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ORIGINAL PAPER

Long-term transformation of submontane spruce-beech forests in the Jizerské hory Mts.: dynamics of natural regeneration

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Abstract
The paper deals with development of the natural regeneration of even-aged spruce-beech forests during their transformation to uneven-aged stands with diversified structure at the Jedlový důl area in the Protected Landscape Area Jizerské hory Mts., Czech Republic. Shelterwood management system and free felling policy based on selection principles has been applied there since 1979 with the support of admixed tree species of the natural species composition, especially silver fir (*Abies alba* Mill.). The research was focuses on structure and development of natural regeneration with the emphasis on ungulate damage and interaction with tree layer from 1979 to 2015. In the course of 36 years, the regeneration structure was diversified towards the close-to-nature tree species composition, spatial and age structure. The number of regeneration recruits increased in average from 941 to 41,669 ind ha^{-1}. During this period share of European beech (*Fagus sylvatica* L.) significantly ($p < 0.01$) increased (by 53.6%), while the share of Norway spruce (*Picea abies* [L.] Karst.) decreased (by 51.5%), such as damage caused by ungulate (by 61.4%) with the highest loses on sycamore maple (*Acer pseudoplatanus* L.), rowan (*Sorbus aucuparia* L.) and silver fir. Moreover, the parent trees had a significant negative influence on natural regeneration at smaller spacing (within a 1 – 5 m radius from the stem). Both, regeneration potential and effective role of the tree layer during the forest transformation has been confirmed as important prerequisites for ongoing forest transformation.

Keywords: regeneration development; forest transformation; shelterwood system; stand structure; browsing damage

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1. Introduction

Currently, many studies are devoted to sustainable forest management and conservation of biological diversity (Fürst et al. 2007; Pretzsch et al. 2008; Pimm et al. 2014; Schulze et al. 2016; Correia et al. 2017). Most national forest strategies have been formulated in support of this trend e.g. 2016–2025 Strategy of Conserving Biological Diversity of the Czech Republic (Mach et al. 2016). There is also a strong emphasis on the transformations of forest stands that were degraded in the past (Stanturf et al. 2014) or have undergone significant changes in the last 70 years. This happened mainly in the former socialist countries of Eastern and Central Europe, where nationalization of forest estates, vast plantations of conifers and subsequent restitutions in the 90s of the 20th century took place (Bouriaud et al. 2015; Podrázský et al. 2014; Schulze et al. 2014). In addition, anthropogenic changes in global ecosystems (Kareiva et al. 2007; Ellis et al. 2013) and assumed impacts of climate change still enhance the need of forest stand transformation (Steffen et al. 2007; Zalasiewicz et al. 2010; Kulla & Sitková 2012). Transformations become part of a broader strategy of climate change mitigation, and other urgent environmental problems of this time such as loss of biological diversity (Thomas et al. 2014; Spiecker et al. 2004). One of the crucial factors influencing the success of performed forest transformations is the existence of natural regeneration that is more productive and resistant to external environmental impacts in comparison with artificial regeneration (Hasanov et al. 2016). At the same time it also is an indicator of forest vitality and stability (Šticha et al. 2010). Natural regeneration is an inherent element of natural forest dynamics and belongs to the general concept of forest adaptation on the basis of forest dynamics and its management including active and passive strategies of forest ecosystem management (Millar et al. 2007).

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Taking into account vast forest areas that are suitable for stand transformations, approaches accentuating the ecosystem functionality can be more beneficial contrary to conventional approaches aimed at predetermined species composition at small area units (Lamb et al. 2012; Oliver 2014). A determinant trait of functional transformations is orientation to sustainability in multifunctional ecosystem processes including hydrological cycles and ecosystem productivity (Stanturf et al. 2014).

In the past there were forest ecosystem transformations with limited success only or that failed completely (Wuethrich 2007). This is the reason why it is important that current and future projects, which usually demand great efforts and many times considerable investments, will be performed in a sustainable and relatively flexible way. In this context Wagner (2004) presented adaptive forest management aimed at maintenance and development of forest functionality as a precondition to meet future needs of forest ecosystems. Such management is defined as a dynamic approach, where the consequences of interventions and particular decisions are monitored and evaluated all the time. This approach continually affects future management steps for the purpose of optimum fulfilment of management objectives (Bolte et al. 2009). Mostly, reasons for forest transformation failure are genetically inconvenient reproductive material not sufficiently adapted to conditions of the given environment and unsuitable silvicultural methods and techniques (Godefroid et al. 2011; Wenying et al. 2013). The reproductive material is very important for transformation because it influences transformation success from both short-term and long-term aspects (Thomas et al. 2014). Genetic suitability positively influences not only individual tree populations (Breed et al. 2012) but also the general ecosystem function and resistance (Thompson et al. 2010; Kettenring et al. 2014).

In the framework of transformations of spruce-beech stands and ongoing climate changes it is to take into account that long-term temperature increase is considered as a reason for higher competitiveness of beech in comparison to spruce (Grundmann et al. 2011). It is to note that spruce is more vulnerable to heat and drought events because of its shallow root system (Schmid 2002; Bolte et al. 2014) and its adaptation to cold and humid climate (Latałowa & van der Knaap 2006). Therefore an increasing proportion of beech is to expect in future at many sites in the Central European region (Menšík et al. 2009).

The objective of the present study is to evaluate natural regeneration in relation to the tree layer within forest stand transformation from 1979 to 2015. The study should answer the following questions:

– which changes have occurred in the species composition of natural regeneration,
– which changes have occurred in the maturity and spatial pattern of regeneration,
– which changes have occurred in the biodiversity of regeneration,
– how ungulates have affected the height structure and species composition of regeneration,
– what is the relation between natural regeneration and tree layer.

The basic hypothesis is that forest stands with this silvicultural strategy have higher ecological stability and biodiversity compared to evenaged spruce-dominated stands.

