Effect of tree layer and microsite on the variability of natural regeneration in autochthonous beech forests

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ABSTRACT

The present study describes natural regeneration on five permanent research plots (PRP) in juvenile growth and development phases (regrowth and advanced growth) in autochthonous beech forests in Broumovské stěny National Nature Reserve located in the Protected Landscape area in the northeast part of Czech Republic. The stands of herb-rich beech forests were studied in the optimum to break-up stage. Natural regeneration was not evenly spaced but rather was clustered. Mean regeneration density ranged from 1,472 to 44,888 recruits per ha. European beech (*Fagus sylvatica* L.) made up 78.5–98.0% of all regeneration. Sycamore maple (*Acer pseudoplatanus* L.) was also relatively abundant. Regeneration dominance and abundance responded to the mature stand canopy, soil skeleton, microrelief, ground vegetation cover, and surface characteristics. The results suggest a relationship between recruit height and microrelief in 4 out of 5 PRPs. We found statistically significant differences in height of natural regeneration ($F_{(2,18843)}$ = 191.8, P <0.001) on mounds (74.0 cm), on slopes (119.5 cm) and on pits (121.0 cm) due to high soil skeleton content on mounds with numerous rock outputs, minimum amount of fine earth and lower water retention, both necessary for recruit growth. In addition to the character of microrelief, the growth of natural regeneration was negatively influenced by mature stand density and canopy indicators.

INTRODUCTION

In the last two decades European beech (*Fagus sylvatica* L.) forests have become the subject of numerous research activities mainly because of importance as a dominant natural forest community in Europe (Peterken 1996, Oheimb *et al.* 2005). Stands with a high degree of naturalness are also often considered as a model for close-to-nature forest management in European forestry (Meyer *et al.* 2003).

European beech is a typical climax tree that occupied 40.0% of the Czech landscape in previous centuries. Today, beech cover in the Czech Republic has decreased to 7%. It is recommended that beech be 18.0% of the forest composition (MZe 2013).

The success of natural regeneration of beech depends on many factors, including climate, site aspect and elevation, seed production and dispersal and biotic factors, such as aphids, herbaceous competition and game browsing (Korpeľ 1978, Dolling 1996, Emborg 1998, Wagner 1999, Szwagrzyk *et al.* 2001, Birkedal *et al.* 2009, Löf and Welander 2004, Čermák and Mrkva 2003, Vacek *et al.* 2013). In European natural forests, windstorms often create canopy gaps that result in changes in light, soil moisture, and nutrient availability (Gálhidy *et al.* 2006). Since light is a key growth factor along with water and nutrients (Madsen 1995), regeneration success in natural forests is often related to structural dynamics and gap formation (Emborg 1998, Bílek *et al.* 2014, Jarčuška 2009, Barna 2011, Mičovský 2013, Kozlowski *et al.* 1991).

At the stand level, natural regeneration is dependent upon a sufficient number of fructifying mature trees with well-developed crowns, seed year occurrence, favorable seed bed conditions, germination and initial growth of recruits and their mortality (Poleno *et al.* 2009, Bílek *et al.* 2009). According to Övergaard (2010) large annual levels of seed production have occurred in recent decades. The intervals between good seed-years has decreased since 1974 from 5 to 2.5 years (Övergaard 2010).

Gap dynamics have been studied intensively using a wide range of modified models (gap models) that are intended to determine basic driving factors (Kaufmann and Linder 1996, Yaussy 2000, Bugmann 2001, Allen *et al.* 2010). Disturbances are commonly scaled from those involving individuals, to groups of overstory trees, and, finally, to large-scale mortality events, sometimes referred to as stand-replacement disturbances (Franklin *et al.* 2007). Where there are overlapping patterns of individual and gap mortality of overstory trees, a complex mosaic structure and multi-cohort development of forest stands are ensured (Zukrigl 1991, Vacek *et al.* 2010, Bílek *et al.* 2014).

To ensure successful natural regeneration, these complex relationships also must be respected in managed forests and are of crucial importance mainly in system with emphasis on natural processes and biotical automation (Saniga and Kráľovič 2009). In these management systems, new recruits are of autochthonous or site-adapted allochthonous origin; they conserve the appropriate characteristics of the maternal population and are well adapted to local conditions (Korpeľ 1989, Vacek *et al.* 2010). Moreover, by conserving local gene pool and the natural composition of site-adapted tree species, such activities increase the vitality and stability of forest stands (Gömöry *et al.* 1998).

Several studies from the Sudetes and central European middle mountains documented the tendency to regular distribution of individuals in the upper canopy level, in contrast to the clustered distribution of regeneration (Vacek *et al.* 2010, Szwagrzyk and Czerwczak 1993). This pattern has also been found in other natural European forests dominated by beech (von Oheimb *et al.* 2005, Commarmot *et al.* 2005). The tendency of clustered establishment and growth of the regeneration is influenced by gap formation and the creation of favorable microsites (Zeibig *et al.* 2005).

The purpose of this presented study is to evaluate the structural diversity of natural regeneration in autochthonous beech stands in the National Nature Reserve Broumovské stěny as a function of microsite. We examined the relationships between microrelief, vegetation cover, mature stand and soil parameters, and height, density and canopy characteristics of natural regeneration recruits. Since in dense beech forest stands the light is for natural regeneration limiting growth factor, its success is often related to gap-formation; higher radiation in gaps often leads to faster growth and generally higher success of tree seedlings, but increased light intensities may also have contradictory effect, when changes in resource availability induce higher ground vegetation cover and intense competition for resources (Collet *et al.* 2001, Petritan *et al.* 2009, Barna 2011). Thus, beside canopy indicators special attention is paid to the characteristics of microrelief that may have strong effect on the initial performance of natural beech regeneration.

