with understory light regimes.

Interspecific variation in light transmission by canopy trees may affect the quantity and quality of incident solar radiation reaching the understory. This variation is a function of both crown depth and structure. Moreover, light conditions under tree canopies depend on solar elevation and sky conditions as well as on spectral properties of leaves (Messier, Bellefleur 1988; Messier, Puttonen 1995). Tree crowns not only limit the amount of light passing to the understory but also change the spectral composition of radiation reaching the forest floor. Broadleaved canopies act as a filter transmitting less energy in the ultraviolet radiation and in PAR (photosynthetically active radiation) than in the far-red and near-infrared spectral regions, as well as less energy in blue and red than in green spectral regions (Messier, Bellefleur 1988). Coniferous canopies partition solar radiation in the various components of shortwave radiation reaching the forest floor, differently than broadleaved canopies (Mai Thu 1978; Mortensen, Sandvik 1988; Parent, Messier 1996).

Tree seedlings and saplings modify their growth according to the understory light regime. The quantity and quality of light influence many different ecological processes, such as photosynthesis (Hoddinott, Hall 1982; Kwestiga et al. 1986) and seed germination (Bormann 1983). Thus, it is very important to describe these two components of light under the canopy of different tree species to identify their effect on the tree growth and development.

Stand structure and composition influence light conditions. Messier and Bellefleur (1988) found that yellow birch (*Betula alleghaninsis* Britton) transmitted more energy than sugar maple (*Acer saccharum* Marsh.) and American beech (*Fagus grandifolia* Ehrh.). It appears important to evaluate both light quality and quantity under different stand canopies in Polish forests.

Silver fir was one of the most important forest tree species in the Sudetes and Karkonosze Mountains in the past. As a result of forest management during the last 200 years, clear cuttings and reforestation with Norway spruce (*Picea abies* [L.] Karst.), forest stands dominated by fir have almost completely disappeared (Boratyński, Filipiak 1997). It is also possible that other factors played an important role in this process. Fir decline has been observed throughout the range in Central Europe. This is a phenomenon of still unknown reasons. It is said that climate change, pollution, soil acidification and browsing have played an important role in the process (Boncina et al. 2002; Bigler et al. 2004). The situation has prompted efforts to restore fir into the forests of the Karkonosze Mts. A large *A. alba* reintroduction project in forest stands of Karkonoski National Park began in 1999 (Barzdajn 2000). Robakowski et al. (2004) investigated the ecophysiological performance of young trees under varying degrees of natural shade. However, it is still little known about the biometric features of fir regeneration and the effect of different tree canopies on the quality of light conditions. One of the main tasks of silver fir restoration is to identify the growth conditions of natural regeneration in the Karkonosze Mts. The specific objectives of this study were: (*i*) to identify the conditions for establishment, growth, and survival of natural silver fir regeneration in different stands in Karkonoski N.P.; (*ii*) to compare the quantity and quality of light reaching the forest floor in stands of different canopies; (*iii*) to compare the growth of silver fir plants under different canopies, and (*iv*) to define the optimal site conditions for silver fir planting under stand canopy.

MATERIAL AND METHODS

Study area of stands with natural regeneration

The study was conducted in Karkonoski N.P. in Poland (50°50'N; 15°32'E). The investigated area was located in the Karkonosze Mts., which is the highest mountain chain in the Sudetes Mts. Mean annual precipitation is 1,141 mm with the mean July temperature of 15.1°C. The main criterion for choosing the study area was the presence of natural silver fir regeneration. Measurements of regeneration were taken in 6 different stands with fir in the canopy (Table 1). The stands were situated at an elevation of 500–700 m in the lower mountain forest zone. The investigated stands grow on wet, deep and rich brown acid soils, frequently not far from streams in the *Luzulo-Fagetum* community. The age of the stands was different and ranged from 94 to 172 years. All investigated stands were planted and normally managed for many years. Nowadays they are partly a protected reserve where some treatments are done, especially sanitary cuts. According to soil analyses $pH_{(KCl)}$ ranged from 3.16 to 3.34 and the C/N ratio varied from 21.3 to 25.5. Major soil nutrient contents in the investigated stands were as follows: organic carbon (%) ranged from 6.64 to 12.66, nitrogen (%) from 0.294 to 0.506 and the sum of exchangeable cations (N, K, Ca, Mg me/100 g of soil) ranged from 1.101 to 2.613.

