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# Spatial pattern of relict beech (*Fagus sylvatica* L.) forests in the Sudetes of the Czech Republic and Poland

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**ABSTRACT**: Horizontal structure of forest stands largely affects the competitive relationships between tree individuals and plays a significant role in the stand dynamics. The present study describes horizontal structure on nine permanent research plots (0.24–0.25 ha) in the regeneration and tree layer of autochthonous European beech (*Fagus sylvatica* Linnaeus) stands in the wide altitudinal gradient in protected areas in the Czech Republic and Poland. The spatial structure was classified in productive herb-rich beech sites, through acidophilic beech sites, exposed sites, to beech fragments near the timberline. The spatial pattern of tree layer was regular in the lowest parts of the altitudinal gradient of beech, random in the middle parts and aggregated in the beech forests under the hilltop phenomenon and extreme edaphic site. Nevertheless, trees in lower tree layers showed a tendency to the aggregated pattern, similarly like the strong aggregation of natural regeneration. In most cases, the parent stand had a significant negative effect on natural regeneration at a smaller distance (to 0.8–4.2 m). The spatial pattern of dead wood was mostly random. Because of the great plasticity of beech crowns, crown centroids were more regularly distributed than tree stems. The average displacement of crown centroids from the stem base was 1.5 m with the prevailing direction of 52.7% down the slope. Projected canopy cover was on average 10.7% higher compared to the canopy simulated by circular crowns.

**Keywords**: European beech; horizontal structure; protected areas; natural forest; crown plasticity

A correct understanding of the spatial pattern of both the upper storey (von Oheimb et al. 2005; Pretzsch 2006; Vacek et al. 2014a) and natural regeneration (Nagel et al. 2006; Vacek et al. 2014b, 2015c) and dead wood (Amanzadeh et al. 2013; Vacek et al. 2015a) is crucial for management aimed at the imitation of natural forest dynamics. The spatial pattern of forest is closely related to the level of competition between tree individuals, and at the same time it substantially affects their establishment, growth and mortality (Newton, Jolliffe 1998; Petritan et al. 2007; Seidling et al. 2014). The tree crown architecture is significantly influenced mainly by light availability in a forest stand (Came-ron, Hands 2010; Rozenbergar, Diaci 2014). Particularly in protected areas the spatial pattern of forest ecosystems is often considered as one of the criterions for determining their degree of naturalness (Schmidt 1997; Moravčík et al. 2010; Vacek et al. 2014b), and thus has also importance for the formulation of management policies on the level of individual forest stands. Leaving forest stands to spontaneous development with a low degree of naturalness results in extensive disturbances (Krejčí et al. 2013).

The initial spatial pattern of near-natural beech stands is usually aggregated or randomly irregu-

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lar and it turns to a moderately regular pattern in favourable conditions (Wijdeven 2003; Vacek et al. 2015b, c). This is a result of the gradual growth and expansion of crowns because beech crowns are able to promptly react to changes in light conditions of the environment (Pretzsch, Schütze 2009). Beech trees are even able to change their architecture in order to increase the light interception and to decrease energy expenditure on respiration while the maximum potential growth space in the stand is utilized (Messier et al. 1999; Rozenbergar, Diaci 2014). The phenotype plasticity of beech is caused not only by biotic interactions between neighbouring trees (Vincent, Harja 2007) but also it can be affected by genotype (Gömöry et al. 1998; Schröter et al. 2012) or by abiotic conditions (Lang et al. 2010). On the other hand, greater shading causes plagiotropic growth (Nicolini 2000) and various stem defects (Wagner et al. 2010), while the crown asymmetry decreases the static stability of trees (Young, Perkocha 1994; Bottero et al. 2011).

In the past, mainly distribution indices based on the tree frequency in quadrats were used to study the horizontal structure of stands (David, Moore 1954; Lloyd 1967; Douglas 1975). In the long term, indices based on a distance of trees to their nearest neighbour have often been used (Clark, Evans 1954), other indices are based on a distance between a randomly selected point and tree positions (Hopkins, Skellam 1954; Mountford 1961) or indices based on angles between neighbouring trees (von Gadow et al. 1998). The research conducted by Corral-Rivas et al. (2010) showed that the individually computed indices of the spatial pattern should be interpreted carefully because they need not always be reliable. Every method has its pros and cons and it is also necessary to take into account the tolerance of tree species to shading. As shown by Ward et al. (1996) or Aldrich et al. (2003) in light-demanding species a decrease in the number of individuals is usually accompanied by a downward trend towards aggregation while shade tolerant species show an opposite trend, which applies to beech in our study (Ellenberg et al. 1992; Kunstler et al. 2005). Recent approaches evaluate the spatial distribution of trees by functions of spatial statistics (Pretzsch 2009). Their advantage compared to spatial indices is that they describe the intensity of the particular types of distribution to different distances and are not transformed to one figure only (Stoyan, Stoyan 1992; Pommerening 2002).

The objective of this contribution was to evaluate the spatial structure of natural beech stands with respect to different environmental conditions. The particular aims were to determine the spatial pattern of regeneration layer individuals and tree layer individuals and dead wood across an altitudinal, climatic and edaphic gradient and to analyse the ability of the crown plasticity of beech trees. We hypothesize that (*i*) tendency towards the aggregated spatial pattern is positively influenced by increasing altitude, (*ii*) tree layer has an effect on the distribution of natural regeneration and (*iii*) centroids of the horizontal crown projection areas of trees are more regularly distributed than their stem bases.

