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PÔVODNÁ PRÁCA – ORIGINAL PAPER

Current and simulated structure, growth parameters and regeneration of beech forests with different game management in the Lány Game Enclosure

Struktura, růstové parametry, obnova a modelový vývoj bukových porostů s odlišným způsobem mysliveckého hospodaření v podmínkách Lánské obory

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Abstract
The paper presents the results of the study of the current and simulated structure of beech forests in the Lány game preserve, which is situated in the Křivoklátsko Protected Landscape Area in the Czech Republic. The research was conducted at two permanent research plots (PRP) of 0.25 ha in size in a mature beech forest using the FieldMap technology. Typological, soil and phytocoenological stand characteristics and the history of management of both PRP are comparable; however, they differ in the protection against wildlife. The results demonstrated that deer species including red deer (*Cervus elaphus* L. – 300 head), sika deer (*Cervus nippon nippon* Temm. – 300 head), mouflon (*Ovis musimon* Pallas – 250 head) and fallow deer (*Dama dama* L. – 300 head) is a limiting factor for successful development of natural regeneration of European beech (*Fagus sylvatica* L.). Natural regeneration on PRP 1 with wild boar herd (*Sus scrofa* L. – 150 head) is sufficient in relation to site and stand conditions. On the contrary, there is no regeneration on PRP 2 with the occurrence of deer species. The results of biometric measurements and subsequent predictions by the SIBYLA forest biodynamics simulator indicate that the stands are insignificantly structured, mature, productive beech stands with the absence of individuals in the lower tree layer.

Key words: *Fagus sylvatica* L.; stand structure and development; natural regeneration; game management; browsing by ungulate game

Abstrakt
V příspěvku jsou prezentovány výsledky studia struktury a dynamiky vývoje bukových porostů v Lánské oboře, která se nachází v Chráněné krajinné oblasti Křivoklátsko v České republice. Výzkum se uskutečnil v dospělém bukovém porostu na dvou trvalých výzkumných plochách (TVP), každá o velikosti 0,25 ha s použitím technologie FieldMap. Typologické, půdní, fytocenologické i porostní charakteristiky obou porovnávaných TVP jsou srovnatelné, odlišují se pouze způsobem ochrany proti zvěři. Výsledky ukázaly, že limitujícím faktorem zdárného vývoje přirozené obnovy buku (*Fagus sylvatica* L.) je vysoká zvěř, a to jelen evropský (*Cervus elaphus* L. – 300 ks), jelen sika (*Cervus nippon nippon* Temm. – 300 ks), muflon (*Ovis musimon* Pallas – 250 ks) a daněk skvrnitý (*Dama dama* L. – 300 ks). Přirozená obnova na TVP 1 s černou zvěří (*Sus scrofa* L. – 150 ks) je dostatečná vzhledem ke stanovištním a porostním poměrům. Naproti tomu na TVP 2 s ostatními druhy zvěře se obnova nevyskytuje. Z výsledků biometrických měření a následných vizualizací pomocí simulátoru biodynamiky lesa Sibyla vyplývá, že se jedná o nevýrazně strukturované, dospělé, produktivní bukové porosty s absencí jedinců spodního stromového patra.

Klíčova slova: *Fagus sylvatica* L.; struktura a vývoj porostů; přirozená obnova; chov zvěře; škody spárkatou zvěří

1. Introduction

The process of regeneration is a highly stochastic phenomenon of forest dynamics that depends to a large extent on many factors involving the habitat, stand characteristics, land use history or the influence of herbivores (Paluch 2007). The spatio-temporal interactions between the particular species are highly dynamic as well: they change variably in relation to soil, climatic and stand conditions (Forrester et al. 2013).

There are a lot of factors influencing natural regeneration of forests. In the conditions of a game enclosure browsing by hoofed game is considered a limiting factor for regeneration. The excessive activity of game due to their increased population densities in forests is a factor demonstrably suppressing the diversity of forest undergrowth and regeneration of the tree layer, particularly of food attractive tree species (Bottero et al. 2011; Vacek et al. 2014). Regeneration of forest stands in connection with high game population densities is currently a frequently discussed issue (Diaci et al. 2010). Many authors defined the basis of damage caused by game. For example Pollanchütz (1995) described these injuries as damage to trees and tree seedlings caused by animals leading to a decrease in financial revenues and increase in costs used for stand protection. Herbivores may have a severe impact on forest regeneration as broadleaved saplings are an important food item (Groot Bruinderink & Hazenbroek 1995). Browsing has a significant effect on growth, morphology, species composition and mortality of natural regeneration (Roth & Suchant 1993; van Hees et al. 1996). Browsing intensity is closely related to population densities of herbivores (Suchomel et al. 2010). The same conclusions were drawn by Côté et al. (2004).

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The obligation to reforest a clearcut area within two years from its origin and to establish a forest stand within seven years is usually very difficult to meet in localities with a high occurrence of game. The Forest Act defines an established forest stand as follows: trees that show sustained height increment, are equally laid out (either individually or in groups), their quantity is not lower than 80% of a minimum number for regeneration or reforestation, they are tall enough to resist forest weed and are not significantly damaged (Forest Act No. 289/1995). Although an increase in damage caused by game to forest stands in the CR was discontinued, the influence of game on the condition and development of mixed and broadleaved stands still persists (Malík & Karnet 2007). In the conditions of a game enclosure the forest authority approaches the reforestation and establishment of forest stands from the aspect of legislation in the same way as in commercial forests. In the Lány game enclosure almost a third of its area (approximately 900 ha) is currently composed of mostly beech stands older than 160 years in the high optimum stage with the absence of the lower tree layer (Working Plan of the Lány Forest District 2010). Besides browsing, vital weeds that appear immediately after the opening-up of the canopy are a crucial problem for the establishment of natural regeneration on fertile sites while the soil preparation increases the costs of forest regeneration (Vacek et al. 1995). This fact was also mentioned by Špulák (2008), who wrote that the competition of forest weed was considered a key factor determining the occurrence and growth of the natural regeneration of beech.