MATERIALS AND METHOD

Area description

Broumovské stěny region – Central Sudetes (450–770 m a.s.l.) represents a part of the Natural Forest Zone number 24 – Sudety Hills and Protected Landscape Area Broumovsko (Fig. 1). The north- and east-facing slopes above Broumov basin are very steep. In contrast, south and west facing slopes are gradual and dissected by many ditches and canyons. Overlaying Jurassic sandstone, soils are predominantly oligotrophic to mezotrophic, mainly Cambisols and Cambic Rankers as well as Cryptopodzols, Regozems and Lithozems in few locations. They are light, sandy to loamy-sandy. Mean annual temperature is 6.1°C and mean annual precipitation is around 857 mm (473 mm in the vegetation season). The growing season is 139 days and the Lang′s rain factor is 140 (Mikeska *et al.* 2000, Vacek *et al.* 2012). The potential natural vegetation consists of the herb-rich beech forests (*Dentario enneaphylli–Fagetum*) and acidic beech forests (*Luzulo–Fagion*). The predominant forest site type is *Acereto–Fagetum lapidosum*. On parts of PRPs 1 and 2,

Table 1. Overview of the basic characteristics of the permanent research plots.

PRP	Altitude (m)	Exposition	Slope (°)	Species	Mean age	Diameter (cm)	Height (m)	Volume (m^3ha^{-1})	Crown projec. (ha)	Basal area (m^2ha^{-1})
1	640	E	31	Pa, Fs, Ap	92	30.4	27.0	549	2.7	40.9
2	644	E	33	Pa, Fs, Ap, Ug	163	31.3	15.0	561	3.2	38.9
3	638	E	35	Pa, Fs, Ap	163	45.3	24.5	491	2.6	30.1
4	645	E	35	Pa, Fs, Ap, Apl, Tc	92	29.5	20.7	601	2.9	44.8
5	614	NE	42	Fs, Sa	163	37.1	22.0	566	2.0	32.5

Notes: Pa – *Picea abies* (L.) H. Karst., Fs – *Fagus sylvatica* L., Ug – *Ulmus glabra* Huds., Ap – *Acer pseudoplatanus* L., Apl – *Acer platanoides* L., Tc – *Tilia cordata* Mill., Sa – *Sorbus aucuparia* L.*;* GPS: 1 – 50°34′25″ N, 16°15′41″ E, 2 – 50°34′29″ N, 16°15′40″ E, 3 – 54°34′33″ N, 16°15′39″ E, 4 – 50°34′36″ N, 16°15′37″ E, 5 – 50°34′43″ N, 16°15′36″ E.

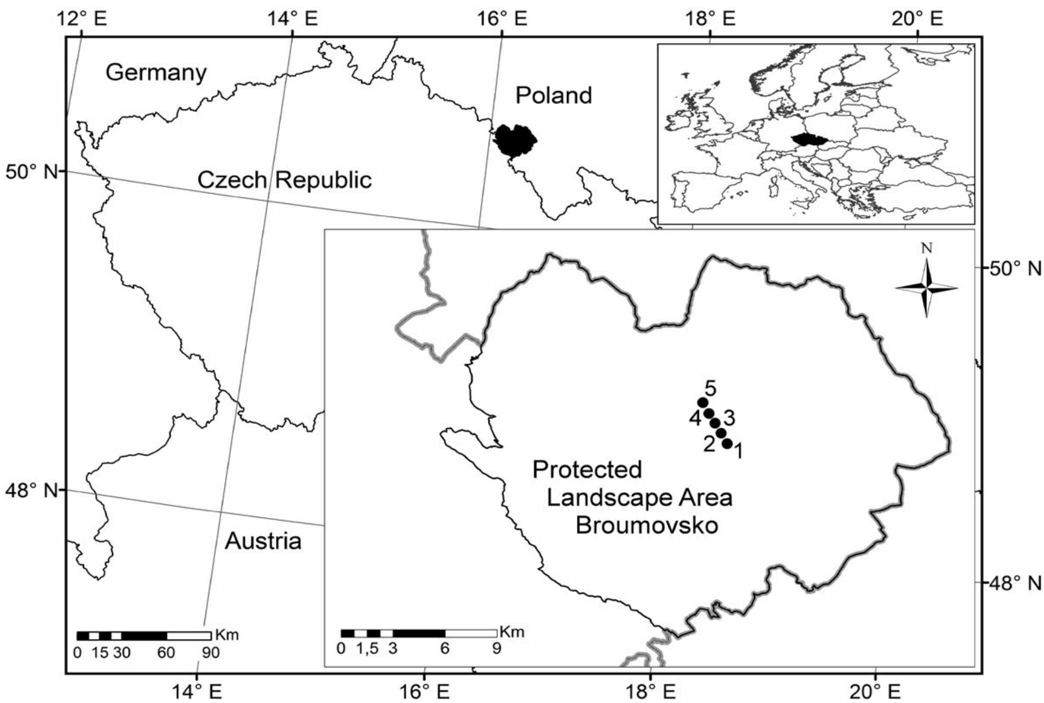

Fig. 1. Location of permanent research plots 1–5 autochthonous beech stands in the Protected Landscape Area Broumovsko – Sudety Hills.