Study area of the experimental plots

To investigate the effect of different stand canopies on the light conditions and growth of fir 500 root-balled silver fir plants were planted under the canopy in each of the following 5 different stands: Scots pine (*Pinus sylvestris* L.), Norway spruce, European beech (*Fagus sylvatica* L.), European larch (*Larix decidua* Mill.) and silver birch (*Betula verrucosa* Roth.) in spring 1999. The investigation was carried out in managed stands which were planted. The seedlings were raised from seeds collected in Karkonoski N.P. and were grown in a local nursery for three years. The studied stands were located in a mixed mountain deciduous forest on brown acidic soil at similar altitudes (around 600 m a.s.l). Soil analyses showed that $pH_{(KCl)}$ ranged from 3.41 (birch stand) to 3.68 (pine stand) and the content of organic carbon varied

Table 1. Characteristics of investigated stands with natural regeneration of silver fir in the Karkonosze Mountains

Compartment	Stand species composition	Age (year)	Altitude (m)	Community	Exposition	Soil type	No. of plots
108a	60 Sp 30 Be 10 Fr	147	600–710	*Luzulo-Fagetum*	N–W	Brown acid	92
113j	70 Sp 30 Be spr. Fr	128	600–690	*Luzulo-Fagetum*	N–W	Brown acid	40
113d	I. 40 Be 30 Fr 20 La 10 Sp II. Be spr. Fr, Sp	142 50	600–690	*Luzulo-Fagetum*	N–W	Brown acid	44
214b	50 Sp 40 Be 10 La spr. Fr	102	500–630	*Luzulo-Fagetum*	N–W	Brown acid	27
215a	70 Sp 10 Be spr. Pn 10 Sp 10 Be	172 120	460–560	*Luzulo-Fagetum*	N	Brown acid	21
215b	70 Sp 20 Pn 10 Be spr. Fr	97	460–560	*Abieti-Piceetum montanum*	N	Brown acid	77
213h	50 Sp 20 Pn 10 Fr 20 Be	94 130	612	*Luzulo-Fagetum*	N	Brown acid	102

Be – European beech; Fr – silver fir; La – European larch; Pn – Scots pine; Sp – Norway spruce; spr. – sporadically

from 4.68% (pine stand) to 9.34% (beech stand). The nitrogen content varied from 0.217% (pine stand) to 0.492 % (beech stand). Contents of exchangeable cations (C, N, K, Mg me/100 g of soil) in beech, birch, pine, larch and spruce stands were: 1.506, 1.207, 0.433, 0.713 and 1.082, respectively.

Growth of fir natural regeneration

In each stand data on natural regeneration and stand structure were collected in circular plots established on 15 × 15 m grid in 1999 and 2000. Each circular sample plot consisted of two concentric circles of radii 1.78 and 5.64 m and areas 10 and 100 m^2, respectively. On the first subplot (area 10 m^2) all seedlings were measured. The second subplot (area 100 m^2) was established for measurements of saplings and trees. The number of research plots was different in each compartment and depended on the area (Table 1).

The following measurements of natural fir regeneration were conducted: height, diameter, "apical dominance ratio" (ratio of the last annual growth increment of the main shoot to the average last annual growth increment of offshoots, Grassi et al. 2004), and determination of vitality and age (by counting the whorls). Then the seedlings were divided into age classes. The following age classes were distinguished: 1-year-old; 2 to 5-years-old and over 6-years-old. For the assessment of fir vitality, three-degree classification was applied based on the vigour and damage by abiotic and biotic factors of the trees. The following vitality classes were chosen: (1) vital trees without damage; (2) weakened trees, partly damaged (browsing, defoliation, discoloration); (3) dying trees, severely damaged.

In the other tree species only measurements of height and diameter were done. Regeneration was divided into the following height classes: short seedlings – height up to 0.10 m, tall seedlings – height 0.11–0.5 m, short saplings – height 0.51–1.3 m, tall saplings – height over 1.31 m and diameter ≤ 5 cm.

Growth of fir artificial regeneration

Biometric measurements of fir plants were done three times (May 1999, autumn 2000 and 2001). All planted firs on five experimental plots were measured. The following parameters were determined: height, diameter at root collar, increment of main shoot and offshoots, vitality, and number of shoots. In 2001 the length and width of needles from the second whorl of 50 plants (100 needles) were measured.

