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Effect of microrelief and vegetation cover on natural regeneration in European beech forests in Krkonoše national parks (Czech Republic, Poland)

Auswirkung des Mikrostandortes und der Bodenvegetation auf die natürliche Verjüngung der Buche in zwei Nationalparks im Riesengebirge (Tschechische Republik, Polen)

Zdeněk Vacek [1], Daniel Bulušek [1], Stanislav Vacek [1], Pavla Hejcmanová [2], Jiří Remeš [1], Lukáš Bílek [1], Igor Štefančík [3]

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Schlüsselbegriffe: Mikrotopographie, Vegetationsmosaik, *Fagus sylvatica*, Zentraleuropa, Riesengebirge

Abstract

Microsite is the key factor for the natural regeneration of forests in their initial developmental stages. In mountain European beech forests the character and process of natural regeneration rely on varied microsite conditions and adverse climatic conditions. The aim of our investigation was to determine the effect of the microrelief and herbaceous vegetation cover on natural regeneration of European beech (*Fagus sylvatica* L.) in two national parks in the Krkonoše Mts. In particular we investigated the relation-

[1] Faculty of Forestry and Wood Sciences, Czech University of Life Sciences in Prague, Kamýcká 129, 169 51 Prague 6 – Suchdol, Czech Republic, Corresponding author: Jiří Remeš (remesj@email.cz)
[2] Faculty of Tropical AgriSciences, Czech University of Life Sciences in Prague, Kamýcká 129, 169 51 Prague 6 – Suchdol, Czech Republic
[3] National Forest Centre, Forest Research Institute, T.G. Masaryka 22, 960 92 Zvolen, Slovak Republic

ship of site and stand parameters on the height and density of natural recruits (from seedlings to DBH < 7 cm) of beech on 10 permanent research plots (PRP), each formed into transect of 5×50 m in size (250 m²). The results indicated that the total density of natural regeneration ranged from 12 080 to 256 400 recruits ha^{-1}. Both, microrelief and vegetation cover had significant effect on height growth of natural regeneration (P<0.001). The lowest heights were measured in the dense cover of *Calamagrostis villosa* and *Avenella flexuosa* and on mound (P<0.001) with the shallowest soil profile compared to other type of microrelief (P<0.001). It indicates that the regeneration is negatively influenced by severe competition of expansive, strongly competitive grasses. The highest average heights were most frequently reached by recruits on the slant and plant surface and without ground vegetation cover (on leaf litter; P<0.001). In addition stand canopy had negative effect on density of natural regeneration, while its mean height increased with increasing height of mature stand. These differences in microsite conditions may be considered in forest tending for more effective promotion of selected individuals.

Zusammenfassung

Die Eigenschaften des Mikrostandortes stellen Bedingungen dar, die entscheidend für die Initialphase der Entwicklung eines Waldbestandes sind. In den Buchenwäldern der montanen Stufe hängt der Erfolg der natürlichen Verjüngung von standörtlichen und klimatischen Verhältnissen ab. Das Ziel dieser Studie war die Wirkung des Microstandortes und der Bodenvegetation auf die natürliche Verjüngung der Buche (*Fagus sylvatica* L.) in zwei Nationalparks im Riesengebirge zu beurteilen. Es wurde die Wirkung vom Standort und Bestand auf die Höhe und dichte der natürlichen Verjüngung (Baumindividuen mit DBH < 7 cm) auf 10 Dauerversuchsflächen mit je einem Transekt 5×50 m (250 m²) analysiert. Die Dichte der natürlichen Verjüngung bewegte sich von 12 080 bis 256 400 Individuen per ha^{-1}. Sowohl Mikrostandort als auch Bodenvegetation haben sich als entscheidend für die Höhe der natürlichen Verjüngung gezeigt (P<0.001). Die niedrigste Höhe wurde auf Erhebungen und mit Konkurrenz von *Calamagrostis villosa* und *Avenella flexuosa* festgestellt (P<0.001). Dies zeigt auf strenges Konkurrenzverhältnis zwischen der natürlichen Verjüngung und ausgewählten Grasarten. Die höchsten durchschnittlichen Höhen wurden auf geneigten und flachen Mikrostandortstypen und ohne Vegetation erreicht (P<0.001). Außerdem der Kronenschluss des Altbestandes hatte negative Auswirkung auf die Dichte der natürlichen Verjüngung, während sich die Höhe der Verjüngung mit der durchschnittlichen Höhe des Altbestandes vergrößert hat. Diese Unterschiede in Mikrostandortstypen sollten in Pflegemaßnahmen in Jungwüchsen berücksichtigt werden.