Abieto–Fagetum saxatile and *Ulmi–Fraxineto–Aceretum saxatile* are also present.

Location of the permanent research plots (PRP) is demonstrated on Fig. 1, their basic characteristics in Table 1. Mezotrophic and modal Cambisols are prevailing on the PRP, on the PRP 1 and 2 also Cambic Rankers occur. The beginning optimum stage was dominant on the PRP 1 and 4, break-up stage on the PRP 2, 3 and partly 5.

Data collection

The Field-Map technology (IFER-Monitoring and Mapping Solutions Ltd.; cf. Šmelko and Merganic 2008) was used to determine the natural regeneration structure as well as the tree layer on five permanent research plots of size 50 × 50 m (0.25 ha). Using these data, we measured the position of all regeneration recruits with diameter at breast height (dbh) outside bark ≤7 cm and recorded tree species, total height, height of green crown base, crown width (to 1 cm accuracy) and diameter at the ground surface (to 1 mm accuracy). For each recruit we classified the site as one of three types of microrelief (mound, pit, slope) at a scale of 1.0 m.

Data analysis

Horizontal spatial arrangement, vertical structure and species composition of the natural regeneration were described. We used the following coefficients to describe the horizontal structure of natural regeneration: Hopkins-Skellam index (Hopkins and Skellam 1954), Pielou-Mountford index (Pielou 1959, Mountford 1961), Clark-Evans index (Clark and Evans 1954); Ripley's *L*-function (Ripley 1981). The David-Moore index (David and Moore 1954) was applied to determine the tree distribution frequency in particular quadrates; 25 quadrates were delimited for each PRP (10 × 10 m).

The program PointPro 2.1 and R 3.1 (Hothorn and Everitt 2014) was used to calculate characteristics describing the horizontal spatial distribution of individuals. Monte Carlo simulation was used to test for significance of deviations. The average values of the *L*-function were estimated as arithmetic means from *L*-functions calculated for 1999 randomly generated point structures. The characteristics of distribution indices are shown in Table 2. Multitype pair correlation function was used to calculate the relationship between natural regeneration and mature overstory according to the coordinates of individuals.

Species diversity was described by using the species richness determination (Menhinick 1964), species heterogeneity characteristics (Simpson 1949, Shannon 1948; 10 tree species were set as default for maximal entropy) and species evenness (Pielou 1975), where the values range between 0 (minimum species diversity) and 1 (the maximum one). Furthermore, biological canopy (sum of crown projections per hectare) and mensurational canopy (crown closure; proportion of a stand covered by the crowns) were calculated.

The heights of regeneration recruits were evaluated with respect to the forest development stage and also with respect to microrelief on particular PRPs. Forest development stages were classified according to Schmidt-Vogt (1985) and Korpeľ (1989).

Analyses were processed in the Statistica 12 software (StatSoft, Tulsa). Data were log transformed to acquire normal distribution and tested by using Kolomogorov-Smirnov procedure. The effects of microrelief on the height of natural regeneration recruits, differences among height of recruits on plots and differences in species diversity of recruits were separately tested by one-way analysis of variance (ANOVA). Significant differences were

Table 2. Overview of indices describing the horizontal structure and their common interpretation.

Index	Mean value	Aggregation	Regularity
Hopkins-Skellam	A = 0.5	A > 0.5	A < 0.5
Pielou-Mountford	α = 1	α > 1	α < 1
Clark-Evans	R = 1	R < 1	R > 1
David-Moore	ICS = 0	ICS > 0	ICS < 0

Table 3. Species composition of the natural regeneration on permanent research plots 1–5.

PRP	Fs	Ap	Pa	Other species	Frequency
	%	%	%	%	ind. ha^{-1}
1	91.3	7.9	0.5	0.3 (Aa)	1 476
2	78.5	20.3	0.8	0.3 (Ug)	9 412
3	80.5	9.9	8.2	1.4 (Sa)	5 624
4	81.2	18.1	0.2	0.6 (Tc, Sa)	14 128
5	98.0	0.9	1.1	<0.1 (Sa)	44 888

Notes: Fs – *Fagus sylvatica*, Ap – *Acer pseudoplatanus*, Pa – *Picea abies*, Ug – *Ulmus glabra*, Sa – *Sorbus aucuparia*, Tc – *Tilia cordata*, Aa – *Abies alba*.

subsequently tested by *post-hoc* comparison Tukey's HSD tests.

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, density and height recruits, tree layer height, slope, ground vegetation cover and similarity of 5 research plots. Data were centred and standardized during the analysis. The results of the PCA were visualized in the form of an ordination diagram constructed by the CanoDraw program.