## MATERIAL AND METHODS

**Description of the area of interest**. A complex of the studied permanent research plots (PRPs) in protected areas is located in the Sudetes range system in the Czech Republic (CZ) and in Poland (PL) (Krkonoše Mountains, Sudetské mezihoří, Orlické hory Mountains). On these PRPs beech forests are represented in different site conditions from the zone of herb-rich beech woods through acidophilous beech woods to fragments of mosaic groups of beech along the timberline, with various impacts of pollutants and different acidification level. In the Krkonoše Mts 3 permanent research plots were chosen (K35 – Chojnik 1, K38 – Łomniczka in PL and K60 – Nad Benzínou 4 in CZ) that were compared with 3 PRPs in the Orlické hory Mts Protected Landscape Area (PLA) (O1 – Pod Vrchmezím, O2 – Bukačka 1, O7 – Trčkov 1) and 3 PRPs in the Broumovsko PLA (B1 – Broumovské stěny 1, B5 – Broumovské stěny 5, B8 – Kozínek 3). The plots in the particular areas were chosen so that they would cover the largest possible altitude range. The permanent research plots were established in the framework of past research projects solved by the Forestry and Game Management Research Institute, Opočno Forest Research Station and Faculty of Forestry and Wood Sciences, Czech University of Life Sciences in Prague. The permanent research plots were established to include mainly semi-natural forests in various stand and site conditions with a high degree of self-thinning processes. Average annual precipitation varies with altitude above sea level from 590 to 1,260 mm and average annual temperature declines with increasing altitude from 7.5 to 2.6°C. The parent bedrock is composed mainly of granites, mica schists and sandstones. At the lowest altitudes Cambisols are dominant while above 1,000 m Cryptopodzols pre-

Table 1. Overview of basic characteristics of permanent research plots sorted according to location and altitude

| Plot | | Altitude (m) | Growing season (day) | Temperature (°C)[1] | Exposition | Slope (°) | Forest type[2] | Age (yr)[3] | DBH (cm)[3] | Height (m)[3] | Volume ($m^3\cdot ha^{-1}$) |
|---|---|---|---|---|---|---|---|---|---|---|---|
| K35 | Chojnik 1 | 580 | 130 | 12.5 | NW | 15 | 4B | 175 | 46.9 | 25.4 | 942 |
| K38 | Łomniczka | 1,040 | 75 | 7.7 | W | 25 | 7K | 124 | 31.3 | 17.4 | 325 |
| K60 | Nad Benzínou 4 | 1,310 | 65 | 7.2 | SW | 24 | 9K | 136 | 16.7 | 8.5 | 212 |
| O7 | Trčkov 1 | 820 | 115 | 11.5 | E | 17 | 6S | 146 | 32.5 | 18.9 | 737 |
| O1 | Pod Vrchmezím | 930 | 110 | 10.7 | NW | 21 | 6K | 163 | 29.8 | 15.3 | 532 |
| O2 | Bukačka 1 | 990 | 95 | 9.2 | W | 5 | 7K | 166 | 32.7 | 12.3 | 234 |
| B8 | Kozínek 3 | 415 | 145 | 12.8 | SE | 27 | 3D | 157 | 44.4 | 26.0 | 601 |
| B5 | Broumovské stěny 5 | 620 | 130 | 11.7 | NE | 46 | 5N | 164 | 32.1 | 20.6 | 556 |
| B1 | Broumovské stěny 1 | 635 | 130 | 11.7 | E | 31 | 5A | 95 | 30.4 | 26.8 | 549 |

[1]mean temperature in the growing season, [2]forest site type according to Viewegh (2004), [3]mean value

GPS: K35 – 50°50'5''N, 15°38'37''E, K38 – 50°45'8''N, 15°44'39''E, K60 – 50°45'1''N, 15°32'2''E, O7 – 50°18'47''N, 16°25'12''E, O1 – 50°21'31''N, 16°21'37''E, O2 – 50°20'10''N, 16°22'42''E, B8 – 50°30'10''N, 16°12'21''E, B5 – 50°34'42''N, 16°15'34''E, B1 – 50°34'25''N, 16°15'42''E

vail. The basic characteristics of these PRPs are documented in Table 1 and Fig. 1.

**Data collection**. Data were collected on 8 PRPs of 50 × 50 m in size (0.25 ha) and on PRP K38 of 60 × 40 m in size (0.24 ha). The FieldMap technology (IFER-Monitoring and Mapping Solutions Ltd., Jílové u Prahy, Czech Republic) was used to determine the structure of natural regeneration, tree layer, dead wood and crown projection areas. The tree layer was divided according to tree classes into upper storey (codominant and dominant trees) and lower storey (suppressed trees) when all individuals with DBH ≥ 4 cm were measured. To study beech natural regeneration a characteristic transect (after pilot study) of 50 × 10 m in size (500 $m^2$) was staked out and stabilized so that it would represent the average abundance and maturity of advance growth on the whole PRP. All individuals of height ≥ 10 cm and DBH < 4 cm present in the particular transects were included

