The effects of cutting regimes on natural regeneration in submountain beech forests: species diversity and abundance

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ABSTRACT: The paper summarizes the results of 15-year natural regeneration for beech of five plots with different densities situated in the Western Carpathians Mts. Three of the plots were subjected to differently intensive shelterwood cuttings (plots L, M, H), one plot was clear-cut (CC), and one was left without intervention – as a control (C). The number of one-year-old seedlings decreased proportionally with increasing cutting intensity. The ANOVA results document a significant influence of cutting intensity on the abundance of both one-year-old and older seedlings. The abundance of beech seedlings was initially increasing with increasing cutting intensity, and, having reached the peak on plot M (medium intensity), there followed a decrease in the seedling abundance. Lower numbers of beech seedlings on plots subjected to less intensive cutting (C, L) result from less favourable growth conditions in comparison with plot M. On the other hand, cutting of higher intensity (H, CC) resulted in lower numbers of fructifying parent trees. The medium cut intervention having provided the plot M with stocking of 0.5 (50% of the stand) resulted in a lower number of seed resources (limiting factor for natural regeneration). However, for the other factor – seedling establishment (survival and recruitment) this plot (M) represents an ecological optimum in beech regeneration in the given conditions.

Keywords: regeneration development; stand density; shelterwood cutting; clear cutting; *Fagus sylvatica* L.

Different woody plants have different demands on the environment. They require specific methods of cultivation, with cutting operations diversified in timing and spatial arrangement (Marušák 2001). The multi-target model of forest management is the only one that is capable to preserve or even to improve the biodiversity. Extensive experiments carried out both in natural and model environment confirmed the crucial importance of biodiversity for performance and stability of the relevant systems (Tilman 1996, 1999; Hector et al. 1999). The correct interpretation of the existing relations, however, is a hot topic (Huston et al. 2000; Kaiser 2000; McCann 2000). In beech stands, natural regeneration is considered to be commercially effective and necessary or inevitable for maintaining the biological balance (Sinner 1974; Korpeľ 1978). In terms of ecology, biology, production and commercial importance, natural regeneration is an efficient tool for ecosystem-oriented forest management. The method has a range of merits: protection and preservation of the local ecotype, abundant natural seeding guaranteeing the further positive development of succession stand, diversified internal stand structure, vigorous root system without deformations (Jaloviar 2006; Jaloviar, Kucbel 2006). It preserves the biological and genetic diversity of forests and contributes to the stability of forest ecosystems (Kucbel 2005). Vološčuk (2004) defined ecological stability as an intrinsic quality of forest

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Table 1. Characteristics of research plots C, L, M, H, CC (A), and of the parent stand on research plots after cutting in February 1989 and at the time of inventory of regeneration, September 2003 (B)

		Plot/intensity of cut									
		C/control plot		L/light cut		M/medium cut		H/heavy cut		CC/clear cut	
A	Cutting intensity (%) according to:										
	basal area	0		24		44		68		100	
	number of trees	0		44		65		82		100	
	Relative illumination (%)	1[a]		8		22		53		100	
	Throughfall (mm): year	465 ± 109[b]		472 ± 106		538 ± 121		607 ± 125		661 ± 164	
	growing season	231 ± 87		236 ± 90		271 ± 98		319 ± 107		347 ± 125	
	Exposition	W		W		WSW		W		W	
	Slope (°)	18		20		20		18		17	
	Area (m^2)	1,500		3,500		3,500		3,500		4,000	
B		1989	2003	1989	2003	1989	2003	1989	2003	1989	2003
	Number of trees/ha	700	627	397	349	243	226	160	160	0	0
	Height (m)	23.6	26.3	25.4	28.6	26.9	29.5	27.7	30.0	–	–
	dbh (cm)	23.9	27.6	29.4	34.5	31.3	38.5	32.0	41.4	–	–
	Basal area (m^2/ha)	40.9	44.5	28.8	36.1	18.6	27.3	13.5	22.4	–	–
	Degrees of stocking[c]	0.9	1.0	0.7	0.9	0.5	0.7	0.3	0.5	0.0	0.0
	Species composition (%):										
	Fagus sylvatica L.	89.5	94.7	76.3	85.2	87.1	89.9	93.0	93.0		
	Abies alba Mill.	5.7	2.1	19.4	11.5	7.1	3.8	0.0	0.0		
	Quercus dalechampii Ten.	1.9	1.1	3.6	2.5	3.5	3.8	5.0	5.0		
	Carpinus betulus L.	2.9	2.1	0.7	0.8	2.3	2.5	2.0	2.0		

[a]Account by Střelec (1992), [b]account by Dubová (2001), [c]the ratio of the real to the original basal area of the stand which is given in the yield tables for yield class and age (Assmann 1970)

ecosystems that utilize their own mechanisms for keeping their consistency.

