doi: 10.17221/98/2015-JFS

How close to nature is close-to-nature pine silviculture?

L. Bílek, S. Vacek, Z. Vacek, J. Remeš, J. Král, D. Bulušek, J. Gallo

Faculty of Forestry and Wood Sciences, Czech University of Life Sciences Prague, Prague, Czech Republic

ABSTRACT: Structural parameters of Scots pine stands (129–191 years) on their natural sites (270–600 m a.s.l.) are described on 6 permanent research plots (PRP; 3 in managed stands using near-natural silvicultural practices and 3 in stands without active forest management for 3 decades at least) in areas of western, central and eastern Bohemia and in the Polish part of the Krkonoše Mts. In the framework of the study structural and growth parameters, horizontal and vertical structure and biodiversity were evaluated on the plots. A comparison of the plots, and of managed and unmanaged plots showed a relatively high variability in different parameters. Nevertheless, the results document that managed stands, compared to forest stands without management, mostly have significantly higher standing volumes (1.5 times in total and 1.7 times in pine), which is caused by more extreme sites. An opposite trend was found out in dead wood volume, which is distinctly higher in unmanaged stands. Differences in the other parameters are not so pronounced, probably because small-scale management is used and because a relatively short time since the stands were left to spontaneous development has elapsed (30–52 years).

Keywords: stand structure; Scots pine; natural pinewoods; managed forests; unmanaged forests

Differences in the structure of woody plant populations may be caused by a number of factors like distinctions in stand conditions (age, area, competitive position, growth rate, genetic properties) and site conditions (soil and climate) (Weiner 1985). They may also result from the heterogeneity of other environmental factors, effects of herbivores or pathogens and occurrence of various disturbances (Oliver, Larson 1990; Weiner 1990; Ambrož et al. 2015). Accordingly, it is possible to quantify the stand structure by a number of attributes including tree density, vertical distribution of crowns, canopy closure, basal area, horizontal distribution of trees, dead wood volume or inclusion of individuals in the respective tree classes (Silver et al. 2013). Differences in structure often reflect the course of disturbances in the past, similarly like particular properties of woody plant species (Vanderwel et al. 2006; D'Amato et al. 2008) while the method and objective of their management are of crucial importance (Kaufmann et al. 2000; Crow et al. 2002; Rouvinen, Kuuluvainen 2005; Bílek et al. 2011; Vacek et al. 2014).

In commercial forests ecological management is generally considered as a tool of homogenization of their stand structure (Uotila et al. 2001, 2002). In this context, a number of studies have been published (Stephenson 1999; Spies 2004) in which, for fear of biodiversity decrease in commercial forests, such management strategies were investigated that would lead to a reduction of differences between commercial forests and natural or near-natural forests, whereas these strategies should ensure higher structural differentiation of commercial forests at the same time (Silver et al. 2013).

For an expansion of silvicultural practices that are inspired by natural variability of forests it is necessary to know structural parameters of particular tree species in near-natural forests (Burrascano et al. 2011). Attention has been focused mainly on climax tree species while rather limited attention has been paid to Scots pine. Exceptions are only pine stands in boreal and Mediterranean areas (cf. Rouvinen, Kuuluvainen 2005; Montes et al. 2005, 2008). The objective of the present paper was

Supported by the Ministry of Agriculture of the Czech Republic, Project No. QJ1520037, and by the Czech University of Life Sciences Prague, Project IGA No. B08/12

to evaluate the structure of managed (PRP 1–3) and unmanaged (PRP 4–6) stands with natural dominance of Scots pine in the conditions of Central Europe. The selection of plots was done deliberately so that it would characterize small-scale silvicultural practices that are rather exceptional in the pine as a light-demanding tree species. The basic hypothesis was that the stands managed in this way have a similar structural variability like stands without active forest management.

MATERIAL AND METHODS

Description of the study sites. The study was conducted at sites with the natural occurrence of Scots pine (*Pinus sylvestris* L.) on six permanent research plots (PRP; 3 managed stands and 3 unmanaged stand for 3 decades at least) in the area of western, central and eastern Bohemia and in the Polish part of the Krkonoše Mts. (Karkonosze). PRPs were mostly 50 × 50 m in size (0.25 ha) but PRP 1 was 25 × 50 m (0.125 ha) and PRP 6 was 40 × 60 m (0.24 ha). The main characteristics of managed stands are use of natural regeneration under the shelter of parent stand, long regeneration and rotation period, free felling policy with the objective to create complex forest structure and rejection of large and abrupt cover release. Cutting frequency is from 5 to 10 years. Measurements were performed in 2014 and 2015 before planned cuttings. Fig. 1 shows the localization of PRPs and Table 1 documents the basic data on PRP.

Data collection. To determine the tree layer structure of woody plants of forest ecosystems the Field-Map technology (IFER-Monitoring and Mapping Solutions Ltd., Strašice, Czech Republic) was used. During particular measurements the position of all

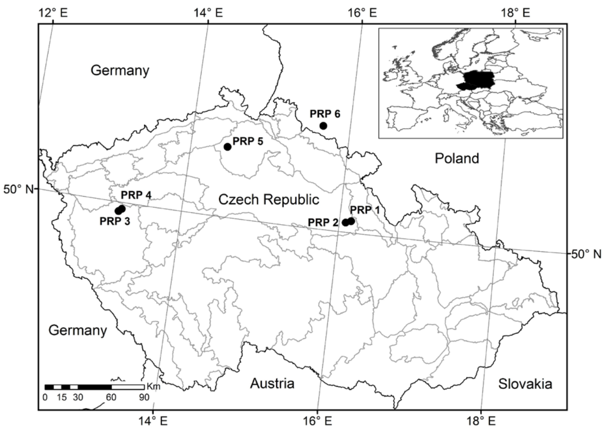

Fig. 1. Localization of PRP 1–6

tree layer individuals of breast height diameter above 8 cm was localized. Tree heights, heights of the live crown base and crown perimeter were measured, at least at 4 directions perpendicular to each other. Breast height diameters were measured with a metal calliper to the nearest 1 mm. Heights and heights of the live crown base were recorded with a laser Vertex hypsometer to the nearest 0.1 m.

Data analysis. In all individuals of the tree layer structural and growth parameters, quantity and quality of production, horizontal and vertical structure and biodiversity were evaluated on particular plots. Tree volume was calculated using the volume equations published by Petráš and Pajtík (1991).