Light quantity

The light quantity under different tree canopies was checked by the measurement of photosynthetically active radiation (PAR). A 1m-line quantum sensor placed on the forest floor was used to measure the light. The measurements of PAR were carried out for 2 days from 5 to 20 hours using a Li-COR system (Li-1000) connected to a sensor and data logger (Parent, Messier 1996). After 2-day measurements in one stand the equipment was moved to another stand and the measurements were continued.

Light quality

Spectral irradiance was measured with Li-1800 spectroradiometer (Li-Cor, Inc., Lincoln, NE) from 300 to 1,100 nm at 5-nm intervals. Light quality on

Table 2. The density of particular species (*N*/ha) of natural regeneration depending on different height classes in the Karkonosze Mountains

Stand (compartment)	Fir	Spruce	Pine	Larch	Beech	Syca-more	Elm	Rowan	Birch	Oak	Dog-wood
h ≤ 0.10 m											
108a	318 [b]	7,728	11	22	1,641	565	0	293	33	22	0
113j	1,027 [ac]	5,919	0	189	8,730	27	0	27	0	0	0
113d	672 [bc]	1,897	0	0	2,974	1,410	0	436	0	26	0
214b	456 [bc]	2,222	0	0	1,852	37	2,444	37	0	0	0
215ab	418 [b]	10,684	0	10	2,071	71	0	71	10	20	0
213h	1,791 [a]	176	0	0	265	353	0	88	0	20	0
h = 0.11–0.5 m											
108a	135 [a]	2,185	0	43	51,728	370	0	1,359	315	185	76
113j	532 [b]	6,540	0	486	128,405	270	0	622	0	0	0
113d	74 [c]	359	0	0	20,974	2,410	0	1,180	0	26	0
214b	163 [a]	444	0	0	4,222	259	0	37	0	0	0
215ab	73 [c]	1,980	0	10	6,837	20	0	316	143	20	0
213h	41 [c]	59	0	0	19,461	1,480	0	853	0	78	0
h = 0.51–1.3 m											
108a	0 [a]	0	0	0	2,380	54	0	706	565	10	22
113j	0 [a]	54	0	0	2,324	27	0	568	54	0	0
113d	0 [a]	0	0	0	846	308	0	282	0	0	0
214b	0 [a]	37	0	0	1,593	74	0	111	0	0	0
215ab	1 [a]	10	0	0	520	10	0	41	5	0	0
213h	0 [a]	0	0	0	3,647	294	0	137	0	0	0
h > 1.3 m											
108a	0 [a]	11	0	0	206	0	0	457	478	0	283
113j	0 [a]	27	0	0	865	54	0	351	0	0	0
113d	0 [a]	0	0	0	333	0	0	26	0	0	0
214b	0 [a]	111	0	0	6,556	185	0	0	37	0	0
215ab	11 [a]	61	0	0	296	10	0	0	51	0	0
213h	0 [a]	9	0	0	1,412	216	0	39	0	0	29

For the column "fir" the values with the same letter are not significantly different at the 0.05 probability level (Kruskal-Wallis test)

the forest floor was measured under different tree canopies in 2001. Measurements were taken between 10 and 14 hours to obviate variations in solar radiations due to the rapidly changing angle of the sun occurring early in the morning and in the late afternoon. Seven repetitions were made under full shade for each different canopy on both sunny and cloudy days. Seven repetitions were made in a nearby open field to estimate above canopy values on cloudy days. All the measurements were done for five sunny days and five cloudy days.

Statistical analyses

Nonparametric methods (Kruskal-Wallis test) were used to test differences between the average quantities of fir in particular regeneration classes. Comparisons of the average amount of fir regeneration according to site conditions in particular regeneration classes were made using the Dunn test (Zar 2002). The significance of interaction between the parameter of fir plant growth and canopy composition was tested by means of analysis of variance

Table 3. The quantity of silver fir natural regeneration in vitality classes according to the age of regeneration in the Karkonosze Mountains