1. Introduction and problem analysis

Availability of microsites and seeds are key factors that potentially may limit recruitment in plant populations (Eriksson and Ehrlén 1992). Microsite, respectively microrelief and vegetation cover, is one of the most important factors for germination and survival of the natural regeneration of forests in their initial developmental stages (Bílek et al. 2014; Vacek et al. 2015a). Natural regeneration of European beech (*Fagus sylvatica* L.) forests relies on a number of microsite conditions, however their temporal and spatial coincidence is necessary. Germination and growth of seedlings depend, for instance, on light quantity and quality, humus form, competition of other tree species, weeds, etc. (Emborg 1998; Topoliantz and Ponge 2000; Špulák 2008). Beech seedlings positively respond to basic growth factors such as moisture content and nutrient reserve of soil and light intensity (Madsen and Larsen 1997; Agestam et al. 2003; Arrietaand and Suárez 2005; Jarčuška 2009). On the other hand, seedlings are very sensitive to drought and water deficit (Silva et al. 2012; Fruleux et al. 2016), especially in pure beech stands due to strong intraspecific competition (Bosela et al. 2015) and high consumption of water by roots of old beech trees (Schieber et al. 2015). Beech seedlings can survive in low light environment for a long time (Barna et al. 2015), but beech requirements for light gradually increase with age and size of recruits, which is evidenced by a gradual decrease in diameter increment with the increasing age of recruits at the same amount of incident light. Diameter growth responds to a change in environmental conditions already in the first year after the given change in environmental conditions has occurred (Collet and Chenost 2006). The competition of surrounding vegetation for soil water and nutrients in relation to the diameter growth of recruits varies according to the size of beech recruits, type of competitor (grasses, dicotyledonous herbs, shrubs or trees) and availability of the other resources light, water and nutrients (Coll et al. 2003; Jaloviar 2005; Provendier and Balandier 2008).

In mountain forests the character and process of natural regeneration are limited and influenced by some additional factors, namely adverse climatic conditions (e.g. climatic fluctuations, cold temperatures, high snow cover) (Šerá et al. 2000). In addition, beech regeneration is indeed sensitive to climatic variations such as late frost (Wagner et al. 2010) or more frequent extreme drought events in growing season (Silva et al. 2004). Disturbances determine the character and division of newly emerging microsites (Hunzinker and Brang 2005; Vodde et al. 2010). Frequent are wind disturbances that increase the intensity of light incidence on the soil surface and change nutrient and water availability as a result of biomass dieback in the overstory and in understory. Another key factor for natural regeneration, very specific for Krkonoše Mts., is allochthonous tree species composition that is not consistent with site conditions. Unsuitable genetic origin of tree species used for reforestation, together with air-pollution disaster in 1980s caused a reduction in the canopy closure of forest stands and impairment of their health status. Opening up of forest stands led to higher infestation by expansive, competitively strong plant species such as *Calamagrostis villosa* or *Vaccinium myrtillus*, which frequently limit natural regeneration (Vacek et al. 2009).

Natural regeneration therefore represents for near-natural forest management indispensable element in order to maintain ecological sustainability (Kuuluvainen and Laiho 2004), while the survival rate of individual species in the natural regeneration can vary considerably (Petritan et al. 2007; Dovčiak and Brown 2014). In the Czech Republic, natural regeneration is currently used to a relatively small extent (its share was 22.1% in 2014) (Ministry of Agriculture - MZe 2015). On the contrary, up to 80% of forest stands in Switzerland come from natural regeneration, even in mountain forests (Brändli 1996). In the Krkonoše National Park the share of natural regeneration is more than twofold compared to the Czech Republic (47.2%). European beech in the Krkonoše National Park (Czech Republic) currently accounts for 3% of forest area and its share in the natural species composition amounted to 24%, however current share of the total regeneration of beech stands, there is currently 19.8% and the share of natural regeneration is 8.9% (Vacek et al. 2012). This trend suggests that natural regeneration should distinctly contribute to a change in the species composition of forest stands in the future when particularly in beech a relatively small number of fertile trees could replace to a great extent the spruce that has been dominant in the Krkonoše Mts. until now (Vacek et al. 2009). A similar trend of significant expansion of beech was reported from Moravia (Magri 2008), from Slovenia (Firm et al. 2009; Poljanec et al. 2010), from the Carpathian Mts. (Vrška et al. 2009), from Italy (Gils et al. 2008) or from Denmark (Olesen and Madsen 2008). Beech population is also very successful on the northeastern border of its expansion in the Baltic region (Janík et al. 2016). The abundance of recruits is the expression of ecological conditions and environmental limits of particular sites and of ecological properties of dominant tree species (Vacek et al. 2010; Vacek and Hejcman 2012).

The aim of our research was to determine the effect of microrelief (plain, slope, mound, pit) and vegetation cover on natural regeneration of European beech in both Krkonoše Mountains national parks (Czech Republic and Poland) in Central Europe. Secondary we investigated relationships among stand canopy, recruit height and density and habitat parameters. We hypothesize that natural regeneration has better growth (1) in depressions with deep soil profile and (2) on leaf litter or on thin cover of mosses and herbs with limited competition of ground vegetation.

2. Material and Methods

2.1. Study area

Study was conducted on ten 0.25 ha (50×50 m) permanent research plots (PRP) with European beech (*Fagus sylvatica* L.) dominant stands in both national parks of the Krkonoše Mountains: 3 and 4 PRP were situated in the eastern and western part of the

Krkonoše National Park (KRNAP) in the Czech Republic, respectively, and 3 PRP in the Karkonoski Park Narodowy (KPN) in Poland (Fig. 1). The basic description of the studied PRP is shown in the Table 1. In studied localities, the mean annual temperature ranged from 3 to 7°C, the mean annual precipitation ranged from 700 to 1300 mm and the length of the growing season ranged from 80 to 130 days.

