

Structural diversity of selected oak stands (*Quercus robur* L.) on the Krotoszyn Plateau in Poland

Janusz Szmyt

Poznań University of Life Sciences, Faculty of Forestry, Department of Silviculture, ul. Wojska Polskiego 69, 60–625 Poznań, Poland

Tel. + 48 61 8487735, e-mail: jszmyt@up.poznan.pl

Abstract. The oak forests growing on the Krotoszyn Plateau are the biggest and most valuable oak forest complexes in Poland. The purpose of this study was to analyze the structural diversity of oak (*Q. robur* L.) stands older than 140 years. Two natural stands located within the forest reserve as well as two managed stands were chosen for investigation. Species and tree size diversity were analyzed using different measures and spatially explicit and inexplicit indices. The results indicate that the structural diversity of the protected oak forests did not differ significantly from that of managed stands. On the contrary, undisturbed natural processes in protected forests can result in a low diversity of some structural attributes in such stands. Although most indices pointed towards a higher structural diversity in protected forests, the differences were not large, especially in the case of spatially explicit indices. The spatial arrangement of live trees was either random, aggregated or regular, with the latter clearly dominating managed, poorly mixed oak stands. Furthermore, a lack of natural disturbances strong hornbeam expansion, in which case strict protection is not favorable for oak sustainability as it creates unsuitable conditions for oak regeneration beneath the hornbeam canopy.

Keywords: *Quercus robur*, structural diversity of forest, structural indices, Krotoszyn Plateau

1. Introduction

The canopy layer of the forest stand, the main part of the forest, is described by using various parameters defining the state of the forest in terms of its vertical profile, size structure, species composition and so on. Stand structure is affected by both external factors (natural disturbances, such as fires and insect infestations) and internal ones (ecological processes, biological and ecological species characteristics, microhabitat variability, etc.) (Müller et al. 2000; Montes et al. 2004; Zenner 2004; Pretzsch 2010; Petritan et al. 2012; Petritan et al. 2015; Zenner et al. 2014; del Rio et al. 2015; Fibich et al. 2016). In managed forests, an additional factor significantly influencing the stand structure in various stages of development is silvicultural practices (Pretzsch, 2010).

Forest structure is the result of different natural processes relating to its development, but, simultaneously, the forest structure itself also affects these processes (Spies 1998; Naumann, Starlinger 2001; Pommerening 2002; Pretzsch 2010; Gadow et al. 2012). These ecological and biological processes occur in various spatial scales and may also overlap, whilst

their intensity varies, depending on the stage of the forest development. For example, natural regeneration often manifests itself in patches of seedlings and saplings, which, as a result of individual competition and increasing tree size, changes with the stand age towards more uniform distribution (Fibich et al. 2016). The process of competition most often involves a tree's nearest neighbours and thus operates at the scale of the immediate surroundings. The result of intense competition is often the death of weaker individuals; however, it also often leads to clearly limiting the growth of weaker trees (Kenkel 1988; Brooker 2006). With age, competition between trees in a forest becomes less intense; hence, the role of this process in older stands is assumed to be less important than in younger ones. Other factors, such as the natural disturbances mentioned earlier, play a greater role in shaping the structure of old-growth forests (Spies 1998; Szymański 2000; Zenner et al. 2011; Gadow et al. 2012).

The structural complexity of a forest is largely determined by the number of tree species but of equal importance is the diversity in the size of individual trees. One of the factors affecting the coexistence of species in a mixed forest

Submitted: 1.03.2016, reviewed: 15.03.2016, accepted after revision: 11.07.2016

is the interactions between individuals of each species, often resulting from different environmental requirements and microhabitats (McElhinny et al. 2005; McIntire, Fajardo 2009; Wilson 2011; Gadow et al. 2012). Aggregations of particular species favour their coexistence in the forest by weakening interspecies competition (Raventós et al. 2009). This is particularly evident in tropical forests. The same effect - to ensure a mixed composition in managed forests - is the intention of using a mix of species in an area at the renewal stage or group cutting to regenerate selected species.

It is assumed that natural forests are often characterised by greater structural diversity than managed forests, where silvicultural practices often excessively unify their species composition and structure. Frequently, forests located in nature reserves or national parks, whose structure is largely the result of natural forces, are provided as examples of highly structured forests. However, long-term studies focused on natural forests indicate that the natural processes occurring in them can lead to the development of a simple system in terms of their species composition and structure (Brzeziecki et al. 2012; Brzeziecki et al. 2016). However, achieving the postulates of having managed forests be as close as possible to natural ones, that is, by using complex forms of fellings, regeneration methods mimicking the natural regeneration of various species and silvicultural practices carried out in forest ecosystems, may even encourage the development of more diverse stands (Paluch, Bielak 2009; Jaworki 2011).

The subjects of this study are the forest stands located on the Krotoszyn Plateau, where the main species is pedunculate oak (*Quercus robur* L.). Four stands were chosen, two located in nature reserves and two in managed stands. The Krotoszyn oak stands are the largest concentration of more than 100-year-old oak stands, occurring in large forest complexes. The conditions that prevail there are not conducive to the natural regeneration of oak, so it is believed that these stands were established by planting and sowing (Szychowiak 2002a, 2002b after Jaworski 2011). At the same time, they are considered as one of the most valuable populations of pedunculate oak in Europe. There are also only a few studies on the dynamics of these forests and their structural diversity. This study, therefore, is a certain supplement to knowledge about their structural diversity under human pressure. In the case of the reserve stands, the results of this study may be helpful in developing strategies for the further protection of forests where the pedunculate oak is an important element. The primary objective of this study was to determine the structural diversity of oak stands in terms of species composition, size (diameter at breast height (DBH) and height) differentiation and the spatial distribution of trees in the stand. On the basis of the calculated indices, an attempt was made to compare the structural diversity of forest stands under various types of human impact.

2. Study area and methodology

2.1. Area and study subjects

Choosing stands for the study was guided by two basic criteria: the proportion of pedunculate oak, which should be the main species, and the age of the stand, which at the time of measurement should not be less than 140 years. An additional premise was to choose stands with different forms of human impact on their structure. Before choosing the study sites, all of the sectors were inspected to locate the most representative fragments of the forest.

Measurements were performed in four plots of four different stands. According to the forest regionalisation, the stands selected for analysis are located in the Wielkopolska–Pomerania Region (III), Krotoszyn (III.8) District (Trampler et al. 1990). The terrain is flat with gleyic stagnosol soils.

Area 1 (Biadki) is a stand established in part of the ‘Dabrowa near Biadek Krotoszyńskich’ reserve, with an area of 16.20 ha, located in the Krotoszyn Forest Division, section 76c of the Borowina Forest District. The dominant phytocenosis of the reserve is the acidophilus hornbeam-oak forest. The tree stand in the fresh broadleaved forest site type has a two-story structure, with the upper story consisted of pedunculate oak and the lower hornbeam (*Carpinus betulus* L.). Individuals of Norway spruces (*Picea abies* L.) also occur as a single mixture. At the time of the measurements, the oaks were approximately 280 years old. Measurements were taken from a plot of 70 m × 50 m (0.35 ha). The reserve was created in 1963 by order of the Minister of Forestry and Wood Industry, with the aim of protecting the ecosystem of deciduous forests, including the acidophilus oak forests typical of the Krotoszyn Plateau.

Area 2 (Smoszew) is a stand located in the ‘Dabrowa Smoszew’ reserve, with an area of 13.85 ha in the Krotoszyn Forest Division, section 56c of the Smoszew Forest District. The dominant (protected) plant community in the reserve is the central European hornbeam forest. The forest site type is described as moist broadleaved forest and has a two-story structure, with pedunculate or sessile oak (*Quercus petraea* Liebl.) in the upper story and hornbeam in the lower. Small-leaved lime (*Tilia cordata* Mill.) occurs in some areas of the reserve as a single mixture. According to the forest management plan, the age of the oak trees at the time of measurement was 151 years (Forestry Management Plan of the Smoszew forest, 2008). A 70 m × 70 m (0.49 ha) measurement plot was established in this stand. The objective of protecting this forest by order of the Minister of Forestry and Wood Industry in 1963 was to maintain the hornbeam and riparian plant associations with the dominating pedunculate oak forest and rare species of plants.