RESULTS

Abundance and species diversity of the natural regeneration

Species composition of the natural regeneration on each PRP is documented in Table 3. The average number of recruits with height ≥10 cm and dbh ≤7 cm was approximately 15,000 ind. ha^{-1}. We recorded the fewest recruits on PRP 1 (1,472 ind. ha^{-1}) and the most on PRP 5 (44,888 ind. ha^{-1}). Considerably higher abundance were found on plots in the break-up stage (PRP 2, 3, 5) compared to plots in the optimum growth stage. Regeneration was predominately European beech (78.5–98.0% of total recruits). Sycamore (*Acer psudoplatanus*) was also fairly abundant, representing approximately 20% on PRPs 2 and 4 (1,908 and 2,556 ind. ha^{-1} respectively). The representation of Norway spruce (*Picea abies*) was 0.2–8.2% of total recruits. Other tree species (*Abies alba*, *Tilia cordata*, *Sorbus aucuparia* and *Ulmus glabra*) accounted for <1% of regeneration.

Statistically significant differences in species diversity of natural regeneration among plots were found ($F_{(4, 15)} = 3.1$, $P < 0.05$). The species diversity (Table 4) can be characterized as low, largely a function of domination by beech. PRP 4 contained the most species (5). According to Menhinick′s index, however, the highest species richness was detected on PRP 1, which was affected by the low number of recruits on this plot. Regardless of the index, the regeneration was species–poor. The indices of species heterogeneity are relatively low to medium rich on PRPs 2, 3 and 4 and extremely low on PRPs 1 and 5. The greatest species homogeneity was found on PRPs 2 and 3, where the disruption process of the overstorey is in progress. The lowest species diversity occured on PRP 5, where beech is dominant in the overstory.

Height structure of the natural regeneration

The height structure of the natural regeneration on PRPs 1–5 (Fig. 2) is fairly heterogeneous on all plots, depending on the dynamics of the development cycle. The largest mean heights are reached by recruits on PRP 5 (148.9 cm ± 0.8 SE) and PRP 3 (93.9 cm ± 1.7 SE), and the smallest mean heights on PRP 1 (29.5 cm ± 4.6 SE). We found that greater regeneration and differentiation of the regeneration coincided with the opening of the canopy in response to the decay of the mature stand, as shown on PRP 5. Here, the recruits were mainly in the height class 80.1–100.0 cm (10,856 ind. ha^{-1}). We also recorded a high percentage of advanced growth taller than 200 cm in PRP: 24.4% (10,956 ind. ha^{-1}). Results were completely different on PRP 1 in the optimum stage, where the height of only 3.1% of the regeneration recruits exceeded 50 cm (46 ind. ha^{-1}). Significantly greater height differentiation was observed in stands in the break–up stage compared to the optimum stage.

Table 4. Indices describing the species biodiversity of natural regeneration.

PRP	m	d (Mei)	λ (Sii)	H′ (Shi)	E (Pii)
1	4	0.108	0.046	0.057	0.095
2	4	0.041	0.342	0.249	0.413
3	4	0.053	0.335	0.290	0.482
4	5	0.042	0.308	0.522	0.324
5	4	0.019	0.040	0.049	0.082

Notes: m – species number, d (Mei) – Menhinick′s index of species richness, λ (Sii) – Simpson′s index of species heterogeneity, H′ (Shi) – Shannon′s index of species heterogeneity, E (Pii) – Pielou′s index of species homogeneity

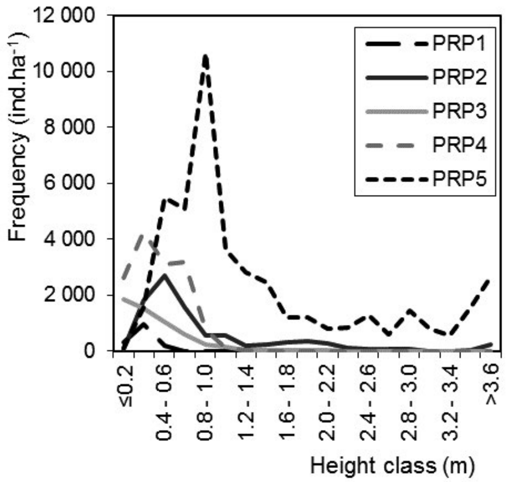

Fig. 2. Frequency of height classes of natural regeneration on permanent research plots.

PRP 3 had the greatest share (28.2%) of the smallest seedlings (those < 20 cm in height). Only the initial phases of regeneration occur on this plot, and light is limited. This smallest seedling are almost absent on PRP 5 (only 0.09% of all recruits) because of competition from advanced growth. On PRPs 1 and 4 (in the optimum overstorey growth stage without the youngest seedlings) 88.9–91.1% of recruits had a root collar diameter <1 cm, whereas on plots in the break-up stage this share of this category ranges between 10.1 and 67.7%. A relatively high number of recruits with diameter on root collar over 4 cm was registered on the PRP 5 (1,246 ind. ha^{-1}, *i.e.* 11.3% respectively).

Statistically significant differences in height of natural regeneration among plots were found (ANOVA, $F_{(4,\ 18843)}$ = 1431.0, *P* <0.001). Higher height values were recorded on plots in the break-up stage (PRPs 2, 5). Height of regeneration on these two plots was significantly different from that on the other plots (ANOVA, *P* <0.001). On the other hand, the hypothesis of homogeneity of PRPs 1, 3 and 4 was not rejected (PRPs 1 and 4: *P* = 0.18; PRPs 1 and 3: *P* = 0.28; PRPs 3 and 4: *P* = 0.99).