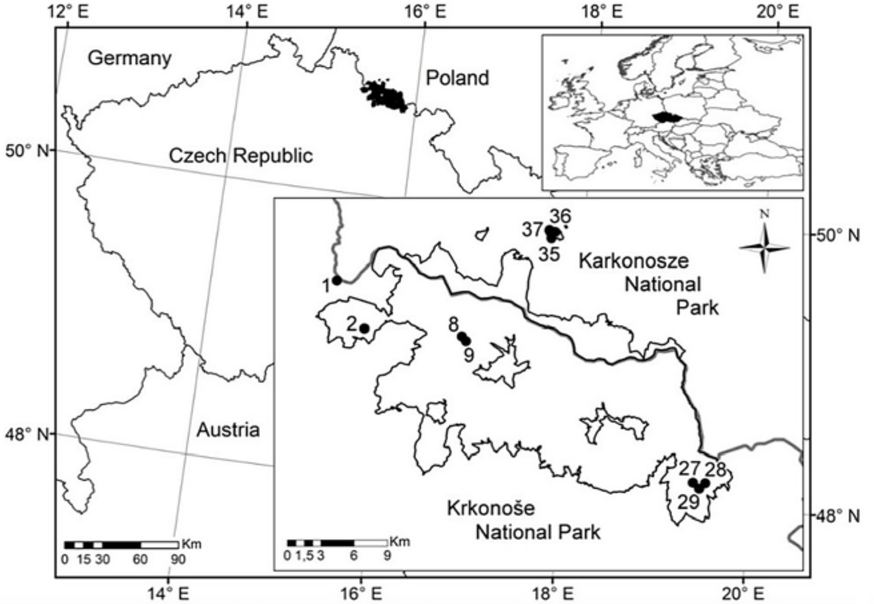

Fig. 1: Localization of the studied PRP in forest stands with dominant European beech in the Krkonoše Mts.

Table 1: Basic description of permanent research plots

PRP	Tree species	Age[1] (year)	Stand height (m)	Mean DBH (cm)	Volume (m^3 ha^{-1})	Canopy[2] (% /ha)	Altitude (m)	Aspect, slope (degree)	Forest site type[3]	Soil type
1 – U Tunelu	beech spruce	139/29	27 26	48 43	382 45	89/1.44	730	SW, 26°	6N4	cambisol
2 – Vilémov	spruce beech larch	180/26	28 27 33	36 40 42	198 128 22	73/1.22	600	SW, 22°	5Y0	ranker
8 – Nad Benzínou 2	beech spruce	165/17	20 26	31 42	220 35	74/0.95	1 190	SW, 24°	7K1	cryptopodsol
9 – Nad Benzínou 1	spruce beech	193/37/17	23 22	40 38	20 240	72/0.83	1 170	SW, 17°	7K1	cambisol
27 – U Bukového pralesa A	beech spruce rowan	178/35/22	15 18 15	30 32 20	82 43 2	89/1.41	1 030	SW, 3°	6Z0	cambisol
28 – U Bukového pralesa C	beech	159/22	24	34	235	88/1.31	940	SW, 15°	6K5	cambisol
29 – U Bukového pralesa B	beech spruce	180/30/16	25 27	47 45	210 23	96/1.31	950	SW, 16°	6S1	cambisol
35 – Chojnik–bučina	beech spruce	178/29/17	28 25	51 31	420 45	93/1.66	580	NW, 15°	4B1	cambisol
36 – Chojnik–jedlová bučina	spruce fir beech pine	125/34/12	28 26 28 26	39 38 35 65	207 157 106 50	76/1.20	520	N, 16°	4S1	cambisol
37 – Chojnik–reliktní bor	pine beech	197/29/18	19 23	42 45	179 22	68/1.12	470	SE, 22°	0Z0	ranker

Notes: [1]Age of tree layer (top/middle/bottom) according to Forest management plan; [2]Canopy of tree layer (crown closure/crown projection are per ha); [3]Forest site type: 0Z – Pinetum relictum humile – scrub pine stand with beech, 4B – Fagetum mesotrophicum – nutrient-rich beech stand, 4S – Fagetum oligo-

mesotrophicum – fresh, nutrient-medium beech stand, 5Y – Abieto-Fagetum saxatile – skeletal fir-beech stand, 6N – Piceeto-Fagetum lapidosum acidophilum – stony-acidic spruce-beech stand, 6Z – Piceeto-Fagetum humile – scrub spruce-beech stand, 6K – Piceeto-Fagetum acidophilum – acidic spruce-beech stand, 7K – Fageto-Piceetum acidophilum – acidic beech-spruce stand.

2.2. Data collection

One transect of 50×5 m (250 m²) was established on each PRP. Total number of recruits for all tree species from seedlings to individuals with diameter at breast height (DBH) < 7 cm and height were counted in each transect. In all recruits we determined tree species and measured their coordinates, height, height of crown base and crown width to the nearest cm. Age of 25 recruits (the first individual to every odd meter of transect on y axis) were determined for each PRP by dendrochronology analysis.

For each recruit we identified four types of the microrelief (plain, slope, mound and pit) and types of vegetation cover in terms of dominant herbaceous vegetation cover (*Avenella flexuosa*, *Calamagrostis villosa*, *Dryopteris dilatata*, *Galium odoratum, Oxalis acetosella, Polytrichum formosum, Vaccinium myrtillus* and leaf litter) at scale of 50×50 cm (network of 1 000 squares for each transect). At each PRP the soil types were also determined (Table 1). Depending on the type of microrelief, 16 soil samples per PRP, differentiated by horizons L, F, H (surface litter) and A (top mineral layer), were taken for determine horizon depth (cf. Matějka et al. 2010). The Field-Map technology (IFER-Monitoring and Mapping Solutions Ltd.) was used to determine the tree layer (tree positions, DBH, height, height of crown base and crown projection).