Areas after former beech stands with an insufficient proportion of beech trees as well as extensive mature and over-mature beech stands with dense weed cover show evidently that practical implementation of natural regeneration in beech stands suffers from severe errors (Korpeľ 1978). In the first phase of regeneration, the primary interest is to reach an appropriate species composition and partitioning – interspecific relations (Saniga 1990). In beech forests, these relations are not complex because beech is privileged in ecology and in growth. The only exception is some communities at its lower distribution range where this woody plant may be suppressed by hornbeam (Bezačinský 1971). Several papers dealing with the survival and growth of succession stand after shelterwood cutting were published (Agestam et al. 2003; Modrý et al. 2004; Karlsson, Nilsson 2005; Stancioiu, O'Hara 2006; Souček 2007). In this paper we have subjected some of them to a more thorough analysis. We explore the influence of common cutting regimes in beech stands on regeneration development – seedling establishment, composition, variability, density.

MATERIALS AND METHODS

Research was carried out in an experimental beech stand situated in the Kremnické vrchy Mts. – the Western Carpathians, Central Slovakia (48°38'N, 19°04'E). The altitude of the site is 470–490 m a.s.l., the mean annual air temperature is 8.2°C, in the growing season 14.9°C, the mean annual precipitation total is 664 mm, in the growing season 370 mm. The soil substrate consists of andesite-tuff agglomerates, the soil type is Andic Cambisol with high skeleton content (20–60%) and mild acid reaction (pH 5.4–6.4), the humus form is acid mull (Kukla 2002). The research was conducted on five research plots. In February 1989, the plots were subjected to different cutting regimes, graded as follows: plot L – light cut, plot M – medium cut, plot H – heavy cut, plot CC – clear cut. The fifth plot was left as control – C. The original stand before the intervention consisted of beech as a dominant species (65–90%), associated with hornbeam, oak and especially fir (20–25% on plots L, M, H and 6–7% on C and CC). The cutting was primarily focused on the admixed species, dying and damaged trees and trees of very low quality. The main characteristics of research plots, cutting intensity and response of stand parameters after the cutting operations in 1989 and 2003 are listed in Table 1. In 2003, the regeneration was subjected to an inventory. Before the research, the stand was managed according to the common forestry practice. Within 30 years preceding the research (1986), the stand was subjected to silvicultural treatments three times. The stand age in 2003 was 105 years. Supplementary information on the site can be found in Pichler et al. (2003), Kuklová et al. (2005), Dubová and Bublinec (2006), Kellerová and Janík (2006).

In February 1989, following a mast year, three plots were subjected to shelterwood cuttings of different intensities. One plot was clear-cut and one plot was left intact. The individual plots were separated by isolation strips (16–30 m). Each strip between the plots was cut at an intensity corresponding to the cutting intensity on the adjacent plot. The experiment was conducted on a rectangular area, 400 × 125 m in size (5 ha). The area was fenced to a height of 1.50 m to avoid game browsing. In natural conditions, game browsing may sometimes be a significant harmful factor (Schweiger, Sterba 1997; Taylor et al. 2006).

Each research plot was divided into three equal longitudinal strips, each of them with a transect identical with the strip axis. On each transect, 20 subplots 1 × 1 m in size were established. The subplots (60 on each plot) were located equidistantly so as the subplot series would cover the whole corresponding transect. We sampled material for the evaluation of variability in the seedling number. For the subplots we evaluated the species composition and numbers of seedlings in natural regeneration.

We sought to identify differences in conditions for seedling development as precisely as possible. For light conditions, we confined to the values of light intensity at the beginning of the experiment, on August 1, 1990 (Střelec 1992). The illumination values were measured at 60 min intervals, on each plot at the same time. The values were recorded with a luxmeter (PU 150 M Blansko) at the vertices of the square 10 × 10 m in size, at a height of 0.5 m above the ground. The data on throughfall were provided by Dubová (2001), who used 10 precipitation collectors (ombrometers) on each plot. The parameter of leaf area index (LAI) was determined in a destructive way – cutting and analyzing three average sample trees (dominant, codominant and subdominant) on each plot. The correlation was calculated with average values for the whole period. The influence of cutting intensity on the amount of natural regeneration was examined using the analysis of variance – ANOVA. The similarity to the normal distribution was tested using the Kolmogorov-Smirnov goodness-of-fit test. For the correct use of ANOVA and