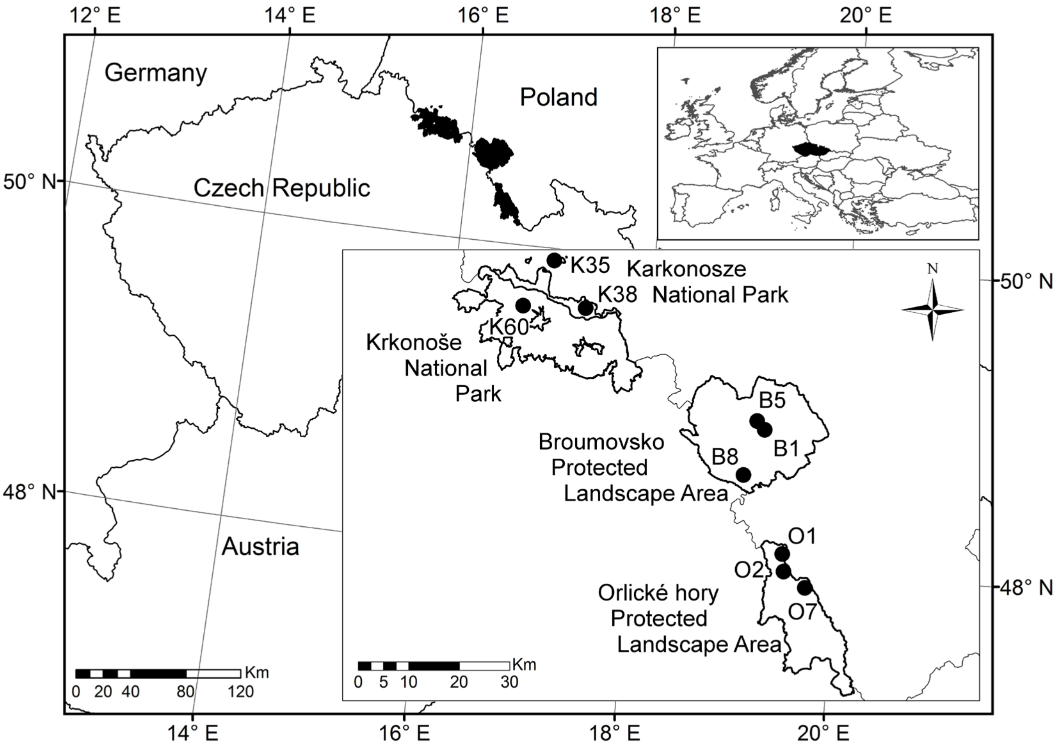

Fig. 1. Localization of permanent research plots in the Sudetes range system

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 | $\alpha = 1$ | $\alpha > 1$ | $\alpha < 1$ |
| Clark-Evans | $R = 1$ | $R < 1$ | $R > 1$ |
| David-Moore | $ICS = 0$ | $ICS > 0$ | $ICS < 0$ |

in measurements of natural regeneration. The following dendrometric characteristics were measured in trees (DBH ≥ 4 cm): DBH, height, base of live crown and crown width at least at 4 directions perpendicular to each other. Position and diameter (D) of stumps were measured from D ≥ 7 cm at a height of 30 cm a.g.l. and logs at the small end D ≥ 7 cm and length ≥ 1 m.

**Data analysis**. Horizontal structure was evaluated separately for natural regeneration, tree layer, dead wood and centroids of horizontal crown projection areas. These indices were computed: Hopkins-Skellam index (Hopkins, Skellam 1954), Pielou-Mountford index (Mountford 1961), Clark-Evans index (Clark, Evans 1954) and Ripley's $L$-function (Ripley 1981; Penttinen et al. 1992). In graphical outputs the black line depicts the $L$-function for real distances of individuals on PRP, the thick grey line shows the middle course for the random spatial pattern of trees and two thinner central curves illustrate the 95% confidence interval. A test of the significance of deviations from the values expected for the random distribution of points was done by means of Monte Carlo simulations. The mean values of $L$-function were estimated as arithmetic means from $L$-functions computed for 1999 randomly generated point structures. If in the figures the black line of tree distribution on PRP is below this interval, it indicates the tendency of individuals towards the regular pattern while if it is above this interval, it shows the tendency towards aggregation. Among distribution indices based on the tree frequency in the particular quadrats, David-Moore index was used (David, Moore 1954). The quadrat size on PRP was 10 × 10 m (25 quadrats) and transects were divided into 80 quadrats (2.5 × 2.5 m each). Table 2 shows the criteria of aggregation indices.

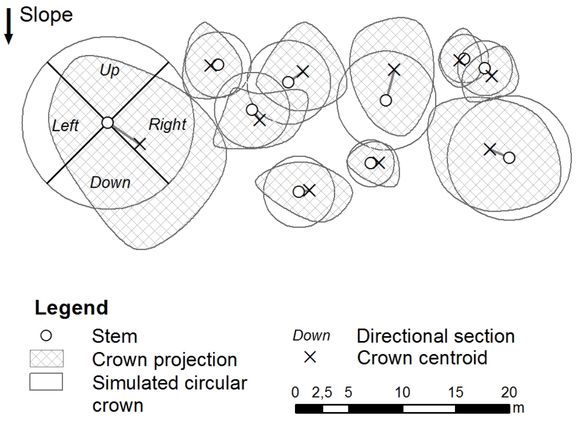

Fig. 2. Illustration of measured crown projections, simulated circular crowns, stems, crown centroids, displacement between stem bases and centroids with distribution of prevailing crown directions of beech trees

To calculate these characteristics describing the horizontal structure of individuals on PRPs the PointPro programme (Version 2.2, 2010) was used. A relationship between tree layer and natural regeneration was analysed using the R software (Version 3.1, 2014) by the pair correlation function. In results statistically significant values ($\alpha = 0.05$) are designated by asterisk.

Situational maps and analysis of crowns were produced in the ArcGIS programme (Version 10.0, 2010; Fig. 2). The crown projection cover (crown closure) was compared with simulated circular areas in the middle of the stem base with radii that were calculated from measured crowns. Absolute displacement between the stem base and the corresponding centroid of the measured crown projection area was used to determine the crown plasticity. Comparing these displacements across crown sizes, relative displacement was defined as the ratio of absolute displacement and the mean crown radius of the respective tree (Longuetaud et al. 2008; Schröter et al. 2012).

Statistical analyses were processed in STATISTICA (Version 12, 2013). Data were log transformed to acquire normal distribution (tested by the Kolmogorov-Smirnov test). The differences between PRPs and canopy of trees were tested by one-way analysis of variance and consequently tested by post-hoc comparison Tukey's honest significant difference tests. Crown plasticity data were analysed by the correlation coefficient. In order to examine the mutual relationships and interactions among stand characteristics (volume, mean age, mean DBH, mean height, tree density, crown closure, crown projection area), site parameters (slope of terrain, altitude, stoniness – content of skeleton was determined from the soil sample, temperature) and indices of horizontal structure, unconstrained principal component analysis (PCA) in the Canoco programme (Version 5.03, 2013) was applied. Data were log-transformed, centred and standardized before the analysis. The results of the PCA were visualized in the form of an ordination diagram.