2.3. Data analyses

In order to evaluate the natural regeneration, we analysed all natural recruits on plots and in addition we distinguished plots with "lower natural regeneration" with the mean height < 40 cm and mean age < 10 year (PRP 9, 27, 35, 36 and 37) and plots with "advanced natural regeneration" with height > 50 cm and age > 12 years (PRP 2, 8 and 28), due to the occurrence of different herbaceous vegetation cover and different growth demands of recruits (competition, habitat). For natural recruit crown projection area (sum of crown projections per hectare) and crown closure (proportion of a stand covered by the crowns) were calculated using devices linked to ArcGIS (© 1999-2010 Esri). The same parameters were measured and calculated for tree layer of the stand using the same technology. Deviation are represented by standard error (SE).

Analyses were processed in Statistica 12 (© 1984-2013 StatSoft, Tulsa). Data were log transformed to acquire normal distribution (tested by Kolmogorov-Smirnov test). The effects of microrelief and vegetation cover on the height of natural regeneration recruits and soil depth of upper horizons were separately tested by one-way analysis of variance (ANOVA) and significant differences were consequently tested by post-hoc comparison Tukey's HSD tests. In addition, stand canopy with density of natural regeneration were tested by the Pearson correlation coefficient. Significance of statistics was noted as follows: $P > 0.05$, $P < 0.05$, $P < 0.01$ and $P < 0.001$.

Unconstrained principal component analysis (PCA) in the CANOCO for Windows 4.5 program (ter Braak and Šmilauer 2002) was used to analyse relationships among canopy cover parameters of recruits and full grown trees, recruit density, recruit height, tree layer height, and similarity of 10 PRP. Data were centred and standardized during the analysis. The results of the PCA analysis were visualized in the form of an ordination diagram constructed by the CanoDraw program. Stand age, soil depth, altitude and slope were supplementary data projected into these relationships in the diagram.

3. Results

3.1. Recruit characteristics

The total density of natural regeneration ranged from 12 080 recruits per hectare on PRP 37 to 256 400 recruits per hectare on PRP 9 (Table 2). The natural regeneration was composed by four dominant species: European beech, Norway spruce (*Picea abies* (L.) Karst.), Rowan (*Sorbus aucuparia* L.) and Sycamore maple (*Acer pseudoplatanus* L.) (Table 2). Beech was the dominant species on all PRP with the exception of PRP 35. The most abundant was on PRP 29 where its share was nearly 99%. Norway spruce was conspicuously abundant on PRP 1, while on other PRP did not exceed 5%. Rowan ranged between 0 and 3.6% and maple was absent on almost all PRP with the exception of PRP 35 where its abundance reached 70.5%. Other tree species were scarce and only on PRP 37 there was a high percentage of the other tree species dominated by sessile oak (*Quercus petraea* (Matt.) Liebl.) (15%). In total, the numbers of recruits were relatively high on all studied PRP, reaching very high values especially on PRP 8 and 9.

Table 2: Base parameters of natural regeneration on permanent research plots

PRP	Age[1]	Height[1]	Density	Canopy[2]	Number of recruits /Relative proportion in regeneration									
					Beech		Spruce		Rowan		Maple		Other	
	year	cm	psc ha^{-1}	%/ha	pcs ha^{-1}	%	psc ha^{-1}	%	psc ha^{-1}	%	psc ha^{-1}	%	psc ha^{-1}	%
1	19.1	97.9	34 880	69/1.18	23 240	66.6	11 360	32.6	280	0.8	-	-	-	-
2	12.0	53.7	41 120	36/0.52	39 400	95.8	1 680	4.1	-	-	-	-	40	0.1
8	13.9	53.9	211 560	52/1.37	206 880	97.8	3 360	1.6	1 280	0.6	-	-	-	-
9	8.4	32.2	256 400	39/1.37	250 640	97.8	5 440	2.1	280	0.1	-	-	-	-
27	9.7	37.4	54 440	5/0.06	51 920	95.4	560	1.0	1 960	3.6	-	-	-	-
28	13.5	65.2	33 440	8/0.09	31 720	94.9	760	2.3	960	2.9	-	-	-	-
29	23.0	130.7	12 200	25/0.51	12 040	98.7	40	0.3	120	1.0	-	-	-	-
35	7.9	30.8	21 800	8/0.09	5 960	27.3	-	-	160	0.7	15 360	70.5	320	1.5
36	4.9	18.3	90 200	10/0.12	81 760	90.6	600	0.7	920	1.0	1 400	1.6	5 520	6.1
37	8.2	19.6	12 080	6/0.08	8 720	72.2	120	1.0	200	1.7	40	0.3	3 000	24.8

Notes: [1]Mean value of nature regeneration, [2]crown closure/crown projection area

The largest mean heights of natural regeneration were reached by recruits on PRP 29 (130.7 cm ± 2.1 SE) with mean age 23.0 ± 0.4 SE and PRP 1 (97.9 cm ± 1.4 SE) with mean age 19.1 ± 0.4 SE (Tab. 2). Because of such more advanced stage of regeneration in relation to other plots, PRP 1 and PRP 29 were discarded from further total mean evaluation of effect of microrelief and vegetation cover on mean height of natural regeneration. The evaluation shows the relatively equivalent average height distribution on PRP 2 53.7 cm, PRP 8 53.9 cm and PRP 28 65.2 cm that were further evaluated as "advanced natural regeneration" with mean age of recruits 12.9 ± 0.4 SE and the five remaining PRP – PRP 9 32.2 cm, PRP 27 37.4 cm, PRP 35 30.8 cm, PRP 36 18.3 cm and PRP 37 19.6 cm where the average height does not exceed 40 cm were evaluated as "lower natural regeneration" with mean age 7.2 ± 0.2 SE (Tab. 2). PRP 1 and 29 are the plots with the longest suitable time for the origin of natural regeneration and its prosperous growth while the time suitable for the origin of regeneration has not practically occurred on PRP 36 and 37 yet.