2. Material and methods

2.1. Study site

The territory of interest in the area of Jedlový důl in the Jizerské hory Mts. is RC1265 Josefodol I Regional Biocentre, which encompass the Josefův důl Gene Resources. At the same time, this territory is part of the Jizerské hory Protected Landscape Area (PLA) and Jizerské hory Bird Conservation Area CZ0511008.

In terms of the CR geomorphological classification according to Demek et al. (1987) the territory of interest belongs to the Krkonoše-Jeseníky range system (province), Krkonoše Mts. subsystem (subprovince), Jizerské hory Mts. area and Jizerská hornatina subarea. The bedrock is composed of porphyritic medium-grained granite or granodiorite of the Krkonoše-Jizerské hory granite pluton (Chaloupský 1989). Cambisols and Cryptopodzols are prevailing soil types. The climate of the area is suboceanic, which is related to the distinctly windward position of the Jizerské hory Mts. Average annual temperature is in the range of 5.2 – 6.5 °C relative to the altitude. Annual precipitation amounts are 1 200 – 1 300 mm. The study territory belongs to humid continental climate characterised by hot and humid summers and cold to severely cold winters (Dfb) with the transition to subarctic climate (Dfc) according to Köppen climate classification (Köppen 1936), respectively by detailed region Quitt distribution (Quitt 1971) to a cold climatic region and CH 7 subregion.

The studied territory is covered by foothills spruce-beech forests of more or less natural type. These are mostly highly structured stands of European beech (*Fagus sylvatica* L.), Norway spruce (*Picea abies* [L.] Karst.), interspersed sycamore maple (*Acer pseudoplatanus* L.), silver fir (*Abies alba* Mill.), rowan (*Sorbus aucuparia* L.) and silver birch (*Betula pendula* Roth.) with ongoing natural regeneration of all above-mentioned species. The fir was introduced into these stands in the 80s and 90s of the 20th century through group underplantings (combined regeneration). In terms of phytocoenology these are mostly acidophilous foothills beech forests (the association *Luzulo luzuloidis–Fagetum sylvaticae* Meusel 1937, *Calamagrostio villosae–Fagetum* Mikyška 1972) and partly impoverished forms of herb-rich beech forests (the association *Dentario enneaphylli–Fagetum* Oberdorfer ex W. et A. Matuszkiewicz 1960).

Figure 1 shows the location of .permanent research plots (PRP) while basic data on PRP are documented in Table 1. On all PRP the growing season length is about 131 days, average temperature in the growing season is around 10.7 °C and rainfall amount in the growing season is 646 mm on average. The bedrock of all PRP is built of porphyritic, medium-grained granite. Soil type is predominantly modal Cambisol.

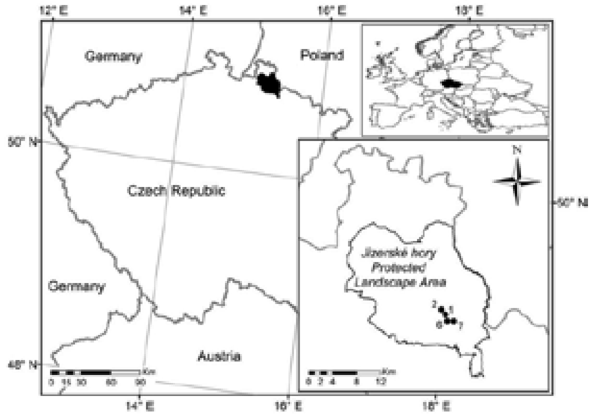

Fig. 1. Localization of spruce-beech forests on permanent research plots 1, 2, 6 and 7 in the Jizerské hory Mts.

2.2. Data collection

To determine the tree layer and regeneration structure of forest ecosystems 4 PRP of 50 × 50 m in size (0.25 ha) were established in 1979 by prof. S. Vacek and Ing. Z. Cipra in cooperation with Forest Research Station at Opočno and PLA Administration Jizerské hory Mts. using theodolite (Vacek & Cipra 1979). In 2015 the FieldMap technology (IFER–Monitoring and Mapping Solutions Ltd.) was used for the re-measurement.

For the individuals of regeneration with breast-height diameter (dbh) < 4 cm and height ≥ 150 cm these characteristics were measured on the whole plot: position, height, distance of live crown base to the ground level, crown width (with a height measuring pole to the nearest cm), root collar diameter and the species was identified. The same parameters were measured for recruits in height range 5 – 150 cm, only on representative subplots 10 × 50 m in size on each PRP. Browsing by ungulate on leading shoots (0 = no browsing, 1 = the first browsing of leading shoot, 2 = repeated browsing of leading shoot) was monitored in all recruits as specified according to the tree species lateral browsing was studied in the same way.

2.3. Data analysis

Structural and growth parameters, abundance, vertical structure, spatial pattern and species diversity were evaluated for all individuals of regeneration on each plot. For evaluation of species diversity of natural regeneration following indices were used: species richness indices D_1 (Margalef 1958) and D_2 (Menhinick 1964), species heterogeneity indices $H´$ (Shannon 1948) and λ (Simpson 1949) and species evenness indices E_1 (Pielou 1975) and E_2 (Hill 1973). The height structure was evaluated by the Gini index G using individual recruit data (Gini 1921). The Gini coefficient was calculated using equation according to Glasser (1962). Criteria for the assessment of these biodiversity indices are shown in Table 2.

For the spatial pattern of regeneration these indices were computed: Hopkins-Skellam index A (Hopkins & Skellam 1954), Pielou-Mountford index α (Pielou 1959; Mountford 1961), Clark-Evans index R (Clark & Evans 1954) and Ripley's K–function (Ripley 1981). Among dis-

Table 1. Basic site and stands characteristics of permanent research plots.