In unfenced hunting grounds where game management is not a priority, the regulation of hoofed game population densities can be considered as the most effective way to diminish losses of forest regeneration caused by game (Čermák et al. 2009). Overall and species-specific browsing intensity notably decreased under the controlled hunting regime (Fichtner et al. 2011). The same was confirmed by Ammer (1996), who studied the influence of ungulates on the structure and dynamics of natural regeneration. Based on the observations he stated that since protection against ungulates is expensive and, due to the slow growth of trees in the mountains impossible to maintain for long periods of time (cf. Mayer 1974), there seems to be no alternative to the long-called-for consistent reduction of these animals (cf. Mayer & Ott 1991; Burschel 1993), which should be realised using the knowledge of wildlife management.

The fencing of young forest plantations prevents them from browsing and fraying damage. Sorges (2001) documented that after the establishment of forest stands the trees from natural regeneration inside the fence were significantly taller than the unprotected ones. The same conclusion was drawn by Kumar et al. (2006). The influence of these measures is positive, but higher costs of plantation protection are incurred. If acceptable population densities of wildlife were maintained, it would not be necessary to fence the natural regeneration, which would bring financial savings (Katona et al. 2013).

Although the game enclosure is considered as a special-purpose facility for game keeping, it is necessary to harmonise forest management and game management so that forest stands will permanently meet the requirements for game keeping and also fulfil other functions. Taking into account the high area share of over-mature stands and the need for their regeneration, such solutions should be found that will not only be functional, but also economically acceptable. From a long-term perspective, it is not economically viable to protect each regeneration segment by fencing individually: the costs will be reduced if we fence larger regeneration blocks, consisting of numerous smaller regeneration segments and also forest stands that are going to be regenerated in the near future. Hromas (1997) states that in game keeping facilities it is necessary to accept either higher forest stand damage caused by game, or higher costs of protection, including more difficult stand regeneration.

The objectives of this paper are as follows: (1) to evaluate the current stage of mature beech stands in the Lány game enclosure with regard to the structure (diameter, height and horizontal), growth parameters and natural regeneration under different game management with the impact of hoofed game (wild boar and red deer), (2) to simulate their future development using the SIBYLA simulator, and (3) to ascertain whether in these stands, subjected to long-term damage caused by hoofed game, the beechnut production is high enough to ensure their natural regeneration, and how wild boar and red deer restrict natural regeneration.

2. Materials and Methods

2.1. The study site

The use of the Lány game enclosure for game hunting has been typical for several centuries. The first records of hunting in this territory date back to 999 while in the Wallenstein era a vast game enclosure of the area of 9,436 ha was established there in 1713 (Ambrož 2012). The restoration of these stands has been difficult because high population densities of wildlife have had to be kept there for the purposes of hunting.

The Lány game enclosure, administered by the Lány Forest District, is situated in the Křivoklátsko Protected Landscape Area (PLA) and in Natural Forest Area 8 – Křivoklátsko and Český kras ranging from 265 to 471 m a.s.l. The bedrock is built of permo-carboniferous rocks and the soil type is modal Cambisols. Average annual temperature fluctuates around 7.5 °C and in the growing season it is around 14.5 °C. Average annual precipitation amount is 486 mm and in the growing season it is 300 mm. The length of the growing season is 158 days. Herb-rich beech forests (*Dentario enneaphylli-Fagetum*) are potential dominant vegetation.

The localisation of permanent research plots (PRP) is shown in Fig. 1 and basic data on PRP are documented in Table 1. Site and stand characteristics are comparable on both plots. PRP 1 is situated in a small concentration enclosure for wild boar of 88.5 ha in size. This enclosure was established in 2011 by the construction of a new fence in the original Lány game enclosure; it is used for the control and regulation of the wild boar (*Sus scrofa* L.) herd (about 150 head). PRP 2 is located in the main part of the game enclosure where besides the wild boar (150 head) there are red deer (*Cervus elaphus* L. – 300 head), sika deer (*Cervus nippon nippon* Temm. – 300 head), mouflon (*Ovis musimon* Pallas – 250 head) and fallow deer *(Dama dama* L. – 300 head). In the last fourty years, the wildlife stocks increased by 35.77%. Wolf et al. (1976) states that there were red deer (301 head), sika deer (151 head), mouflon (153 head) and fallow deer (243 head) in the Lány game enclosure in 1974. Based on historical afforestation records, forest stands in the vicinity of PRPs were established by sowing in the Fürstenberg period. The origin and subsequent management of these forest stands were regulated by the Jáchym Egon of Fürstenberg Hunting Regulations from 1817. Via these regulations he ordered the division of the original big Wallenstein game enclosure into two smaller parts – the Lány game enclosure (intended for red deer), where both PRPs are situated, and the Řevničov game enclosure (intended for wild boar) (Ambrož 2012). After 1817, mainly beech and oak stands were established in the newly created Lány game enclosure, whereas in other parts of the Křivoklát area, the acreage of beech stands was decreasing since it was used as a supply of fuel wood to local ironworks. The newly established stands were fenced. Based on the historical survey of the property of the Lány Forest District, the stands at both PRPs were managed in the same way – with respect to both silvicultural (stand regeneration and tending) and game management (hoofed game population). This fact is further documented by the data from individual working plans of the Lány Forest District from previous decades (Novák & Hošek 1969).

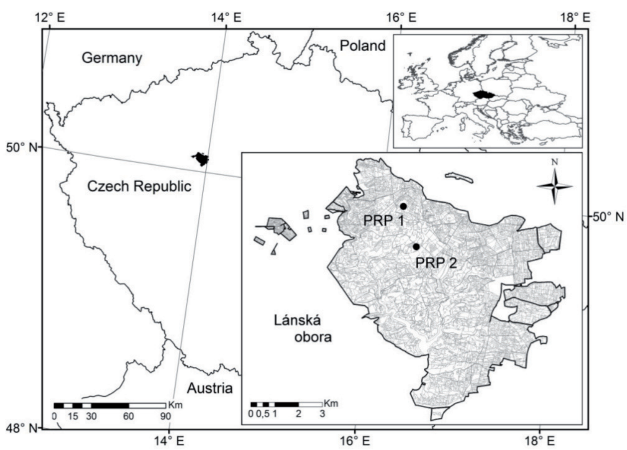

Fig. 1. The localisation of permanent research plots 1 and 2 in the Lány game enclosure.