Stand (compartment)	Age classes								
	1-year			2–5 years			≥ 6 years		
	1*	2*	3*	1	2	3	1	2	3
108a	60 [a]	1 [a]	0 [a]	314 [a]	47 [ab]	0 [a]	13 [a]	21 [a]	0 [a]
113j	224 [ab]	8 [ab]	0 [a]	935 [b]	54 [a]	0 [a]	319 [b]	19 [ab]	0 [a]
113d	333 [bc]	36 [c]	0 [a]	274 [a]	41 [ab]	0 [a]	59 [c]	3 [b]	0 [a]
214b	267 [cd]	4 [ac]	0 [a]	111 [c]	41 [ac]	0 [a]	130 [bd]	67 [c]	0 [a]
215ab	179 [bd]	36 [bc]	0 [a]	122 [c]	31 [bc]	1 [a]	112 [cd]	22 [a]	2 [a]
213h	17 [e]	11 [bc]	1 [a]	1,506 [b]	235 [e]	5 [a]	28 [a]	29 [ac]	1 [a]

For each column the values with the same letter are not significantly different at the 0.05 probability level (Kruskal-Wallis test)
* vitality class

(ANOVA and Kruskal-Wallis test). The analysis of light parameters between different stand canopies was first evaluated by the Kruskal-Wallis test, followed by the Dunn test for individual variables. All statistical calculations were conducted with Statistica 5.5 software.

RESULTS

Natural regeneration of different tree species

Ten different species of trees and shrubs regenerated in the stands of the Karkonosze Mts. (Table 1). The fir was not a dominant tree in all size classes from seedlings to saplings. Seedlings (both phases) of spruce, beech, sycamore (*Acer pseudoplatanus* L.) and rowan (*Sorbus aucuparia* L.) were found in all studied stands. However, the most abundant tree species was beech. Tall beech saplings dominated in stands and their quantity ranged from 4,222 to 128,405 individuals per hectare. The seedlings of larch and pine were observed only in few stands. The highest variability of natural regeneration was found in compartment 108a, where some saplings of dogwood (*Frangula alnus* L.) were observed.

The density (N/ha) of fir varied in the different stands (the Kruskal-Wallis statistic, H, was H = 54.08 for short seedlings, H = 128.09 for tall seedlings and H = 48.05 for tall saplings and was significant at $P < 0.001$) (Table 2). The best site conditions for fir seedling establishment were noticed in compartments 213h and 113j. There were no short fir saplings in all investigated stands. Tall fir saplings were found only in one stand.

There were significant differences in fir seedling (1-year-old) vitality between the studied sites (Table 3). The differences for vitality classes 1 and 2 were statistically significant ($H_1 = 62.19$ and $H_2 = 21.46$ for $P = 0.000$). The differences in fir vitality were found also for age class II ($H_1 = 130.42$; $H_2 = 65.94$ for

Table 4. Growth of fir natural regeneration in different stands in regard to age classes in the Karkonosze Mountains

Stand (compartment)	Age classes					
	2–5 years			≥ 6 years		
	height (cm)	main shoot increment	offshoot increment	height (cm)	main shoot increment	offshoot increment
108a	10.53 [a]	2.24 [a]	5.07 [a]	13.82 [ab]	2.38 [ab]	5.35 [ab]
113j	9.94 [ab]	1.51 [b]	4.28 [c]	19.42 [d]	2.69 [a]	6.40 [a]
113d	9.11 [b]	1.46 [bc]	3.65 [b]	14.29 [ab]	1.53 [cd]	4.37 [bc]
214b	9.11 [abc]	1.11 [bd]	3.33 [b]	15.38 [bc]	1.24 [c]	4.26 [c]
215ab	7.54 [c]	1.10 [d]	3.12 [b]	24.93 [ac]	1.71 [d]	5.03 [b]
213h	9.68 [ab]	1.30 [cd]	3.55 [b]	11.93 [c]	1.63 [bcd]	3.40 [c]

For each column the values with the same letter are not significantly different at the 0.05 probability level (Kruskal-Wallis test)

Table 5. Comparison of the height and diameter growth of silver fir plants planted under different stand canopies in the Karkonosze Mountains in 1999–2001

Stand canopy	Diameter (mm)		Height (cm)		
	1999	2001	1999	2000	2001
Spruce	3.20 [a]	5.69 [a]	11.13 [ab]	17.89 [a]	21.98 [a]
Pine	2.90 [b]	6.73 [b]	10.73 [a]	18.34 [a]	25.00 [b]
Birch	3.31 [a]	7.16 [c]	11.55 [bcd]	20.45 [b]	24.80 [b]
Larch	3.50 [c]	8.19 [d]	11.17 [ac]	19.34 [c]	28.13 [c]
Beech	3.29 [a]	5.03 [e]	11.91 [d]	16.72 [d]	19.07 [d]