PRP	GPS coordinates	Altitude [m]	Exposition	Slope [°]	Forest site type[1]	Tree species[2]	Felling (1979–2015) [m³ ha⁻¹]	Year of record	Age of tree layers (y)	Stand volume [m³ ha⁻¹]	Number of trees [trees ha⁻¹]
1	50°47´26˝ N 15°15´02˝ E	750	SE	9	6S	FS, PA, AA, SA	63	1979 2015	153/22 117	559 604	408 1032
2	50°47´28˝ N 15°14´59˝ E	730	SE	8	6S	FS, PA, AA, AP	150	1979 2015	153/26 117	604 536	420 1464
6	50°47´24˝ N 15°15´04˝ E	765	SE	7	6S	FS, PA, AA, SA, BP	67	1979 2015	153/26 117	489 530	380 1464
7	50°47´25˝ N 15°15´11˝ E	725	SE	11	6S	FS, PA, AA, AP	82	1979 2015	153/22 117	400 497	444 1424

Explanatory notes: [1]6S – *Piceo-Fagetum oligomesotrophicum*, *Calamagrostio villosae-Fagetum* Mikyška 1972; Species[2]: FS – *Fagus sylvatica*, PA – *Picea abies*, AA – *Abies alba*, SA – *Sorbus aucuparia*, AP – *Acer pseudoplatanus*, BP – *Betula pendula*.

Table 2. Overview of the indices describing regeneration diversity and their interpretation.

Criterion	Quantifiers	Label	Reference	Evaluation
Species diversity	Heterogeneity	H´ (Shi) λ (Sii)	Shannon (1948) Simpson (1949)	minimum H´ (λ) = 0, higher H´ (λ) = higher values
	Evenness	E_1 (Pi) E_2 (Hi)	Pielou (1975) Hill (1973)	range 0 – 1; minimum E = 0, maximum E = 1
	Richness	D_1 (Mai) D_2 (Mei)	Margalef (1958) Menhinick (1964)	minimum D = 0, higher D = higher values
Horizontal structure	Index of non-randomness	α (P&Mi) A (H&Si)	Pielou (1959); Mountford (1961) Hopkins & Skellam (1954)	mean value α = 1, aggregation α > 1, regularity α < 1 mean value A = 0.5, aggregation A > 0.5, regularity A < 0.5
	Aggregation index	R (C&Ei)	Clark & Evans (1954)	mean value R = 1, aggregation R < 1, regularity R > 1
	Index of cluster size	CS (D&Mi)	David & Moore (1954)	mean value CS = 0, aggregation CS < 0, regularity CS > 0
Vertical structure	Gini index	G (Gi)	Gini (1921); Glasser (1962)	range 0 – 1; low G < 0.3, very high differentiation G > 0.7

tribution indices based on the tree frequency in particular quadrats the David-Moore index *CS* (David & Moore 1954) was used. The chosen size of quadrats on PRP was 10 × 10 m (25 quadrats). To compute these characteristics describing the horizontal structure of individuals on the plot the PointPro 2 programme (© 2010 CULS, Zahradnik & Pus, Prague) was used. The test of significance of deviations from the values expected for the random pattern of points was done by Monte Carlo simulations (95% confidence interval). The mean values of the *K*–function were estimated as arithmetical means of the *K*–functions computed for 1999 randomly generated point structures. The spatial relations of natural regeneration and tree layer were evaluated by the cross-type pair correlation function *g(r)* – (Stoyan & Stoyan 1992).

Statistical analyses were processed in Statistica 13 (© 2016 Del Inc., Tulsa). Differences in tree species composition, game damage and diversity indices of natural regeneration recruits in course of time and among PRP were tested by one-way analysis of variance (ANOVA) and significant differences were consequently tested by post-hoc comparison Tukey's HSD tests. Significance of statistics was noted as follows: $p > 0.05$, $p < 0.05$, $p < 0.01$ and $p < 0.001$. Unconstrained principal component analysis (PCA) in the CANOCO for Windows 5 program (© 2013 Biometris, ter Braak & Smilauer, Wageningen) was used to analyse relationships among natural regeneration parameters, characteristic of tree layer, tree species, time and similarity of 4 PRP. Data were centred and standardized during the analysis. The results of the PCA analysis were visualized in the form of an ordination diagram.

3. Results

3.1. Species composition and density

The number of natural regeneration on PRP in 1979 was from 680 (PRP 7) to 1,152 (PRP 6) recruits ha^{-1}. The proportion of beech on PRP at that time was 13 – 26%, spruce 67 – 83%, fir 0 – 1%, rowan 0 – 2%, birch 0 – 5% and sycamore maple 0 – 4%. The number of recruits (in fir also partly of individuals of combined regeneration – fir underplanting from denser natural seeding in the given stands was performed in 1980–1984) in 2015 ranged from 24,964 (PRP 1) to 77,036 (PRP 6) recruits ha^{-1}. The proportion of beech on PRP was 43 – 84%, spruce 15 – 52%, fir 0 – 6%, rowan 0 – 3% and the proportions of sycamore and birch were negligible (Table 3).

In the course of 36 years, the total number of natural regeneration significantly increased (44 times; $F_{(1,6)} = 11.7$, $p < 0.01$), respectively density of all main tree species ($F_{(1,30)} = 6.9$, $p < 0.01$). Specifically, significant increase ($p < 0.05$) were observed in spruce, beech and fir. In the study period, share of beech significantly increased ($F_{(1,6)} = 28.9$, $p < 0.01$) by 53.6%, while the share of spruce significantly decreased ($F_{(1,6)} = 30.0$, $p < 0.01$) by 51.5 %. There were no significant differences in density dynamics of fir ($F_{(1,6)} = 1.6$, $p > 0.05$; increase by 1.6%) and rowan ($F_{(1,6)} = 0.8$, $p > 0.05$; decrease by 0.9%).