To determine the spatial distribution Hopkins-Skellam index (Hopkins, Skellam 1954), Pielou-Mountford index (Pielou 1959; Mountford 1961), Clark-Evans index (Clark, Evans 1954) and Ripley's *L*-function (Ripley 1981) were computed. The David-Moore index (David, Moore 1954) was used as a distribution index based on tree frequency in the particular quadrats. The size of

Table 1. An overview of basic characteristics of forest stands included in the study (stand structural data from forest management plans)

Stand ID	Plot name	Coordinates (WGS84)	Age (yr)	Height (m)	DBH (cm)	Volume ($m^3 \cdot ha^{-1}$)	Altitude (m)	Exposure	Slope gradient (°)	Forest site type*
1	Vysoké Chvojno 1	50.0551672N 16.1497353E	132	23	33	278	270	–	0	2I7
2	Vysoké Chvojno 2	50.0886833N 16.0471461E	129	25	32	357	300	–	0	2M2
3	Plasy manag.	49.9055694N 13.2062422E	145	20	32	162	600	E	5	0Q5
4	Plasy non-manag.	49.9099036N 13.1998936E	142	17	27	211	590	–	0	0Q5
5	Kostelecké bory	50.5697825N 14.4599611E	190	14	25	180	430	SW	4	0Z3
6	Chojník bory	50.8374794N 15.6412489E	191	19	42	179	470	NE	22	0Z0

*according to Viewegh et al. (2003)

quadrats on PRP was 10 × 10 m. The PointPro 2.1 (Zahradník, Puš, Prague, Czech Republic) was used to calculate these characteristics describing the horizontal structure of individuals across the plot. The test of significance of the deviations from the values expected for random distribution of points was done using Monte Carlo simulations. The mean values of *L*-function were estimated as arithmetical means from *L*-functions calculated for 1999 randomly generated point structures. The respective expected values of these indices were computed by means of numerical simulations for each particular case separately. In results statistically significant values (exceeding the confidence interval) are designated by asterisk. Structural characteristics were computed using the Sibyla growth simulator (Fabrika, Ďurský 2005).

In graphical outputs the black line represents the *L*-function for actual distances of individuals on PRP, the thick blue line shows the mean curve of random spatial distribution of trees and two thinner central curves document the 95% reliability interval. When the black line of tree distribution on PRP is below this interval, it indicates the tendency of regular distribution of individuals, and if it is above this interval, it shows the tendency of aggregated spatial pattern. Stand density, biological canopy (the sum of all crown projection areas/total area of PRP) and mensurational canopy (the horizontal area covered by crowns/total area of PRP) were derived during the study of horizontal structure on PRP. Situational maps were created in the ArcGIS (ESRI, Redmont, USA).

In the framework of biodiversity evaluation these indices were computed: diameter differentiation index (TM_d), height differentiation index (TM_h, values of indices 0–1) (Füldner 1995), species diversity index (Shannon 1948), species evenness index (Pielou 1975), Arten-profil index (*A*, values of indices 0–1) (Pretsch 2006) and total diversity index ($B < 4$ – monotonous structure and $B \geq 9$ – highly structured stands) (Jaehne, Dohrenbusch 1997). Index *D* (*Mi*) and index *G* (*Gi*) (Gini 1921; Sterba 2008) were also calculated.

Unconstrained principal component analysis (PCA) in Canoco for Windows 4.5 (ter Braak, Šmilauer 2002) was used to analyse the relationships between volumes of living trees, mean diameter at breast height, mean height, living tree density, crown projection area, and structural diversity indices in order to reveal similarity of all records. Data were log-transformed, centred and standardized before the analysis. The results of the PCA analysis were visualized in the form of an ordination diagram constructed by CanoDraw.

RESULTS

Tree layer structure

Table 2 shows the basic stand characteristics. The numbers of living trees (DBH ≥ 8 cm) in the tree layer are between 556 and 1,248 trees·ha^{-1}

Table 2. An overview of basic stand characteristics of tree layer on PRPs

PRP	Age	QMD ± SD (cm)	h (m)	h_{95} (m)	f	v (m^3)	*N* (indd·ha^{-1})	BA (m^2·ha^{-1})	V (m^3·ha^{-1})	h/DBH	CC (%)	CPA (ha)	SDI
Pinus sylvestris													
1	132	23.7 ± 12.1	16.3	25.0	0.592	0.425	1,072	47.0	456	68.7	78.0	0.99	0.92
2	129	29.8 ± 9.7	18.7	23.0	0.499	0.649	476	33.2	309	62.6	55.4	0.60	0.64
3	145	24.9 ± 11.3	15.8	22.0	0.566	0.434	552	26.8	240	63.3	65.2	1.06	0.55
4	142	27.2 ± 7.8	17.8	22.0	0.483	0.501	488	28.3	245	65.6	68.6	1.16	0.56
5	190	23.0 ± 11.3	12.1	19.1	0.593	0.298	592	24.6	177	52.6	78.6	0.89	0.52
6	191	35.1 ± 15.3	14.7	22.1	0.562	0.797	200	19.3	159	41.8	34.5	0.36	0.35
All trees													
1	132	22.8 ± 11.7	15.8	24.2	0.597	0.384	1,248	50.9	480	69.3	82.2	1.22	0.98
2	129	27.6 ± 10.7	17.3	23.0	0.525	0.544	588	35.1	320	62.8	66.6	1.32	0.68
3	145	24.8 ± 11.3	15.7	22.0	0.569	0.430	556	26.9	240	63.3	65.3	1.06	0.55
4	142	25.3 ± 8.8	16.7	21.9	0.502	0.420	620	31.1	260	65.8	76.3	1.44	0.62
5	190	22.9 ± 11.1	12.1	19.1	0.580	0.289	624	25.8	181	52.8	80.4	0.94	0.55
6	191	24.4 ± 12.6	12.7	20.9	0.572	0.340	712	33.1	242	52.0	82.6	1.00	0.64

Age – average stand age, QMD – mean quadratic breast height diameter, SD – standard deviation, h – mean height, h_{95} – top 95% height, f – form factor, v – average tree volume, *N* – number of trees, BA – basal area, V – stand volume, h/DBH – slenderness quotient, CC – canopy closure, CPA – crown projection area, SDI – stand density index