## RESULTS

### Tree layer

**Krkonoše Mts National Park (PRP K35, K38, K60)**. The spatial pattern of the canopy trees of a productive herb-rich beech forest situated at the lowest altitude on PRP K35 was moderately regular according to *A*, *R* and *ICS* indices while it was random according to α index (Table 3, Fig. 3). The regular and random pattern of the canopy trees according to their distances was also indicated by the *L*-function (Fig. 4). In the distance range of 1–7 m the tree distribution on the plot was regular and random to a distance of 1 m and from 7 m. A more detailed analysis of the upper and lower storey documents that co-dominant and dominant trees showed a regular pattern inclining towards randomness ($A$ = 0.317*, α = 0.805*, $R$ = 1.331*). On the contrary, the horizontal structure of shaded and intermediate trees was aggregated ($A$ = 0.907*, α = 6.159*, $R$ = 0.614*). The tree layer of an acidophilous beech wood on PRP K38 was distributed randomly as shown identically by all computed structural indices (Table 3) and *L*-function (Fig. 4). The spatial pattern of the canopy trees on PRP K60 situated at the highest altitude around the timberline was aggregated according to the four computed indices (Table 3). The *L*-function shows that the highest intensity of aggregation occurred at a tree distance of 3 to 6 m (Fig. 4).

**Orlické hory Mts PLA (PRP O7, O1, O2)**. Similar results like in the Krkonoše Mts National Park were obtained in the Orlické hory Mts PLA (Table 3, Fig. 4). The plot at the lowest altitude (PRP O7), characterized by the most favourable climatic and site conditions, had the regular spatial pattern of the canopy trees according to structural indices. The *L*-function illustrates that the random pattern of trees for distances within 1.6 m was typical of this plot and at longer distances regular distribution prevailed. At a longer distance (more than 8 m) both types of spatial pattern alternated. Trees on PRP O1 were distributed randomly, and only at a distance within 1 m the spatial pattern was moderately regular. It resulted also from the *L*-function. PRP O2 is situated on the ridge of the Orlické hory Mts and is considerably influenced by the hilltop phenomenon. It explains the aggregated horizontal structure of tree layer on this plot. For PRP O2 the *L*-function shows the initial pronounced intensity of aggregation at the distance of 0.5–4.5 m. At a distance less than 0.5 m and more than 5 m the tree layer structure was random.

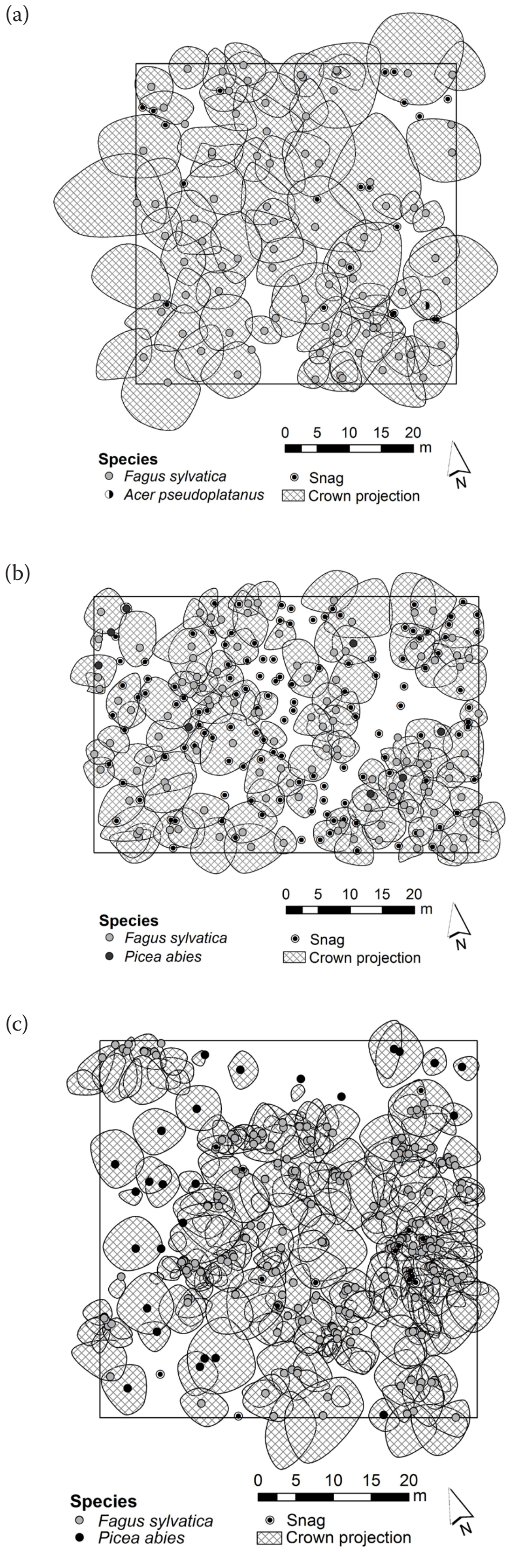

Fig. 3. Horizontal structure of the autochthonous beech forest in the Krkonoše Mts National Park on permanent research plots K35 – Chojnik 1 (a), K38 – Łomniczka (b) and K60 – Nad Benzínou 4 (c) in 2014 represented by all three variants of the spatial pattern – regular, random and aggregated

Table 3. Indices describing the horizontal structure of selected entities on permanent research plots (PRPs)