Area 3 (Jelonek) is a two-story managed stand in the Krotoszyn Forest Division, compartment 162d, growing in a moist broadleaved forest site type. The upper story consists of pedunculate oak, whose age was estimated at 164 years at the time of measurement. The upper story also includes beech (*Fagus sylvatica* L.). The lower story consists of hornbeam. In this stand, which was managed according to the management plan in force, a measurement plot of about 0.50 ha (50 m × 100 m) was established.

Area 4 (Piaski) is located in the managed stands of the Piaski Forest Division, compartment 291j. The forest type is specified as a fresh broadleaved forest site type. The age of the oak trees was estimated at 145 years. The admixture of Norway spruce (*P. abies* Karst.) occurred in the lower story. An area of 140 m × 60 m (0.84 ha) was established as the measurement plot.

2.2. Methodology

During field work, DBH ($d_{1.3}$, cm), total tree height (H , m) and species identification of live trees in all of the stands were determined. The coordinates (x , y) of each tree was determined for the spatial analysis.

The structural diversity of the forests was determined using the Shannon species diversity index (H_{gat} , E_{gat}), the species profile index of vertical differentiation by Pretzsch (A) and the Gini index (GI). In order to take into account the spatial distribution of trees, the Clark–Evans aggregation index (R), the spatial size differentiation index for DBH (TD) and height (TH) and the spatial species mingling index (SM) were calculated. The mathematical formulas of each index are presented in Table 4.

Species diversity index (H_{gat}) has a greater value when a higher number of species is present in an area and their proportions are more balanced (Brzeziecki, 2002; Pretzsch 2010). If a stand is made up of one species, the index H_{gat} is equal to 0, whereas its maximum value H_{max} , specifying the maximum diversity of tree species, is equal to $\ln(S)$, where S is the number of species. Comparing the diversity of different forest stands, the index of evenness for species diversity of $E_{gat} = H_{gat} / H_{max}$ is often used, specifying the extent to which the observed variation of H_{gat} deviates from the maximum diversity (H_{max}). If the proportion of species in the forest stand is the same, and their mix is the greatest, then $E_{gat} = 100$, and vice versa, E_{gat} approaches 0 when the species diversity is low (Pretzsch, 2010).

The profile index (A) describes the vertical structure of a stand with regard to the participation of species in its different vertical layers. Trees are allocated to three vertical classes: layer I, less than 50% of the maximum height of the trees; layer II, 50–80% of the maximum height of the trees; layer III, greater than 80% of the maximum height of the trees in the stand (Pretzsch 2010; Petritan et al. 2012).

The lowest values of the index are found for single-story and single-species stands, it increases in multi-storied but single-species stands and has the highest value in mixed stands with a complex vertical structure. The maximum value of A is calculated by using the following formula:

$$A_{max} = \ln(S \times Z)$$

where

S is the number of species,

Z is the number of layers in the tree stand.

In order to compare the variation in height amongst different forest stands, the standardised, A_{rel} , index is used, which is described by the formula $A_{rel} = (A/A_{max}) \times 100\%$ (Pretzsch 2010). The A_{rel} index determines the extent to which the analysed stand differs from the maximum variation for the given conditions.

The Gini index (GI) is the next measure of the diversity of the study population's characteristics (e.g. DBH) (Lexerød, Eid 2006; Sterba 2008; Zenner et al. 2015). It can take values in the range of $GI \hat{I}$ (0, 1), wherein the low values indicate that the trees are characterised by, for example, a diameter close to the mean (little variation in the characteristic), whilst higher values indicate greater GI diversity in the population's analysed characteristics.

The Clark–Evans aggregation index (R) defines the pattern of the distribution of trees based on the comparison of the average observed distance between the trees with the average distance of their random distribution. The maximum value ($R=2.15$) is reached with a hexagonal arrangement of trees. Values of $R > 1$ indicate a regular distribution, whilst $R < 1$ indicates aggregate distribution. The random distribution of individuals in an area is indicated by a value of $R = 1$ (Donnelly 1978; Kint et al. 2000). This indicator takes into account corrections resulting from the edge effect (Donnelly 1970). Significant deviations from the random distribution were determined by 999 Monte Carlo simulations.

Indices of the spatial differentiation of DBH and height (TD and TH , respectively) define the differences in the DBH (or height) of trees at the scale of the immediate neighbourhood. The index ranges from 0 to 1, with $TD = 0$ indicating a lack of differentiation of the measured feature of nearest neighbours and $TD = 1$ indicating very large differences of the measured feature (Pretzsch 2010; Szmyt, Ceitel 2011; Szmyt 2012). The proportion of pairs of trees of varying DBH can be determined based on the distribution of TD amongst classes of diversity: 0.00–0.30, little variation; 0.30–0.50, average variation; 0.50–0.70, large variation; and 0.70–1.00, very large diversity of features between nearest neighbours (Pommerening 2002).

The indicator of the spatial species mingling (SM) defines the mutual distribution of species at the scale of the immediate neighbourhood. SM value can vary from 0 to 1, wherein in

the analysis of the four nearest neighbours, *SM* may have five values: 0, 0.25, 0.5, 0.75 and 1. The higher the index value, the greater is the diversity of species at a small spatial scale. The analysis of the distribution of *SM* allows the proportion of homogeneous groups and diverse species of trees in the stand to be specified (Kint et al. 2000; Gadow, Hui 2002).

Structural measures were calculated with R (R Core Development Team 2015), using the ‘Spatstat’ package (Baddeley, Turner 2015).

3. Results

3.1. Characteristics of the oak stands

As shown in Table 1, three of the four analysed stands, including two in the reserves, had similar basal areas (40.70–46.39 m² ha⁻¹, $N = 444\text{--}968$ szt.×ha⁻¹). The managed stand in Jelonek had almost twice the combined *G* ($G = 40.70$ m²×ha⁻¹) than the managed stand in Piaski ($G = 24.66$ m²×ha⁻¹).

Stands in the reserves (Biadki, Smoszew) had a greater range of DBH, but the range of the height was similar in both types of stands. The lowest average DBH of all live trees was found in Biadki ($d_{1.3} = 17.07$ cm) and the highest was in the managed stands in Piaski ($d_{1.3} = 46.5$ cm). Oaks, of course, had the highest DBH in each stand, but the lowest DBH of oaks was found in Piaski (Table 1). The highest average height was found for the oaks in Jelonek site (31.84 m) and then in Smoszew, Piaski and Biadki. Except for Piaski, hornbeam was the most abundant species in the stands. The trees of this species comprised the understory layer of the stands in Biadki, Smoszew and Jelonek. The average DBH of hornbeam ranged from 12.76 to 19.58 cm, whilst the height varied from 14.44 to 18.05 m (Table 1).