For each column the values with the same letter are not significantly different at the 0.05 probability level (Kruskal-Wallis test)

Table 6. Changes in the "apical dominance ratio" (length of main annual shoot/average length of annual offshoots) of silver fir plants in the experimental plots in the Karkonosze Mountains in 1998–2001

Stand canopy	Main shoot/offshoots			
	1998	1999	2000	2001
Spruce	0.59 [a]	0.58 [a]	0.50 [a]	0.53 [a]
Pine	0.56 [b]	0.49 [c]	0.59 [b]	0.63 [b]
Birch	0.58 [a]	0.58 [ab]	0.64 [c]	0.60 [c]
Larch	0.19 [c]	0.56 [b]	0.65 [c]	0.73 [d]
Beech	0.61 [a]	0.59 [ab]	0.43 [d]	0.46 [e]

For each column the values with the same letter are not significantly different at the 0.05 probability level (Kruskal-Wallis test)

$P = 0.000$). The vitality of 1-year-old and 2 to 5-years-old seedlings was high. The most vital seedlings were found in compartments 113j and 108a. The quantity of the oldest phase of regeneration varied between studied stands ($H_1 = 76.12$; $H_2 = 16.20$ for $P = 0.000$). The best quality characterized firs growing in the stands (comp. 113j and 113d) where 94–95% of trees belonged to quality class 1. In other stands fir vitality was rather poor.

2 to 5-years-old fir seedlings dominated in study stands (Table 3). The percentage of this age class ranged from 25 to 95% and the highest number was found in compartment 213h (1,746/ha). The percentage of 1-year-old seedling was different and varied from 2 to 50%. The lowest quantity of those seedlings was found in compartment 213h (298/ha) and the highest in compartment 113d (369/ha).

The parameters of fir growth depended on site conditions ($P < 0.001$). All seedlings and saplings gained very slowly in height (Table 4). The increment of main shoots of 2 to 5-years-old firs ranged from 1.10 (comp. 215a,b) to 2.24 cm (comp. 108a)

Table 7. Characteristics of needles of silver fir plants depending on stand canopy

Stand canopy	Needle length (cm)			Needle width (mm)		
	mean	min	max	mean	min	max
Spruce	2.03 [a]	1.2	3.05	1.95 [a]	1.8	2.2
Pine	2.30 [d]	1.5	3.10	2.07 [b]	1.8	2.5
Birch	2.03 [ab]	1.4	2.85	1.99 [c]	1.5	2.3
Larch	1.76 [c]	0.8	2.60	1.82 [d]	1.2	2.2
Beech	1.88 [bc]	1.2	2.80	1.84 [d]	1.3	2.3

For each column the values with the same letter are not significantly different at the 0.05 probability level (ANOVA, Tukey's test)

Table 8. Light characteristics under different stand canopies in the Karkonosze Mountains

Stand canopy	Time of measurement (hour)						
	6–9	9–11	11–15	15–17	17–20	6–20	max
Relative light radiation (%)							
Spruce	4.16 [a]	7.16 [a]	7.92 [a]	7.90 [a]	6.56 [a]	6.96 [a]	12.25
Pine	6.53 [b]	7.68 [a]	17.41 [b]	17.18 [b]	14.57 [b]	12.81 [b]	53.91
Birch	8.77 [c]	11.35 [c]	13.04 [c]	13.79 [c]	9.78 [c]	11.08 [c]	25.31
Larch	15.29 [d]	21.12 [d]	22.13 [d]	22.58 [d]	17.22 [b]	19.19 [d]	20.12
Beech	4.39 [a]	3.63 [e]	4.03 [e]	4.14 [e]	4.39 [d]	4.17 [e]	20.26

For each column the values with the same letter are not significantly different at the 0.05 probability level (Kruskal-Wallis test)

and from 1.24 to 2.69 cm for older regeneration. The mean increment of offshoots varied from 3.12 to 5.07 and from 3.40 to 6.4 cm (for both age classes, respectively).