3.2. Effect of microrelief

Microrelief had a significant effect on the height of natural recruits ($F_{(3,\ 19644)} = 55.3$, $P<0.001$). The mean height of recruits on plain was 41.1 cm ± 0.8 SE, on slope was 43.4

cm ± 0.4 SE, on mound was 21.0 cm ± 2.1 SE and on pit 36.6 cm ± 0.8 SE. The highest recruits were found on PRP 29, especially on plain (146.8 cm ± 4.5 SE), followed by PRP 1, particularly on slope (101.5 cm ± 1.8 SE). The lowest recruit mean heights were found on PRP 36, especially on plain (16.6 cm ± 2.6 SE), followed by PRP 37, particularly on mound (15.8 cm ± 2.6 SE; Fig. 2). On most PRP, recruits were the highest on slope followed directly by or not different from plain, and the lowest on mound (Fig. 2). On PRP 9 and 36 there were no differences in recruit heights among microrelief types. Lower natural regeneration was the highest on plain (31.2 cm ± 0.5 SE) and pits (31.0 cm ± 0.5 SE) and the lowest on mound (17.9 cm ± 1.3 SE; $F_{(3, 11786)} = 57.4$, $P<0.001$) whereas advanced regeneration was the highest on slope (56.8 cm ± 0.5 SE) and plain (56.1 cm ± 1.4 SE) and the lowest on mound (27.1 cm ± 3.1 SE; $F_{(3, 6906)} = 43.2$, $P<0.001$; Fig. 3).

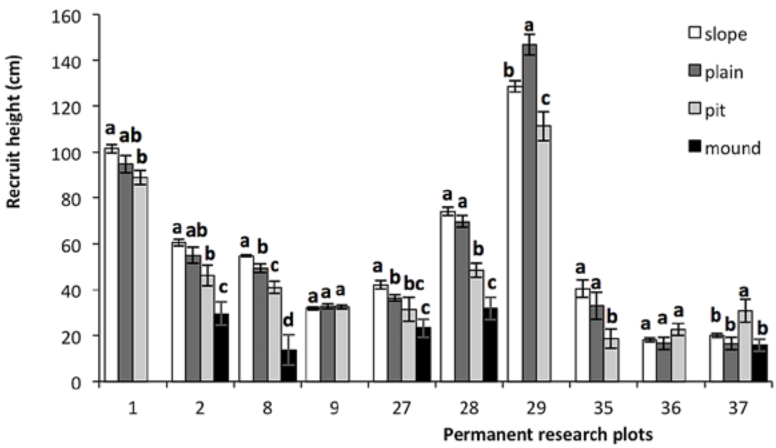

Fig. 2: Average height of natural regeneration on PRP according to microrelief; significant differences (P<0.05) among microreliefs on each PRP separately are indicated by different letters; error bars represent SE

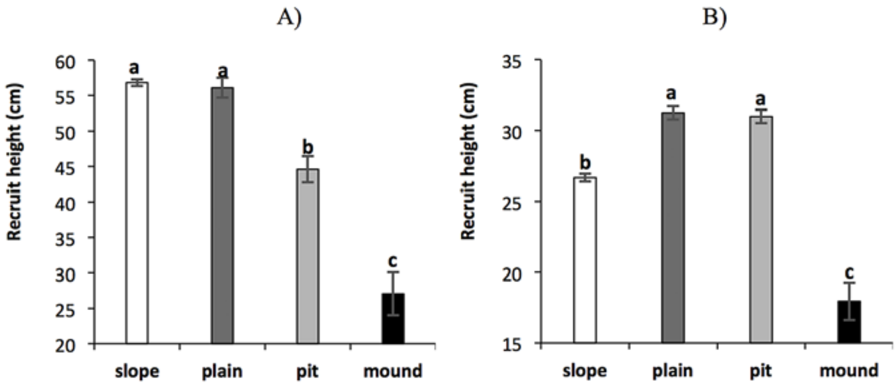

Fig. 3: Average height of A) advanced natural regeneration and B) lower natural regeneration on each microrelief type; significant differences (P<0.05) among microreliefs are indicated by different letters; error bars represent SE

Significant differences among mean soil depth of upper horizons (L, F, H and A) was also found ($F_{(3, 36)} = 7.3$, $P<0.001$; Tab. 3). Significantly ($P<0.001$) the deepest mean upper soil horizon was by pit (22.8 cm ± 2.1 SE) compared to the shallowest by mound (11.5 cm ± 1.5 SE). No difference was found between soil depth by slope (17.6 cm ± 1.8) and plain (18.6 cm ± 1.7; $P>0.05$).