3.2. Diversity

Table 4 shows the indices describing species diversity of natural regeneration on PRP. Species richness evaluated by the index of the relative measure of species diversity D_1 was medium on all PRP while it was low according to the D_2 index. According to the λ index the species diversity was medium on all PRP and by the entropy H' index it was medium on PRP 2 and 6, high on PRP 1 and low on PRP 7. The species evenness of natural regeneration according to the Pielou index of was low to medium and according to Hill index it was medium to high. Comparing individual PRP, there were observed similarity ($F_{(3,24)}=0.2$, $p > 0.05$) in diversity (except aggregation indices).

The spatial pattern of natural regeneration on all plots in 2015 was significantly aggregated ($A = 0.708 – 0.851$, $\alpha = 1.997 – 3.796$, $R = 0.714 – 0.832$, $CS = 5.516 – 8.477$) with the highest trend of clumpiness on PRP 7 (Table

Table 3. Per-hectare numbers (share) of natural regeneration (height ≥ 5 cm, dbh < 4 cm) specified according to tree species in 1979 and 2015.

PRP	Year	*Fagus sylvatica*		*Picea abies*		*Abies alba*		*Sorbus aucuparia*		*Betula pendula*		*Acer pseudoplatanus*		Total density
		recruits	%	recruits	%	recruits	%	recruits	%	recruits	%	recruits	%	recruits
1	1979	248	26.1	640	67.2	4	0.4	12	1.2	48	5.1	0	0	952
	2015	19,804	79.3	3,852	15.4	644	2.6	660	2.6	4	0	0	0	24,964
2	1979	136	13.9	816	83.3	8	0.8	4	0.4	16	1.6	0	0	980
	2015	13,888	42.5	16,968	51.9	1,816	5.6	4	0	0	0	0	0	32,676
6	1979	168	14.6	932	80.9	4	0.3	48	4.2	0	0	0	0	1,152
	2015	58,372	75.8	16,824	21.8	496	0.6	1,340	1.8	0	0	4	0	77,036
7	1979	88	12.9	540	79.4	8	1.2	16	2.4	0	0	28	4.1	680
	2015	26,896	84.1	5,036	15.7	64	0.2	4	0	0	0	0	0	32,000

Table 4. The indices describing the diversity of regeneration on permanent research plots 1, 2, 6 and 7 in 2015.

PRP	D_1 (Mai)	D_2 (Mei)	λ (Sii)	H' (Shi)	E_1 (Pi)	E_2 (Hi)	α (P&Mi)	A (H&Si)	R (C&Ei)	CS (D&Mi)	G (Gi)
1	0.466	0.068	0.454	0.856	0.532	0.615	0.795*	2.886*	0.791*	5.809*	0.399
2	0.349	0.054	0.354	0.631	0.455	0.624	0.815*	3.715*	0.832*	5.516*	0.459
6	0.433	0.049	0.306	0.562	0.349	0.583	0.708*	1.997*	0.819*	8.477*	0.499
7	0.365	0.066	0.524	0.307	0.221	0.958	0.851*	3.796*	0.714*	5.926*	0.518

Explanatory notes: D_1 and D_2 – indices of species richness, λ and H' – indices of species heterogeneity, E_1 and E_2 – indices of species evenness; α, A, R and CS – aggregation indices (* statistically significant at level $\alpha = 0.05$)); G – index of vertical structure.

4). The aggregation of recruits smaller than 1.5 m was higher on all PRP than that of all recruits. The aggregated pattern of recruits according to their distance (spacing) is indicated by Ripley's K-function (Fig. 2). The most distinct clumpiness was on PRP 7. Higher clumpiness was demonstrated in beech than in spruce. The vertical structure reached medium (PRP 1, 2) to high (PRP 6, 7) differentiation.

3.3. Height development

In 1979 natural regeneration on PRP was mostly unestablished (96% of recruits were smaller than 50 cm), while substantial development and differentiation of natural regeneration occurred until 2015, in fir partly of the combined established regeneration. The height structure of recruits in 2015 was mostly left-skewed. Most recruits belong by their height to classes in the range of 30 to 120 cm (67.7 – 82.6%), in beech it was 46.1 – 81.5% and in spruce 51.9 – 85.6% (Fig. 3). Established regeneration (above the height of 50 cm) was dominant on all PRP. The proportion of unestablished regeneration (lower than 50 cm of height) on PRP ranged of 23.2 – 38.7%, in beech it was 14.4 – 26.3%, in spruce 20.8 – 58.9% and in fir 0 – 62.1%.

The mean height of recruits was comparable on all plots, ranging from 97 to 169 cm, in beech it was 105 – 149 cm, in spruce 68 – 120 cm, in fir 92 – 227 cm, in sycamore maple 150 cm, in rowan 104 – 255 cm and in birch 38 – 330 cm. In recruits smaller than 150 cm the range was 69 – 82 cm, in beech 77 – 88 cm, in spruce 58 – 86 cm, in fir 53 – 70 cm, in rowan 68 – 72 cm and in birch 38 cm. In recruits taller than 150 cm the height range was 238 – 266 cm, in beech 285 – 314 cm, in spruce 222 – 232 cm, in fir 204 – 232 cm, in sycamore maple 150 cm and in rowan 190 – 391 cm. On the particular PRP the natural regeneration development specified according to tree species was of similar character.

3.4. Damage by wildlife

In 1979 natural regeneration was severely and repeatedly damaged by ungulate game, especially by red deer (*Cervus elaphus* L.) and roe deer (*Capreolus capreolus* L.). The greatest damage was caused by browsing of the leading shoot to sycamore maple, rowan and fir (100%), 93% in beech, 69% in spruce and 66% of leading shoots were damaged in birch. Browsing of lateral shoots in sycamore maple amounted to 100% on average, 94% in rowan, 90% in fir, 82% in beech, 48% in spruce and 45% in birch.