2.2. Field measurements

The FieldMap technology was used to determine the structure of the tree layer of tree species where two permanent research plots (PRP) of 50 × 50 m in size (0.25 ha) were established. Using this system the positions of all individuals of the tree layer were localised at both PRP. Total tree height and height to crown base were measured with a Vertex hypsometer to the nearest 0.1 m. To determine the crown width, the measurements in four mutually perpendicular directions were performed. Diameter at breast height (dbh ≥ 4 cm) was measured with a metal calliper to the nearest 1 mm. Presence of fork in the major stem axis was identified in 4 classes: no fork, fork below 1.3 m, from 1.3 to 7 m and over 7 m.

Natural regeneration (recruits) on PRP was measured on nine circular subplots of 3 m in radius (254.47 m^2). Recruit height (h > 5 cm), dbh < 4 cm and height to the living crown base were measured to the nearest 1 cm. A pole was used for these measurements. For the localisation of recruit positions the Field-Map technology was applied. The total number of beechnuts including germinating and full beechnuts was evaluated on nine identical subplots as for natural regeneration (9 × 28.26 m^2) on each PRP and was converted per m^2.

2.3. Data processing

The structure of the studied stands was visualised and their development was simulated by the SIBYLA growth model (Fabrika & Ďurský 2005). The modelling of spontaneous development of stands was realised for both PRPs for a span of the next 50 years (in five ten-year periods) assuming an ecologically stable environment. The characteristics of individual trees were used as input data (coordinates, height, dbh, crown width, crown base, age). Site input data were following: NOx concentration in air, CO_2 concentration in air, soil nutrient supply, number of days in the vegetation period, annual temperature amplitude, mean daily temperature in the vegetation period, soil moisture and precipitation amount in the vegetation period. In addition, damage by animals, biotic and abiotic losses on seeds and vegetative cover were set for natural regeneration model. Soil moisture and nutrients in the range from 0 (minimum) to 1 (maximum) were derived from the typological classification system of ÚHÚL (Plíva 1987). Climate data were obtained from the Lány meteorological station. For a higher statistical significance of prediction the simulation was repeated 25× (5× repetition of structure generating, 5× repetition of prognosis). Using the resultant value the arithmetical mean of variables from repeated simulations was computed, and subsequently the nearest simulation to the mean was chosen.

Stand diversity from the point of horizontal and vertical structure, frequency of their representation and tree species composition was evaluated by the following indices: Artenprofil index (Pretsch 2001), diameter and height differen-

Table 1. An overview of the basic characteristics of forest stands where the permanent research plots are located.

Plot	Tree species	Age	Height [m]	DBH [cm]	Standing volume [m^3 ha^{-1}]	Altitude [m]	Aspect	Slope [°]	Forest site type	Danger zone
PRP 1	Beech	179	34	49	335	451	NW	3.1	3H5	D
	Pine		28	46	52					
	Larch		40	48	11					
	Oak		32	47	8					
PRP 2	Beech	194	31	61	368	432	S	1.8	3H5	D
	Hornbeam		20	28	9					

Explanatory notes: 3H5 – *Querceto-Fagetum illimerosum mesotrophicum* – mesotrophic loamy oak-beech stands; danger zone D – zone of dynamics deterioration of health status by 0–2% of dead trees per year; age – mean age of trees according to forest management plan; GPS coordinates: PRP 1 – N 50° 07‘ 05“ E 13° 54‘ 31“, PRP 2 – N 50° 06‘18 “ E 13° 55‘ 12“.

tiation index (Füldner 1995), aggregation index according to Clark & Evans (1954), Pielou-Mountford aggregation index (Pielou 1959; Mountford 1961), Hopkins-Skellam aggregation index (Hopkins & Skellam 1954), David-Moore aggregation index (David & Moore 1954), stand diversity index (Jaehne & Dohrenbusch 1997) and *L*–function (Ripley 1981). The *L*–function of natural regeneration was computed for a plot created by combining all subplots in PointPro 2.1 software. Development of the tree layer density (enumeration canopy, biological canopy, stocking, stand density index; Fabrika & Ďurský 2005) was also computed. Situational maps were created in the ArcGIS 10.0 programme (Esri). Statistical analyses (ANOVA) were processed in the Statistica 12 software (StatSoft, Tulsa).

3. Results

3.1. Diameter and height structure of tree layer and natural regeneration

The histograms of diameter classes of tree layer in Fig. 2 document the variability of tree frequencies in diameter classes at both PRPs. The diameter structure at PRP 1 resembles a Gaussian curve indicating the man-made even-aged stand with the highest frequency in the class of 48–52 cm. Diameter distribution gradually decreases at both ends of the curve with the boundaries of 26.4 cm and 95.2 cm. European beech (*Fagus sylvatica* L.) trees with diameter in the range of 68–72 cm and 56–60 cm are also abundant. There are eight trees of admixed European larch (*Larix decidua* Mill.) per hectare, its dbh is 52–57 cm.

The frequencies of beech diameter classes at PRP 2 are almost even. However, at both PRPs some classes are empty due to the relatively low number of trees on the plots. The highest frequencies of trees are in diameter classes of 34–40 and 52–56 cm. Average dbh for beech is around 57.2 cm 59.0 cm at PRP 1 and 2, respectively. Beech trees of smaller dimensions (24 cm) are relatively more frequent at PRP.

The height of both tree species occurring on PRP 1 sharply increases with diameter at breast height at first, but almost immediately the vertical structure of the stand evens out and creates the hall structure typical of an even-aged stand (Fig. 2). From the coenotic aspect, the larch in the upper tree layer reaches a dominant position with the maximum height of 42.9 cm. The height of the tallest beech trees is 41.9 m.

The relation between the height of beech trees and dbh is positive on PRP 2; this relation shows a fast increase at first, then it decreases very slowly. From the breast height diameter of 40 cm (similarly like on PRP 1) its dependence on height is stabilised ca. at 39 m. The average height of beech is 30.5 m (by 8.5 m less than on PRP 1), while the maximum height is 41.9 m but there are a lot of overtopped trees of 11–15 m in height. The relationship between the breast height diameter and the height of beech on PRP is shown in Fig. 3.