Table 3: Mean soil depth of upper horizons L, F, H and A (summary in cm) on PRP differentiated by microreliefs; significant differences (P<0.05) among microreliefs summary on all PRP are indicated by different letters

PRP	Mound	Pit	Slope	Plain
1	8.1	28.7	20.3	20.4
2	10.9	23.7	18.3	19.7
8	17.0	25.5	19.8	21.1
9	15.2	24.6	19.3	21.1
27	13.8	27.0	22.0	20.2
28	17.4	26.1	22.7	21.6
29	15.1	27.0	21.3	23.2
35	4.1	12.8	7.4	9.0
36	10.6	24.1	20.1	21.1
37	3.2	8.4	4.9	5.8
All PRP	11.5[a]	22.8[c]	17.6[b]	18.3[b]

3.3. Effect of vegetation cover

Vegetation cover had a significant effect on the height of natural recruits ($F_{(7, 19644)}$ = 58.1, P<0.001), the mean height of recruits on leaf litter was 42.1 cm ± 0.3 SE, on *Galium odoratum* was 30.3 cm ± 2.8 SE, on *Calamagrostis villosa* was 34.4 cm ± 3.5 SE, on *Avenella flexuosa* was 15.9 cm ± 2.6 SE, on *Vaccinium myrtillus* was 44.3 cm ± 1.0 SE and on *Polytrichum formosum* was 27.4 cm ± 2.3 SE. The highest recruits were found on PRP 29, especially on leaf litter (139.0 cm ± 10.5 SE), followed by PRP 1, in particularly also on leaf litter (117.7 cm ± 6.5 SE). Natural regeneration prospers very well also on subplots with the *Galium odoratum* dominance. The lowest recruit height was on PRP 36 on *Avenella flexuosa* (15.9 cm ± 0.5 SE) and on PRP 37 on *Vaccinium myrtillus* (16.6 cm ± 0.8 SE; Fig. 4). On most PRP, recruits were the highest on leaf litter where there is not any competition of herbaceous or moss vegetation for natural regeneration, followed by *Galium odoratum*. Also on the PRP with *Vaccinium myrtillus* was achieved relatively greater heights. In the remaining dominants of soil cover shown in Fig. 4 height growth and recruit height are limited to a greater extent as a result of competition or less favourable edaphic conditions. The lowest heights were on *Avenella flexuosa* and *Callamagrostis villosa* (Fig. 4). Lower natural regeneration was the highest on *Vaccinium myrtillus* (31.2 cm ± 0.7 SE) and the lowest on *Avenella flexuosa* (15.9 cm ± 1.4 SE; F(5, 11786) = 35.5, P<0.001) whereas advanced regeneration was the highest on leaf litter (56.4 cm ± 0.5 SE) followed *Polytrichum formosum* (48.5 cm ± 4.5 SE) and the lowest on *Callamagrostis villosa* (34.4 cm ± 3.0 SE; $F_{(4, 6906)}$ = 31.0, P<0.001; Fig. 5).

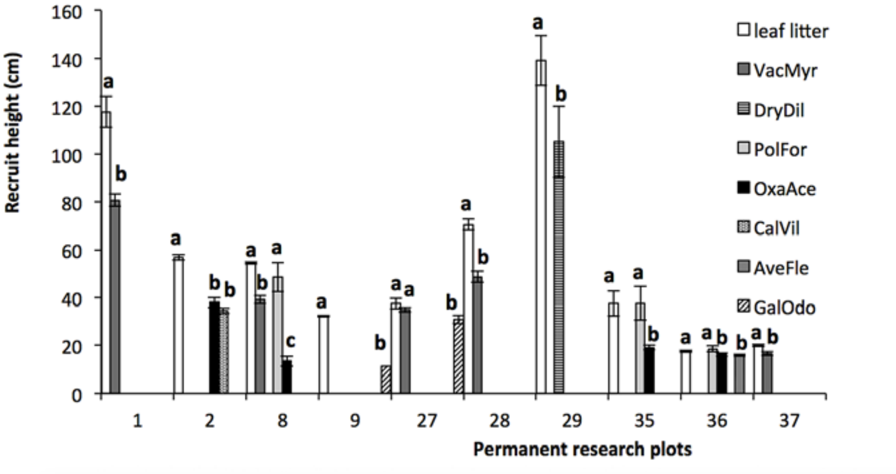

Fig. 4: Average height of natural regeneration according to different vegetation cover with differentiated by PRP; significant differences (P<0.05) among types of vegetation cover are indicated by different letters, error bars represent SE

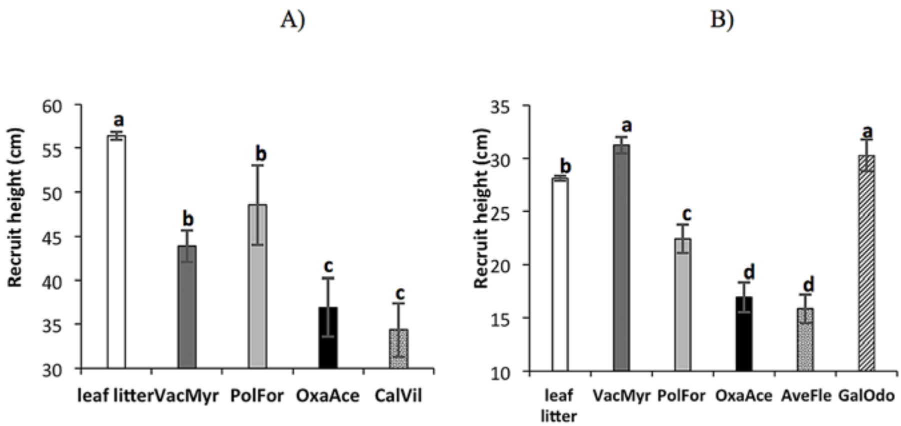

Fig. 5: Average height of A) advanced natural regeneration and B) lower natural regeneration on each vegetation cover; significant differences (P<0.05) among types of vegetation cover are indicated by different letters, error bars represent SE

3.4. Relationships among tree layer, natural regeneration and plot parameters

Results of the PCA analysis are presented in the form of the ordination diagram in Figure 6. The first ordination axis explained 48.2 % of the variability and represented recruit density together with stand canopy. Recruit density was negatively correlated with canopy of tree layer, especially crown projection area had significantly negatively effect on the occurrence of natural regeneration (r = -0.66, $P<0.05$). Crown projection area and crown closure of recruits were positively correlated with altitude and plot slope. Second axis explained 33.1 % of the variability in data and represented the height of tree layer and recruits and the soil depth. Together the first four axes in total explained 95.4% of data variability. The age of upper tree layer, microrelief and vegetation cover showed low significance to mutual relationships among density, height and canopy cover parameters. Comparing types of microrelief, mound showed the largest effect on recruit height, respectively *Galium odoratum* and *Calamagrostis villosa* in vegetation cover.