3.2. Spatial distribution of trees

Live trees were regularly distributed only in the managed stand in Piaski ($R = 1.12$; $p = 0.05$). In Smoszew and Piaski,

Table 1. Characteristic of oak stands on the measurement plots (*N* – trees number/plot, *Db* – common oak, *Gb* – hornbeam, *Jw* – sycamore, *Bk* – European beech)

	Forest stand					
	<i>N</i>	$d_{1.3, sr}$ [cm]	<i>G</i> [m ² ha ⁻¹]	min-max [cm]	<i>H</i> [m]	min-max [m]
Biadki (0.35 ha)						
Live trees	339	17.07	46.39	7.10–120.0	15.24	12.99–33.70
Db	34	55.74	33.14	7.20–120.00	22.47	13.32–33.70
Gb	305	12.76	13.26	9.10–38.55	14.44	11.50–19.43
Smoszew (0.49 ha)						
Live trees	259	26.10	40.71	7.00–90.40	19.54	10.30–38.40
Db	67	52.37	31.67	14.7–90.4	28.70	10.30–38.40
Gb	185	16.45	9.04	7.00–38.00	16.23	10.85–21.05
Jw	7	29.49	1.06	18.25–42.75	20.79	16.10–27.00
Jelonek (0.50 ha)						
Live trees	222	29.89	40.70	8.00–72.00	22.43	8.00–37.00
Db	51	54.46	24.48	16.00–72.00	31.84	15.00–37.00
Gb	128	19.58	8.54	8.00–42.20	18.05	8.00–26.00
Bk	43	31.15	7.42	10.00–58.50	24.05	10.00–31.00
Piaski (0.84 ha)						
Live trees	114	46.50	24.66	7.10–71.20	25.07	12.00–31.30
Db	114	46.50	23.85	7.10–71.20	25.19	15.20–31.30

no significant deviations from the random distribution were found, whilst in Biadki, the trees were aggregated (Table 2). Oaks were regularly distributed, except for Biadki, where they were found to occur randomly, despite a trend towards a regular distribution. Hornbeams, most frequently, had a random distribution except for those in Biadki, where the deviations from the random pattern towards clumped distribution were statistically significant ($R = 0.90$; $p = 0.05$). Sycamores were also found to have an aggregated distribution in Smoszew, whilst beech in Jelonek showed no statistically significant deviation from a random pattern (Table 2).

3.3. Species diversity and mix in the stands

The species diversity index, H_{gat} , had the highest value in the managed stands in Jelonek. Lower values were obtained for both the reserve stands, $H_{gat} = 0.69$ for Smoszew and $H_{gat} = 0.35$ for Biadki. The lowest level of species diversity was found in Piaski stands, which had a single admixture of spruce. The standardised Shannon index, E_{gat} , indicated the same trend (Table 3). The analysis of species diversity amongst the nearest neighbour trees (SM) confirmed that the stand in Jelonek was the most diverse in terms of species mingling (Table 3). The oak stand in Smoszew also had a high value of species mingling index ($SM = 0.45$). The stand in Biadki had a lower value of SM , similar to that of Piaski ($SM = 0.13$; $SM = 0.05$, respectively). In analysing the share of trees, whose nearest neighbourhood was characterised by a low, medium or high species diversity (Fig. 1), we can conclude that the stand in Jelonek had trees whose share in the different categories was relatively even. In Smoszew, the share of trees, whose neighbours were more homogeneous ($SM \leq 0.25$), was slightly higher. The remaining two stands – Biadki and Piaski – although clearly distinguishable in their average SM values, were characterised by the highest share of trees, whose neighbours did not exhibit species diversity, that is, $SM = 0$ (Fig. 1). Both stands were characterised by the lowest share of individuals growing next to different spe-

cies (Fig. 1). An analysis of the surroundings of oaks indicated that in case of three of the four stands, they were often found next to trees of a different species ($SM = 0.75, 1.0$) (Fig. 1). Only the Piaski stand had oaks growing next to each other (90% of cases).

3.4. Diversity of DBH and height of trees in the oak stands

The DBH structure of live tree of the different stands is presented in Figure 2. Its shape was similar in the reserve stands and the managed stand of Jelonek, indicating two peaks, one in the low diameter classes and the second in the moderate classes. It is also notable that the oaks occurred almost exclusively in large diameter classes (DBH > 30 cm), whilst the share of this species in the lower classes was sporadic. The structure of DBH in Piaski showed a unimodal shape, with the maximum found in the 40- to 60-cm diameter classes. The Gini index (GI) confirmed the differences in the DBH variability of the stands. The stands located in the reserves showed higher variation in DBH, and less diversity of DBH was found in both managed stands, with the stand in Piaski having the lowest value of GI index. The coefficient of variation calculated for DBH (CV_{db}) indicated the same trend with regard to the diversity of the diameter of trees (Table 2). Figure 3 and Table 2 show the spatial differentiation of tree diameters expressed as the average TD index and the share of trees in each differentiation class. The highest mean TD value was found in the Smoszew reserve ($TD = 0.46$), indicating an average differentiation of the nearest neighbours. Stands in Biadki (reserve) and Jelonek (managed stand) showed slightly lower but similar mean TD values. The lowest average diameter differentiation index was found in the managed stand located in Piaski ($TD = 0.21$). The distribution of TD values (Fig. 3) shows that the stand with the greatest average diversity of diameter (Smoszew) had the most cases of closest neighbours differing in DBH by 30–70%. A similar situation was found in Jelonek site,

Table 2. Mean values of structural indices for analyzed oak stands (*significance level, $\alpha = 0.05$)

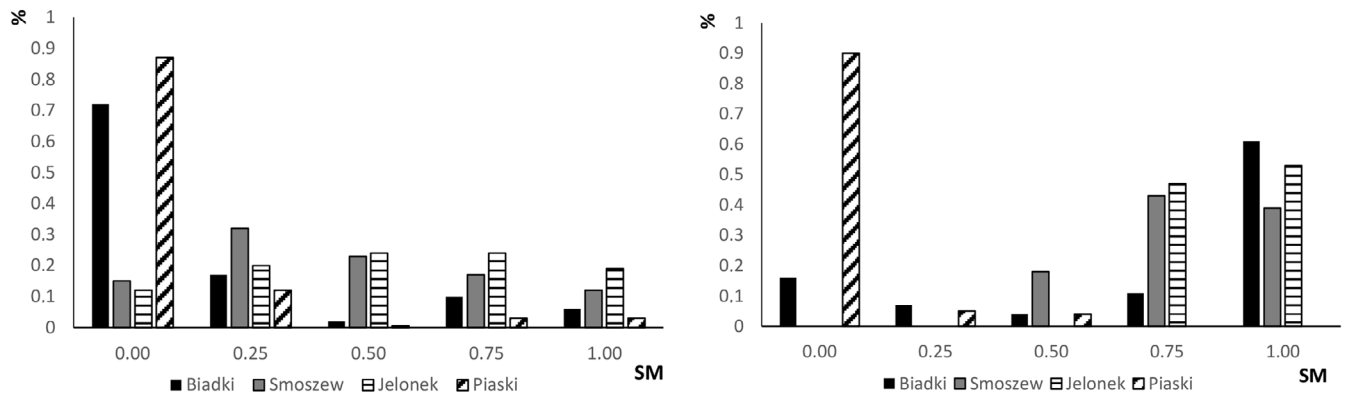
Wskaźnik	Biadki			Smoszew				Jelonek			Piaski	
	Live trees	Db	Gb	Live trees	Db	Gb	Jw	Live trees	Db	Gb	Bk	Db
R	0.9*	1.10	0.90*	1.02	1.13*	0.99	0.52*	0.96	1.18*	0.96	0.82	1.12*
SM	0.13	0.74	0.06	0.44	0.80	0.31	0.95	0.54	0.88	0.38	0.69	0.05
TD	0.36	0.65	0.30	0.46	0.60	0.41	0.35	0.40	0.56	0.35	0.38	0.21
TH	0.16	0.37	0.41	0.20	0.40	0.23	0.24	0.27	0.37	0.25	0.23	0.10

Explanation: R – Clark-Evans index, TD – spatial differentiation index for diameter, TH – spatial differentiation index for height, SM – spatial mingling index

Table 3. Mean values of structural indices for analyzed oak stands (spatial inexplicit indices)

Study plot	$H_{gat} (H_{max})$	E_{gat}	$A (A_{max})$	A_{rel}	GI	$CV_{d1.3}$	CV_H
Biadki	0.35 (0.69)	0.51	1.22 (1.79)	0.68	0.45	1.11	0.29
Smoszew	0.69 (1.09)	0.63	0.62 (1.79)	0.34	0.36	0.70	0.33
Jelonek	0.97 (1.39)	0.70	0.62 (2.48)	0.25	0.30	0.55	0.31
Piaski	0.14 (0.69)	0.20	0.53 (2.20)	0.24	0.11	0.21	0.12

Explanation: H_{gat} – Shannon index of species diversity, H_{max} – max. value of H_{gat} index, E_{gat} – evenness index for species diversity, A – profile index by Pretzsch, A_{max} – max. value of A index, A_{rel} – relative A index, GI – Gini index, $CV_{d1.3}$ – coefficient of variation for diameter, CV_H – coefficient of variation for tree height

**Figure 1.** The share of live trees (left panel) and oaks (right panel) in the dependence on the number of neighbors (1–4) belonging to the different species than reference tree based on the SM index

although its share of trees with a DBH diversity of <30% was higher. In Biadki, neighbouring trees most often had DBH differences of 30–50%. Managed stand in Piaski was characterised by the largest share of trees (84%) with the lowest level of DBH diversity between nearest neighbours (<30%) (Fig. 3).