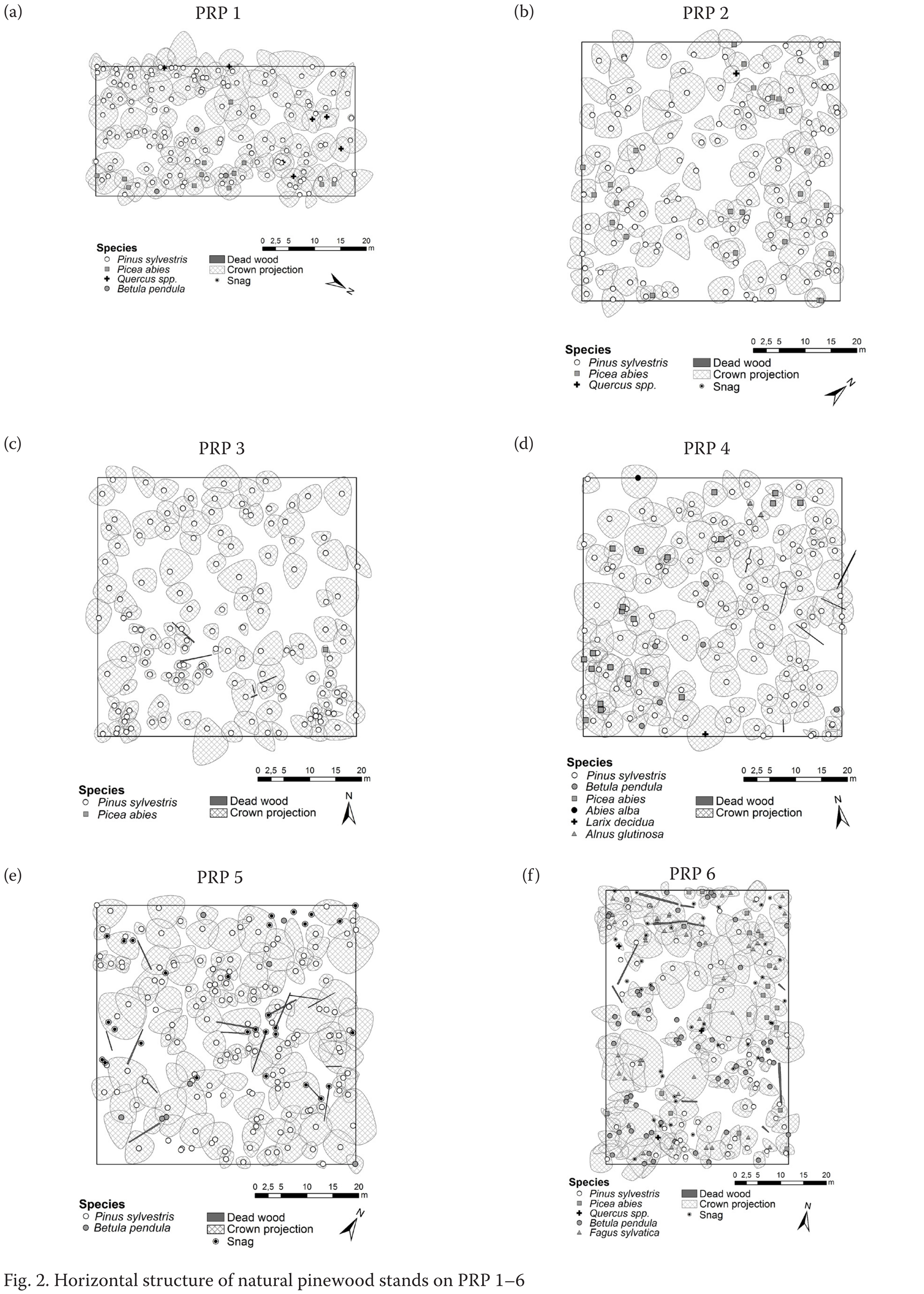

Fig. 2. Horizontal structure of natural pinewood stands on PRP 1–6

and in Scots pine they are between 200 and 1,072 trees·ha^{-1}. The relative stand density (SDI) is consistent with these numbers, which is between 0.55 and 0.98 in the tree layer and in pine it is between 0.35 and 0.92. The average basal area is very different in the particular PRPs due to their site

Table 3. Indices describing the horizontal structure of tree layer on PRPs

Index	PRP					
	1	2	3	4	5	6
All trees						
Hopkins-Skellam	0.447	0.441	0.380*	0.439	0.509	0.506
Pielou-Mountford	0.987	0.901	0.886	1.061	1.117	1.101
Clark-Evans	1.144	1.099	1.229*	1.170	1.040	1.031
David-Moore	0.125	–0.013	–0.008	–0.252	0.053	0.065
Trees DBH < 20 cm						
Hopkins-Skellam	0.447	0.637	0.858*	0.545	0.602*	0.578*
Pielou-Mountford	0.987	1.928*	5.104*	1.502	1.643*	1.325
Clark-Evans	1.144	0.964	0.794*	1.020	0.980	0.919*
David-Moore	0.125	0.232	1.163*	0.116	0.529*	0.527*
Trees DBH ≥ 20 cm						
Hopkins-Skellam	0.409	0.374*	0.390	0.414	0.519	0.378*
Pielou-Mountford	0.917	0.836*	0.974	0.929	1.007	0.903
Clark-Evans	1.217	1.238*	1.299*	1.216*	0.938	1.273*
David-Moore	–0.206	–0.202*	–0.355*	–0.333*	0.118	–0.266*

*statistically significant at $\alpha = 0.05$

conditions and in all tree woody species it ranges from 25.8 to 50.9 $m^2 \cdot ha^{-1}$ and in pine it is 19.3 to 47.0 $m^2 \cdot ha^{-1}$. There are also great differences in standing volumes on the particular plots. As for all woody plants on PRPs they range from 181 to 480 $m^3 \cdot ha^{-1}$ and in pine this range is from 159 to 456 $m^3 \cdot ha^{-1}$. Compared to managed forests, standing volumes in unmanaged forest stands are mostly considerably lower (1.5 times in total and 1.7 times in pine).