| Index | PRP | | | | | |
|---|---|---|---|---|---|---|
| **Krkonoše Mts National Park** | K35 | K38 | K60 | K35 | K38 | K60 |
| | tree layer | | | natural regeneration | | |
| Hopkins-Skellam | 0.355* | 0.528 | 0.915* | 0.682* | 0.821* | 0.969* |
| Pielou-Mountford | 0.878 | 1.245 | 5.131* | 2.565* | 3.858* | 6.538* |
| Clark-Evans | 1.318* | 1.048 | 0.470* | 0.822* | 0.788* | 0.489* |
| David-Moore | –0.123* | –0.020 | 0.811* | 1.589* | 2.998* | 2.578* |
| | crown centroids | | | stumps | | |
| Hopkins-Skellam | 0.292* | 0.368* | 0.694* | 0.471 | 0.482 | 0.630 |
| Pielou-Mountford | 0.753* | 0.829* | 2.158* | 1.081 | 1.075 | 1.459 |
| Clark-Evans | 1.469* | 1.264* | 0.736* | 0.949 | 1.124 | 0.741* |
| David-Moore | –0.238* | –0.220* | 0.466* | –0.188 | 0.008 | 0.750* |
| **Orlické hory Mts PLA** | O7 | O1 | O2 | O7 | O1 | O2 |
| | tree layer | | | natural regeneration | | |
| Hopkins-Skellam | 0.388* | 0.522 | 0.732* | 0.841* | 0.887* | 0.963* |
| Pielou-Mountford | 0.924 | 1.159 | 1.857* | 10.992* | 5.497* | 11.563* |
| Clark-Evans | 1.201* | 1.058 | 0.633* | 0.742* | 0.636* | 0.459* |
| David-Moore | –0.310* | –0.133 | 0.434* | 3.152* | 2.290* | 3.347* |
| | crown centroids | | | stumps | | |
| Hopkins-Skellam | 0.362* | 0.422* | 0.646* | 0.618 | 0.561 | 0.668 |
| Pielou-Mountford | 0.805* | 0.998 | 1.647 | 1.448 | 1.337 | 1.689 |
| Clark-Evans | 1.268* | 1.127* | 0.891* | 0.962 | 1.021 | 0.855* |
| David-Moore | –0.397* | –0.133 | 0.030 | 0.089 | –0.293 | 0.263 |
| **Broumovsko PLA** | B8 | B1 | B5 | B8 | B1 | B5 |
| | tree layer | | | natural regeneration | | |
| Hopkins-Skellam | 0.324* | 0.519 | 0.674* | 0.739* | 0.942* | 0.976* |
| Pielou-Mountford | 0.806 | 1.170 | 1.608 | 3.232* | 8.892* | 14.225* |
| Clark-Evans | 1.341* | 1.088 | 0.838* | 0.731* | 0.682* | 0.469* |
| David-Moore | –0.233* | –0.067 | 0.496* | 2.679* | 3.217* | 4.165* |
| | crown centroids | | | stumps | | |
| Hopkins-Skellam | 0.305* | 0.402* | 0.573 | 0.661 | 0.651 | 0.501 |
| Pielou-Mountford | 0.724* | 0.967 | 1.406 | 1.779 | 1.435 | 1.634 |
| Clark-Evans | 1.489* | 1.234* | 0.964 | 1.018 | 1.062 | 1.069 |
| David-Moore | –0.283* | –0.240* | –0.073 | –0.152 | –0.150 | 0.333 |

*statistically significant (α = 0.05), PLA – Protected Landscape Area, PRP: K35 – Chojnik 1, K38 – Łomniczka, K60 – Nad Benzínou 4, O1 – Pod Vrchmezím, O2 – Bukačka 1, O7 – Trčkov 1, B1 – Broumovské stěny 1, B5 – Broumovské stěny 5, B8 – Kozínek 3

**Broumovsko PLA (PRP B8, B1, B5)**. Similar results of horizontal structure to those from the Krkonoše Mts National Park and Orlické hory Mts PLA were found out in the Broumovsko PLA (Table 3, Fig. 4). On the plot at the lowest altitude (PRP B8) the canopy trees showed a regular spatial pattern according to all structural indices, but according to α index it was not statistically significant. The *L*-function indicates that for a distance within 3 m the random spatial pattern of trees was typical of this plot and at a longer distance the regular distribution prevailed. Trees on PRP B1 were distributed randomly, only at a distance of 0.9–1.3 m their distribution was moderately regular. On the contrary, PRP B5 was situated at the same altitude as PRP B1, but on a very steep rocky slope with the shallow soil profile with high skeleton content and local rock outcrops. It explains the aggregated horizontal structure of tree layer on this plot (PRP B5), which was statistically significant in all cases except α index.

### Tree crown plasticity

Structural indices from the Krkonoše Mts listed in Table 3 demonstrate that the structure of tree crowns on PRP K35 was regular. A comparison of the indices of the centroids of horizontal crown projection areas with the centroids of stem bases of trees shows a still larger shift towards regular structure. The *L*-function also documents a regular spatial pattern, already at a distance from 1 to 9.5 m (only to 7 m in the tree layer). The regular spatial pattern of crown centroids on PRP K38 is evident from Table 3 and also from the *L*-function while the tree structure was random. At a distance of 5 to 30 m the distribution of crown centroids on the plots was regular, in the other cases it was random. On PRP K60 the indices of horizontal structure listed in Table 3 document that the spatial pattern of crown centroids was aggregated. A comparison of the indices of crown centroids with the stem base of trees indicates considerably smaller aggregation of crowns. In some cases the centroids of beech crowns were at a distance of more than 3.2 m from the stem base while the mean height of the stand was 8.5 m. *L*-function also shows a shift towards the regular spatial pattern compared to tree positions. At a distance within 2 m the horizontal structure of crowns was random, from 2 m aggregated distribution prevailed.

On all three PRP in the Orlické hory Mts PLA the spatial pattern of the crown centroids of trees was more regular than that of their stem bases (Table 3). On PRP O7 the crown centroids were distributed regularly. Identically, the crown centroids on PRP O1 were distributed significantly regularly according to *R* and *A* indices while the stem distribution was fully random. As for tree crowns, the most pronounced shift towards a more regular spatial pattern was observed on PRP O2. Similarly, the crown centroids of trees on all three PRP in the Broumovsko PLA were distributed more regularly compared to their stem bases (Table 3). On PRP B8 the values of α index also show a statistically regular distribution. The spatial pattern of crown centroids on PRP B1 was significantly regular according to *A*, *R* and *ICS* indices