The total number of recruits per hectare is 62,935 individuals, out of this beech accounts for 100%. Very high numbers of recruits have been established since the fence against red deer, mouflon and fallow deer was built there three years ago.

Height structure of natural regeneration on PRP 1 is shown in Fig. 4. The highest number of recruits belongs to the class of 10–15 cm (29,365 seedlings ha^{-1}), fewer recruits belong to the class of 15–20 centimetres (25,276 seedlings ha^{-1}) and the lowest number of recruits is in the class above 30 cm (157 seedlings ha^{-1}). Seedlings > 20.1 cm in height account for only 6.7% of the total number, which corresponds to the duration of protection against wildlife. The majority of the recruits of 10 to 20 cm in height come from the mast year 2012. Beech recruits ≤ 10 cm in height amount to 4,088 seedlings ha^{-1}. No natural regeneration occurs on PRP 2 with the enormous pressure of red deer, mouflon and fallow deer.

3.2. Horizontal structure of tree layer and natural regeneration

Situational representation of the horizontal structure of tree layer and natural regeneration on PRP 1 is shown in Fig. 5, and the spatial pattern expressed by Ripley's *L*–function is illustrated in Fig. 6. According to all four determined structural indices, the individuals of the tree layer are distributed randomly (Table 2). The random distribution of the individuals of the tree layer was also confirmed by Ripley's *L*–function

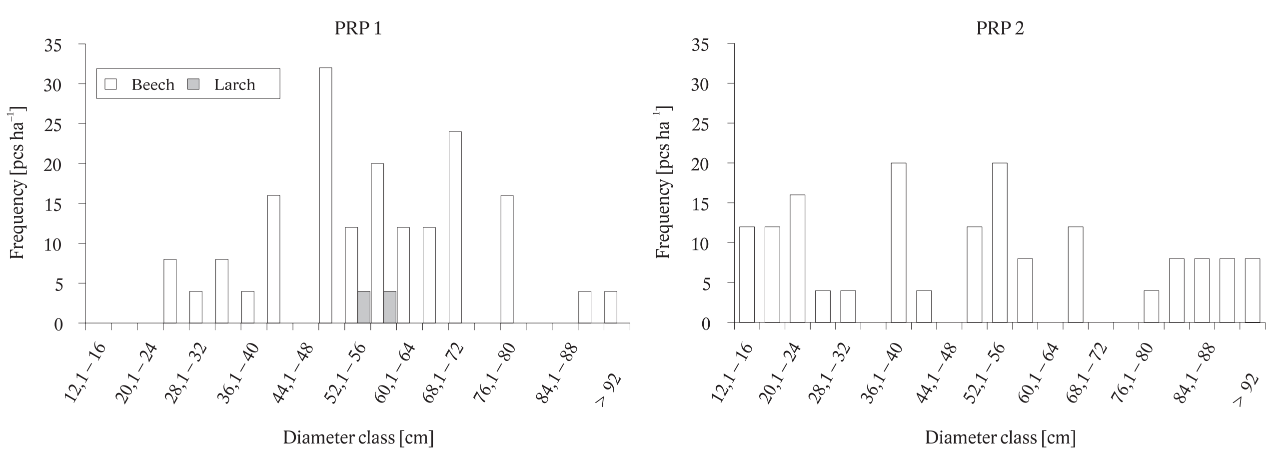

Fig. 2. Histograms of frequencies in diameter classes in the beech stands on the permanent research plots PRPs differentiated by tree species.

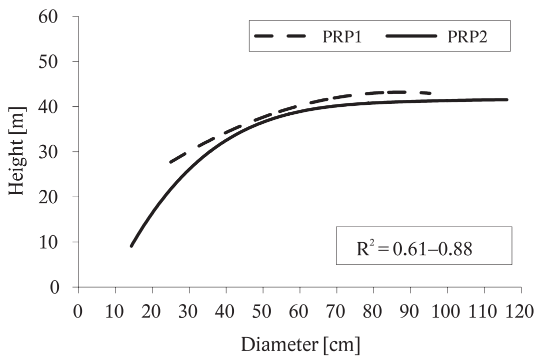

Fig. 3. The relationship between the breast height diameter and the height of beech on PRPs.

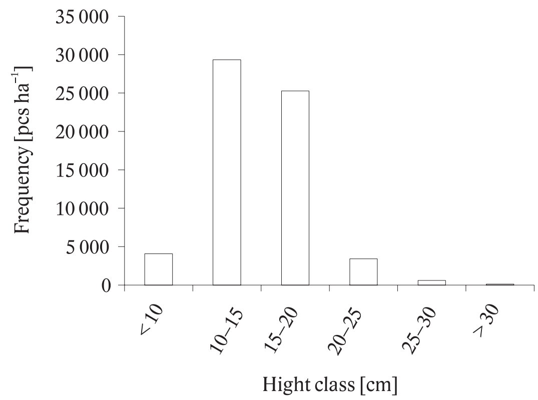

Fig. 4. Histogram of tree frequencies in height classes in the beech stand on PRP 1 in the Lány game enclosure.

from the spacing of 2 m. If the spacing is smaller (less than 2 m), their horizontal structure is aggregated. *L*–function also confirms the considerably aggregated structure of natural regeneration. The highly aggregated structure results from the indices based on a distance from the randomly selected point to the nearest tree (A = 0.977, α = 22.193), on the average distance of trees to their nearest neighbours (R = 0.551) and on the tree frequency in the particular quadrats (CS = 27.137).

Situational representation of the horizontal structure of the tree layer on PRP 2 is shown in Fig. 4 and expression by *L*–function in Fig. 7. According to the majority of the determined structural indices (Hopkins-Skellam, David-Moore and Clark-Evans) the distribution of all individuals of the tree layer on this PRP is aggregated, while according to the Pielou-Mountford index it is random (Table 3). The random distribution of individuals of the tree layer according to their distance (spacing) is also indicated by Ripley's *L*–function, only at a smaller spacing (less than 3 m) the distribution of trees on the plot is aggregated. Compared to PRP 1, the aggregation at initial spacing is more distinct. Since natural regeneration is completely missing, its horizontal structure could not be studied. As for structural indices (A = 0.444, α = 1.384, R = 1.197) and *L*–function, the distribution of beech and relatively well-preserved oak stumps from the last generation (often exceeding the dbh of 130 cm) across the plot is quite random similarly like in the preceding PRP.