Fig. 2. illustrates the layout of the horizontal structure of tree layer on PRPs 1–6, where fallen stems are also seen when their amount is markedly higher in unmanaged forests. Table 3 shows the horizontal structure of tree layer by means of structural indices. According to the computed structural indices, regular distribution is dominant in all individuals of the tree layer in managed stands (PRPs 1–3). Only the David-Moore index shows aggregated distribution on PRP 1 and random one on PRP 3. According to the studied indices the aggregated distribution of individuals with breast height diameter within 20 cm is dominant on these plots, only on PRP 1 the distribution is regular according

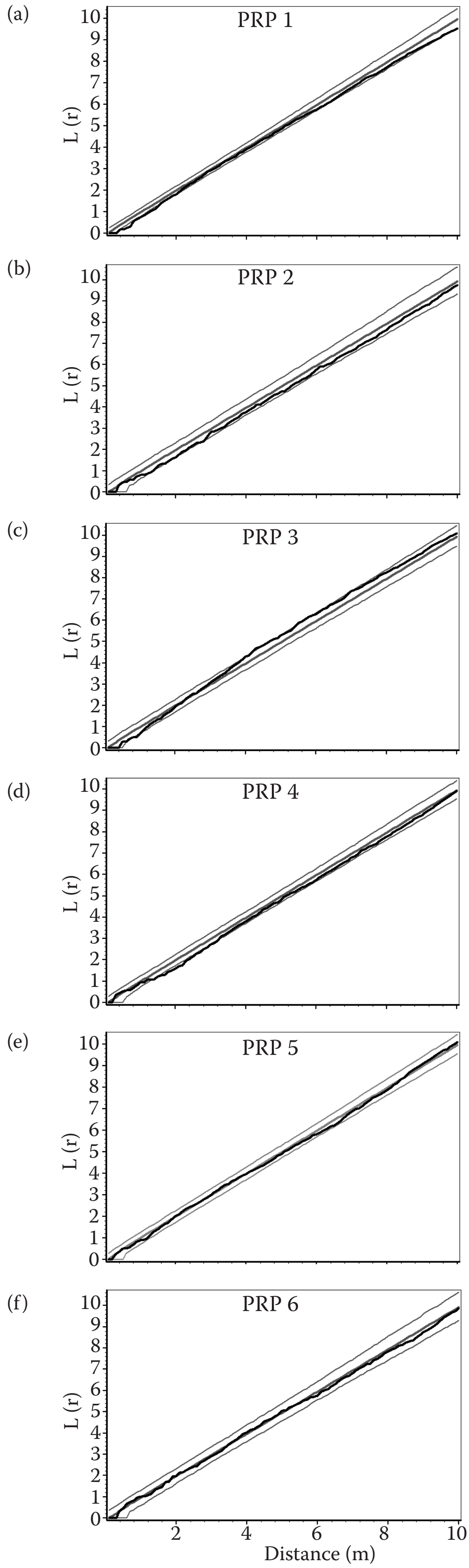

Fig. 3. Horizontal structure of tree layer on PRP expressed by the *L*-function, explanatory notes in Data analysis

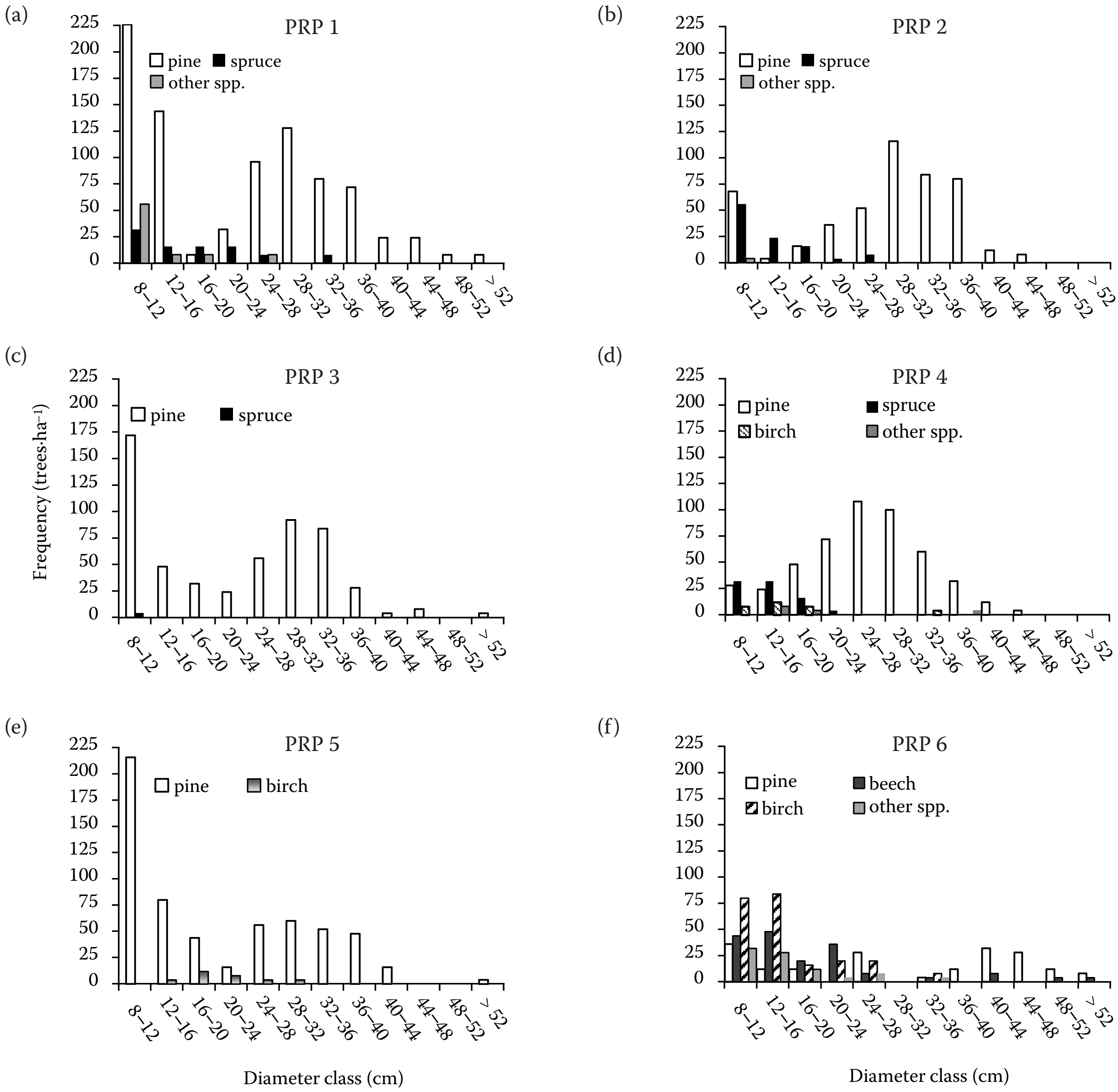

Fig. 4. Histogram of diameter classes on PRP differentiated by main tree species

to all indices with the exception of David-Moore index. In individuals with breast height diameter larger than 20 cm the distribution is regular in all cases.