Effect of microrelief

A significantly higher proportion of natural regeneration recruits was found on pits and slopes (ANOVA, $F_{(2,\ 18843)}$ = 191.8, *P* <0.001) than on mounds. There was no difference in mean height of recruits on pits and slopes (ANOVA, *P* = 0.44). The mean height of recruits on mounds was 74.0 cm ± 2.2 SE, on slopes 119.5 cm ± 0.7 SE and on pits 121.0 cm ± 1.7 SE (Fig. 3). The tallest recruits were found on PRP 5, especially on pits (161.5 cm ± 1.8 SE), followed by PRP 2, particularly on slopes (102.9 cm ± 1.8 SE). Recruits with the shortest mean heights were found on PRP 3, especially on mounds (22.5 cm ± 4.5 SE), followed by PRP 1, particularly on mounds (27.0 cm ± 10.6 SE). On most plots, recruits were the tallest on pits and the shortest on mounds (Fig. 3). On PRP 1 there were no differences in recruit heights among microrelief types (test, *P* > 0.05).

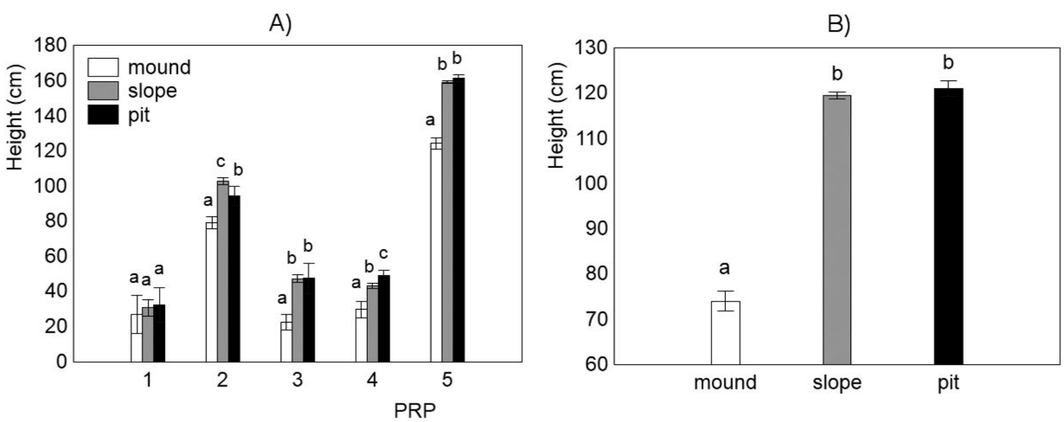

Fig. 3. Average height of natural regeneration among plots with respect to microrelief types A) and clustered for all plots B); significant differences (*P* <0.05) among microreliefs are indicated by different letters; error bars represent standard error of the mean.

Horizontal structure of the natural regeneration

The natural regeneration was considerably aggregated (Table 5, Fig. 4) based on our results using applied structural indices (Hopkins-Skellam, Pielou-Mountford, David-Moore, Clark-Evans). Ripley's *L*-function also supported the conclusion that regeneration recruits had a clumped distribution (Fig. 5). PRP 2 was the most highly aggregated (A = 0.987, α = 14.546, ICS = 27.222, R = 0.469), whereas according to the *L*-function, PRP 1 was the most highly aggregated, twice as much as PRP 3. The most clustered tree species was beech. Beech and sycamore regeneration were concentrated in groups of different size. Spruce regeneration was located in larger gaps and on sites with favourable edaphic conditions. Fir (*Abies alba)*, rowan (*Sorbus aucuparia*), lime-tree (*Tilia cordata)* and elm (*Ulmus glabra*) seedlings are interspersed. Considerably higher spatial diversity was observed in break-up stages (PRP 2, 3, 5) than in the optimum growth stage (Fig. 4).

Results of multi-type pair correlation analysis showed a negative effect of the parent stand on the natural regeneration at smaller spacing (1.0–2.5 m). Distribution at higher spacing across the plots is mostly random (no spatial relationship).

Relationships among canopy, recruit height and density and plot parameters

Results of the PCA are presented in the form of the ordination diagram in Fig. 6. The first ordination axis explained 61%, the first two axes together 82% and the first four axes together 99% variability of data. The first axis x represented plot slope and soil depth, together with canopy indicators of recruits. Second axis y represented stand height. Recruit density, stand age, crown projection of recruits and crown closure of recruits were positively correlated with plot slope and soil depth. These parameters were negatively correlated with stand density and canopy indicators of the stand. Stoniness was positively correlated with stand height and negatively correlated with recruit height and density. Vegetation cover was negatively correlated with stand density and canopy indicators of the stand. Stand age and vegetation cover had less effect on mutual relationships among canopy, recruit height and density and plot parameters.

DISCUSSION

The success of natural regeneration management in forestry obviously depends on the abundance and survival of seedlings. Korpeľ (1978) determined that the values of the natural regeneration abundance (≤3 years) were approximately 25,000 ind. ha^{-1} in natural beech forests of Slovakia at altitudes between 600–760 m a.s.l. For successful development and growth of the regeneration he concluded that the minimum number of recruits should be 20,000 ind. ha^{-1}. In our study, natural regeneration numbers (height of recruits ≥ 10 cm and dbh <7 cm) averaged 15,100 ind. ha^{-1}. Nagel *et al.* (2006) found similar numbers of natural regeneration in southeatern Slovenia in fir-beech forests, ranging from 11,654 to 14,615 ind. ha^{-1}. Lower regeneration density was documented in the acidophillic and mesophyllic beech stands of the north-eastern Germany (Oheimb *et al.* 2005), where the abundance of regeneration was on average 3,202 with a maximum of 9,408 ind. ha^{-1}. Meyer *et al.* (2003), however, reported higher values in natural beech forests of Albania, ranging from 19,259 to 29,844 ind. ha^{-1}. Bílek *et al.* (2014) found even higher seedling densities (9,020 to 75,778 ind. ha^{-1}) in Central Bohemia in the Voděradské bučiny Natural Reserve. Korpeľ (1989) reported be-

Table 5. Indices describing the horizontal structure of natural regeneration.