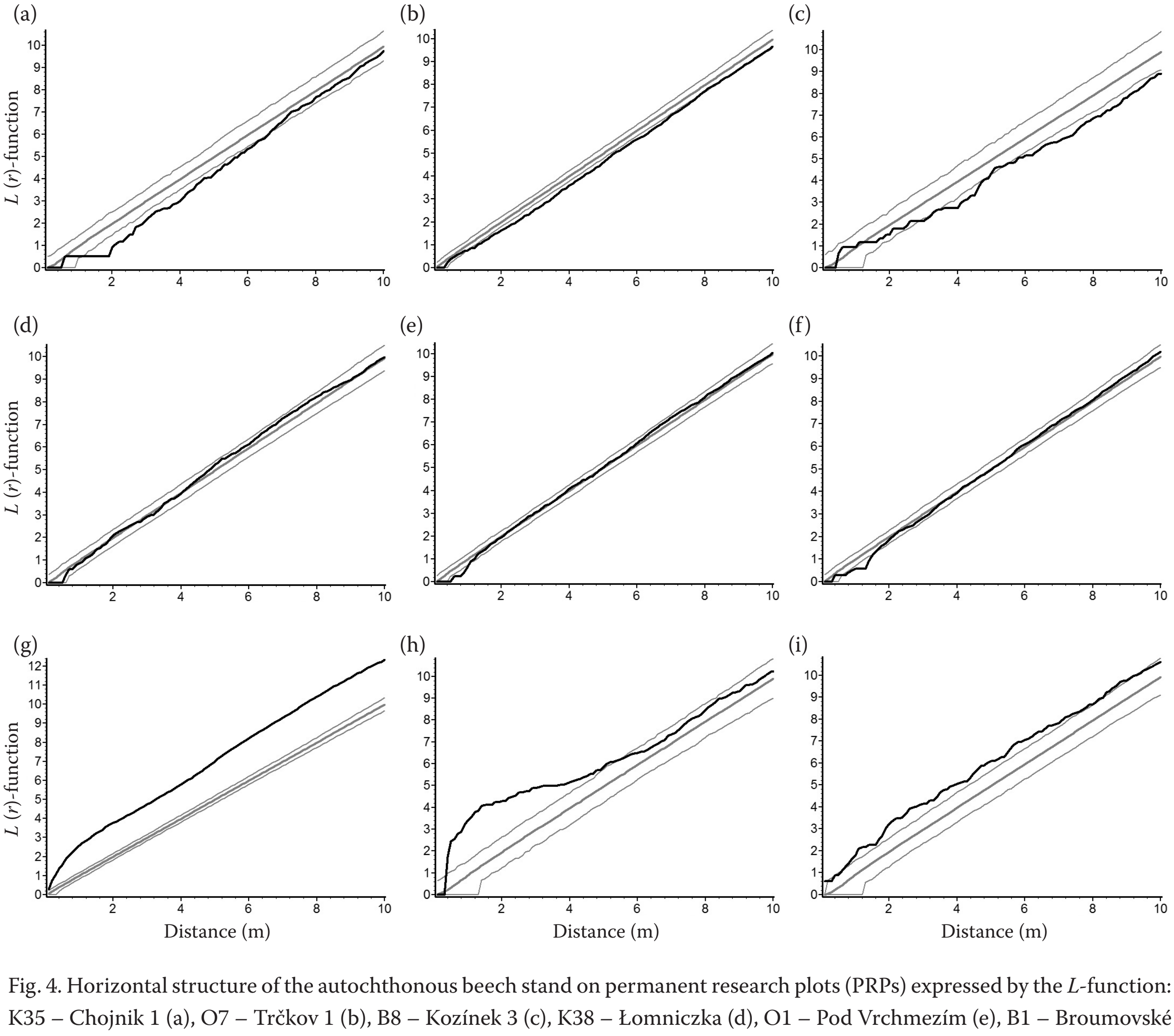

Fig. 4. Horizontal structure of the autochthonous beech stand on permanent research plots (PRPs) expressed by the *L*-function: K35 – Chojnik 1 (a), O7 – Trčkov 1 (b), B8 – Kozínek 3 (c), K38 – Łomniczka (d), O1 – Pod Vrchmezím (e), B1 – Broumovské stěny 1 (f), K60 – Nad Benzínou 4 (g), O2 – Bukačka 1 (h), B5 – Broumovské stěny 5 (i); the black line depicts the *L*-function for real distances of individuals on PRP, the thick grey line shows the middle course for the random spatial pattern of trees and two thinner central curves illustrate the 95% confidence interval; *r* – radius defining limiting distance from the selected point (tree)

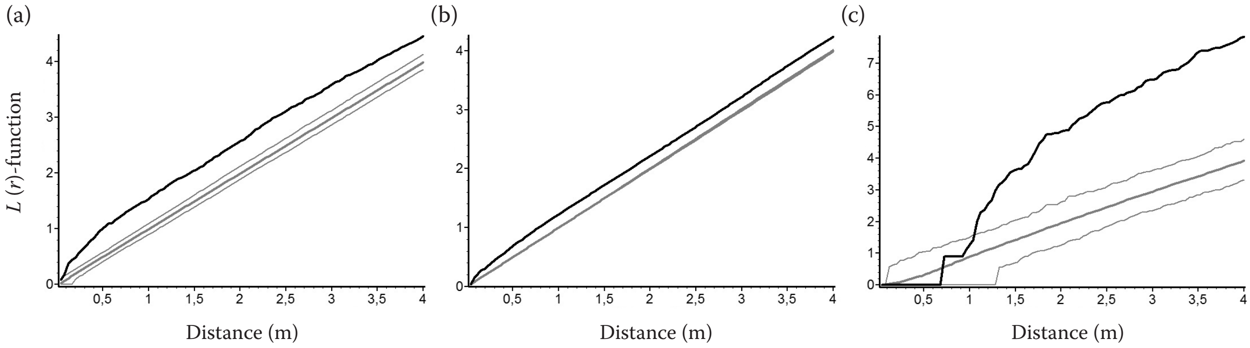

Fig. 5. Horizontal structure of the natural regeneration of autochthonous stands with dominant beech in the Krkonoše Mts National Park on permanent research plots (PRPs) expressed by the *L*-function: K35 – Chojnik 1 (a), K38 – Łomniczka (b), K60 – Nad Benzínou 4 (c); the black line depicts the *L*-function for real distances of individuals on PRP, the thick grey line shows the middle course for the random spatial pattern of trees and two thinner central curves illustrate the 95% confidence interval; *r* – radius defining limiting distance from the selected point (tree)

when the distribution of stems was random. On PRP B1 the *L*-function at a distance of 1–4 m shows the regular spatial pattern of crown centroids. In spite of the values of aggregated structure of trees the distribution of crown centroids on PRP B5 was random.