3.3. Growth parameters and simulation of tree layer and natural regeneration development

The yield table obtained from the simulation of spontaneous stand development on PRP 1 is shown in Table 4. The beech stand with individually admixed larch is a moderately spatially differentiated, even-aged stand. The mature forest consists of the upper and middle layers. Natural regeneration of beech occurs almost across the whole plot, it is abundant in

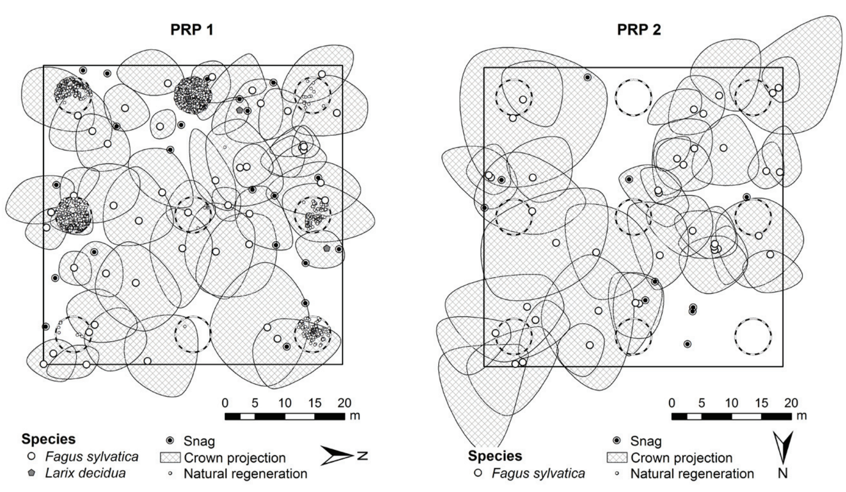

Fig. 5. Horizontal structure of the tree layer of the beech forest on PRPs in the Lány game enclosure.

Table 2. Indices describing the horizontal structure of the beech stand on PRP 1 in the Lány game enclosure.

Index	Tree layer				Natural regeneration			
	Observed value	Expected value	Lower bound	Upper bound	Observed value	Expected value	Lower bound	Upper bound
Hopkins-Skellam	0.448	0.498	0.364	0.660	0.977*	0.500	0.476	0.526
Pielou-Mountford	1.016	1.158	0.762	1.822	22.193*	1.027	0.962	1.111
David-Moore	−0.035	0.004	−0.250	0.309	27.137*	0.008	−0.281	0.316
Clark-Evans	1.125	1.066	0.900	1.239	0.551*	1.011	0.980	1.039

* Statistically significant (confidence interval 0.95).

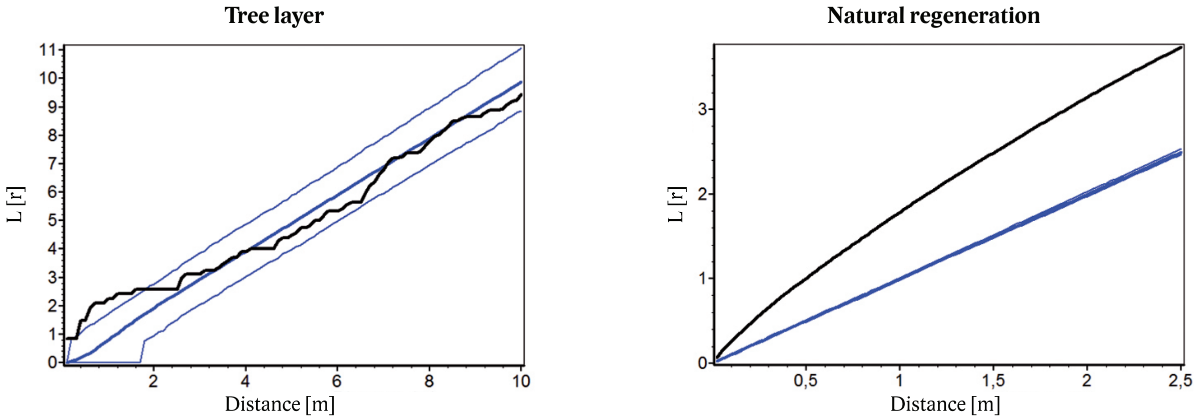

Fig. 6. Horizontal structure of the beech stand on PRP 1 in the Lány game enclosure expressed by *L*–function.

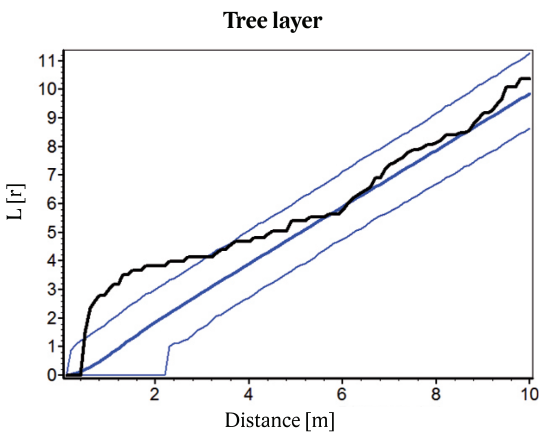

Fig. 7. Horizontal structure of the beech stand on PRP 2 in the Lány game enclosure expressed by *L*–function.

Table 3. Indices describing the horizontal structure of the beech stand on PRP 2 in the Lány game enclosure.

Index	Tree layer				Natural regeneration			
	Observed value	Expected value	Lower bound	Upper bound	Observed value	Expected value	Lower bound	Upper bound
Hopkins-Skellam	0.748*	0.497	0.350	0.675	Not found			
Pielou-Mountford	1.727	1.173	0.740	1.855				
David-Moore	0.567*	0.000	−0.408	0.513				
Clark-Evans	0.695*	1.074	0.878	1.257				

* Statistically significant (95% confidence interval).

gaps. Natural regeneration is not abundant in the proximity of wallows and cribs. The utilisation of the productive space is currently high, but codominant and dominant trees reaching their maximum physiological age will be dying naturally. The stand protected against red deer, fallow deer and mouflon has sufficient regenerative capacities.