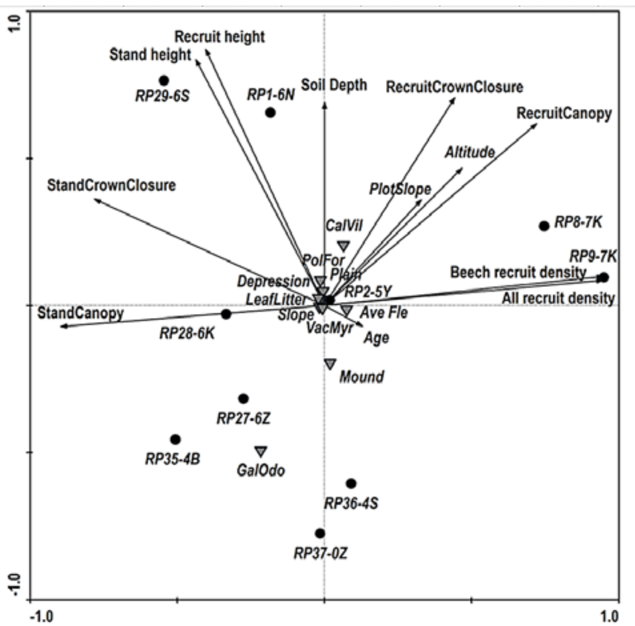

Fig. 6: Ordination diagram (PCA) of relationships among canopy cover parameters (crown closure, canopy – crown projection area) of recruits and tree layer (stand), recruit density, recruit height, tree layer height (stand height) and PRP attributes (plot slope, altitude, soil depth), four types of microrelief (plain, slope, mound, depression) and six types of vegetation cover (leaf litter, CalVil – Calamagrostis villosa, AveFle – Avenella flexuosa, VacMyr – Vaccinium myrtillus, GalOdo – Galium odoratum, PolFor – Polytrichum formosum); circles: PRP; triangles: vegetation cover and microreliefs

4. Discussion

For successful development of the natural regeneration study from natural beech forests of Slovakia indicated that minimum number of recruits should be 20 000 pcs ha^{-1} (Korpeľ 1978), while the abundance of natural regeneration is mainly influenced by the supply of seeds in the seed bank, germination success and survival during growth (Sagnard et al. 2007; Barna 2015). In our study from Krkonoše Mts., natural regeneration ranged from 12 080 to 256 400 pcs ha^{-1}, with average 76 812 pcs ha^{-1}. This number of regeneration was higher than average number 15 100 pcs ha^{-1} presented by study Vacek et al. (2015a) from herb-rich beech forests in Broumovsko Mts. Also Meyer et al. (2002) from natural beech forests of Albania reported lower values (19 259 to 29 844 pcs ha^{-1}) or Nagel et al. (2006) in Slovenia in fir-beech forests (11 654 to 14 615 pcs ha^{-1}). Bílek et al. (2014) found nearest number of seedlings (maximum 75 778 pcs ha^{-1}) in Central Bohemia in the Voděradské bučiny Natural Reserve.

Besides the species composition is a very significant aspect reflecting the role of microsite (Liira et al. 2011). On 9 out of 10 PRP European beech was a markedly dominant tree species in nature regeneration while its share was higher than 90% on seven PRP, similarly as reported in other mountain areas in the Czech Republic (Vacek et al. 2009), in Germany (von Oheimb et al. 2005), in Poland (Jaworski et al. 2002) or in Romania (Petritan et al. 2015). On the only plot (PRP 35) sycamore maple with almost 71% share was the dominant species, probably due to the surrounding stands with a high representation of sycamore. Janík et al. (2016) reported positive correlation between the occurrence of natural regeneration and old trees of sycamore, while in beech this association can be negative (Martinez et al. 2013). On the studied PRP spruce was mostly admixed or interspersed tree species, such as rowan and silver fir in the regeneration.

Our results suggest that natural regeneration in beech forests with an admixture of spruce, sycamore maple and fir on the studied PRP has a relatively variable structure in comparison with results in study Vacek et al. (2009) from beech–spruce forest stands, for instance variation in recruit density was more than threefold. Even though there is a number of factors influencing natural regeneration in the Krkonoše Mts., among the very important ones are microsite conditions and anthropogenic factors, such as air-pollution disaster and its long-term negative impacts, inappropriate forest management practices mainly in the last centuries, disturbance of structure and dynamics by the wildlife population or grazing of farm animals in forests that was quite frequent in the past (Vacek et al. 2010; Král et al. 2015; Vacek et al. 2015b).

Our results showed that microrelief and vegetation cover had significant effect on quantity and height growth of natural regeneration, similarly as reported by many authors (Diaci 1997; Hunziker and Brang 2005; Kathke and Bruelheide 2010; Vacek et al. 2015a).