Index	PRP 1	PRP 2	PRP 3	PRP 4	PRP 5
Hopkins-Skellam	0.943*	0.987*	0.983*	0.960*	0.920*
Pielou-Mountford	9.082*	14.546*	9.613*	9.794*	6.164*
David-Moore	10.773*	27.222*	7.415*	25.285*	29.983*
Clark-Evans	0.475*	0.469*	0.547*	0.635*	0.622*

* statistically significant

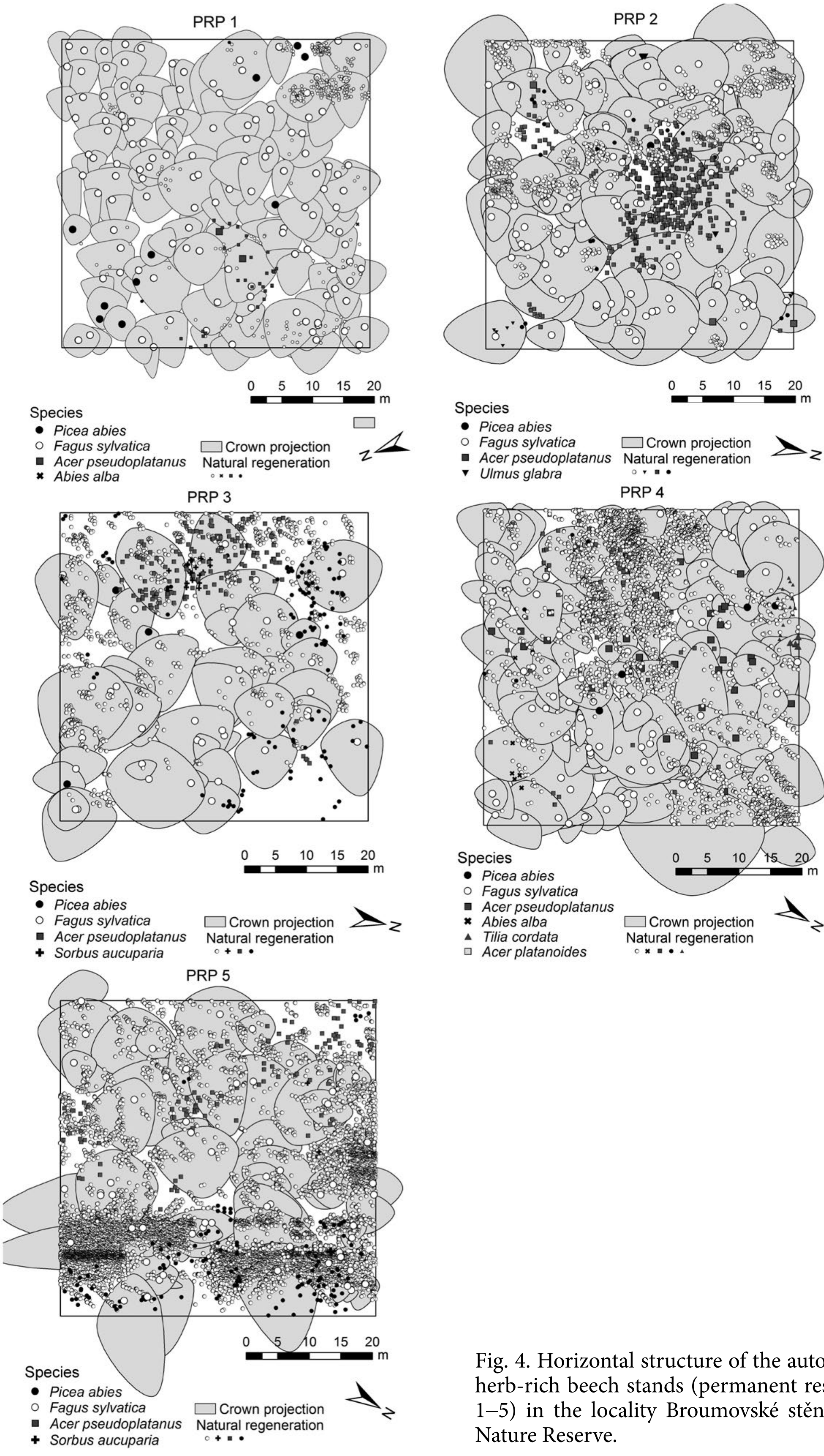

Fig. 4. Horizontal structure of the autochthonous herb-rich beech stands (permanent research plot 1–5) in the locality Broumovské stěny National Nature Reserve.