At present (2014), the total standing volume of large timber ≥ 7 cm in diameter o.b.) in the stand is 975 m^3 ha^{-1}, of this beech accounts for 934 m^3 and larch accounts for 41 m^3. In 2064 a decrease by 400 m^3 ha^{-1} is expected due to the transition to the advanced stage of disintegration or the initial growing-up stage. The number of individuals of the tree layer is 184 trees per ha, while in the fifty-year simulation period the tree number will increase by 19% as a result of trees growing-up to the registration limit. Productive capacities of the stand are very good with regard to site and stand conditions. Current annual increment in 2014 is 7.5 m^3 ha^{-1} year^{-1} and mean annual increment is 5.6 m^3 ha^{-1} year^{-1}.

The yield table obtained from the simulation of spontaneous stand development on PRP 2 is shown in Table 5. The phase of regeneration is missing there and any natural regeneration is destroyed by kept red deer. The utilisation of the productive space was relatively good until now, but in recent years the natural dieback of trees reaching their maximum physiological age has occurred in the over-storey. The unprotected stand against the high population densities of wildlife does not have sufficient self-regulation capacities, especially from the aspect of regeneration.

In 2014 the total standing volume of large timber in the beech stand was 732 m^3 ha^{-1}, and in 2064 its decrease by 54% is expected (by 337 m^3 ha^{-1}), which will be caused by the transition to the final stage of disintegration with the absence of growing-up regeneration. The number of individuals of the tree layer is 152 trees per ha, while in the course of 50-year development the original number of trees will be reduced by 72 trees per ha. Taking into account site and stand conditions, productive capacities of the stand have been relatively good until now. Current annual increment in 2014 is around 4.7 m^3 ha^{-1} year^{-1} and mean annual increment is 3.9 m^3 ha^{-1} year^{-1}.

Table 4. Overview of the simulated stand characteristics of the beech stand on PRP 1 in the Lány game enclosure under the assumption of spontaneous development.

Year	t	dbh±σ	h	h_{95}	f	v	N	G	V	h:d	CAI	MAI	TVP
2014	175	59.0±15.5	39.04	42.2	0.497	5.300	184	50.3	975	66.2	7.5	5.57	975
2024	185	58.5±21.0	36.55	42.5	0.535	5.252	200	53.6	1051	62.5	7.0	5.68	1050
2034	195	57.5±21.1	35.83	42.6	0.543	5.048	144	37.2	727	62.3	6.4	5.72	1115
2044	205	55.6±27.8	30.83	42.9	0.637	4.765	152	36.6	724	55.4	5.6	5.75	1179
2054	215	52.0±30.5	26.99	43.3	0.728	4.170	156	32.9	651	51.9	4.6	5.71	1227
2064	225	41.3±30.8	17.68	43.1	1.104	2.615	220	29.1	575	0.428	4.5	5.65	1272

Explanatory notes: t – average stand age, dbh±σ – average breast height diameter ± standard deviation (cm), h – mean stand height (m), $h_{95\%}$ – top height – 95% quantile (m), f – form factor, v – average tree volume (m^3), N – number of trees per ha, G – basal area (m^2 ha^{-1}), V – stand volume (m^3 ha^{-1}), h:d – height diameter ratio, CAI – current annual increment (m^3 ha^{-1} $year^{-1}$), MAI – mean annual increment (m^3 ha^{-1} $year^{-1}$), TVP – total volume production (m^3 ha^{-1}).

Table 5. Overview of the simulated stand characteristics of the beech stand on PRP 2 in the Lány game enclosure under the assumption of spontaneous development.

Year	t	$d_{1,3}$±σ	h	h_{95}	f	v	N	G	V	h:d	CAI	MAI	TVP
2014	188	57.5±27.9	30.45	41.4	0.609	4.390	152	39.2	732	0.530	4.7	3.89	732
2024	198	59.1±30.9	30.90	41.6	0.604	5.116	152	41.4	778	0.523	4.3	3.93	778
2034	206	57.2±29.8	28.74	41.2	0.631	4.657	108	27.5	503	0.502	3.9	3.98	819
2044	215	57.4±29.1	28.68	40.7	0.622	4.613	104	26.7	480	0.500	3.5	3.98	856
2054	225	59.9±29.9	28.79	41.1	0.622	5.048	96	26.8	485	0.481	2.9	3.96	890
2064	232	60.2±31.3	27.90	41.1	0.641	4.940	80	22.5	395	0.450	2.1	3.94	914

Explanatory notes: see Table 4.

3.4. Biodiversity of tree layer and natural regeneration

The development of structural indices of the tree layer and its density on PRP 1 are documented in Table 6. With continuous dynamics of the stand in the stage of advanced optimum, the initially invariable trend of random structure of the tree layer gradually changes into an insignificantly aggregated distribution. At first the stand is characterised by low spatial diversity, and later by intermediate spatial diversity that will probably gradually increase due to the growing-up understorey. Total diversity of this homogeneous stand (B = 3.829) will gradually increase and during the studied years it will reach the value of 6.345, which indicates an uneven structure. A similar situation will occurwith diameter and height differentiation of the stand that will be first low and will gradually increase up to 7 times in the next 50 years. At the end of the 50-year period, the stand will show a clear structural differentiation. The species diversity on PRP 1 is very low (from the aspect of species richness, heterogeneity and evenness) and its moderate decrease is expected in the future.

Table 6. Indices describing the diversity of the beech stand on PRP 1 in the Lány game enclosure quantified from the simulation results of spontaneous stand development.

Year	Index					Density		
	A (Pri)	B (J&Di)	TM_d (Fi)	TM_h (Fi)	R(C&Ei)	CP	CC	SDI
2014	0.174	3.829	0.230	0.072	1.125	2.24	0.89	0.69
2024	0.176	5.268	0.308	0.187	1.181	2.36	0.90	0.74
2034	0.231	5.853	0.341	0.258	1.069	1.73	0.82	0.52
2044	0.253	6.295	0.463	0.378	1.041	1.73	0.82	0.52
2054	0.289	6.241	0.452	0.389	0.934	1.54	0.79	0.48
2064	0.355	6.345	0.531	0.518	1.021	1.48	0.77	0.47

Explanatory notes: A – Arten-profil index, B – total diversity index, TMd – diameter differentiation index, TMh – height differentiation index, R – aggregation index, CC – crown closure, CP – crown projection area, SDI – relative stand density index.