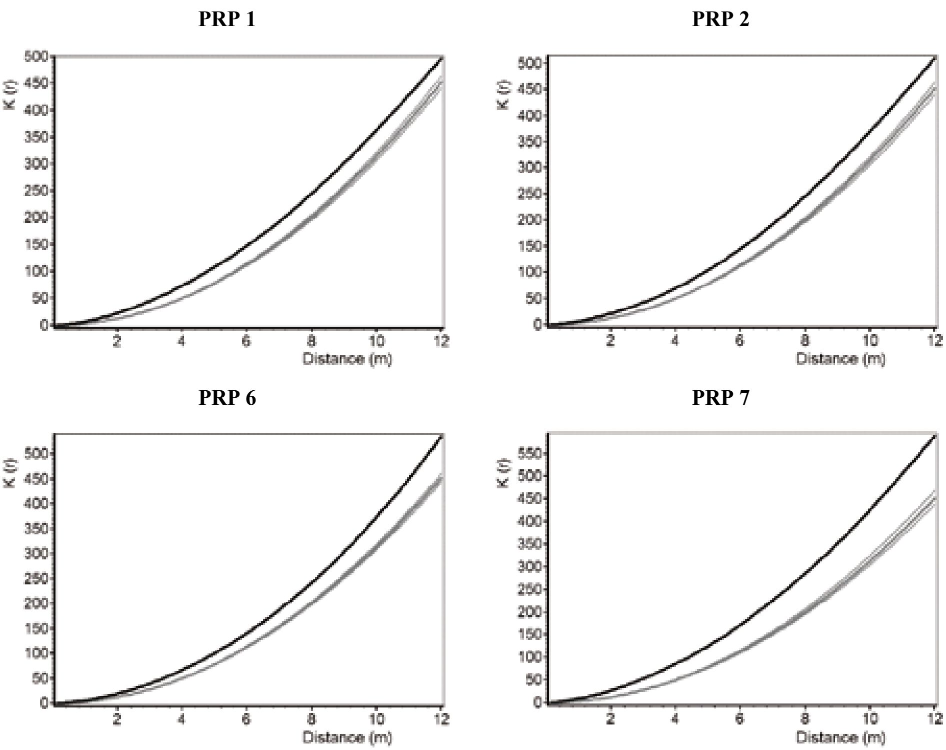

Fig. 2. Horizontal structure of natural regeneration on particular permanent research plots in 2015; the black line represents the *K*–function for real distances of recruits on PRP, the thick grey line illustrates the random spatial distribution of recruits and two thinner central curves represent a 95% confidence interval; when the black line of recruits distribution on PRP is below this interval, it indicates a tendency of individuals toward regular distribution, and if it is above this interval, it shows a tendency toward aggregation.

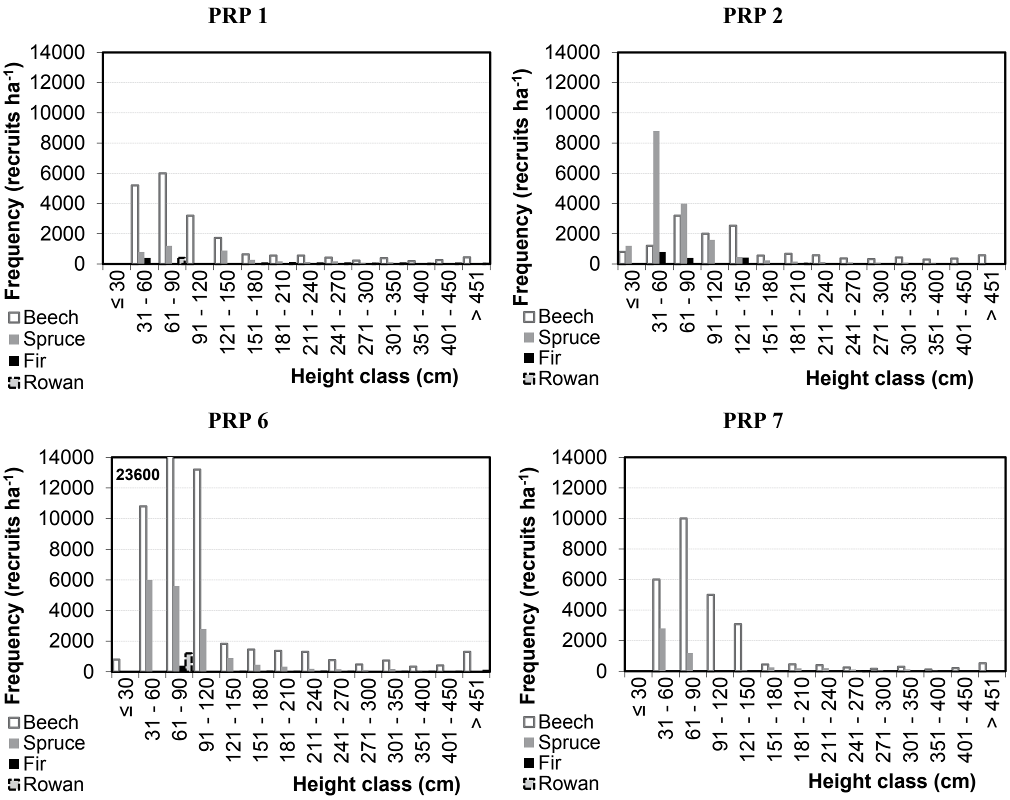

Fig. 3. Histogram of the height structure of recruits specified according to dominant tree species on permanent research plots 1, 2, 6 and 7 in 2015.