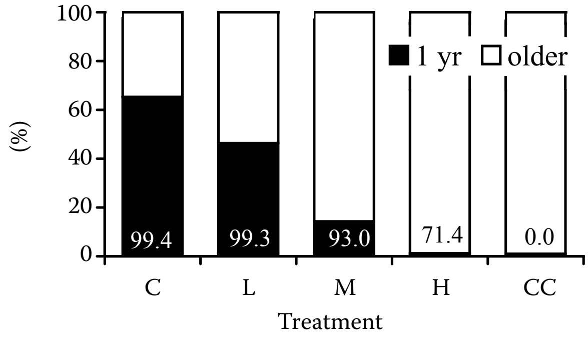

Fig. 1. Comparison of one-year-old and older-than-one-year regeneration between the plots (C, L, M, H, CC see Table 1). The numerical data in columns express proportions of beech in the one-year regeneration in percent

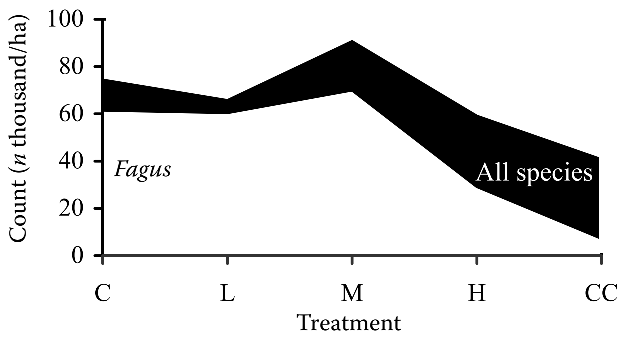

Fig. 2. Amount of natural regeneration on the plots (C, L, M, H, CC see Table 1) – beech and all species

Pearson's correlation, the measured values were subjected to transformation. For the regeneration of the except-one-year seedlings we used the transformation $x` = \sqrt{x} + \sqrt{(x + 1)}$. The significance of differences between the means was determined by their multiple comparisons – repeatedly used Duncan's test ($\alpha \leq 0.05$). For calculations we used the Statistica Software, Inc. Tulsa OK.

RESULTS

The overall natural regeneration was differentiated according to: (*i*) species composition; (*ii*) age (one-year-old and older), due to the high mortality of one-year-old seedlings (Béland et al. 1999; Knott et al. 2004). Fig. 1 illustrates a dependence of the number of one-year-old seedlings on cutting intensity. The highest proportion (65%) of one-year seedlings was found on the control plot with 431 fructifying trees per hectare, the lowest values (1%) were on plots H and CC with 158 and 0 fructifying trees per ha, respectively. Beech is a dominant (95–85% – Table 1) woody plant on all the plots in the parent stand; consequently, the proportion of one-year-old beech seedlings in natural regeneration is also the highest (99–71%), except plot CC (Fig. 1). Beech is mostly governing the course of natural regeneration (Fig. 2). In abundance, it is followed by hornbeam (4–28%), also present on research plots in the parent stand (1–3%), and linden (3–33%), not occurring on the plots, only in the surrounding stand (up to 3%).

The highest number of seedlings was found on plot M (more than 90,000 per ha), out of which beech represented 70,000 per ha. The lowest number was on plot CC (40,700 per ha), and also the beech proportion was much lower: 18.1%. A similar situation was in the case of relative numbers per m^2 (Fig. 3). The highest value was obtained for plot M – 9.18 individuals/m^2, lower on plots C and L; however, the difference was not statistically significant. These plots also have the highest numbers of fructifying trees, and Duncan's test confirmed ($P < 0.05$) that they form one homogeneous group. The lowest relative values were obtained for plots CC (4.08 ind/m^2) and H (5.88 ind/m^2), but without a significant difference in comparison with plot L. The trend in numbers of seedlings older than one year is different. In this case, the largest difference in comparison with one-year-old seedlings was found on plots with the most closed canopy (C and L) and with the least favourable conditions for seedling survival. The abundance of seedlings increased significantly with the extent of canopy opening: from control (C – 2.55 ind/m^2) to

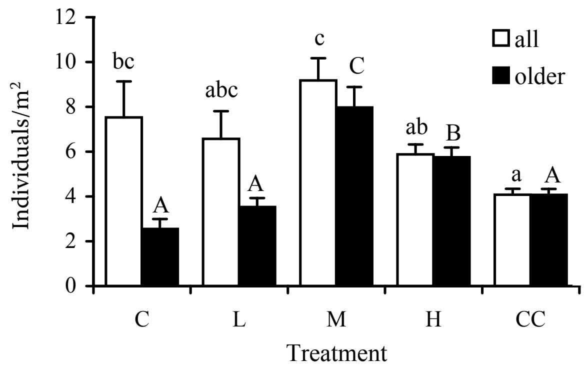

Fig. 3. Effect of cutting regimes (C – control, L – light, M – medium, H – heavy cutting intensity, CC – clear cut) on the density of natural regeneration of all and older-than-one-year individuals. Vertical bars indicate ±SE from the mean. Different letters indicate statistically significant differences between the means; small letters for all seedlings, capital letters for seedlings older than one year; Duncan's test applied ($P \leq 0.05$)