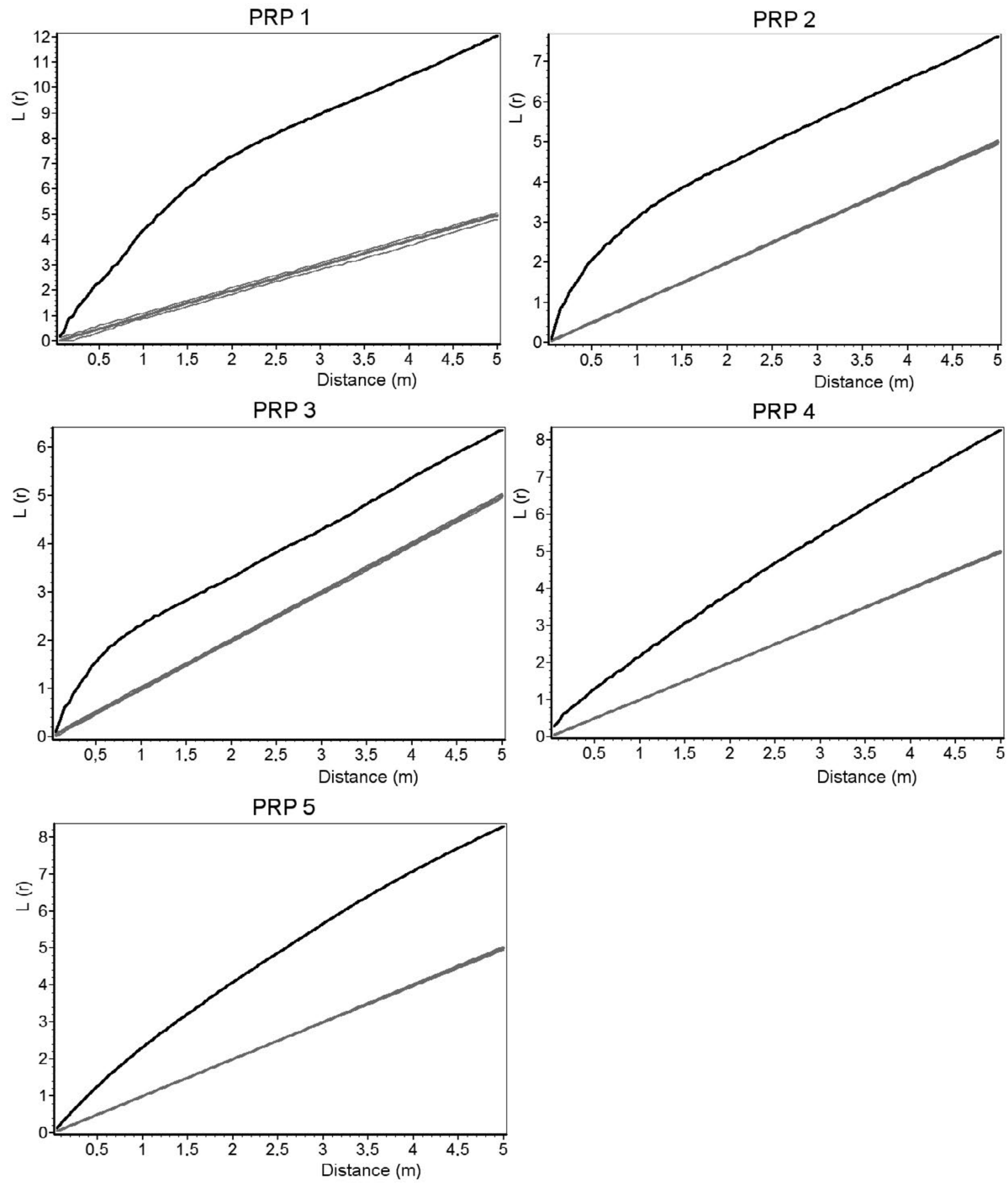

Fig. 5. Horizontal structures of natural regeneration on permanent research plots 1–5 expressed by Ripley´s *L*-function; the black line represents the *L*-function for real distances of trees on the permanent research plot; the bold blue line represents the mean course for random spatial distribution of trees and the two thinner central curves represent 95% interval of reliability; when the black line of tree distribution on the plot is below this interval, it indicates a tendency of trees toward regular distribution, and if it is above this interval, it shows a tendency toward aggregation.

tween 11,674 and 21,345 recruits ha^{-1} in forest reserves in middle elevations of Slovakia (Vihorlatský Kyjov, Rožok a Havešová). High variability was evident in all cases, depending particularly on the size of the canopy opening and on gap formation contrary to the closed forest environment.

Korpeľ (1978) stated that 5-year-old beech regeneration in single cohort management systems can reach a height ≥40 cm only if canopy closure is less than 0.5. Similar stand conditions were in our study observed on PRP 5 with stocking 0.5 and the most advanced beech regeneration in the height class

80.1–100.0 cm. The lowest seedling density and mean height of beech regeneration was observed on PRP 1, which had an overstory stocking 0.9. These results are similar to those of Bílek *et al.* (2013). They documented the best growths of seedlings on the locations with canopy 0.5, satisfactory on sites with canopy 0.6 and unsatisfactory on sites with canopy 0.8, ten years after a heavy seed crop. Expressed differences in recruit heights between plots can be explained as a result of different levels of overstory tree density, gap disturbances and prevailing habitat conditions. Reduced levels of variation in recruit heights within sample plots are in line with other similar research that report close to normal distribution for initial natural regeneration, whereas on PRP 1 and 5 advanced regeneration displayed a shift to right-skewed height-classes distribution as the strongest individuals start to differentiate within the regeneration cohort (Vacek *et al.* 2014).