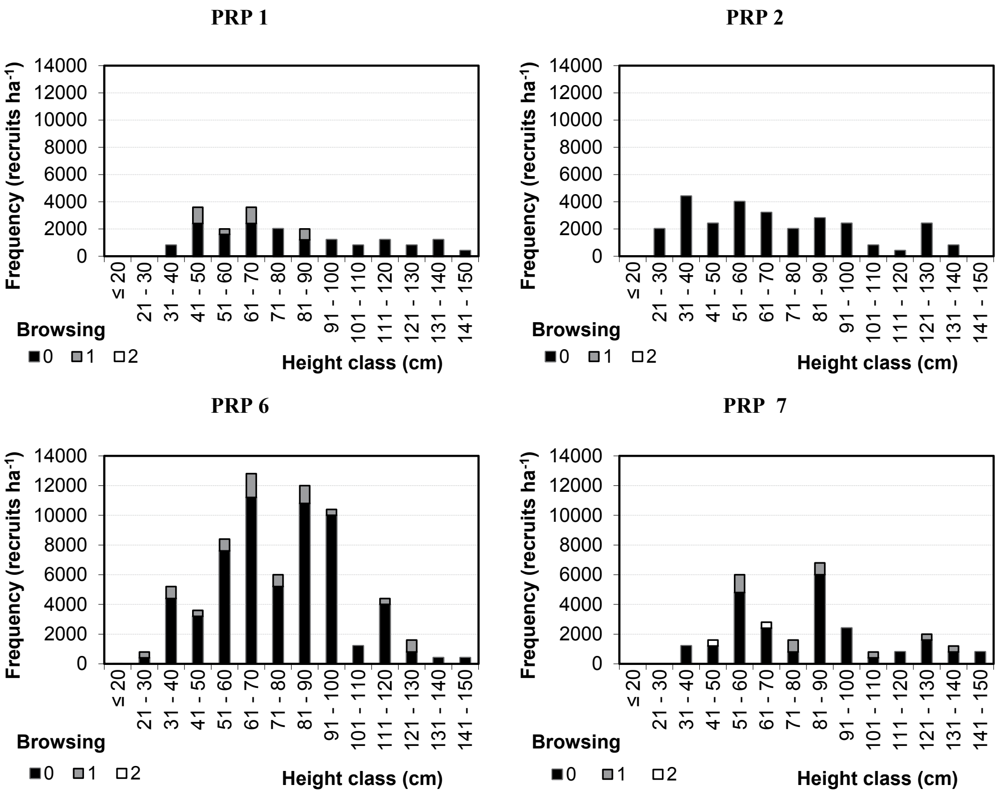

Fig. 4. Distribution of browsing of leading shoots in height classes of regeneration on permanent research plots in 2015; 0 = no browsing, 1 = the first browsing of leading shoot, 2 = repeated browsing of leading shoot.

In 2015 the proportion of recruits damaged by browsing of the leading shoot was from 0 to 23%. 22.5% of recruits on PRP 1 were damaged by the first browsing of the terminal shoot, while it was 0% on PRP 2, 12.8% on PRP 6 and 17.2% of recruits on PRP 7. On PRP 7 0.7% of recruits suffered damage by repeated browsing of the terminal shoot. The highest losses due to browsing were observed in sycamore maple (100%), followed by rowan (57%), fir (36%), beech (12%) and the lowest loss was incurred in spruce (3%). Fig. 4 shows browsing distribution in height classes of regeneration. The greatest damage by ungulate game was caused to recruits of 40 – 90 cm in height and with the root collar diameter of 6 – 12 mm. Sycamore seedlings were almost totally eliminated by hares (*Lepus europaeus* Pallas) there and rowan seedlings to a large extent. Browsing of lateral shoots on PRP accounted for 1 – 18%. The first browsing of lateral shoots damaged 18.2% of recruits on PRP 1, 0% on PRP 2, 8.8% on PRP 6 and 14.4% of recruits on PRP 7. 0.4% of individuals were damaged by repeated browsing of lateral shoots on PRP 7. In the course of 36 years, damage by browsing significantly decreased ($F_{(1, 34)} = 35.0$, $p < 0.01$) across all tree species due to high density of natural regeneration. Comparing individual tree species, there were observed significant differences ($F_{(4, 31)} = 3.6$, $p < 0.05$) in the size of damage by browsing. The significantly highest ungulate damage was observed in maple, while the significantly lowest damage was in spruce ($p < 0.05$).

3.5. Relations of regeneration and tree layer

On all PRP the spatial pattern of recruits in relation to the tree layer was evaluated as random at distances longer than 5 – 7 m, only on PRP 1 from a distance of 1 m (Fig. 5). The regular pattern was observed at shorter distances, while especially within 1 m it was a distinctly regular distribution, significant on all plots. This pattern reflects a negative influence of the tree layer on natural regeneration at small distances.

Relationships among natural regeneration parameters, characteristic of tree layer, tree species and time are presented in the form of the ordination diagram (PCA) in Fig. 6. The first ordination axis explains 49.1%, the first two axes together 84.2% and the first four axes