The similar effect of microrelief on the height of recruits was observed for lower and advanced regenerations grown on mounds and plain compared to differences on slope and pit. Absolutely the lowest heights were measured in individuals of natural regeneration on the mound that were up to two times smaller than on other types of microrelief. Similarly, the natural regeneration of beech was the shortest on mounds (74.0 cm) and the tallest on pits (121.0 cm) from Protected Landscape Area Broumovsko (Vacek et al. 2015a). Mounds have very shallow soil profile with a large proportion of skeleton, minimum amount of fine earth and low water retention, both necessary for recruit growth, because they are exposed in the long run to the soil erosion is very negatively affected their growth (Vodde et al. 2010; Vacek et al. 2015a), that it is consistent with our results. Other conditions limiting growth recruit on mounds and especially beech are its sensitivity to drought and frost (Wagner et al. 2010). For this reason, silviculture management in the form of planting and supporting of beech should avoid of these habitats in mountain areas. In turn, in pits the edaphic conditions offer to recruits deeper soils with humus horizon and with favourable water content for recruit growth. In the advanced regeneration, however, competitive interactions among recruits outweigh edaphic conditions and probably light become limiting (cf. Poleno et al. 2009) lower heights of recruits in pits compared on slope presents a study Sutinen et al. (2010). The heights of recruits on slope and plain were more or less comparable, because also edaphic and light conditions could be comparable between these two microreliefs, although for advanced regeneration the slope may enable to individual recruits to catch more light than on plain.

Concerning vegetation cover effect on the height of recruits, the lowest heights were measured in individuals of natural regeneration in a microhabitat dominated by *Avenella flexuosa* that were nearly up to three times smaller than other types of vegetation cover. On PRP with *A. flexuosa*, shallow poorest-in-nutrients soils were observed from all studied variants of vegetation cover (Bulušek, unpublished data). Also low heights were measured in individuals of natural regeneration on *Calamagrostis villosa* where the growth of seedlings is limited by severe competition of this grass. Study Hanssen (2003) reported, that grasses are often found in dense carpets and prevent germination, growth and cause mortality of regeneration. The reason is the strong competition for nutrients, soil moisture and light (Valkonen and Maguire 2005). Comparing to near-natural beech forest in Central Bohemia, the same genus *Calamagrostis (C. epigejos)* increased also competition for natural regeneration, especially in gap (Bílek et al. 2014). In Krkonoše Mts. the highest recruits were on leaf litter where there was not any competition of herbaceous or moss vegetation for natural regeneration, followed from *Galium odoratum*, where the highest content of microelements, especially of N and Ca, was found out in soil horizons F, H and A (Bulušek, unpublished data). Therefore these habitats are suitable for artificial regeneration. The herb layer represents to recruits a competition for resources (Simon et al. 2011), however our results suggest that the level of this competition depends primarily on its plant species composition. Conversely, research Durak (2012) showed, that beech may also have markedly negative effect on structure of herb layer which subsequently undergoes homogenization due to reduced heterogeneity habitats. We can thus assume a decrease of number of herbs on the studied plots in the future.

Results of multivariate analysis showed that microrelief and vegetation cover in comparison to other factors had relatively low importance for recruit density, height and canopy. These were related more likely to canopy of tree layer and site parameters. Considering that most of our PRP were located on SW exposition and on a steep slope, according Diaci et al. (2005) direct radiation had probably important impact on ground vegetation and consequently on other environmental features such as soil moisture or reduced frost. The canopy on the stand correlated negatively with the number of individuals of natural regeneration, similarly as reported in other studies (Olesen and Madsen 2008; Sefidi et al. 2011; Bílek et al. 2014; Vacek et al. 2015b). For beech as shade-tolerant tree species, the gaps in the canopy support positively the growth of natural regeneration (Szwagrzyk et al. 2001). However, the relationship between stand canopy and density of recruits of natural regeneration can be rather variable and may vary considerably depending on local competition (Collet and Le Moguedec 2007) and game damage (Ficko et al. 2011; Vacek et al. 2015c). The height of recruits was positively correlated with stand canopy and the age of recruits, both parameters interacting together what it is consistent with study Jarčuška and Day (2013). The height of recruits also positively correlated with the depth of soil because substantially deeper soils are richer in Krkonoše Mts., suitable for recruit growth in mountain beech forests, similar results presented studies Madsen and Larsen (1997) and Diaci et al. (2005). Recruit canopy was positively correlated with plot slope due to better space utilization of recruit crowns on steeper slopes. There was no specific relation between recruit height and recruit crown closure and the density of recruits probably because at such an early stage of regeneration the effect of self-thinning still has not been too strong. However the self-thinning, which displays competition of recruits for resources leading to higher mortality, depends primarily on the density of recruits (Kathke and Bruelheide 2010) and on the age of recruits, thus it may take, for instance, almost six years before any effect of self-thinning on the natural regeneration arise (Collet and Le Moguedec 2007).

5. Conclusions

Forest stands in the Krkonoše Mts. have high capacity for natural regeneration of beech. Nevertheless, better knowledge about the influence of microrelief and vegetation cover on the vitality of beech regeneration is important for the formulation of active silviculture principles, where planting and/or seeding is needed. Lower mortality rates and better growth is to expect on microrelief types: slope, plane and on skeletal soils also in depression. Generally it is to avoid mounds with often inadequate soil profile and higher risk of drought. For artificial regeneration areas without dense cover of *Calamagrostis villosa* and *Avenella flexuosa* should be always preferred. Even though study is based on a large data set, impact of additional factors on nature regeneration such as different site parameters, human intervention and other aspects should be considered when interpreting the results.

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