Silver fir and sycamore numbers and relative dominance in our study were comparable to numbers reported by Korpeľ (1978, 1989), who found 2,400–6,750 ind. ha^{-1} of fir recruits in similar conditions. In the overstory the share of this species was 14%. Nagel *et al.* (2006) found similar numbers of silver fir regeneration, slightly lower than those in Oheimb *et al.* (2005).

Our study found the regeneration was strongly aggregated horizontally, similar to other studies (Rozas 2003, Nagel *et al.* 2006, Paluch 2007, Szewczyk and Szwagrzyk 2010, Vacek *et al.* 2010). The clustered nature of the recruit distribution was evident in our study not only near the canopy gaps, but also relatively far from them. Abundance and size of recruits of natural origin is strongly affected by the canopy closure of the parent overstory. Significantly higher species as well as spatial variability including height distribution form was documented in the break-up stage comparing to the optimum stage.

The recruits were significantly taller in the terrain depressions (pits) and slopes compared to those growing on mounds. This was even emphasized by the high soil skeleton content on mounds with numerous rock outputs, minimum amount of fine earth and lower water retention, both necessary for recruit growth (Vodde *et al.* 2010). Limiting growth of recruits on mounds is also connected with sensitivity to frost and drought (Wagner *et al.* 2010). This is in contrast to the situation in the Giant Mts., where taller regeneration and more vigorous growth was found on the elevated sites (Vacek *et al.* 2009). This results was likely due to different climatic conditions of the Giant Mts. and by soil factors with much lower soil skeleton content.

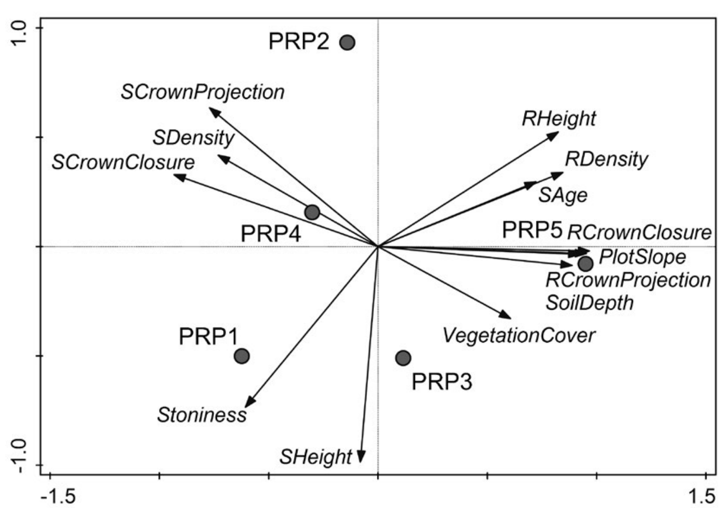

Fig. 6. Ordination diagram showing results of PCA analysis of relationships among canopy parameters (crown closure, crown projection) of recruits (marked as 'R') and stand (marked as 'S'), density, height, stand age, vegetation cover and research plot attributes (plot slope, stoniness, soil depth); indicate the research plots.

The quantity of the natural regeneration was also strongly modified by the topography and soil herb and moss cover found in this part of Central Sudetes (Vacek and Matějka 2003) as well as in the primeval and natural forests of the Slovakia in Vihorlatský prales Kyjov, Rožok and Havešová (Korpeľ 1989).

Results of multivariate analysis showed that mature stand canopy (crown projection, crown closure), soil depth and stoniness was important for recruit density and recruit canopy characteristics. Similar result were confirmed by many authors (cf. Madsen and Larsen 1997, Madsen and Hahn 2008), who demonstrated a significantly positive effect of increasing light levels on natural regeneration (Ammer *et al.* 2008, Sefidi *et al.* 2011, Bílek 2014 *et al.*). However, this relationship between mature stand canopy and the density of natural regeneration recruits is not linear and may vary considerably depending on local competition (Collet and Le Mogeudec 2007). Analysis also showed a negative effect from stony soil and positive effect of soil depth on the growth of recruits (Madsen and Larsen 1997, Diaci *et al.* 2005).

It has been shown that unmanaged old-growth forest stands support high variability of natural regeneration recruits concerning their height, tree species and spatial pattern. Natural regeneration is typically variable in time and space as result of ongoing gap dynamics with absent or very limited large-scale break-up of senescent parent stands. This is in accordance with other studies conducted in similar natural conditions in stands dominated by European beech. Therefore it is expected that multi-aged management regimes are better suited for the retention of structural and spatial attributes characteristic for these forest ecosystems.

CONCLUSION

High variability of natural regeneration was documented on all studied plots. Natural regeneration of beech dominated stands was predominantly aggregated with rather uniform size structure within clusters of natural regeneration and more expressed differences in heights of recruits among plots. Changes of horizontal structure are influenced mainly by microrelief types, competition of parent stand and soil parameters. The occurrence and growth of recruits was negatively influenced by parent stand density and canopy closure. Regeneration was in general more prospering on pits and slopes with more favourable moisture characteristics. This is in contrast to the situation in other parts of the Sudetes, where taller regeneration and more vigorous growth was found on the elevated sites (Giant Mts.). This results was likely due to different climatic conditions of the Giant Mts. and by soil factors with much lower soil skeleton content.

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