Table 2. Density of natural regeneration of all and older-than-one-year individuals on research plots (C – control, L – low, M – medium, H –heavy cutting intensity, CC – clear cut) according to tree species (individuals/m^2)

Species	C		L		M		H		CC	
	all	older	all	older	all	older	all	older	all	older
Fagus sylvatica L.	6.20 b	1.33 c	6.03 b	3.02 b	7.00 b	5.80 b	2.90 c	2.87 c	0.73 c	0.73 c
Carpinus betulus L.	0.20 a	0.20 a	0.15 a	0.15 a	1.08 a	1.03 a	1.13 b	1.13 b	1.13 d	1.12 d
Abies alba Mill.	0.12 a	0.12 a	0.17 a	0.15 a	0.48 a	0.47 a	0.15 a	0.15 a	0.17 ab	0.17 ab
Quercus dalechampii Ten.	0.03 a	0.03 a	0.08 a	0.08 a	0.17 a	0.10 a	0.03 a	0.03 a	0.07 ab	0.05 ab
Tilia cordata Mill.	0.88 a	0.85 b	0.10 a	0.10 a	0.38 a	0.38 a	1.50 b	1.48 b	1.18 d	1.18 d
Acer pseudoplatanus L.[a]	0.05 a	0.05 a	0.02 a	0.02 a	0.07 a	0.07 a	0.08 a	0.08 a	0.10 ab	0.10 ab
Salix caprea L.							0.67 a	0.03 a	0.45 bc	0.45 bc
Populus tremula L.									0.20 ab	0.20 ab
Alnus incana L.									0.03 ab	0.03 a
Fraxinus excelsior L.			+[b]	+					+	+
Ulmus glabra Huds.							+	+		
Betula verrucosa Ehrh.									+	+
Cerasus avium Moench.									+	+

[a]On plot M, *Acer campestre* L. was found, for simplification classified to the group *Acer pseudoplatanus,* [b]sporadic occurrence, less than 0.5%. Different letters indicate statistically significant differences between the means; Duncan's test applied ($P \leq 0.05$)

Table 3. ANOVA treatment effect of different cutting regimes (by plots) on natural regeneration (seedling abundance) for beech alone and for all species in total

Seedlings	d.f.	*F*	*P*
Fagus sylvatica L.	4	7.0171	0.0000
– older than 1 year	4	22.1193	0.0000
All species	4	3.3606	0.0104
– older than 1 year	4	15.6315	0.0000

Error d.f. = 295; total d.f. = 299

plot after medium cutting (M – 7.97 ind/m^2), and then followed by a significant decline again. A similar trend was found for the beech alone: the highest abundance on plot M (5.80 ind/m^2), the lowest on plots C and CC (1.33 and 0.73 ind/m^2).

The list of all the species participating in natural regeneration is in Table 2. Six woody plant species occur on all the plots – beech, hornbeam, oak, fir (that are present also in the parent stand), linden and sycamore. On plots with the most intensive cutting (H and CC) there also occur pioneer species – mainly willow, aspen and alder. The highest proportion in the species composition belongs to beech. On each plot with parent stand, beech forms an independent homogeneous group, statistically different from the other woody plants. These woody plants do not have a significant influence on the total numbers of seedlings on plots C, L and M. On plot H, linden and hornbeam are more abundant and form the second homogeneous group. On plot CC, the two woody plants are already the most abundant: 1.18 and 1.13 individuals per one m^2 on average, followed by beech and willow (0.73 and 0.45 ind/m^2). In the case of individuals older than one year, the species composition is similar, the difference is in lower numbers. Beech is the most abundant (C – 51.6, L – 85.8, M – 74.7, H – 49.2%) except for CC (18.1%), where linden and hornbeam are the most abundant species, followed by a homogeneous group consisting of beech and willow.