In unmanaged stands (PRPs 4–6) the aggregated distribution of trees across the plots generally prevails in all individuals of tree layer. The evaluation by Clark-Evans index is an exception on all plots because the distribution is regular, similarly like on PRP 1 by Hopkins-Skellam index and David Moore index. In individuals with breast height diameter within 20 cm aggregated distribution is dominant on these plots according to the studied indices, only on PRP 4 the distribution is regular according to Clark-Evans index. In individuals from 20 cm of breast height diameter the distribution is regular on PRP 4 and 6 and mostly aggregated on PRP 5, only according to Pielou-Mountford index the distribution is random.

The horizontal structure of woody plants of tree layer on PRPs 1–6 is mostly random according to the *L*-function (Fig. 3). Only on PRP 1 it is regular within 1.8 m, on PRP 2 it is regular in the range of 1–2.5 m and on PRP 3 between 1.5 and 3.5 m. PRP 3 is also an exception where trees with the spacing of 4–6 m show a tendency of moderate aggregation.

Figs 4 and 5 illustrate diameter frequencies of tree layer and the relation of breast height diameter to tree height on PRP. The distribution of diameter classes indicates differences between particular PRP, especially with regard to their regeneration potential, which is very pronounced on PRPs 1, 3 and 5 as a result of the high representation of individuals in the first two diameter classes, which causes an atypical distribution of diameter classes for pine stands. The succession of the growing-

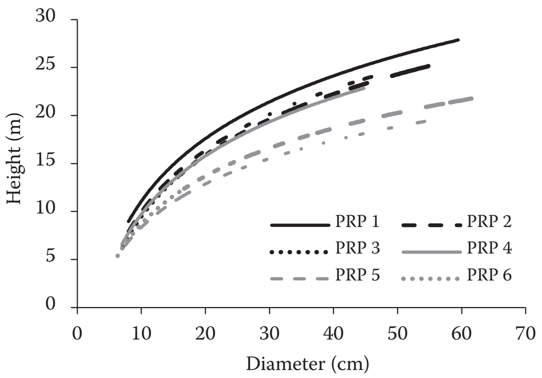

Fig. 5. The relationship between breast height diameter and tree height on PRP 1–6

up stage individuals is evident on PRPs 2, 4 and 6. There is a specific situation on PRP 6, where the mortality of the youngest individuals is very high due to very extreme site conditions of relict pinewoods. Unlike the other PRPs, regeneration on this plot is not cyclical while it is more or less continuous but very sporadic.

The relation of breast height diameter and tree height on PRP suggests differences between stands on natural pinewood sites (PRPs 1–4) and in relict pinewoods (PRPs 5 and 6).

Tree layer biodiversity

Table 4 documents the indices describing tree layer diversity on PRPs 1–6. Species richness of the tree layer evaluated by *D*(*Mi*) index is low on PRP 3 and 5, intermediate on PRP 1 and 2, high on PRP 6 and very high on PRP 4. Species diversity of the tree layer according to entropy *H´*(*Si*) is minimum on PRP 3, low on PRPs 1, 2, 4 and 5 and intermediate on PRP 6. Species evenness of the tree layer according to *E* (*Pii*) index is minimum on PRP 3, low on PRPs 1, 2, 4 and 5 and high on PRP 6. Vertical structure is relatively variable as it is moderately differentiated on PRPs 1–4, strongly differentiated on PRP 5 and very strongly differentiated on PRP 6. According to the diameter differentiation index TM_d (*Fi*) differentiation is small on PRP 3 and moderate on the other plots; according to the height differentiation index TM_h (*Fi*) small differentiation is on PRPs 2–6 and moderate differentiation on PRP 1. With regard to complex diversity *B* (*J&Di*) even structure is on PRP 3, uneven structure is on PRPs 1, 2, 4 and 5 and differentiated structure on PRP 6. High values of index *G* (*Gi*) typical of stands with the negatively exponential distribution of diameter classes were found out on PRPs 1, 3, 5 and 6 and lower values typical of stands with normal distribution were observed on PRP 2 and 4.

Table 4. Indices describing the diversity of tree layer on PRPs

PRP	*D* (*Mi*)	*H´* (*Si*)	*E* (*Pii*)	*A* (*Pri*)	TM_d (*Fi*)	TM_h (*Fi*)	*B* (*J&Di*)	*G* (*Gi*)
1	0.421	0.142	0.236	0.400	0.432	0.337	6.403	0.560
2	0.314	0.091	0.191	0.389	0.387	0.298	6.481	0.390
3	0.158	0.005	0.017	0.386	0.275	0.208	5.576	0.474
4	0.778	0.184	0.236	0.375	0.324	0.225	7.121	0.372
5	0.155	0.081	0.272	0.578	0.314	0.259	6.348	0.526
6	0.609	0.481	0.688	0.756	0.355	0.294	8.241	0.662

D – index of species richness, *H´* – index of species heterogeneity, *E* – index of species evenness, *A* – Arten-profil index, TM_d – diameter differentiation index, TM_h – height differentiation index, *B* – total diversity index, *G* – Gini index

Result of PCA analysis

The first ordination axis explained 47.2% of data variability, the first two axes in total explained 72.8% and the first four axes in total explained 95.4% of data variability (Fig. 6). The first y-axis represented number of trees and stand volume by diameter differentiation index and height differentiation index. The second x-axis represented DBH and precipitation by Arten-profil index, both aggregation indices and Gini index. Mean height of trees was positively correlated with temperature, crown projection and DBH, while these parameters were negatively correlated with altitude. Number of trees was positively correlated with diameter differentiation index, height differentiation index and species richness index. Stand volume was negatively correlated with altitude. Precipitation, species evenness index, species diversity index, Gini index, Pielou-Mountford aggregation index and total diversity index were positively correlated with one another, while these parameters were negatively correlated with DBH and Clark-Evans aggregation index. Diameter (DBH) and species richness index were of relatively small importance to explain the data variability. PRPs were very different from one another, but managed plots occupied the left upper part of the diagram typical of higher stand volume, while higher aggregation and partially higher structural diversity (vertical and tree species) were characteristic of unmanaged stands. On the other hand, some structural characteristics of the studied managed plots are very similar to those of stands without active management.