Absolute displacement between the stem base and the corresponding centroid of measured crown projection area ranged from 0.92 m on PRP O1 to 2.32 m on PRP K60 (max. reached up to 5.5 m). Comparing canopy, the cover of crown projections was significantly higher ($F_{(1,\,16)} = 22.1$, $P < 0.001$) by 10.7 ± 6.4% compared to the canopy simulated by circular crowns. The highest differences were found on PRP K60 (23.8%), followed by PRP B5 (16.9%). The lowest differences were found on PRP K35 (3.1 %), followed by PRP O7 (5.1%). As for the prevailing direction of crown displacement, the slope had a significant effect on crown morphology ($F_{(3,\,32)} = 29.5$, $P < 0.001$). A significantly prevailing direction of crown displacement was downhill 52.7%, other crowns were displaced uphill 7.7%, to the right 23.2% and to the left 16.4% in relation to the slope direction. Only on PRP O2 with the slope 5° a prevailing direction of crown displacement was to the right (45.0%). The crown area varied considerably and ranged from 2.1 to 263.6 $m^2$, the mean crown area was 29.6 ± 6.4 $m^2$. Comparing displacements across crown sizes, there was a significant correlation between the crown size and the relative displacement of crown centroids from the stem base $r = 0.43$ ($P < 0.001$).

### Natural regeneration

According to the computed indices on PRP in the Krkonoše Mts the spatial pattern of natural regeneration on PRP K35 and K38 was aggregated (Table 3). The clumpy distribution of recruits according to their distance is also documented by the *L*-function (Fig. 5). On PRP K60 the indices of horizontal structure of recruits from generative and mostly vegetative regeneration (layered branches) indicated the clearly clumpy distribution (Table 3). The clumpy distribution of layers according to their distance was also evident from *L*-function, at a distance of more than 1 m, at a distance shorter than 1 m the layers within clonal groups were distributed randomly (Fig. 5). Natural regeneration in the Orlické hory Mts PLA was distinctly aggregated on all PRPs (Table 3) and the situation was identical in the Broumovsko PLA (Table 3). Regeneration on PRP B5 was the most highly aggregated from all plots ($A = 0.976^*$, $\alpha = 14.225^*$, $R = 0.469^*$, $ICS = 4.165^*$), whereas according to the *L*-function it was the case of PRP K60.

Results of the cross-type pair correlation function for a multitype point pattern showed a significant negative effect of the parent stand on natural regeneration at a shorter distance on seven PRPs (from stem base to 0.8–4.2 m). Distribution at longer distances across the plots was mostly random (no spatial relationship). Conversely, on PRP O2 the tree layer had a positive effect on beech natural regeneration to a distance of 2.1 m (spatial pattern was aggregated), and/or of 3.8 m on PRP K35 caused by natural layering.

### Dead wood

As for the spatial pattern of stumps on PRP in the Krkonoše Mts, random distribution was dominant (Table 3), with a tendency towards aggregation in thinner trees with DBH < 12 cm. The distribution of stumps on PRP K35 was mostly random with moderate aggregation at a distance within 2 m. In the Orlické hory Mts the structure of stumps was also mostly random (Table 3), only on PRP O2 it was indistinctly aggregated. On PRP O7 the random and aggregated spatial patterns of stumps alternate from a distance of 4 m. On PRP O2 according to the value of *R* index (0.855*) the distribution of stumps was clumpy like in the upper storey. Similarly like in the Krkonoše Mts National Park and Orlické hory Mts PLA, in the Broumovsko PLA the structure of stumps on PRP was mostly random (Table 3).

Coarse woody debris (thick ends of logs) on all PRPs was distributed randomly with a tendency to aggregated structures ($A = 0.585$, $\alpha = 1.379$, $R = 0.948$, $ICS = 0.114$), especially on plots at a high altitude.

### Interactions of stand and site characteristics

Results of the PCA analysis are presented in the form of an ordination diagram in Fig. 6. The first ordination axis explains 59.8% of the variability of data, the first two axes explain together 79.3% and the first four axes explain together 95.4% of the variability of data. The first x-axis represents altitude, temperature and stoniness with average height of trees and volume. The second y-axis represents slope of terrain, average age of the stand and canopy characteristics (crown projection area and crown closure). Stoniness and altitude were positively correlated ($P < 0.05$) with one another and with aggregation indices (or negatively with *R* index), while these parameters were negatively correlated with temperature, DBH, height and volume. Live tree density was positively correlated with altitude and aggregation indices and negatively with DBH, height and temperature. Canopy characteristics were positively correlated with one another and with age, while these parameters were negatively correlated with slope. Average age of the stand was of relatively small importance to explain the data variability. Most of PRPs were very different from one another, with the exception of K38 and B5, which were very similar. Permanent research plots at the highest altitude (K60, O2) have an aggregated spatial pattern of trees, while stands tend to regularity at the lowest elevations (K35, B8).

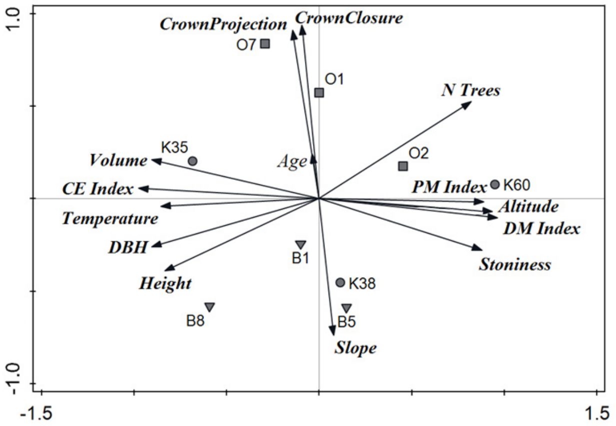

Fig. 6. Ordination diagram showing results of the principal component analysis of relationships between stand characteristics (*N* trees – number of live trees, DBH, height – average height, age, volume, crown closure, crown projection area), stand parameters (altitude, slope, temperature, stoniness) and horizontal indices of tree layer (*HS* (Hopkins-Skellam) index, *CE* (Clark-Evans) index, *PM* (Pielou-Mountford) index, *DM* (David-Moore) index), Broumovsko Hills, Krkonoše Mts, Orlické hory Mts, permanent research plot: B1 – Broumovské stěny 1, B5 – Broumovské stěny 5, B8 – Kozínek 3, K35 – Chojnik 1, K38 – Łomniczka, K60 – Nad Benzínou 4, O1 – Pod Vrchmezím, O2 – Bukačka 1, O7 – Trčkov 1