Oaks were markedly different in terms of the DBH of their immediate neighbours in three of the four analysed stands (Fig. 4). The exception was the Piaski site, where the differentiation of the nearest neighbours of the oaks was usually not greater than 30% (Fig. 3).

The most diverse vertical profile of the stands was found in both reserve stands ($A_{rel} = 0.68$ and $A_{rel} = 0.34$). Jelonek and Smoszew had the same index A value. These stands varied, however, in the differences between the standardised A_{rel} index, which allows us to state that the Smoszew stand has a somewhat greater variation of vertical structure (Table 3). The least diverse was the managed stand in Piaski. Similar results in terms of variation in height were obtained by calculating the coefficient of variation (Table 2).

The spatial diversity of tree height (TH) was significantly lower than the diameter variations. The average TH index fluctuated between $TH = 0.10$ and $TH = 0.27$ (Table 3). It is worth noting that both managed stands had radically different values of tree height diversity, but the stands in the reserves had similar mean TH values (Table 3). The share of trees in each class of height difference indicated that neighbouring trees were predominantly similar in terms of this feature. Only the stand in Smoszew had greater diversity, and in the case of 20% of the trees, these differences reached above 70% (Fig. 4). The trees surrounding oaks were characterised by greater height diversity than the average for the stand (Fig. 4). The oaks in the managed stand in Piaski were the exception. In 93% of cases, the difference in height between the oaks and their surrounding trees was not greater than 20%. In the remaining stands, most of the differences were in the average class of height variation. The share of oaks whose surrounding trees differed in height by 50–70% did not exceed 20% in any of the stands (Fig. 4).

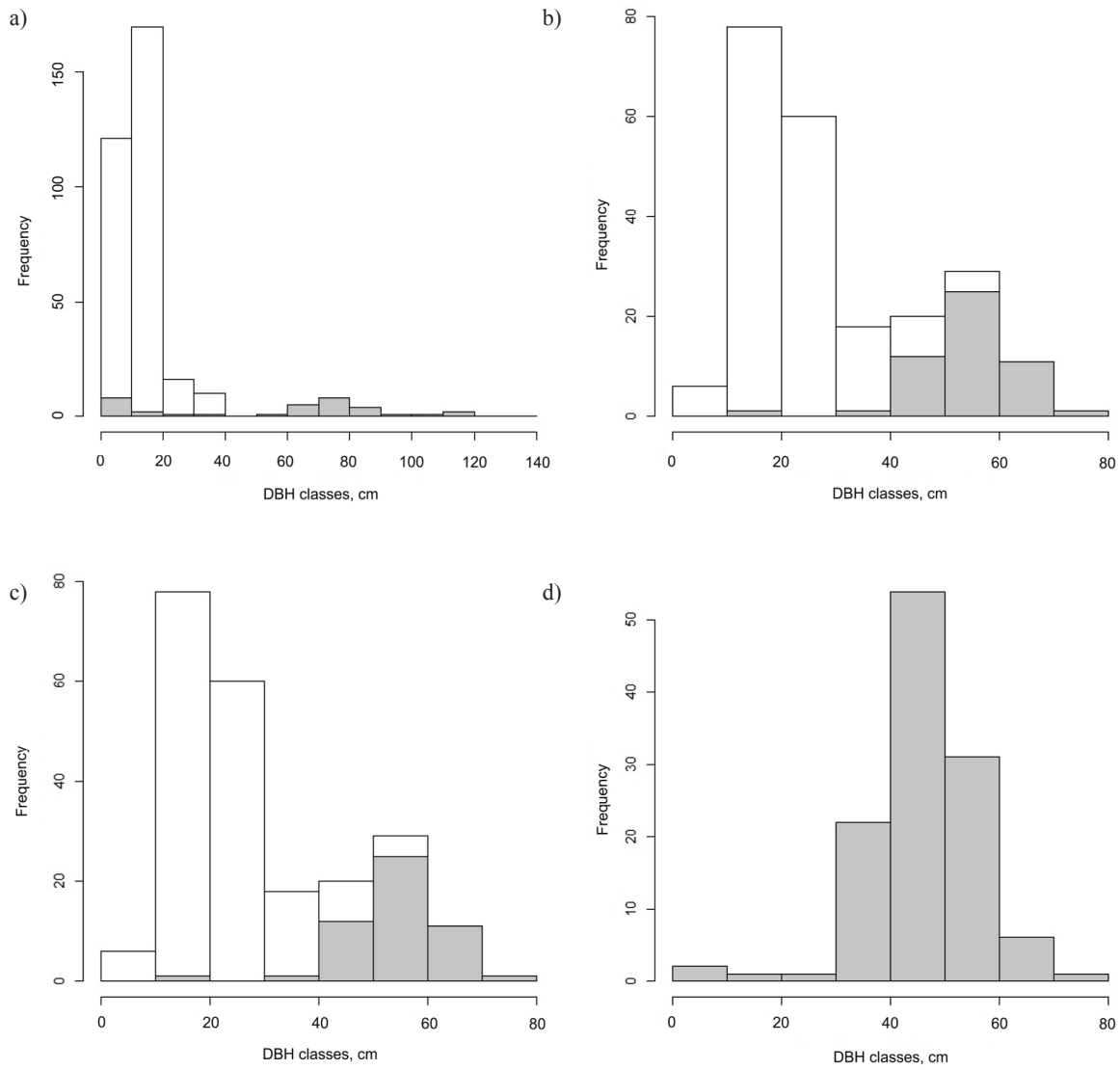


Figure 2. Diameter structure of analyzed stands: a) Biadki, b) Smoszew, c) Jelonek and d) Piaski (grey bars – oak, white bars – other species)

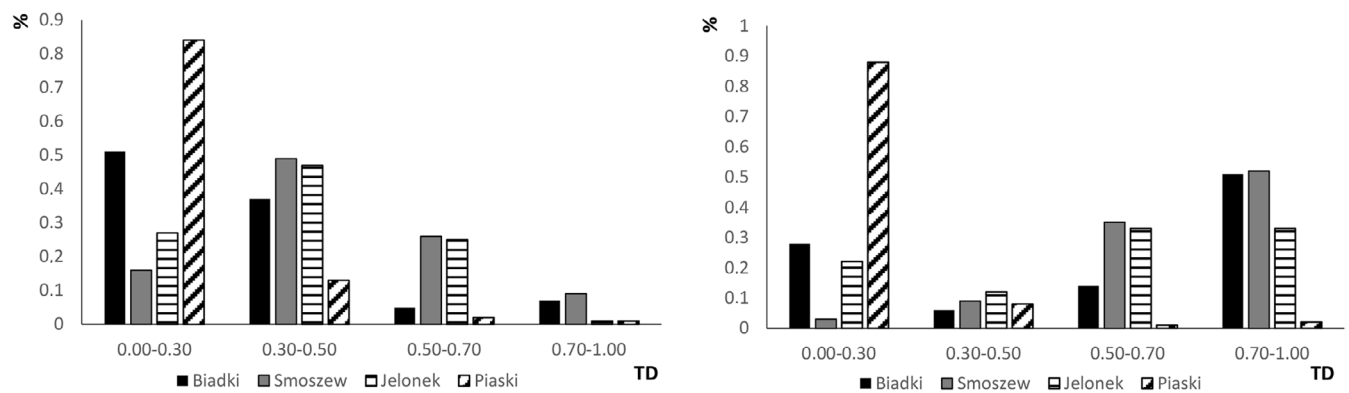


Figure 3. Distribution of TD values in diameter differentiation classes for live trees (left panel) and oaks (right panel) in the analyzed stands.