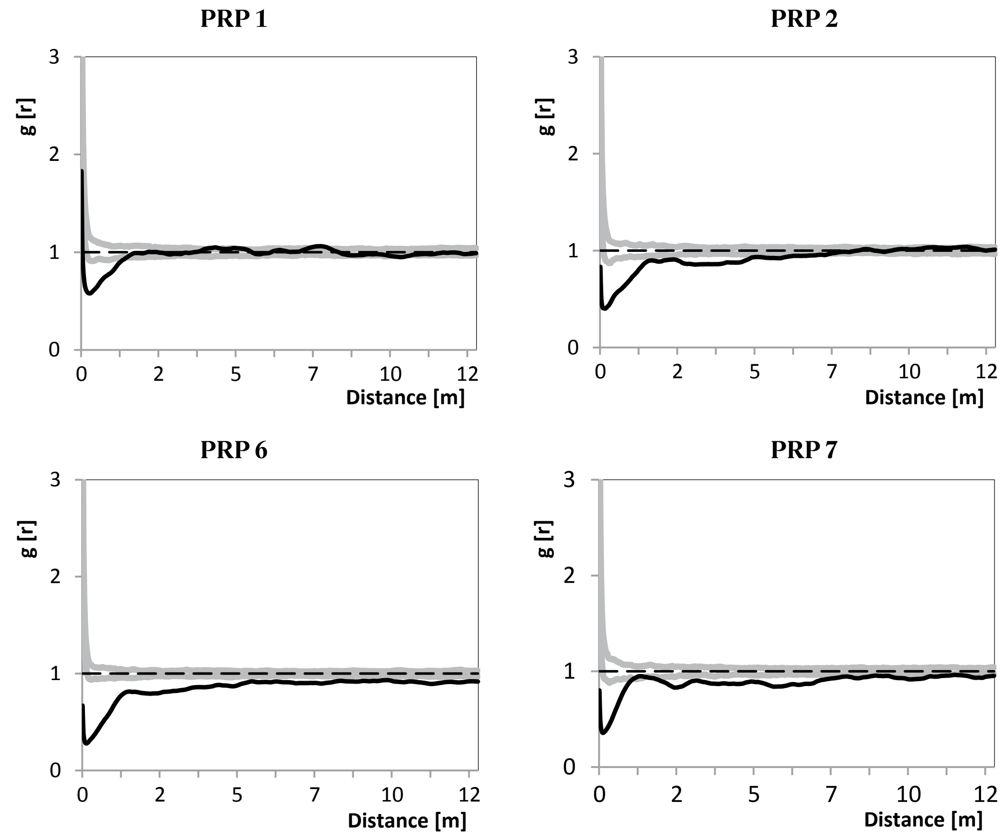

Fig. 5. The relation between natural regeneration and the tree layer of all tree species in a mixed stand on particular permanent research plots; the bold black line represents the cross-type pair correlation function for real distances of individuals; the dashed black line on the level of g (r) = 1 represents the mean course for random spatial distribution of trees and the two grey curves 95% confidence interval; when the observed value exceeds the upper limit of the simulation interval, it indicates significant aggregation – positive relationship between two tested groups, and if it is under this interval, it shows inhibition – negative relationship.

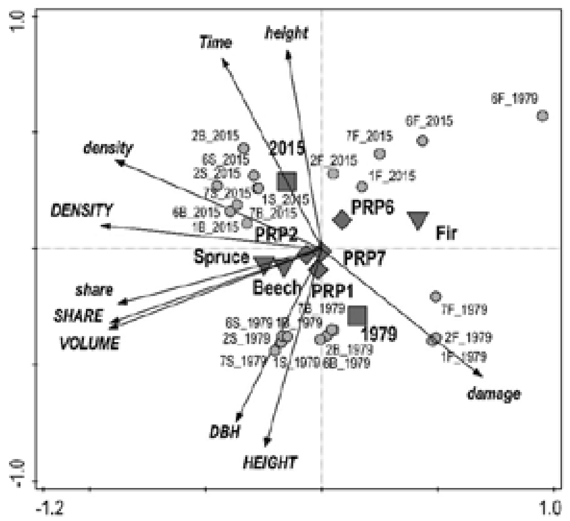

Fig. 6. Ordination diagram showing results of PCA analysis of relationships among natural regeneration parameters (*density* – number of recruits, *height*, *share* of tree species, *damage* – browsing by game), characteristic of tree layer (*DENSITY* – number of trees, *HEIGHT*, *DBH* – diameter at breast height, *SHARE* of tree species, stand *VOLUME*) and time (*Time*); large codes: ▼ indicate tree species (*Fir*, *Beech*, *Spruce*), ■ year of measurement (*1979*, *2015*), ◆ PRP (*1*, *2*, *6*, *7*); small codes: ● indicate PRP with tree species and year of measurement.

together explain 96.2% variability of the data. The first axis X represented density of tree layer. The second axis Y represented mean height of tree layer and natural regeneration. Regeneration species composition was positively correlated with species composition of tree layer. In course time, the mean height of regeneration was increasing, while DBH and height of tree layer and damage on regeneration caused by game were decreasing over 36 years. Particular PRP showed relatively similarity (instead of PRP 6) compared to great differences between years of measurement and tree species. Differences of species were remarkable for fir as marks of each record were relatively distant from one another whereas marks for spruce and beech were fairly close together in the diagram. Fir with the highest browsing damage occupied the right part of the diagram, while higher stand volume, share and density were typical for beech and spruce (left part).

4. Discussion

Modern silvicultural approaches are based on continuous improvement and gradual management of forest ecosystems in order to reduce risks and uncertainties related to climate change and other environmental factors (Schelhaas et al. 2010). According to Schelhaas et al. (2015) two methods are applicable for these approaches. The one consists in shortening the rotation period and the other in the adjustment of species composition in favour of tree species in which their better adaptability to changing climatic conditions is expected. In our study we focused especially on natural regeneration during forest transformation whose long-term development is continually associated with a change in species composition.

The results of our study explicitly document a significant increase in the proportion of beech (by 53.6%) recruits in natural regeneration over 36 years, mainly at the cost of spruce (decrease by 51.5%). This trend is in agreement with the results of some long-term studies that confirmed beech expansion at many locations in Europe (Emborg et al. 2000; Rohner et al. 2012). Poljanec et al. (2010) expected that along with climate changes the beech representation would be increasing also in future. Similar conclusions were drawn by Dakskobler (2008), who predicted beech expansion particularly into older spruce stands and pioneer forests but did not assume beech expansion into locations not so favourable for beech like frost pockets, water-logged, very steep, rocky or too dry sites. The representation of other tree species occurring as admixed ones at these localities showed quite few changes in their proportions during the studied period when the increased proportion of fir was a result of artificial regeneration – underplantings of this species in forest stands.