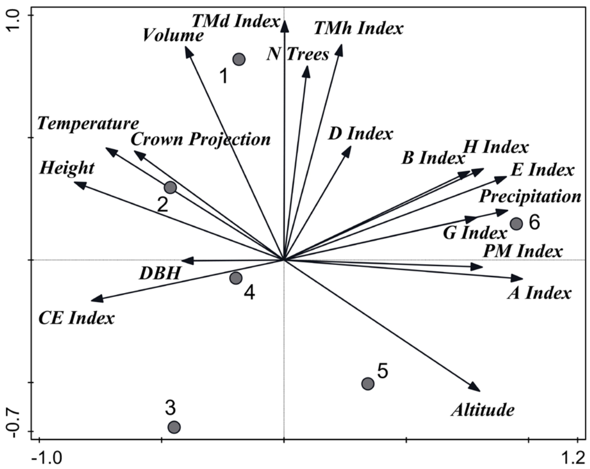

Fig. 6. Ordination diagram showing the results of PCA analysis of relationships between living tree characteristics (*N trees*, *DBH*, *Height*, *Volume* and *Canopy*), stand parameters (*Altitude*, *Temperature*, *Precipitation*) and structural indices (*D index*, *E index*, *H index*, *CE index*, *PM index*, *A index*, *TMd index*, *TMh index*, *G index*, *B index*)

N trees – number of living trees per hectare, *DBH* – quadratic diameter at breast height, *Height* – mean height, *Volume* and *Canopy* – crown projection area, *D index* – species richness index, *E index* – species evenness index, *H index* – species diversity index, *CE index* – Clark-Evans aggregation index, *PM index* – Pielou-Mountford index of non-randomness, *A index* – Arten-profil index, *TMd index* – diameter differentiation index, *TMh index* – height differentiation index, *G index* – Gini index, *B index* – total diversity index; codes indicate each record of data; code abbreviations: ● number – identification of permanent research plot

DISCUSSION

Our study was focused on a comparison of pine stands without active forest management and intensively managed stands using near-natural silvicultural practices. Related to this topic, more information is available from the area of southern and northern Europe (Angelstam, Kuuluvainen 2004; Montes et al. 2005; Poyatos et al. 2013; Martín-Alcón et al. 2015), but in conditions of central Europe researchers paid attention mainly to stands being composed of shade-tolerant species such as spruce, beech and fir.

Our study did not reveal any larger differences in the density of commercial stands and stands without management. This trend is also evident from a comparison of diameter frequencies in particular diameter classes when there are no distinct differences between managed and unmanaged plots. Nevertheless, the distribution of breast height diameters in the stand is similar like in other papers where unimodal, multimodal, decreasing or irregular distribution is usually reported (Maltamo et al. 2000). It is to note that the unimodal distribution of breast height diameters occurs e.g. after the total bark beetle disturbance of parent stand with relatively fast natural regeneration, while after a smaller disturbance a part of trees remains in the stand, which increases its structural variability (Franklin et al. 2002). In this case, in relation to subsequent diversification of regeneration, multimodal, decreasing or irregular distribution of breast height diameters occurs (Lampainen et al. 2004).

Based on the evaluation of results describing the horizontal structure of tree layer it is to state that a regular distribution of trees is dominant in general in the studied managed forests while unmanaged stands show an aggregated tree distribution. In both variants of management trees with DBH ≤ 20 cm tend to aggregation. Such a trend was also documented by Larson et al. (2012) or Lydersen et al. (2013). Tuten et al. (2015) also found out a high degree of aggregated distribution of trees in a pine stand, especially within a distance of 10 m. Sánchez et al. (2011) documented statistically significant aggregated distribution to a distance smaller than 40 m with the peak of aggregation at a distance of 6–8 m. In studied Scots pine stands aggregated structures of younger trees may indicate inclination to gap regeneration dynamics related to autogenic disturbances (mortality and self-thinning) or cohort dynamics related to partial disturbances (Angelstam, Kuuluvainen 2004). In natural pine stands partial and low-intensity disturbances are mainly caused by fire or windthrow. In managed forests these disturbance regimes are replaced by final harvest, which creates the opportunity for establishment of new tree cohorts. The size and texture then depend on the spatial pattern and intensity of silvicultural treatment. In general, for the regeneration of light-demanding tree species more intense treatment is required.

Biodiversity plays a crucial role in all ecosystem components (Mace et al. 2012), and in recent decades efforts aimed at its increase or maintenance have become a new objective of forest managers (Millar et al. 2007; Bauhus et al. 2009; Fraver, Palik 2012). An important influence of stand structure on the formation of ecosystem processes and biological diversity was well documented by Spies (1998).

The evaluation of tree layer biodiversity on the basis of selected structural indices shows relatively distinct differences within the studied plots. These results are generally consistent with Gao et al. (2014), who demonstrated that mature stands with multilayer structure usually have higher species diversity, especially in mixed conifer-broadleaved forests with disturbed canopy. Barbier et al. (2008) or Chávez and MacDonald (2012) considered combined effects of several factors such as age, canopy density and species composition to be determinant for species diversity. According to Smith et al. (2008) and Coote et al. (2013) a change in species composition is closely related to differences in light conditions, developmental stages and tree species composition of the stand. Last but not least, stand biodiversity is significantly influenced by forest management (Zobel et al. 1993). Lust et al. (1998) stated that in old pine stands some tree species may grow as spontaneous intermediate trees which subsequently contribute to more complex structure and higher biological diversity. Similar results were published by MacLachlan et al. (2000) or Liira et al. (2007), who described lower heterogeneity, density or lower complexity of structural attributes from stands with strong anthropogenic impacts. In some cases, development and especially the spontaneous growth of intermediate trees of autochthonous species in pine stands may be disturbed by undesirable expansion of allochthonous species (Maddelein et al. 1990).

Peterken (1981) specified measures that help increase the total diversity of forest ecosystems. They involve a long conversion period, longer rotation period, use of autochthonous species, support of natural regeneration or specific measures for the protection of heterogeneous microsites. Lindenmayer and Franklin (2002) considered a longer rotation period as an especially important principle because it subsequently allows the higher complexity of structural parameters and larger similarity to natural forests (Silver et al. 2013).