Growth and development of silver fir plants

The species composition of canopy influenced the height (H_{2000} = 162.42; H_{2001} = 424.98, P = 0.000) and diameter (H_{2001} = 846.91, P = 0.00) of fir plants (Table 5). The optimal conditions for fir growth were found under larch canopy. That was demonstrated by the highest increment of height (P < 0.01), diameter and offshoots (P < 0.001). The worst conditions for fir growth were under beech and spruce canopy, which was indicated by the lowest diameter and height. The ratio of main shoot length to average offshoot length was the best parameter for plant growth classification (Table 6). It was found that the stand species composition influenced the "apical dominance ratio". The lowest value of the ratio (P < 0.001) was observed under beech canopy, whereas the highest value of the parameter was found under larch canopy. Morphological characteristics of fir needles from different stands are given in Table 7. The species composition of stand canopy influenced the length (F = 25.98 for P = 0.000) and width (H = 76.91 for P = 0.000) of fir needles. Needles developed under the canopy of larch were longer and wider than those from the other stands (P < 0.05). Under pine and birch canopy the length of fir needles was similar. The canopy composed of spruce and beech caused a decrease in the length of fir needles.

Table 9. Spectral irradiance (nm) under different stand canopies in the Karkonosze Mountains

Stand canopy	Spectral irradiance (W/m²)						
	UV 300–400	PAR 400–700	FR 700–800	NIR 800–850	Total 300–850	BAP 300–500	R:FR
Sunny days							
Spruce	3.38	36.34	26.50	13.88	80.10	13.42	0.71
Pine	14.62	231.93	127.38	79.15	435.08	73.35	0.90
Birch	15.77	291.32	150.27	93.86	551.22	91.75	0.72
Larch	18.15	312.50	164.33	47.18	542.16	96.31	1.01
Beech	3.49	59.67	69.55	38.91	171.62	17.94	0.36
Cloudy days							
Spruce	5.44	82.35	44.62	20.21	152.62	26.91	0.93
Pine	3.97	56.45	28.81	12.37	101.60	18.96	1.12
Birch	7.03	111.36	73.89	35.24	227.52	35.42	0.75
Larch	6.17	89.02	47.47	20.94	163.60	29.81	1.02
Beech	1.24	19.58	23.67	13.92	58.41	6.11	0.49
Control	35.09	516.42	212.11	80.64	844.26	173.96	1.23

UV – ultraviolet radiation, PAR – photosynthetically active radiation, FR – red radiation, NIR – near-infrared radiation, BAP – biologically active points, R – red radiation, FR – far-red radiation

Light quantity and quality under stand canopy

Stand canopy affected the light quantity reaching the forest floor (the Kruskal-Wallis statistic calculated for light quantity from 6 a.m. till 8 p.m. was $H_{6-20} = 232.08$, $P = 0.000$). The effect of forest canopy on the light conditions was found not only during the whole day but at different times of day (Table 8). The highest differentiation of light conditions in the investigated stands was observed at midday (hours 11–15). The highest PAR was recorded under pine canopy, whereas the lowest one under beech canopy. The quantity of light under the investigated canopies was very low in comparison with the open area (< 20%). It was observed that even during the day the quantity of light reaching the forest floor was below the threshold of photosynthetically active radiation (2 µmol/m^2/s) (Messier, Bellefleur 1988).

Spectral irradiance was higher on sunny days than on cloudy ones (Table 9). On sunny days, the birch stands transmitted more total energy (between 300 and 1,100 nm) than the other stands. The beech stands transmitted twice the amount of total energy than the spruce canopy. During cloudy days the least energy was transmitted by the beech canopy. For PAR the differences were even greater. The lowest PAR was found under beech stand both on sunny and cloudy days. The R:FR ratios varied among canopies. The beech stand induced a lower R:FR ratio than the other tree species both on sunny and cloudy days. The highest ratio was found under the canopy of larch and pine stands. The UV was different under studied canopies. The lowest values were observed under spruce and beech canopies. However, the highest values were detected under birch and larch stands, both on sunny and cloudy days. Larch and birch stands transmitted the highest BAP energy. The lowest BAP was found under beech and spruce canopy. On both days the highest value of NIR was observed also under birch canopy. Spruce (sunny days) and beech (cloudy days) transmitted the lowest NIR energy.

DISCUSSION

The lack of fir saplings and a small quantity of seedlings showed that there was no continuity in silver fir regeneration in Karkonoski N.P. The process of fir decline in the studied stands was very advanced (Jaworski 1979). Few fir saplings of weak vitality, those mainly growing close to the stream, will not be able to play an important role in future. The density of fir seedlings in Karkonoski N.P. was lower than in other protected stands (Korpeľ, Vinš 1965; Niemtur et al. 1994). Research on silver fir in the Sudetes Mts. pointed out very poor regeneration of this species and constantly decreasing share of younger age classes in the tree stands (Jaworski 1979; Filipiak et al. 2003). However, the results of the study did not answer the question why fir did not regenerate naturally in the Sudetes Mts.