The results of ANOVA in Table 3 indicate a significant influence of different cutting operations on the number of all regenerating individuals, of all individuals older than one year, of all beech seedlings and the number of all beech individuals older than one year. Fig. 4 illustrates the average values of natural regeneration older than one year and their variability. Six woody plants occurring on all research plots were evaluated. In the case of beech we can see a gradual increase up to the peak reached on plot M and followed by a decrease in numbers. Cutting operations in the stand also had a significant influence on linden and hornbeam regeneration (F = 14.02 and 13.13, P < 0.0001 for both). Both woody plants represent two homogeneous groups with a statistically significant difference (Fig. 4). Linden is not present in the parent stand, but its seed can be well transported by wind. We can see from the results of Pearson correlation in Table 4 that the amount of linden

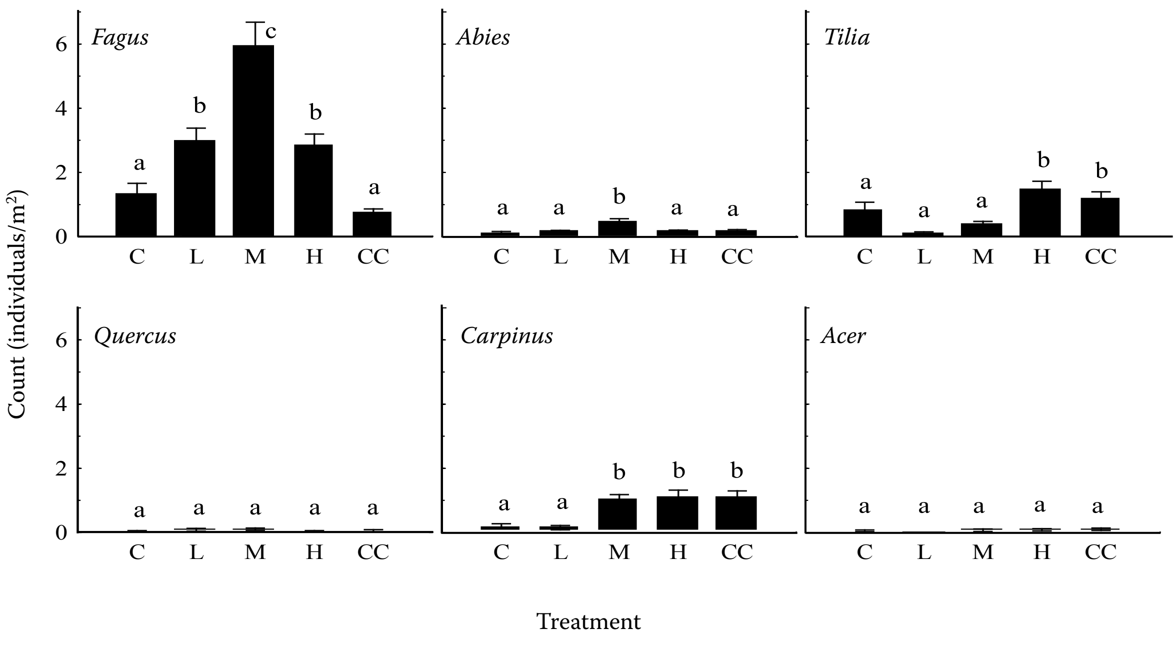

Fig. 4. Amount and variability of natural regeneration older than one year on research plots (C, L, M, H, CC see Table 1). Different letters indicate statistically significant differences between the means; Duncan's test applied ($P \leq 0.05$)

Table 4. Results of Pearson's correlation describing a relation between the number of beech, hornbeam, fir, oak, linden and sycamore seedlings and the number of fructifying trees, stand density, illumination in the growing season – GS (illumination account by Střelec 1992), leaf area index (LAI), annual throughfall and throughfall in the growing season – GS (throughfall account by Dubová 2001)

Seedlings	Number of fructifying trees	Stand density	Illumination in GS	LAI	Annual throughfall	Throughfall in GS
***Fagus sylvatica* L.**						
correlation – r (X,Y)	0.2217	0.1673	–	0.3568	–0.2648	–0.2618
determination – r^2	0.0492	0.0280	–	**0.1273**	0.0701	0.0685
P-value	**0.0001**	**0.0037**	–	**0.0000**	**0.0000**	**0.0000**
Older than 1 year						
correlation – r (X,Y)	0.0263	–0.0444	–0.1904	0.2187	–0.1170	–0.1095
determination – r^2	0.0007	0.0020	0.0362	0.0478	0.0137	0.0120
P-value	0.6506	0.4432	**0.0009**	**0.0001**	**0.0429**	0.0582
***Carpinus betulus* L.**						
correlation – r (X,Y)	0.2531	–0.3274	0.2897	–0.2751	0.3397	0.3364
determination – r^2	0.0640	**0.1072**	0.0839	0.0757	**0.1154**	**0.1132**
P-value	**0.0000**	**0.0000**	**0.0000**	**0.0000**	**0.0000**	**0.0000**
***Abies alba* Mill.**						
correlation – r (X,Y)	–0.0284	–0.0583	–0.0349	0.0427	–0.0012	–0.0097
determination – r^2	0.0008	0.0034	0.0012	0.0018	0.0000	0.0001
P-value	0.6241	0.3139	0.5469	0.4617	0.9830	0.8676
***Quercus dalechampii* Ten.**						
correlation – r (X,Y)	–0.0107	0.0193	–0.0622	0.0568	–0.0476	–0.0526
determination – r^2	0.0001	0.0004	0.0039	0.0032	0.0023	0.0028
P-value	0.8533	0.7394	0.2826	0.3269	0.4117	0.3637
***Tilia cordata* Mill.**						
correlation – r (X,Y)	–[a]	–0.1246	0.2169	–0.2052	0.2370	0.2438
determination – r^2	–	0.0155	0.0470	0.0421	0.0562	0.0594
P-value	–	**0.0000**	**0.0002**	**0.0003**	**0.0000**	**0.0000**
***Acer pseudoplatanus* L.**						
correlation – r (X,Y)	–	–0.0783	0.0947	–0.0901	0.1016	0.1010
determination – r^2	–	0.0061	0.0090	0.0081	0.0103	0.0102
P-value	–	0.1763	0.1017	0.1193	0.0790	0.0807