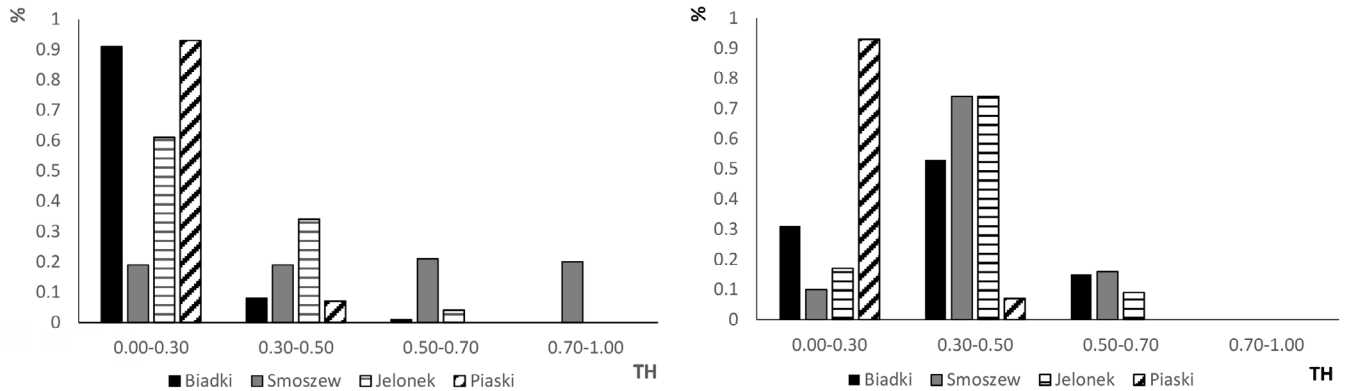


Figure 4. Distribution of TD values in tree height differentiation classes for live trees (left panel) and oaks (right panel) in the analyzed stands.

4. Discussion

The relationship between the stand structure and the functioning of the forest ecosystem has made it one of the most important features, enabling the current state of the forest to be analysed as well as to determine, with greater or lesser probability, the direction of its future development (Oliver, Larson 1996; Spies in 1998; Brzezicki et al. 2012). For managed forests, the analysis of forest structure can provide an essential tool to use in deciding the scope of silviculture efforts to develop more structurally diverse stands that are less vulnerable to adverse external factors (Drozdowski et al. 2014a, b). For protected forests (nature reserves, national parks, etc.), knowledge about their structure can provide important information for undertaking conservation work to maintain or improve the living conditions of the protected objects, such as, plant associations and threatened species (Petritan et al. 2012; Iszkuło et al. 2013).

4.1. Diversity of the size of the trees in the stands

The simplest measures of population diversity in terms of the selected features are descriptive statistical measures, for example, their range or coefficient of variation. The ease of their interpretation, on one hand, ensures their popularity, whilst, on the other hand, their cognitive limitation is the fact that they characterise the variability of the analyzed traits in a synthetic way, at the level of the stand, for example. Both measures applied in the analysed oak stands indicated that the protected stands are a little more diverse in terms of tree diameters than the managed stands, whilst DBH was a more variable trait than tree height.

The DBH structure indicated that forest stands located in reserves and the managed stand in Jelonek are characterised

by a bimodal distribution of DBH, with a first maximum attributable to the lower size classes and the second to higher size classes. A bimodal shape of DBH structure was also observed by Pach and Podlaski (2015) in the protected stands in mountains. Such a DBH distribution was common in protected or natural forests (Bobinac 2000; Kucbel et al. 2012; Petritan et al. 2012). A high representation of trees with small DBHs indicates that intensive renewal processes are taking place in the stand, which may prove the stability and sustainability of the analysed population. The lack of potential young trees may indicate the decreasing importance of a species and may be related to the ageing of the population (Bernadzki et al. 1998; Brzezicki et al. 2012). In the analysed oak stands, the first case is represented by hornbeam (especially in the reserves), whilst oak represents the second case, where nearly all the individuals are old trees found in the upper story of the forest. Only the managed stand in Piaski was typical, a single species and even-aged stand, with a unimodal DBH distribution.

The diversity of tree stands can also be inferred from an analysis of the results obtained using the profile index A (height) and the Gini index (DBH). The profile index, which takes into account the share of individual species in the three vertical layers of the stand, has a greater value when there is a greater share of species in a stand and when they are more proportionally distributed in the particular layers of the stand (Biber, Weyerhaeuser 1998; Aguirre et al. 2006; Petritan et al. 2012; del Rio et al. 2015). Using the original version of A index in comparing the diversity of different stands, however, poses difficulties of interpretation, and therefore, it is often used indirectly by determining the so-called A_{rel} standardised index (Pretzsch, 2010). This index showed a greater diversity in the vertical structure of the stands in both reserves. The lowest variation in vertical structure was

Table 4. Stand structural indices

Index	Formula	Description
Species diversity index (H_{sp})	$H = -\sum_{i=1}^s p_i \cdot \ln p_i$	s – number of species in the stand \ln – natural logarithm p_i – share of the species in the study population ($p_i = n_i/N$, where n_i is the number of individuals of i species and N is the number of trees in the stand)
Stand profile index (A)	$A = -\sum_{i=1}^s \sum_{j=1}^z p_{ij} \cdot \ln(p_{ij})$	s – number of species in the stand z – number of height classes ($z = 3$) p_{ij} – share of species in the classes ($p_{ij} = n_{ij}/N$) n_{ij} – share of i species in j height class N – number of trees
Gini inequality index (G)	$G = \frac{\sum_{j=1}^n (2j - n - 1)d_{1.3j}}{\sum_{j=1}^n d_{1.3j} (n - 1)}$	$d_{1.3j}$ – DBH of a j th rank tree j – rank of a tree in an increasing order from 1, ..., n n – number of trees in the population
Spatial mingling index (DM)	$DM_i = \frac{1}{n} \sum_{j=1}^n V_{ij}$	$V_{ij} = 0$ – when neighbour j and tree i are the same species, otherwise $V_{ij} = 1$ n – number of nearest neighbours (established $n = 1$)
Spatial differentiation index (TD/TH)	$TD = \frac{1}{n} \sum_{j=1}^n 1 - \frac{\min(d_{1.3i}, d_{1.3j})}{\max(d_{1.3i}, d_{1.3j})}$	$d_{1.3}$ – DBH of tree i and j n – number of nearest neighbours ($n=1$)
Aggregation index (R)	$R = \frac{r_A}{r_E} = \frac{\frac{1}{N} \sum_{i=1}^N r_i}{0.5 \cdot \left(\frac{A}{N}\right)^{1/2} + 0.0514 \cdot \frac{P}{N} + 0.041 \cdot \frac{P}{N^{3/2}}}$	r_A – average distance between nearest neighbours r_E – average expected (theoretically) distance between nearest neighbours r_i – distance between individual i and its nearest neighbour (m) N – number of individuals in the measurement plot A – area (m ²) P – circumference (m)

found in the managed stand located in Piaski. High value of A index was found by Petritan et al. (2012) in stands with greater species diversity than in stands consisting of a small share of species.

Relevant information concerning the forest stand diversity is provided by indicators of the spatial pattern of trees. In the case of tree height, these indicators showed little variation amongst adjacent trees in the studied stands. A more complete picture, however, is provided by the analysis of the share of trees in each height differentiation class. Such

analysis indicated that most trees fell into the class of the lowest variation (differences of up to 30%), regardless of the character of the stands. It is worth noting that the results obtained for the Biadki and Piaski stands were very similar. The analysis of the surroundings of oaks, however, indicated a distinctly higher variation of their neighbours in terms of height. Frequently, the differences between nearest neighbours of oaks were up to 30–50%. The exception was the stand in Piaski, where the trees surrounding oaks usually did not differ in height by more than 30%. The spatial differentia-

tion of DBH in the studied stands was clearly greater than that of height. The differences reached even 70% amongst some neighbouring trees. The trees surrounding oaks were characterised by an average DBH variation, except for Piaski stand, where the trees surrounding oaks were very similar to the reference trees.