## DISCUSSION

With respect to stand structural characteristics, on the PRP K60 situated at the highest altitude (1,310 m a.s.l.) the aggregated spatial pattern of the tree layer prevails, which is caused by extreme conditions of the hilltop phenomenon. In these conditions the growth of individuals takes place in compact clonal groups. This trend of a departure from random distribution is enhanced by vegetative propagation as adaptation to extreme conditions of growth (Doležal, Šrůtek 2002; Vacek, Hejcman 2012). A similar trend was observed in the tree layer of acidophilous mountain beech woods in the Orlické hory Mts PLA or in exposed beech woods with extreme edaphic conditions (high skeleton content, steep slope and shallow soil profile) in the Broumovsko PLA. It is to conclude that the aggregation of the canopy trees in forest stands left to spontaneous development is caused by extreme climatic and edaphic conditions (Vacek et al. 2015b).

On permanent research plot K38 situated at a lower altitude in the zone of acidophilous mountain beech woods the random spatial pattern of the tree layer was dominant, which is typical of the majority of forest stands at the advanced stage of optimum and initial stage of disintegration. Similar results were obtained in Orlické hory Mts PLA (PRP O1) and Broumovsko PLA (PRP B1). The very frequent random spatial pattern of forest stands was demonstrated e.g. in the upper storey of near-natural beech fragments in Germany (von Oheimb et al. 2005). In the Boubín Virgin Forest, at the beginning of measurements Šebková et al. (2011) also described a dominant random structure that gradually turned to an aggregated structure. Similar results were reported by Janik et al. (2013), who documented a tendency towards mostly an aggregated structure in mixed stands in the Western Carpathians.

Tree distribution on PRP K35 in a highly productive herb-rich beech stand at the stage of optimum showed a tendency towards a regular spatial pattern like on PRP O7 and B8. The regular spacing that occurs in natural conditions only to a small extent is caused by competition between neighbouring trees. The upper storey on PRP K35 was distributed regularly but the trees in lower layers showed an aggregated spatial pattern. Such a pattern was also observed in beech woods on the Czech side of the Krkonoše Mts (Vacek et al. 2015b), in Slovenia (Rugani et al. 2013) or in other European natural forests with dominant beech (Szwagrzyk, Czerwczak 1993; Commarmot et al. 2005). The tendency towards aggregation in the lower storey is a result of the prosperous growth of natural regeneration in canopy gaps that originated after dead trees (Zeibig et al. 2005; Szwagrzyk, Szewczyk 2008). Transition from markedly aggregated distribution of recruits through random distribution to regular spatial pattern of trees (from DBH > 32.5 cm) was also observed in near-natural forests in France (Wijdeven 2003). However, different mean age of trees (95–175 years) and irregular distribution along the altitudinal gradient of compared plots must be considered when interpreting the present results of spatial pattern.

Similarly like in other studies of beech natural regeneration (Nagel et al. 2006; Vacek et al. 2014b, 2015c; Ambrož et al. 2015) the horizontal structure of regeneration was found to be distinctly aggregated. The amount of natural regeneration is differentiated according to the herb layer cover (Bílek et al. 2014) and topography (Vacek et al. 2015c).

The centroids of beech crowns were distributed significantly more regularly than the tree stems. Crown plasticity decreases intraspecific competition in this way and allows the more effective utilization of growth space, which provides a potential to maintain the high productivity of forest stand (Longuetaud et al. 2008; Schröter et al. 2012). In our study, the displacement between crown centroids and stem base was about 1.5 m, the highest mean distance was observed on PRP K60 close to the timberline (2.3 m). The slope had a significant effect on crown morphology, when the prevailing direction of crown centroid displacement was downhill 52.7%, the opposite direction was uphill 7.7%. The only exception was confirmed on PRP O2 with the negligible slope of terrain (5°). The projected canopy area was on average 10.7% higher compared to the canopy simulated by circular crowns, similarly (about 10%) like in old-growth beech forests in Germany (Schröter et al. 2012).

The spatial pattern of stumps was mostly random. This type of snag distribution was also indicated from beech woods in Germany (von Oheimb et al. 2005) and from fir-beech stands in the Western Carpathians (Janik et al. 2013). The clumpiness of small-diameter stumps can be explained by regeneration in groups and their subsequent self-thinning while the random distribution of large-diameter stumps is a result of the mortality of individual trees caused by reaching physical maturity (Rouvinen, Kouki 2002). According to studies from Sweden (Edman, Jonsson 2001) and Finland (Rouvinen, Kouki 2002) the stumps revealed a different spatial structure – thin stumps showed clumpy distribution and thick stumps random distribution. A similar type of distribution was confirmed on PRP O1, where the aggregated pattern of stumps of DBH < 12 cm was found. This trend can be explained by regeneration of individuals in groups and their subsequent self-thinning while the random spatial pattern of large-diameter stumps is a result of the mortality of individual trees caused by reaching physical maturity (Rouvinen, Kouki 2002).

## CONCLUSIONS

The spatial pattern of tree layer was significantly different in selected beech stands in the Sudetes range system. The study proved the influence of site (climatic and edaphic) conditions on horizontal structure. A tendency towards the clumpy spatial pattern of forest stand was positively influenced by increasing altitude above sea level and extreme conditions of the site (rocky slope with shallow soil profile) as well as by stand density. Similarly, natural regeneration and initial growth phases had an aggregated spatial pattern that turns through random to regular distribution of mature trees on favourable sites. We drew a conclusion that beech crowns have a high ability of plasticity and adaptation to exposed sites and of responding to changes in canopy closure. Because of the great plasticity of beech crowns, crown centroids were more regularly distributed than tree stems.

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