n = 300, the correlation is significant at $P < 0.05$ (bold), determination values in bold are used for effects higher than 10%,
[a]linden and sycamore do not occur in the parent stand on the research plot

regeneration was dependent on the stand density ($P < 0.0001$). The situation in hornbeam was similar to that of linden, with the difference that fructifying trees are present on plots M and H. More abundant regeneration of hornbeam is on plots M, H and CC (Fig. 4). A significant influence of cutting on fir regeneration was also found ($F = 5.19$, $P < 0.0005$). We can see in the figure that this influence was found positive on plot M only.

Fig. 5 illustrates the influence of cutting on changes in the species composition of natural regeneration in comparison with the parent stand. The more intensive the cutting (greater canopy opening), the less abundant the species from the parent stand in natural regeneration. The only exception was the control plot with fructifying linden in neighbourhood. The commonly recognized fact that pioneer species regenerate vigorously in open-canopy conditions was

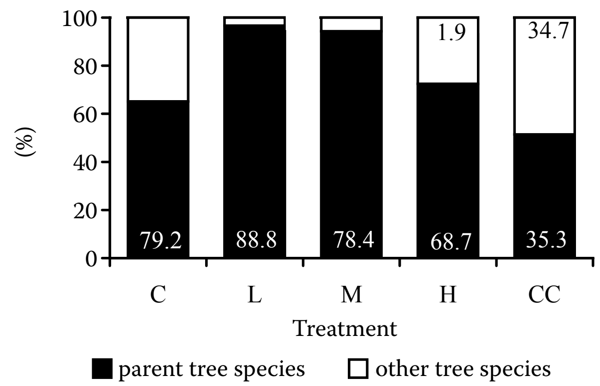

Fig. 5. Proportions of woody plant species from the parent stand and of other woody plants in relation to seedlings older than one year. White numbers correspond to the (percent) proportions of beech seedlings in the group of parent woody plants, black numbers express proportions of the pioneer species (see Table 2) in relation to the number of seedlings of the other woody plants

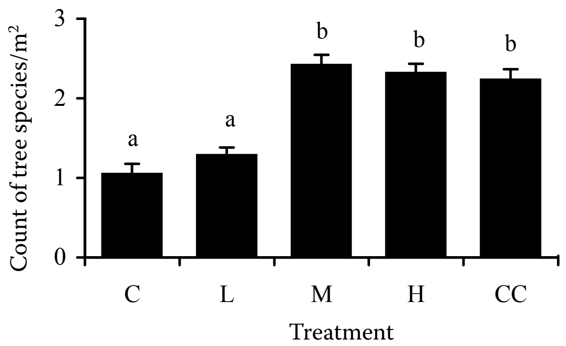

Fig. 6. Effect of cutting regimes (C – control, L – low, M – medium, H – heavy cutting intensity, CC – clear cut) on the number of different tree species in natural regeneration older than one year. Different letters indicate statistically significant differences between the means; Duncan's test applied ($P \leq 0.05$)

also confirmed. We recorded the occurrence of pioneer species on plots H and CC (1.9 and 34.7%). We can see in Fig. 6 that cutting intensity also influences the dispersal of seedlings of different species. The plots were classified in two homogeneous groups: the first consisting of plots C and L, on which one woody plant species occurs per m^2, and plots after more intensive cutting on which there are more than two different species per each m^2, however, the species composition on plot M is the same as on C and L (Table 2).