The small differences in the size of trees observed in the managed stands is often the result of the silviculture practices carried out, favouring the structural homogenisation of forest stands. But there are a number of opportunities available to increase the diversity of the composition and structure of managed forests, for example, through the use of complex renewal cuttings or structural and selective thinning or felling (Bilski, Brzeziecki, 2005; Paluch, Bielak 2009; Jaworski 2011). In protected forests using passive protection, natural processes shape the structure and composition of the forests. As shown by many years of research on the dynamics of these forests, their structural diversity can be surprisingly low (Brzeziecki et al. 2016).

4.2. Species diversity of the stands

One of the frequently used indicators of species diversity of plant communities, including forests, is the Shannon diversity index (Magurran 2004; Pretzsch 2010). Its significant disadvantage, however, is the excessive weight it assigns to a rare species in terms of its share in species composition, with little attention paid to abundant species. As a result, the value of this index disproportionately increases in communities consisting of only few species. As with the profile index, the use of the evenness index, E_{gat} (Pretzsch 2010), is recommended in order to compare the species diversity amongst the different forest stands. Species diversity was the highest in the managed stand in Jelonek and then in both of the protected stands. The lowest species diversity was found in the Piaski managed stand. The number of species and their share in species composition do not reveal information about the spatial relationships in the distribution of species. The spatial distribution of species can be inferred based on the SM index. The higher the value, the greater is the mingling of the species. The highest diversity of the studied oak stands was found in the Jelonek managed stand and then in the Smoszew reserve. In both stands, the share of trees in each diversity class was substantially uniform. On the basis of the distribution of SM index values for the oaks, it was found that this species was dispersed in the forest as an individual admixture, so the trees surrounding the oaks mainly consist of other species (hornbeam, sycamore or beech). The moderate species diversity found in the analysed oak stands was consistent with the studies of Müller et al. (2000) and Indira et al. (2013). Strong uni-

formity of species composition and age structure of stands growing in the strictly protected stands in the Świętokrzyski National Park was found by Brzeziecki et al. (2011) over many years of observation. During the 45-year study period, spruce and fir clearly decreased in favour of deciduous species, that is, beech and sycamore, which in the same period increased their share in the stand. The mutual replacement of species is often the result of competition between them, won by the stronger species. The weaker species in the analysed oak stands is oak. As a heliophilous species, it is not finding favourable regeneration sites under the dense canopy of hornbeam. Interesting research spanning several decades on the variability of species composition in the protected forests of Białowieża National Park (BNP) is presented by Bernardzki et al. (1998), Brzeziecki et al. (2012) and Brzeziecki et al. (2016). Whilst analysing the growth and development of stands at permanent experimental plots, they found that some of the so-called primeval species, such as oak, pine, ash and aspen, are now ageing populations, threatened by an at least temporary disappearance from the stand layer. The most expansive species in areas under strict protection proved to be hornbeam and lime (Brzeziecki et al. 2012; Brzeziecki et al. 2016). The authors also pointed out that the likely loss of some forest tree species in the stand will result in a decrease of the overall diversity of the forest ecosystems in Białowieża Forest. Strict protection consisting only of preserving natural ecological processes does not necessarily translate into increased forest biodiversity. The homogenisation of species composition relating to hornbeam expansion and the elimination of oak (the disintegration of the stand) may be taking place in the studied reserves. Both phenomena are of course natural processes, but keep in mind that the purpose of the protection of both reserves is to preserve specific deciduous forest communities, of which oak is an important element. Taking this into account, it seems reasonable to consider the possibility of instituting the more active protection of these communities in order to ensure the sustainability of oak. Such possibilities are provided by appropriate silviculture practices. Drozdowski et al. (2012) obtained interesting results of the impact of such practices on the formation of species composition and the status of various species' dynamics in the managed stands of Białowieża Forest in its Hajnówka and Białowieża Forest Divisions. Studies have shown that the homogenisation of species composition in the BNP was similar in both the managed forests as well as the strict reserve, yet through the efforts of breeding practices (renewal cuttings), the process was significantly slower in the managed stands. Another example of research that indicates the rational use of active forms of nature conservation through the use of appropriate breeding and renewal cuttings are the studies of Petrit et al.

(2012) in the oak and beech forests of Romania, where oak renewal was prevented by the expansive beech. The difficulties in natural regeneration of oak on a largely shaded forest floor under conditions of conservation protection is being observed by Wiczyńska et al. (2013) and Horodecki et al. (2014) in the Czmoń nature reserve. In light of the results obtained and data from the literature, it can, therefore, be assumed that the sustainability of acidophilous oak and hornbeam forests with the dominating pedunculate oak in the analysed forest reserves is threatened, given the absence of natural disturbances and the lack of active protection methods used in forest management. The hornbeams dominating in these forests, a shade-tolerant species that heavily dims the forest floor, effectively prevents the renewal of heliophilous oaks. In continuing to maintain conservation protection, only the occurrence of a natural disturbance will disrupt the dense canopy layer of hornbeam to result in favourable ecological conditions for the renewal of oak.

4.3. The spatial pattern of the trees

A regular spatial distribution of live trees was confirmed only in the Piaski managed stand. This is most likely the result of intense silviculture practices promoting the proper growth and development of the most valuable oak trees by removing the surrounding trees that could restrict this (Müller et al. 2000; Brzeziecki, 2005; Bončina et al. 2007; Indira et al. 2013). In the second of the analysed managed stands, the distribution of all live trees, as well as beech and hornbeam, was random. A regular pattern was observed in the case of oak. In the protected sites (forests reserves) where no management activities were carried out for the past 50 years, a more or less regular spatial distribution of trees in the stand is also not uncommon. This regularity becomes more apparent as the stand ages, resulting from the competitive interaction between individuals in the immediate vicinity. More often, however, natural or nearly natural forests have a spatial distribution of trees that is aggregate or random (Szwagrzyk 1992; Brzeziecki, 2005; Das et al. 2011; Petritan et al. 2012; Forrester 2014; Wehenkel et al. 2015; Zenner et al. 2015). The results obtained from the two reserves are, therefore, consistent with earlier studies. The aggregations of trees encourage a spatial mosaic of habitat conditions, varied ecological and biological requirements of species and the manner of their renewal (Müller et al. 2000; Wiegand et al. 2007, 2009; Zhang et al. 2010). The clustered arrangement of trees in Biadki resulted, amongst others, from the aggregate occurrence of hornbeams, which comprised 90% of quantitative share of species. The oaks were arranged regularly only in Smoszew and Biadki, but their incidence did not differ from a random pattern.

5. Conclusions

The analysis of human impact on the structural diversity of mixed oak stands using different structural indicators allows the following conclusions to be formulated:

The use of different indicators of the structural diversity of trees, and in particular spatial indicators, provides more detailed information on the stand, its diversity in terms of species, construction and structure. Commonly used synthetic indicators, such as the coefficient of variation and Gini indices, characterise the study population in general terms, whilst spatial indices (*SM*, *TD / TH* and *R*) allow the state of the stand to be analysed in more detail.

The conservation of the old reserve stands of pedunculate oak is conducive to an increasing uniformity of their structure, especially in terms of species diversity.

Both the reserve stands and managed stands can have a similar level of diversity in terms of their construction and structure. On one hand, the intensive silviculture practices conducted in the less species diverse oak stands lead to their structural homogenisation. On the other hand, silviculture practices in managed stands with a more diverse species composition can promote the formation of a more complex structure and construction.

The results obtained, supported by the results of earlier studies by other authors, suggest that under conditions of passive protection, in the absence of natural disturbances and the presence of the strongly competitive and expansive hornbeam, the sustainability of oak in protected forest teams is not ensured. An alternative may be to carry out active protection measures, which, under skilfully guided breeding and renewal cuttings, will provide the favourable conditions for the establishment, growth and development of oak, ensuring the sustainability of this protected species for future generations.