CONCLUSIONS

Where required, close-to-nature silviculture is a viable model for creating more complex forest structure in stands naturally dominated by Scots pine. The use of natural regeneration under the shelter of parent stand, longer regeneration and rotation period than usual, and rejection of large and abrupt cover release have led to forest structures that are relatively similar to stands without active forest management for 30–52 years. Nevertheless, for the continuous viable regeneration of managed pine stands, constantly lower canopy density is a necessity. For a better understanding of the growth and productivity of such stands, a longer research period is needed.

References

Ambrož R., Vacek S., Vacek Z., Král J., Štefančík I. (2015): Structure, growth parameters and regeneration in relation to model development of beech forests with different game management in the Lány Game Enclosure. Lesnícký časopis – Forestry Journal, 61: 78–88.

Angelstam P., Kuuluvainen T. (2004): Boreal forest disturbance regimes, successional dynamics and landscape structures – a European perspective. Ecological Bulletins, 51: 117–136.

Barbier S., Gosselin F., Balandier P. (2008): Influence of tree species on understory vegetation diversity and mechanisms involved – a critical review for temperate and boreal forests. Forest Ecology and Management, 254: 1–15.

Bauhus J., Puettmann K., Messier C. (2009): Silviculture for old-growth attributes. Forest Ecology and Management, 258: 525–537.

Bílek L., Remeš J., Zahradník D. (2011): Managed *vs.* unmanaged. Structure of beech forest stands (*Fagus sylvatica* L.) after 50 years of development, Central Bohemia. Forest Systems, 20: 122–138.

Burrascano S., Sabatini F.M., Blasi C. (2011): Testing indicators of sustainable forest management on understorey composition and diversity in southern Italy through variation partitioning. Plant Ecology, 212: 829–841.

Clark P.J., Evans F.C. (1954): Distance to nearest neighbour as a measure of spatial relationship in populations. Ecology, 35: 445–453.

Coote L., Dietzsch A.C., Wilson M.W., Graham C.T., Fuller L., Walsh A.T., Irwin S., Kelly D.L., Mitchell F.J.G., Kelly T.C., O'Halloran J. (2013): Testing indicators of biodiversity for plantation forests. Ecological Indicators, 32: 107–115.

Crow T.R., Buckley D.S., Nauertz, E.A., Zasada, J.C. (2002): Effects of management on the composition and structure of northern hardwood forests in Upper Michigan. Forest Science, 48: 129–145.

D'Amato A.W., Orwig D.A., Foster D.R. (2008): The influence of successional processes and disturbance on the structure of *Tsuga canadensis* forests. Ecological Applications, 18: 1182–1199.

David F.N., Moore P.G. (1954): Notes on contagious distributions in plant populations. Annals of Botany, 18: 47–53.

Fabrika M., Ďurský J. (2005): Stromové růstové simulátory. Zvolen, EFRA: 112.

Franklin J.F., Spies T.A., Pelt R.V., Carey A.B., Thornburgh D.A., Berg D.R., Lindenmayer D.B., Harmon M.E., Keeton W.S., Shaw D.C., Bible K., Chen J. (2002): Disturbances and structural development of natural forest ecosystems with structural implications, using Douglas-fir forests as an example. Forest Ecology and Management, 155: 399–423.

Fraver S., Palik B.J. (2012): Stand and cohort structures of old-growth *Pinus resinosa*-dominated forests of northern Minnesota, USA. Journal of Vegetation Science, 23: 249–259.

Fuller R.J., Gill R.M.A. (2001): Ecological impacts of increasing numbers of deer in British woodland. Forestry, 74: 193–199.

Gao T., Hedblom M., Emilsson T., Nielsen A.B. (2014): The role of forest stand structure as biodiversity indicator. Forest Ecology and Management, 330: 82–93.

Gini C. (1921): Measurement of inequality on income. The Economic Journal, 31: 22–43.

Hopkins B., Skellam J.G. (1954): A new method for determining the type of distribution of plant individuals. Annals of Botany, 18: 213–227.

Chávez V., MacDonald S.E. (2012): Partitioning vascular understory diversity in mixed wood boreal forests: the importance of mixed canopies for diversity conservation. Forest Ecology and Management, 271: 19–26.

Jaehne S.C., Dohrenbusch A. (1997): Ein Verfahren zur Beurteilung der Bestandesdiversität. Forstwissenschaftliches Centralblatt, 116: 333–345.

Kaufmann M.R., Regan C.M., Brown P.M. (2000): Heterogeneity in ponderosa pine/Douglas-fir forests: age and size structure in unlogged and logged landscapes of central Colorado. Canadian Journal of Forest Research, 30: 698–711.

Lampainen J., Kuuluvainen T., Wallenius T.H., Karjalainen L., Vanha-Majamaa I. (2004): Long-term forest structure and regeneration after wild fire in Russian Karelia. Journal of Vegetation Science, 15: 245–256.

Larson A.J., Keyes C.R., Stover K.C. (2012): Effects of restoration thinning on spatial heterogeneity in mixed-conifer forest. Canadian Journal of Forest Research, 42: 1505–1517.

Liira J., Sepp T., Parrest O. (2007): The forest structure and ecosystem quality in conditions of anthropogenic disturbance along productivity gradient. Forest Ecology and Management, 250: 34–46.

Lust N., Muys B., Nachtergale L. (1998): Increase of biodiversity in homogeneous Scots pine stands by an ecologically diversified management. Biodiversity and Conservation, 7: 249–260.

Lydersen J.M., North M.P., Knapp E.E., Collins B.M. (2013): Quantifying spatial patterns of tree groups and gaps in mixed-conifer forests: reference conditions and long-term changes following fire suppression and logging. Forest Ecology and Management, 304: 340–382.

Mace G.M., Norris K., Fitter A.H. (2012): Biodiversity and ecosystem services: a multilayered relationship. Trends in Ecology & Evolution, 27: 19–26.

Maddelein D., Lust N., Meyen S., Muys B. (1990): Dynamics in maturing Scots pine monocultures in North-East Belgium. Silva Gandavensis, 55: 69–80.

Maltamo M., Kangas A., Uuttera J., Torniainen T., Saramäki J. (2000): Comparison of percentile based prediction methods and the Weibull distribution in describing the diameter distribution of heterogeneous Scots pine stands. Forest Ecology and Management, 133: 263–274.

Maltamo M., Kangas A., Uuttera J., Torniainen T., Saramäki J. (2000): Comparison of percentile based prediction methods and the Weibull distribution in describing the diameter distribution of heterogeneous Scots pine stands. Forest Ecology and Management, 133: 263–274.