The development of structural indices of the tree layer and its density on PRP 2 is shown in Table 7. With continuous dynamics at the stage of advanced optimum or initial stage of disintegration the trend of aggregated structure of the tree layer is more or less invariable at first, later it becomes more intensive. At the beginning of the simulation the spatial diversity is intermediate, but gradually there will be a transition to the sharp differentiation of vertical structure. Total diversity of this forest stand with even structure will obviously continue decreasing due to the absence of the regeneration phase. The situation will be opposite with the low diameter and height differentiation of the stand that should increase in the course of spontaneous development due to the dieback of the more numerous over-storey. When comparing both PRPs, the difference between the structural indices (except for Clark-Evans index) during fifty years was statistically significantly higher in PRP 1 ($F_{1,6}$ = 7.9; P > 0.05), which indicates distinctly increasing stand diversity.

Table 7. Indices describing the diversity of the beech stand on PRP 2 in the Lány game enclosure quantified from the simulation results of spontaneous stand development.

Year	Index					Density		
	A (Pri)	B (J&Di)	TM_d (Fi)	TM_h (Fi)	R(C&Ei)	CP	CC	SDI
2014	0.430	4.611	0.406	0.311	0.695	2.67	0.86	0.55
2024	0.433	4.482	0.400	0.302	0.685	2.79	0.88	0.57
2034	0.462	4.401	0.508	0.415	0.697	1.89	0.80	0.38
2044	0.507	4.301	0.492	0.398	0.670	1.64	0.77	0.36
2054	0.519	4.218	0.482	0.391	0.627	1.66	0.76	0.36
2064	0.626	4.042	0.497	0.403	0.636	1.41	0.69	0.28

Explanatory notes: see Table 6.

All characteristics of stand density are currently at the intermediate level but they will decrease sharply during further development. Over the years the highly differentiated enumeration canopy (perfect to broken canopy; 0.86 on average) will diminish along with density index (0.55) as the stage of disintegration will be progressing. The total area of crown projections is currently 2.67 ha per ha of the stand. As the tree layer develops, the decrease in the stocking of the main stand to 0.21 is expected by 2064 due to the continuous stage of disintegration, which means that a very sparse stand with solitary trees will be gradually created.

3.5. Regeneration potential and the impact of hoofed game

On PRP 1, on average 265 beechnuts per m^2 were found at the end of October 2013, of them 232 full beechnuts. At the beginning of April 2014 there were only 37 beechnuts per m^2, of them 27 full beechnuts. On PRP 2, there were on average 288 beechnuts per m^2 at the end of October 2013, of them 264 full beechnuts, and at the beginning of April 2014 only 18 beechnuts per m^2 were recorded, of them 5 full beechnuts. Hence, the numbers of beechnuts were heavily reduced by hoofed game in the autumn and winter season. On PRP 2, the loss was higher due to a greater pressure of wild boar and other species of hoofed game.

On PRP 1 the number of beech recruits amounted to 62,935 seedlings per ha, while on PRP 2 the natural regeneration of beech was completely destroyed by deer. The influence of browsing by hoofed game during the formation of the current stand is evident also from an enormous number of stem deformations, especially tree forks. On PRP 1, tree forks were observed on 8.5%, 14.9%, and 8.5% of trees at a height below 1.3 m, from 1.3 to 7 m, and above 7 m, respectively. On PRP 2, tree forks at a height below 1.3 m, from 1.3 to 7 m, and above 7m were found on 26.3%, 5.3%, and 15.8% of trees, respectively

4. Discussion

Height and diameter differentiation of the growing-up natural regeneration is expected on PRP 1 with progressive canopy opening-up and stand disintegration. The occurrence and quantity of recruits depend on the canopy closure, characteristics of the soil surface and cover of the herb layer. Natural regeneration in gaps with suitable site conditions is limited only by the activity of wild boars (in the proximity of cribs and wallows).

An ideal situation is when the so-called optimum population density is reached, when all individuals have sufficient food, resting and hiding opportunities for their prosperous development. When forest tree species are damaged by browsing or gnawing, the threshold of the so-called maximum population density is exceeded and game stocks should be reduced (Fichtner et al. 2011). A positive effect of reduced stocks of hoofed game on natural regeneration is confirmed by the statistically significant presence of undamaged natural regeneration on PRP 1 where the above-mentioned deer has been excluded. This limiting factor is evident also from the simulation of stand development by the growth model. In addition, other papers that used the SIBYLA simulator in the context of damage by game (Vacek et al. 2013) confirmed relatively high quality of its predictions (Špulák & Souček 2010).

An enormous quantity of tree forks was also observed on PRP (27.5% ± 4.1 SD). The formation of leading shoot forks is mostly caused by damage to the leading shoot at a young age, which results in the formation of two or more stems near the ground surface. Based on the observed stem deformations of the lower part of beech stems it may be concluded that the high stocks of game must have already existed at the time of the establishment of these stands. Browsed beeches have less leaf biomass and thus a smaller leaf area, but more branch biomass than unbrowsed beeches with the same shoot biomass (Vera 2000).

Successful natural regeneration depends first of all on its abundance and/or on seedling survival. In the Lány game enclosure there is a sufficient amount of seed material of European beech for the natural regeneration also in the stands of 179 and 194 years of age. On PRP the amount of full beechnuts that fell per 1 m^2 was on average in the range of 232–264 beechnuts.

Similar values were reported from Germany – from 200 to 500 beechnuts per m^2 in a heavy mast year and 5 – 60 beechnuts in a weak mast year (Röhring et al. 1978). Schmidt (2006) carried out a research in the area of Gottingen between the years 1981 and 2004. His results imply that in this period the annual mast production exceeded 16 × 150 beechnuts. Vacek & Jurásek (1986), who performed research in beech stands of the Krkonoše Mts. and Podkrkonoší at the beginning of air-pollution disasters between 1978 and 1982, reported more than 200 beechnuts per 1 m^2 in a heavy mast year, 30 – 200 beechnuts per 1 m^2 in a moderate mast year, and maximum 30 beechnuts per m^2 in a weak mast year.