Conflict of interest

The author declares no conflicts of interest.

Acknowledgements and sources of funding

The research was funded by the Silviculture Department of the Poznań University of Life Sciences.

References

- Aguirre O., Hui G., Gadow K. Von, Jiménez J. 2003. An analysis of spatial forest structure using neighbourhood-based variables. *Forest Ecology and Management* 183: 137–145.

- Baddeley A., Turner R. 2005. Spatstat: An R Package for Analyzing Spatial Point Patterns. *Journal of Statistical Software* 6: 1–42. <http://www.jstatsoft.org/v12/i06/> [1.02.2016].
- Biber P., Weyerhaeuser H. 1998. Numerical methods for characterizing structure and diversity applied to a natural tropical forest and an even aged teak stand, in: Natural and Socioeconomic analysis and modelling of forest and agroforestry systems in Southeast Asia. (ed. E. Mies). <http://www.wwk.forst.tu-muenchen.de/info/publications/OnlinePublications/482.pdf>. [2.02.2016].
- Balanda M. 2012. Spatio-temporal structure of natural forest: a structural index approach. *Beskydy* 5: 163–172
- Bernadzki E., Bolibok L., Brzeziecki B., Zajęzkowski J., Żybura H. 1998. Compositional dynamics of natural forests in the Białowieża National Park, northeastern Poland. *Journal of Vegetation Science* 9: 229–238.
- Bilski M., Brzeziecki B. 2005. Wpływ trzebieży przerębowej na zróżnicowanie strukturalne drzewostanu. *Sylvan* 4: 21–34.
- Bobinac M. 2000. Stand structure and natural regeneration of common oak in the nature reserves “Vraticna” and “Smogva” near Morovic. *Glasnik za sumske pokuse* 37: 295–309.
- Boncina A., Kadunc A., Robic D. 2007. Effects of selective thinning of growth and development of beech (*Fagus sylvatica* L.) forest stands in south-eastern Slovenia. *Annals of Forest Science* 64: 47–57.
- Brooker R.W., Brooker R.W. 2006. Plant – plant interactions and environmental change. *New Phytologist* 171: 271–284.
- Brzeziecki B. 2002. Wskaźniki zróżnicowania struktury drzewostanu. *Sylvan* 4: 69–88.
- Brzeziecki B. 2005. Wpływ trzebieży na zróżnicowanie strukturalne drzewostanów sosnowych. *Sylvan* 10: 11–20.
- Brzeziecki B., Janicki S., Wiech M. 2011. Wieloletnia dynamika drzewostanów na dawnym zrębie kulisowym w warunkach ochrony ścisłej (Łysica, Góry Świętokrzyskie). *Sylvan* 8: 518–530
- Brzeziecki B., Keczyński A., Zajęzkowski J., Drozdowski S., Gawron L., Buraczyk W., Bielak K., Szeliński H., Dzwonkowski M. 2012. Zagrożone gatunki drzew Białowieżskiego Parku Narodowego (Rezerwat Ścisły). *Sylvan* 156(4): 252–261
- Brzeziecki B., Pommerening A., Miścicki S., Drozdowski S., Żybura H. 2016. A common lack of demographic equilibrium among tree species in Białowieża National Park (NE Poland): evidence from long-term plots. *Journal of Vegetation Science* 27: 460–469. DOI 10.1111/jvs.12369.
- Ceitel J. 2006. Lasy dębowe w Polsce, in: Dęby. Nasze drzewa leśne. Instytut Dendrologii PAN, Kórnik.
- Das A., Battles J., Stephenson N.L. van Mantgem P.J. 2011. The contribution of competition to tree mortality in old-growth coniferous forests. *Forest Ecology and Management* 261: 1203–1213. DOI 10.1016/j.foreco.2010.12.035.
- Del Rio M., Pretzsch H., Alberdi I., Bielak K., Bravo F., Brunner A., Condes S., Ducey M.J., Fonseca T., Lupke N. von, Pach M., Peric S., Perot T., Souidi Z., Spathelf P., Sterba H., Tijardovoc M., Tome M., Vallet P., Bravo-Oviedo A. 2015. Characterization of the structure, dynamics, and productivity of mixed-species stands: review and perspectives. *European Journal of Forest Research* 135(1): 23–49. DOI 10.1007/s10342-015-0927-6.
- Donnelly K.P. 1978. Simulation to determine the variance and the edge effect of total nearest-neighbor distances, in: Simulation methods in Archeology (ed. I. Hodder). Cambridge Press, London, 91–95.
- Drozdowski S., Bielak K., Buraczyk W., Gawron L., Jaros R., Żybura H. 2014a. Planowanie hodowlane w drzewostanach jodłowych o złożonej strukturze z wykorzystaniem metody BDq w Nadleśnictwie Zagnańsk. *Sylvan* 9: 651–661.
- Drozdowski S., Andrzejczyk T., Bielak K., Buraczyk W., Gawron L. 2014b. Planowanie hodowlane z wykorzystaniem metody DBq w drzewostanach świerkowych na siedliskach bagiennych. *Sylvan* 10: 733–743.
- Eichhorn M.P. 2010. Pattern reveals process: spatial organization of Kamchatkan stone birch forest. *Plant Ecology and Diversity* 3: 281–288.
- Fibich P., Leps J., Novotny V., Klimes P., Tesitel J., Molem K., Damas K., Weiblen G. 2016. Spatial patterns of tree species distribution in New Guinea primary and secondary lowland rain forest. *Journal of Vegetation Science* 27(2): 328–339. DOI 10.1111/jvs.12363.
- Forrester D.I. 2014. The spatial and temporal dynamics of species interactions in mixed-species forests: From pattern to process. *Forest Ecology and Management* 312: 282–292.
- Gadow K. von, Zhang C.Y., Wehenkel C., Pommerening A., Corral-Rivas J., Korol M. et al. 2012. Forest structure and diversity, in: Continuous Cover Forestry. Managing Forest Ecosystems (eds. T. Pukkala, K. Gadow). Springer Science+Business Media B.V.
- Gadow K. v. Hui G. 2002. Characterising forest spatial structure and diversity, in: Sustainable forestry in temperate regions. (ed. L. Bjoerk). Materiały konferencyjne IUFRO, Lund, 20–30.
- Getzin S., Dean C., He F., Trofymow J.A., Wiegand K., Wiegand T. 2006. Spatial patterns and competition of tree species in a Douglas-fir chronosequence on Vancouver Island. *Ecography* 29: 671–682.
- Hobi M., Commarmot B., Bugmann H. 2015. Pattern and process in the largest primeval beech forest of Europe (Ukrainian Carpathians). *Journal of Vegetation Science* 26: 323–336.
- Horedecki P., Wiczyńska K., Jagodziński A.M. 2014. Odnowienie naturalne w rezerwacie przyrody „Czmoń” (Wielkopolska). *Leśne Prace Badawcze* 75: 61–75. DOI 10.2478/frp-2014-0007.
- Indir K., Balenovic I., Paladinic E., Marjanovic H., Szirovicza L., Vuletic D. 2013. Spatial structure indices of mature pedunculate oak stands in NW Croatia. SEEFOR South-East European Forestry.
- Iszkuło G., Didukh Y., Giertych M.J., Jasińska A.K., Sobierajska K., Szmyt J. 2013. Weak competitive ability may explain decline of *Taxus baccata*. *Annals of Forest Science* 69: 705–712.
- Jaworski A. 2011. Hodowla lasu: Sposoby zagospodarowania, odnowienie lasu, przebudowa i przemiana drzewostanów. PWRiL, Warszawa.
- Kenkel N.C. 1988. Pattern of self-thinning in jack pine: testing the random mortality hypothesis. *Ecology* 69: 1017–1024