Calculating Pearson correlation coefficients, we have identified a significant influence of specified stand variables (fructifying trees, stand density, LAI) on the amount of beech seedlings (principal woody plant) in natural regeneration. A significant influence of two principal climatic variables (moisture and light conditions) on the growth and survival of seedlings was also proved (Table 4). For beech seedlings older than one year, the relation was significant only in the cases where the *P*-value is printed in bold. The values of determination coefficient (r^2) represent the contribution to the total variance (the measure in what a change in one variable causes a change in the other). As for the other examined woody plants, the influence of the discussed factors was confirmed for linden and hornbeam – in all cases. The correlation between the abundance of overall natural regeneration was found in throughfall only, the abundance of individuals older than one year was also significantly dependent on the stand density and LAI.

DISCUSSION

The irregular fructification of beech trees may cause problems in connection with planning and implementation of natural regeneration for beech stands. The observations show evidently that the statements about scarce mast years, separated by long sterile periods, in European beech stands are exaggerated. Every two or three years the production of beechnuts is sufficient for regeneration in conditions of suitably prepared soil and appropriately applied regeneration cuts (Korpeľ 1978; Peters 1997). In the second phase of shelterwood regeneration – seed cutting accomplished in the mast year after the fruit fall, the stocking is lowered to 0.7–0.6 (Bílek et al. 2004). A sufficient supply of light, heat and water necessary for vigorous emergence and survival of seedlings is guaranteed in such a way. Reducing the stocking value below 0.6 significantly decreases the survival of seedlings at an age of 1–3 years (Korpeľ 1978). The assessment of natural regeneration done after 15 years has confirmed our former hypothesizing. However, the highest number of older seedlings – the most important from the aspect of the succession stand, was found on plot M. The results obtained on our research plots situated in the submountain zone allow us to hypothesize that natural beech regeneration should be most promoted in these conditions by lowering the stocking value to 0.5 (50% of the basal area of parent stand according to tabular values), which corresponds to the model plot M (Table 1). This measure will however reduce the number of seed sources – one of the crucial factors limiting the natural regeneration success (Clark et al. 1998). On the other hand, this plot (M) presents the ecological optimum for seedling survival and growth (Fig. 3). Our explanation is that the threat of herbal synusia to beech stands in the submountain zone is not so great as in the mountain zone. The beech stands are sufficiently compact, relative illumination in the year after the cut was "only" 22% (Table 1). The proportions of beech trees belonging to the first and second classes in the parent stand are high, and consequently the seed production is good.

The emergence of viable seeds is controlled by physical conditions: temperature, moisture and light (Kozlowski et al. 1991). The seedling growth depends on the overall supply of nutrients (Burgess, Wetzel 2000), water (Löf et al. 1998) and light (Lüpke 1995; Schmid et al. 2005); the survival is influenced by the presence of predators and pathogens. However, the insufficient seed supply can also have disposition effects (Kozlowski et al. 1991). From this perspective, we also must interpret the results of Pearson correlation used for assessment of the influence of some stand variables on regeneration abundance (Table 4). Before performing a further analysis, it is necessary to point out the significance of source density and dispersal in the process of natural regeneration. For beech seedlings in total (also one-year-old ones) a positive influence of stand density on the seedling abundance was found. In seedlings older than one year, no similar dependence was found, because namely this factor (dense stand) caused the worsening of survival conditions. This influence was still stronger than the influence of precipitation on seed emergence and survival rate. Beech prefers well moistened soils (Pueke et al. 2002; Fotelli et al. 2005) – in spite of this fact, we obtained a negative correlation in throughfall. For older beech individuals, this correlation was calculated on much lower significance levels ($P = 0.0429$ and $P = 0.0582$ – in this case immediately beyond the significance limit) because they were not significantly influenced by the number of fructifying trees any longer ($P = 0.6506$). It is evident that the number and abundance of seed sources is an important interactive factor.