It is known that one of the main reasons for fir decline was forest management (Boratyński, Filipiak 1997). The Karkonosze Mts. were covered by very rich forests composed of different tree species: oaks (*Quercus robur* and *Q. sessilis*), beech, fir, sycamore and hornbeam (*Carpinus betulus* L.) (Boratyński, Filipiak 1997). From the 17th to 19th century forests were cut for people's settlements and mining purposes. Clear-cuttings and forestation with Norway spruce converted the very much diversified stands growing in the lower mountain forest zone into monocultures (Boratyński, Filipiak 1997). Silver fir is very sensitive to air pollution (Bernadzki 1983). Although the SO_2 and NO_x contamination has decreased in the last years, the effects of air pollution have been observed. The vitality of fir crowns was very low. Crowns of many mature fir trees are short and much defoliated (Dobrowolska 2001). The phenomenon of fir dying has been observed not only in the Karkonosze Mts. but also in the whole natural range of this species (Bernadzki 1983; Krause et al. 1986; Larsen 1986; Boratyński, Filipiak 1997; Rozenbergar et al. 2007). In the 1990s fir recovered in many countries (Boncina et al. 2002; Thomas et al. 2002; Filipiak, Ufnalski 2004). The same was observed in Polish forests but not in the Karkonosze Mts. (Dobrowolska 1998b). The reasons for a lack of natural regeneration in that region are still unknown. Why did many seedlings appear after the mast year but why did they die within a few years?

Natural regeneration enables the continuity of a forest both in space and time. Therefore, the correct understanding of natural regeneration dynamics and of the conditions that may enhance it is of great importance for the sustainability of silvicultural systems (Grassi et al. 2004). The best conditions for fir establishment and growth were found in Jagniatków area (compartments 113j and 108a), where the higher contents of organic carbon and exchangeable cations were recorded (Dobrowolska 2001). The vitality of fine roots of natural fir regenerations was significantly higher in Jagniatków stands (Farfał 2001).

Other parameters of soils like the content of micro- and macroelements and the activity of soil enzymes did not influence the quantity of fir regeneration (Dobrowolska 2001). The species composition and cover of vegetation plants was investigated. No allopathic effect of plants on natural fir regeneration was found in the studied stands (Dobrowolska 2001).

In Karkonoski N.P. stands with fir undergo a significant shift in the species composition. The increasing contribution of beech and other deciduous tree species to the regeneration indicated that coniferous trees were replaced by broadleaved ones. European beech is one of the most expansive tree species in a mountain area (Matic et al. 1996; Szwagrzyk et al. 1996; Rozenbergar et al. 2007). Hence, the beech competition can significantly limit the regeneration of fir in Karkonoski N.P., especially because beech has smaller requirements regarding the soil moisture. In such circumstances the best conditions for fir establishment should be provided and fir should be planted simultaneously.

One of the important environmental factors that influence the plant growth both directly and indirectly was the spectral composition of solar radiation. Silver fir planted under varied stands experienced a range of light conditions determined by species-specific structural characteristics of the canopy. The best conditions for fir planting were under larch canopy, where the highest PAR was recorded. Deciduous tree species – beech and birch – transmitted less energy in ultraviolet (UV) radiation and in PAR than in far-red and near infrared spectral regions. The same results were obtained by Messier and Putonen (1995). The least UV radiation was transmitted by beech canopy, but FR was the highest. The highest BAP was transmitted by larch and pine canopies. It may be concluded that the light environment under larch and pine stands was more conducive to fir growth than that created by beech and spruce.

It is documented that the light quality affects plant growth and morphology (Mortensen, Sandvik 1988; Tuller, Peterson 1988). Fir, similarly like many other tree species, achieved higher increments at low shading than under a denser tree canopy (Bellon et al. 1983; Gazda 1988; Skrzyszewski, Gomółka 1998; Magnuski et al. 2001). It was found that light intensity and spectral irradiance under different canopy determined the growth of firs. The tallest and thickest plants with the greatest increment of main shoots or offshoots grew under the larch stand, where the length and width of needles were significantly greater than on other plots. Fir needles from the larch stand were not only thicker but also had greater dimensions of some internal structures (Robakowski et al. 2004).