- Kint V., Lust N., Ferris R., Olsthoorn A.F.M. 2000. Quantification of forest stand structure applied to Scots pine (*Pinus sylvestris* L.) forests. *Investigación Agraria: Sistemas y Recursos Forestales: Fuera de Serie* 1: 147–163.
- Kucbel S., Saniga M., Jaloviar P., Vencurik J. 2012. Stand structure and temporal variability in old-growth beech-dominated forests of the northwestern Carpathians: A 40-years perspective. *Forest Ecology and Management* 264: 125–133. DOI 10.1016/j.foreco.2011.10.011.
- Longuetad F., Seifert T., Leban J.M., Pretzsch H. 2008. Analysis of long-term dynamics of crowns of sessile oaks at the stand level by means of spatial statistics. *Forest Ecology and Management* 255: 2007–2019.
- Lexerød N.L., Eid T. 2006. An evaluation of different diameter diversity indices based on criteria related to forest management planning. *Forest Ecology and Management* 222 (1–3): 17–28.
- Lähde E., Laiho O., Norokorpi Y. 1999. Diversity-oriented silviculture in the Boreal Zone of Europe. *Forest Ecology and Management* 118 (1–3): 223–243.
- Magurran A.E. 2004. Measuring biological diversity. Blackwell Science Ltd.
- Matuszkiewicz J.M. 2011. Przemiany w zespołach leśnych Puszczy Białowieskiej w drugiej połowie XX wieku (Rezerwat Ścisły BPN). *Czasopismo Geograficzne* 82: 69–105
- McElhinny C., Gibbons, P. Brack, C. Buhus, J. 2005. Forest and woodland stand structural complexity: Its definition and measurement. *Forest Ecology and Management* 218(1–3): 1–24.
- Mosandl R., Kleinert A. 1998. Development of oaks (*Quercus petraea* (Matt.) Liebl.) emerged from bird-dispersed seeds under old-growth pine (*Pinus sylvestris* L.) stands. *Forest Ecology and Management* 106(1): 35–44.
- Montes F., Cañellas I., Río M. del 2004. The effects of thinning on the structural diversity of coppice forests. *Annals of Forest Science* 61: 771–779.
- Müller S., von Ammer C., Nusslein S. 2000. Analyses of stand structure as a tool for silvicultural decisions – a case study in a *Quercus petraea*-*Sorbus torminalis* stand. *Forstwissenschaftliches Centralblatt* 119: 32–42.
- McIntire E.J., Fajardo A. 2009. Beyond description: the active and effective way to infer processes from spatial patterns. *Ecology* 90: 46–56.
- Neumann M., Starlinger F. 2001. The significance of different indices for stand structure and diversity in forests. *Forest Ecology and Management* 145: 91–106.
- Oliver C., Larson B.C. 1996. Forest stand dynamics. John Wiley & Sons, Inc. Chichester.
- Paluch R., Bielak K. 2009. Przebudowa drzewostanów z wykorzystaniem naturalnych procesów sukcesyjnych w Puszczy Białowieskiej. *Leśne Prace Badawcze* 70(4): 339–354.
- Pastorella F., Paletto A. 2013. Stand structure indices as tools to support forest management: An application in Trentino forests (Italy). *Journal of Forest Science* 59(4): 159–168.
- Petritan A.M., Biris I.A., Merce A., Turcu D.O., Petritan I.C. 2012. Structure and diversity of natural temperate sessile oak (*Quercus petraea* L.) European beech (*Fagus sylvatica* L.) forest. *Forest Ecology and Management* 280: 140–149.
- Petritan I.C., Commarmot B., Hobi M.L., Petritan A.M. Bigler C., Abrudan I.V., Rigling A. 2015. Structural patterns of beech and silver fir suggest stability and resilience of the virgin forest Sinca in the Southern Carpathians, Romania. *Forest Ecology and Management* 356: 184–195.
- Pommerening A. 2002. Approaches to quantifying forest structures. *Forestry* 75: 305–324.
- R Core Team 2015. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/> [3.02.2016].
- Pretzsch H. 1996. The effect of various thinning regimes on the spatial stand structure, in: Effects of environmental factors on tree and stand growth. Conference materials, 183–191.
- Pretzsch H. 2010. Forest Dynamics, growth and yield. Berlin Heidelberg, Springer-Verlag.
- Sterba H. 2008. Diversity indices based on angle count sampling and their interrelationships when used in forest inventories. *Forestry* 81(5): 587–597.
- Raventós J., Wiegand T., De Lusie M. 2010. Evidence for the spatial segregation hypothesis: a test with nine-year survivorship data in a Mediterranean shrubland. *Ecology* 91: 2110–2120.
- Szwagrzyk J. 1992. Small-scale spatial patterns of trees in a mixed *Pinus sylvestris*-*Fagus sylvatica* forest. *Forest Ecology and Management* 51: 301–315.
- Saunders M.R., Wagner R.G. 2008. Long-term spatial and structural dynamics in Acadian mixedwood stands managed under various silvicultural systems. *Canadian Journal of Forest Research* 38(3): 498–517.
- Spies T. 1998. Forest structure: a key to the ecosystem. *Northwest Science* 72(2): 34–39. <http://scholar.google.com/scholar?hl=en&btnG=Search&q=intitle:Forest+Structure+:+A+Key+to+the+Ecosystem#0> [6.02.2016].
- Szmyt J., Ceitel J. 2011. Zróżnicowanie przestrzenne i grubościowe drzew w niepielegnowanych drzewostanach sosnowych o różnym zagęszczeniu początkowym. *Sylwan* 155: 749–759
- Szmyt J. 2012. Spatial structure of managed beech-dominated forest: Applicability of nearest neighbors indices. *Dendrobiology* 68: 69–76.
- Szymański S. 2000. Ekologiczne podstawy hodowli lasu. PWRiL, Warszawa.
- Trampler T., Kliczkowska A., Dmyterko E., Sierpińska A., Matuszkiewicz W. 1990. Regionalizacja przyrodniczo-leśna na podstawach ekologiczno-fizjograficznych. PWRiL, Warszawa.
- Wehenkel C. Brazao-Protazio J.M., Carillo-Parra A., Martinez-Guerrero J.H., Crecente-Campo F. 2015. Spatial distribution patterns in the very rare and species-rich *Picea chihuahuana* tree community (Mexico). *PLoS ONE* 10(10): e0140442. DOI 10.1371/journal.pone.0140442.
- Wiczyńska K., Horodecki P., Jagodzińska A.M. 2013. Stand structure and species composition in the „Czmoń” nature reserve. *Nauka Przyroda Technologie* 7: #69.
- Wiegand T., Gunatilleke S, Gunatilleke N, Okuda T. 2007. Analyzing the spatial structure of a Sri Lankan tree species with multiple scales of clustering. *Ecology* 88(12): 3088–3102.
- Wiegand T., Martinez I., Huth A. 2009. Recruitment in tropical tree

- species: revealing complex spatial patterns. *American Naturalist* 174: E106–E140.
- Wilson J.B. 2011. The twelve theories of co-existence in plant communities: The doubtful, the important and the unexplored. *Journal of Vegetation Science* 22: 184–195. DOI 10.1111/j.1654-1103.2010.01226.x.
- Youngblood A., Max T., Coe K. 2004. Stand structure in eastside old-growth ponderosa pine forests of Oregon and northern California. *Forest Ecology and Management* 199(2–3): 191–217.
- Zenner E.K. 2004. Does old-growth condition imply high live-tree structural complexity? *Forest Ecology and Management* 195 (1–2): 243–258.
- Zenner E.K., Lähde E., Laiho O. 2011. Contrasting the temporal dynamics of stand structure in even- and uneven-sized *Picea abies* dominated stands. *Canadian Journal of Forest Research* 41(2): 289–299.
- Zenner E.K., Peck J.E., Hobi M.L., Commarmot B. 2015. The dynamics of structure across scale in a primeval European beech stand. *Forestry* 88: 180–189. DOI 10.1093/forestry/cpu042.
- Zhang Z.H., Zhang, Hu G., Zhu J.D., Luo D.H., Ni J. 2010. Spatial patterns and interspecific associations of dominant tree species in two old-growth karst forests, SW China. *Ecological Research* 25: 1151–1160.