Martín-Alcón S., Coll L., Salekin S. (2015): Stand-level drivers of tree-species diversification in Mediterranean pine forests after abandonment of traditional practices. Forest Ecology and Management, 353: 107–117.

McLachlan J.S., Foster D.R., Menalled F. (2000): Anthropogenic ties to latesuccessional structure and composition in four New England hemlock stands. Ecology, 81: 717–733.

Millar C.I., Stephenson N.L., Stephens S.L. (2007): Climate change and forests of the future: managing in the face of uncertainty. Ecological Applications, 17: 2145–2151.

Montes F., Rubio A., Barbeito I., Cañellas I. (2008): Characterization of the spatial structure of the canopy in *Pinus silvestris* L. stands in central Spain from hemispherical photographs. Forest Ecology and Management, 255: 580–590.

Montes F., Sanchez M., del Rio M., Canellas I. (2005): Using historic management records to characterize the effects of management on the structural diversity of forests. Forest Ecology and Management, 207: 279–293.

Mountford M.D. (1961): On E. C. Pielou's index of non randomness. Journal of Ecology, 49: 271–275.

Näslund M. (1936): Skogsförsöksanstaltens gallringsförsök i tallskog. Meddelanden från Statens Skogsförsöksanstalt, Swedish Institute of Experimental Forestry, 29: 169.

Oliver C.D., Larson B.C. (1990): Forest Stand Dynamics. New York, McGraw-Hill: 544.

Peterken G.F. (1981): Wooland Conservation and Management. London: Chapman & Hall: 328.

Petráš R., Pajtík J. (1991): Sústava Česko-slovenských objemových tabuliek drevín. Lesnícky časopis: 7, 49–56.

Pielou E.C. (1959): The use of point-to-plant distances in the study of the pattern of plant populations. Journal of Ecology, 47: 607–613.

Pielou E.C. (1975): Ecological Diversity. New York, Wiley: 165.

Poyatos R., Latron J., Llorens P. (2003): Land use and land cover change after agricultural abandonment – the case of a Mediterranean Mountain Area (Catalan Pre-Pyrenees). Mountain Research and Development, 23: 362–368.

Pretzsch H. (2006). Wissen nutzbar machen für das Management von Waldökosystemen. Allgemeine Forstzeitschrift/Der Wald, 61: 1158–1159.

Ripley B.D. (1981): Spatial Statistics. New York, John Wiley & Sons: 252.

Rouvinen S., Kuuluvainen T. (2005): Tree diameter distributions in natural and managed old *Pinus sylvestris* -dominated forests. Forest Ecology and Management, 208: 45–61.

Sánchez Meador A.J., Parysow P.F., Moore M.M. (2011): A new method for delineating tree patches and assessing spatial reference conditions of ponderosa pine forests in northern Arizona. Restoration Ecology, 19: 490–499.

Shannon C.E. (1948): A mathematical theory of communications. Bell System Technical Journal, 27: 379–423.

Silver E.J, D'Amato A., Fraver S., Palik B.J., Bradford J.B. (2013): Structure and development of old-growth, unmanaged second-growth, and extended rotation *Pinus resinosa* forests in Minnesota, USA. Forest Ecology and Management, 291: 110–118.

Smith G.F., Gittings T., Wilson M., French L., Oxbrough A., O'Donoghue S., O'Halloran J., Kelly D.L., Mitchell F.J.G., Kelly T., Iremonger S., McKee A.M., Giller P. (2008): Identifying practical indicators of biodiversity for stand-level management of plantation forests. Biodiversity and Conservation, 17: 991–1015.

Spies T.A. (1998): Forest structure: a key to the ecosystem. Northwest Science, 72: 34–39.

Spies T.A. (2004): Ecological concepts and diversity of old-growth forests. Journal of Forestry, 102: 14–20.

Stephenson N.L. (1999): Reference conditions for giant sequoia forest restoration: structure, process, and precision. Ecological Applications, 9: 1253–1265.

Sterba H. (2008): Diversity indices based on angle count sampling and their interrelationships when used in forest inventories. Forestry 81: 587-597.

ter Braak C.J.F., Šmilauer P. (2002): CANOCO Reference Manual and CanoDraw for Windows User›s Guide: Software for Canonical Community Ordination (version 4.5). Ithaca, NY, USA. Available at www.canoco.com

Tuten M.C., Meador A.S., Fu P.Z. (2015): Ecological restoration and fine-scale forest structure regulativ in southwestern ponderosa pine forests. Forest Ecology and Management, 348: 57–67.

Uotila A., Maltamo M., Uuttera J., Isomaki A. (2001): Stand structure in seminatural and managed forests in eastern Finland and Russian Karelia. Ecological Bulletins, 49: 149–158.

Uotila A., Kouki J., Kontkanen H., Pulkkinen P. (2002): Assessing the naturalness of boreal forests in eastern Fennoscandia. Forest Ecology and Management, 161: 257–277.

Vacek S., Vacek Z., Podrazský V., Bilek L., Bulušek D., Štefančik I., Remeš J., Šticha V., Ambrož R. (2014): Structural diversity of autochthonous beech forests in Broumovske Stěny national nature reserve, Czech Republic. Austrian Journal of Forest Science, 131: 191–214.

Vanderwel M.C., Caspersen J.P., Woods M.E. (2006): Snag dynamics in partially harvested and unmanaged northern hardwood forests. Canadian Journal of Forest Research, 36: 2769–2779.

Viewegh J., Kusbach A., Mikeska M. (2003): Czech forest ecosystem classification. Journal of Forest Science, 49: 74–82.

Weiner J. (1985): Size hierarchies in experimental populations of annual plants. Ecology, 66: 743–752.

Weiner J. (1990): Asymmetric competition in plant populations. Trends in Ecology and Evolution, 5: 360–364.

Zobel K., Zobel M., Peet R.K. (1993): Change in pattern diversity during secondary succession in Estonian forests. Journal of Vegetation Science, 4: 489–498.

Received for publication October 22, 2015
Accepted after corrections December 4, 2015

Corresponding author:

Ing. Lukáš Bílek, Ph.D., Czech University of Life Sciences Prague, Faculty of Forestry and Wood Sciences, Kamýcká 1176, 165 21 Prague 6-Suchdol, Czech Republic; e-mail: bilek@fld.czu.cz