The worst conditions for fir growth were under the canopy of beech. All biometric features of fir plants were significantly lower at beech plots. Conditions for fir growth under the canopy of birch and pine were similar. In the following years the greater variability of growth ratio was found depending on the canopy.

The quantity of light under tree canopy was very small in comparison with the open area. The relative light intensity was lower than 20% in all studied stands. The lowest value of relative intensity was observed under beech and spruce canopies (only 4–7%, respectively). The best light conditions were found under larch canopy (20%). The results of light intensity are related to fir growth and development on the study areas (the greater the PAR, the greater the growth of fir seedlings). It is known that fir seedlings need 10–33% of full light, and relative intensity for optimal growth is 15–25% (Jaworski, Zarzycki 1983; Dobrowolska 1998b). The "relative minimum of light" for fir seedlings is 1.7–2.7% of full light (Jaworski, Zarzycki 1983). Only under beech canopy the relative intensity was lower than 5%. The same results were reported by Szwagrzyk et al. (2001). In other investigated plots the relative intensity was close to optimal. The results suggest that fir should be planted under different canopies, except poor beech stands.

The climate influences the development and growth of regeneration. It was noticed that the PAR was below the threshold (2 $\mu mol/m^2/s$) under spruce and beech stands. The Karkonosze are the foggiest mountains in Poland. The highest point in the mountains notes over 300 days of mist and wind. The average precipitation is over 1,500 mm. In such climatic conditions there must be a lot of days when the radiation under beech and spruce canopy is below the PAR threshold and the firs are not able to photosensitize.

CONCLUSIONS

The lack of fir saplings indicated that there is no continuation of fir regeneration in stands of Karkonoski N.P. The small amount of slowly growing seedlings shows that fir has no chance to come to the next generation of canopy trees. Stands with fir share undergo a significant shift in the species composition, with coniferous trees being replaced by broadleaved ones, which was indicated by the percentage of beech and other deciduous tree species in the regeneration. Planting of silver fir should be done to protect the population of fir in the Karkonosze Mts. The optimal conditions for silver fir planting were under larch canopy, whereas the worst conditions were in pure beech and spruce stands. Silver fir should also be planted under pine and birch stand canopy. The results provided useful information to ensure, through silvicultural practices, favourable conditions for the regeneration processes and fir reintroduction to the Karkonosze Mts.

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Růst a vývoj jedle bělokoré (*Abies alba* Mill.) – obnova a regenerace této dřeviny v Krkonoších

ABSTRAKT: Hlavním cílem výzkumu bylo zjistit růstové podmínky přirozené obnovy jedle bělokoré v Krkonoších (Polsko). V článku je hodnocena kvalita a kvantita slunečního záření dopadajícího na povrch půdy v porostech s různým stupněm zápoje. Cílem studie bylo také definovat optimální stanovištní podmínky pro jedlové podsadby. Data zahrnující údaje o přirozené obnově a porostní struktuře v každém zkoumaném porostu byla získávána na kruhových plochách v síti 15 × 15 m v letech 1999 a 2000. Biometrická měření jedlových sazenic v podsadbách pod různým stupněm zápoje byla provedena třikrát (květen 1999, podzim 2000 a 2001). Bylo zjištěno, že jedle nebyla dominantním stromem v žádné velikostní třídě od semenáčků po odrostlejší nárosty. Obě kategorie semenáčků (do 0,1 m, 0,11–0,5 m) smrku, buku, javoru klenu a jeřábu ptačího se vyskytovaly ve všech zkoumaných porostech. Optimální podmínky pro vývoje jedle byly zjištěny pod zápojem modřínu. To bylo doloženo nejvyšším přírůstem výšky, tloušťky a bočních výhonů. Nejhorší podmínky pro růst jedle, indikované nejnižší tloušťkou a výškou, byly pod zápojem buku a smrku. Nejvyšší hodnoty PAR byly zaznamenány pod zápojem borovice, zatímco nejnižší pod zápojem buku. V bukových porostech bylo dosaženo menšího poměru R:FR než u ostatních dřevin, a to jak při oblačném, tak i slunečném dni. Nejvyšší poměr R:FR byl zjištěn v porostech modřínu a borovice.

Klíčová slova: přirozená obnova; výsadba; světlo; biometrická měření

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