As for the other woody plants, significant influences of some stand parameters on regeneration abundance were found only in hornbeam and linden (Table 4), but with a reverse tendency than in beech. The only exception was the influence of the number of adult fructifying hornbeam trees on regeneration abundance where a positive correlation was found. The number of seedlings for this species significantly increased with decreasing stand density. It is so because its seeds are winged, and they can be transported by wind to longer distances. On the other hand, stand density is a significant factor ($P < 0.00001$) negatively influencing the dispersal of such seeds. The seed dispersal is the third (after seed sources and seedling establishment) most important factor limiting the natural regeneration (Clark et al. 1999; Xiao et al. 2004). Stand density influences the seedlings number positively when the stand contains fructifying trees of the same species. This is the case of beech. We can see in Table 2 that the most intensive beech regeneration was on plot M – 7 ind/m^2 or 70,000 per ha. The average regeneration rate on plots C and L is 6 ind/m^2 (60,000 per ha). In beech, a gradual increase was found followed by a decrease. The peak was on plot M (medium cut). Lower numbers on denser plots C and L (left) probably result from less favourable growth conditions (Hille Ris Lambers et al. 2002). On the other hand, the most opened plots H and CC, regenerating at a rate of 1–3 ind/m^2, were negatively influenced by severely lowered numbers of fructifying trees. Korpeľ (1978) suggested that successful natural regeneration in conditions of Central Europe required a minimum of 20,000 biologically guaranteed seedlings per ha (2 ind/m^2). Because we deal with older seedlings, in Table 2 we will focus on the group of seedlings older than one year. We can see that the requirement is met on all the plots. In the case of beech alone, plots C and CC will be eliminated where the regeneration density is only 1.33 ind/m^2 and 0.73 ind/m^2, respectively. For comparison: in the past, the stands were generally planted with three-years-old seedlings, in an amount of 4,000–6,500 individuals per ha (Wijdeven 2003). For pine, more than 5,000 overgrown seedlings per ha are suggested to be present before the felling starts (Kerr 2000).

Fig. 3 shows (linearly) decreasing variability of seedlings on the plots with decreasing stand density: standard error (SE) 1.60–0.26. One-year beech seedlings cause this. Beech has the most variable and the least uniform regeneration from all the examined woody plants. A possible explanation is that the seed belongs to the heaviest ones and falls onto the ground nearby the fructifying tree. If the conditions are favourable, one-year seedlings form dense patches. In the case of older seedlings, less abundant due to mortality, the variability is lower, primarily on plots C and L, and also on plot M to some extent. It is evident that the growth conditions for beech are the most favourable there, thanks to the highest survival success.

CONCLUSIONS

Releasing the canopy and lowering the stand density markedly promote the formation of increments (Pretzsch 2005) and fecundity in the remaining trees (Paar et al. 2000), and they also promote the emergence and growth of seedlings (Madsen, Larsen 1997; Collet et al. 2001; Curt et al. 2005). Evaluation of results collected over 15 years (15 vegetation periods in 1989–2003) of natural beech regeneration on the plots with different densities allows us to decide on the way and extent of the initial cut. The aim is the optimum species composition and abundant natural regeneration (Gonzáles-Martínez, Bravo 2001). The series of regeneration cuts of different intensities adjusted site ecological conditions for seedling emergence, survival and species variability. The results suggest that the ecological conditions on model plots M and H can guarantee the suitability of application of the second cut 10 to 15 years later and to perform the whole regeneration with two cuttings. From the aspect of natural regeneration, the model plot M (stocking 0.5) seems to be more favourable because more denser beech regeneration has a decisive positive effect on the qualitative structure of the future stand (Saniga 1994). The upper limit of 15 years is more suitable if we want to meet the secondary objective of the understorey cutting (primary objective is the formation of successive stand) increasing increments in the parent trees (Sedmák et al. 2006).

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Vplyv obnovných postupov na prirodzenú obnovu v podhorských bučinách: diverzita a abundancia

ABSTRAKT: Vyhodnocujeme 15ročné výsledky prirodzenej obnovy buka na piatich plochách s rôznou denzitou v Západných Karpatoch. Na troch plochách bol aplikovaný clonný rub rôznej sily (plochy L, M, H), na jednej ploche maloplošný holorub (CC) a jedna bola kontrolná (C). Počet jednoročných semenáčikov priamo úmerne klesal so silou ťažby, s preriedením porastu. Výsledky ANOVA poukazujú na významný vplyv rôznej sily ťažbových zásahov na početnosť jedincov z prirodzenej obnovy: jednoročných, starších, semenáčikov buka a všetkých semenáčikov spolu. U buka bol zistený postupný nárast početnosti a potom pokles s vrcholom na ploche M (medium cut – stredne silný ťažbový zásah). Menší počet semenáčikov buka na hustejších plochách (C, L) je výsledkom zhoršených rastových podmienok a na opačnej strane, na plochách so silnejšími zásahmi (H, CC), bol menší počet fruktifikujúcich stromov. Aj keď sa znížením zakmenenia na 0,5 (50 % porastu) znížil počet semenných zdrojov (jeden z limitujúcich faktorov prirodzenej obnovy), pre ďalší faktor – zaistenie semenáčikov (ich prežívanie a odrastanie) sa táto plocha (M) prejavila ako ekologické optimum.

Kľúčové slová: vývoj prirodzenej obnovy; hustota porastu; clonný rub; holorub; *Fagus sylvatica* L.

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