In natural beech stands at an altitude of 600–760 m a.s.l. Korpeľ (1978) counted on average 25,000 seedlings per ha as the number of biologically established seedlings (at 3 years of age and older). For successful regeneration in these conditions he assumed a minimum number of 20,000 seedlings per ha. On studied PRP 1 in the Lány game enclosure the average number of recruits from the mast years 2011 and 2012 was 62,935 seedlings per ha, of this beech accounted for 100%. Referring to Korpeľ (1978) the seedling number on PRP 1 can be considered as sufficient. However, on PRP 2 the natural regeneration was completely destroyed by deer (red deer, sika deer, fallow deer and mouflon). Similar numbers of beech recruits like on PRP 1, though fluctuating in a wide range (9,020–75,778 seedlings per ha) were reported by Bílek et al. (2013) from the Voděrady beech forests, growing at comparable site and stand conditions. Moderately lower numbers of beech recruits (19,259–29,844 seedlings per ha) in natural beech forests in Albania were documented by Meyer et al. (2002). For selected objects of primeval forest type in the 4th forest altitudinal zone in Slovakia Korpeľ (1989) reported from 11,674 to 21,345 seedlings per ha.

On PRP 1, seedlings in height classes of 10–20 cm were the most abundant. Korpeľ (1978) stated that beech regeneration may reach the height of 40 cm and more only at stocking lower than 0.5. At stocking higher than 0.7 deceleration of height growth was observed as a result of shading by the parent stand. These findings are consistent with the results of Bílek et al. (2013), who stated that in ten years after the mast year in 2003 the growth of beech seedlings was fastest in stands with stocking 0.5, sufficient in stands with stocking

0.6, and rather insufficient in stands with stand density 0.8. From this aspect the growth of seedlings on PRP 1 at stocking 0.69 can be considered as sufficient.

Similarly to other studies of European beech natural regeneration (Rozas 2003; Nagel et al. 2006; Paluch 2007; Szewczyk & Szwagrzyk 2010; Vacek et al. 2010, 2014), the evaluation of the horizontal structure showed that the distribution of regeneration was distinctly aggregated. The relatively distinctly aggregated distribution of natural regeneration on all PRP 1 subplots is indicated not only by spatial indices but also by Ripley's *L*–function. The aggregated distribution of recruits occurs mainly in the gaps of the tree layer canopy, but the regeneration of this shade-loving tree species can spread relatively far behind the gap edge (Vacek et al. 2010). Similar results were obtained by Korpeľ (1989), who analysed the structure and development of beech natural forests in Slovakia in detail. This finding is consistent with the results from the studied PRP in the Voděrady beech forests (Bílek et al. 2013).

In the conditions of the Lány game enclosure the abundance of hoofed game is many times higher than is usual in nature. Vera (2000) concluded that for the successful growth of natural regeneration admissible stocks are 0.5–3 head of red deer per 100 ha and 4–5 head of roe deer per 100 ha. Of course, it is virtually impossible to reduce the stocks of wildlife in the game enclosure to such low numbers; hence, all attempts on natural regeneration and cultivation of young forest plantations must include fencing. Hromas (1997), for instance, recommends the following optimum wildlife stocks in a game enclosure: 12 head of red deer per 100 ha, 35 head of fallow deer per 100 ha, 45 head of mouflon per 100 ha, and 30 head per 100 ha in the case of the combination of fallow deer and mouflon. The abundance of game was a determining factor when the stands in the Poněšice game enclosure (South Bohemia, Czech Republic) were regenerated. The original wildlife stocks were reduced to approximately 10 head of red deer per 100 ha. The reduction of wildlife stocks, an increase in the carrying capacity of the game enclosure and a year-round high-quality feeding had a positive impact on the forest stands and led to the development of natural regeneration (Vaněk 2000, Řehoř & Zasadil 2010). In the Lány game enclosure, however, such a drastic reduction of wildlife stocks cannot take place since the area is used by the guests of the Office of the President of the Czech Republic. Therefore, it is necessary to handle the regeneration of the Lány game enclosure in a different way. The fencing of larger regeneration blocks was employed successfully in the Lány game enclosure in the past. The results confirming an efficient application of this management model were also reported from the Soutok game enclosure (South Moravia, Czech Republic), where red deer, fallow deer, wild boar and roe deer are kept. In this game enclosure mature stands were fenced between the years 1999 and 2000. This measure brought about a dynamic increase of natural regeneration inside the fence (Tureček 2013). The winter stocks of all game species kept in the Lány game enclosure comprise 43 head per 100 ha. These extremely high stocks logically cause absolute destruction of natural regeneration of European beech, which is evident on PRP 2 where red deer, sika deer, fallow deer and mouflon are present. Natural seeding is totally destroyed even though the game regularly receives supplementary feeding. The smaller enclosure (PRP 1), from which all hoofed game species except for wild boar are excluded, is positive for the presence of natural regeneration even though the density of wild boar is 169 wild boars per 100 ha in the period from September to January. Therefore, the wild boar does not seem to be a limiting factor for the successful growth of natural regeneration.

5. Conclusion

Our surveys document that with the present stocks of wildlife in the Lány game enclosure the limiting factor for the natural regeneration of old beech forests in the conditions of a game enclosure is not wild boar but other species of hoofed game (red deer, sika deer, fallow deer and mouflon) that completely destroy natural regeneration due to their high stocks. The model prediction of the development of beech forests on PRPs indicates that with the absence of natural regeneration there will be gradual disintegration of these forests and the obligation of reforestation will arise. Artificial reforestation and fencing of small regeneration segments inside these plots would require enormously high financial costs. Hence it seems more effective to develop a conception of controlled natural and/or combined regeneration of these stands on the basis of their differentiation according to age and stocking. The fertility of these old beech forests is sufficiently high to ensure natural regeneration if the influence of deer is eliminated. The oldest stands with reduced stocking should be integrated into larger blocks and protected by good fencing. A reduction in hoofed game stocks would be desirable because the gradual fencing of regeneration will diminish the productive area providing food.

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