The total number of recruits on PRP in the studied period significantly increased from 941 to 41,669 ind ha^{-1}. Similar numbers like those were reported by others researches in the Czech Republic from spruce-beech near-natural forest in the Orlické hory Mts. – 37,230 recruits ha^{-1} (Vacek et al. 2014; Králíček et al. 2017), while higher regeneration density were observed in the Voděrady Beechwoods – 60,859 recruits ha^{-1} (Bílek et al. 2014), in Krkonoše Mts. – 75,395 recruits ha^{-1} (Vacek et al. 2015a) or in old-growth forest in Slovenia – 62,000 recruits ha^{-1} (Dusan et al. 2007). The number of recruits differs on the particular plots in relation to vegetation cover of the herb layer, topography (Štícha et al. 2010; Vacek et al. 2015b) and canopy cover of mature forest (Madsen & Hahn 2008; Sefidi et al. 2011). Light availability strongly affects the survival, growth rate and form of recruits (Grassi et al. 2004; Mountford et al. 2006). Taking into account an increasing beech proportion and generally relatively high numbers of recruits it is to state that the stand transformation currently develops well and should result in more stable forest stands better adapted to climate change in future. According to Bolte et al. (2010), in conditions of climate changes the beech shows an increased resistance to abiotic and biotic factors in comparison with spruce.

The ongoing development and related changes at the studied localities are in fact in line with the conclusions of Alexander et al. (2011), who stated that one of the proposed objectives of ecological transformations from the aspect of the Society for Ecological Restoration is the reintroduction of autogenic ecological processes. Subsequently, these processes should lead to the arrangement of tree species into a functional and resistant ecosystem that will adapt itself to changing conditions of the environment and at the same time will provide crucial ecosystem functions (Thomas et al. 2014). Relative to the arrangement of forest ecosystems we focused on stand diversity within particular PRP. Generally, mainly lower to medium diversity was indicated in studied stands. Nevertheless, we expect its further increase with ongoing forest transformation. Knoke et al. (2008) reported that the relatively structurally complex close-to-nature mixed stands have, compared to the relatively structurally simple monospecific forests, higher stability and resistance to disturbances. The horizontal pattern of natural regeneration on all PRP was significantly aggregated, which is in agreement with many studies on natural regeneration (Nagel et al. 2006; Paluch 2007; Ambrož et al. 2015; Vacek et al. 2015a). Particularly in beech as a shade-tolerant tree species, the tendency to clumpiness in our study was more significant than in spruce. The pronounced clumpiness is due to the occurrence of recruits in small gaps in the canopy (Szwagrzyk et al. 2001; Grassi et al. 2004). But the relationships between natural regeneration and canopy density can be quite variable depending on local conditions (Collet & Le Moguedec 2007) and damage caused by the wildlife (Ficko et al. 2011; Vacek et al. 2014; Mattila & Kjellander 2017).

Monitoring of game damage on the studied PRP has revealed a generally high pressure on natural regeneration during the whole period of study. Nevertheless, there was a marked significant decrease (by 61.4%) in damage in the studied period because of 44 times higher regeneration density. However, we repeatedly observed total elimination of sycamore maple (100%) and a great part of rowan (57%) and fir (36%) were also damaged. On the contrary the lowest damage was caused to spruce (3%). These results are consistent with Vacek et al. (2014), who presented a marked suppression or even disposal of natural regeneration of fir, sycamore and rowan recruits, while the lowest damage was also reported for spruce. The attractiveness of sycamore and rowan for game was also confirmed by studies from the Italian Alps (Motta 2003), from Krkonoše Mts. (Čermák & Grundmann 2006) and from Slovakia (Konôpka & Pajtík 2015). A high pressure on fir and factually the disposal of its natural regeneration by game browsing were described by Bottero et al. (2011) in Bosna and Herzegovina, by Jaworski et al. (2002) in the Western Carpathians or by Klopcic et al. (2010) in Slovenia; the latter authors reported about unfenced fir-beech stands, where great damage to fir recruits or even the total disposal of fir regeneration by browsing was observed. In relation to the high game pressure Vrška et al. (2001) concluded that selected forest stands should be fenced to provide natural spontaneous development of the regeneration of spruce-fir-beech forests. In our case the reducing of still increasing ungulate populations (Konôpka et al. 2015; Vacek 2017) and mechanical or repellents protection with focusing on support of fir, sycamore maple and other species largely suffering from browsing seems to be necessary (Olesen & Madsen 2008; Häsler & Senn 2012).

In terms of spatial relations between regeneration and tree layer, the spatial pattern of recruits relative to the tree layer was evaluated as random at distances over 1 – 5 m. At shorter distances the individuals of the tree layer had negative influence on natural regeneration, which was mostly revealed in Sudetes Mts. (Bulušek et al. 2016; Králíček et al. 2017). On the other hand, in those studies a positive relationship of recruits and tree layer in beech was confirmed on plots with extreme site conditions due to natural layering. In these conditions the tree layer creates better microsite conditions for regeneration (Vacek & Hejcman 2012).

5. Conclusion

A shelterwood system with the application of selection principles has become the main objective of close-to-nature silvicultural management in the forest sector in the Czech Republic, where natural regeneration plays a crucial role. One of these examples are studied forest stands in the Jizerské hory Mts. at more advanced phase of transformation as a result of the combination of spontaneous development and intentional silvicultural practices emerging structurally diversified forest stands. Currently, site and growth conditions in the area are, unlike those at the time of the air-pollution disaster culminating in the 1980s, more favourable for close-to-nature stand structures, which is manifested by a decreased share of spruce in natural regeneration mainly in favour of beech. In the stand transformation process the maximum utilization of natural regeneration should further continue for a relatively long time when particularly natural regeneration of fir, which suffers very much from damage by game, should be supported. In a limited period certain economic risks can be expected relative to the loss of timber value mainly in beech (false heart) caused by its relatively high age. These trees will have to be left in forest stands many times in order to maintain the relevant stand structure. On the other hand, it is to expect in future a pronounced reduction in the costs of regeneration and tending. Moreover structurally diversified stands normally show higher ecological stability and biodiversity.

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