Effect of game browsing on natural regeneration of European beech (*Fagus sylvatica* L.) forests in the Krušné hory Mts. (Czech Republic and Germany)

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Abstract

Tree damage by game browsing is one of the biggest threats to forest ecosystems at the time of climate change and large-scale forest disturbances. The aim of the paper was to determine the effect of browsing by ungulates on the diversity, abundance and species composition of natural regeneration in forest stands dominated by European beech (*Fagus sylvatica* L.). The research was conducted on 10 permanent research plots in the Krušné hory Mts. in the Czech Republic and Germany. The density of natural regeneration was in the range of 23,300–114,100 recruits ha⁻¹. A higher proportion of silver birch (*Betula pendula* Roth.) and rowan (*Sorbus aucuparia* L.) was found in the regeneration compared to the mature stands. A total of 78% of recruits was damaged by browsing. The most frequently damaged tree species were sycamore (*Acer pseudoplatanus* L.; 98%) and black alder (*Alnus glutinosa* [L.] Gaertn.; 97%), while Norway spruce (*Picea abies* [L.] Karst; 31%) and sessile oak (*Quercus petraea* [Matt.] Liebl.; 50%) were the least affected. Seventy-nine percent of European beech recruits were damaged. The game significantly reduced the height of regeneration by up to 40%, especially by terminal browsing. Browsing also negatively affected the quality and abundance of regeneration. For successful dynamics of species-rich natural forest ecosystems, it is necessary to minimize tree damage by game browsing. These main measures include the reduction of ungulate population levels and the optimization of their age structure and sex ratio, an increase in the number of overwintering enclosures and food fields for game and a change in the political approach to game management with sufficient consideration of forestry interests.

Key words: tree damage; forest structure; biodiversity; forest protection; Central Europe

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1. Introduction

Central European forest stands are characterized in the climax stage by occasional disturbances (Glončák 2009), which can be described by the gap disturbance regime (Korpel 1995; Jaworski & Kołodziej 2002). From this point of view, natural disturbances contribute positively to the dynamics of climax stands (Yamamoto 2000; Franklin et al. 2002; Sage et al. 2003; Manning 2007). Disturbance in the form of the death of a small number of trees contributes to the release of production space for new individuals of the tree layer that will occupy these newly opened niches in future (Kneeshaw & Gauthier 2003; Angelstam & Kuuluvainen 2004; Kuchel et al. 2010; Rugani et al. 2013). Natural regeneration, as a basic and essential element of forest dynamics, forms and ensures the continuity of the forest ecosystem (Veblen

1992; Vacek et al. 2010; Wagner et al. 2010). One uses this element and transforms it according to current and local needs (Paluch 2005; Collet & Chénost 2006; Collet et al. 2008). Through its intervention in this system, additional energy is created, without which the current concept of forest establishment could not exist (Korpel 1995; Pretzsch 2009; Trotsiuk 2012). In addition to disadvantages such as the specificity of the time of seedling of the mature stand (Ambrož et al. 2015; Vacek et al. 2017a), inequality of seedling density (Kantor 2001; Wagner et al. 2010) and the restoration of only such species composition that is already in the stand (Poleno et al. 2009), natural regeneration has also its advantages. Typical advantages include, for example, ensuring the natural occurrence of genetically native tree species (Korpel et al. 1991; Gömöry et al. 2011; Gallo et al. 2020a) that can make use of the local microrelief in an outstanding

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way (Barna 2004; Poleno et al. 2009; Vacek et al. 2015b). With its high adaptability, non-deformed root system (Mauer 2005) and, last but not least, its high number of individuals (Reininger 1992; Hájek et al. 2020), natural regeneration is a prerequisite for seed, shelterwood and selection silvicultural systems (Slanař et al. 2017; Vacek et al. 2019b). The specifics of natural regeneration are based on the precisely timed moment of intersection of individual assumptions that ensure its origin (Jarčuška 2009; Barna 2011; Jarčuška 2011). These assumptions include the occurrence of the seed year of the tree species present, optimum temperature, condition of the seed germination bed, light conditions and also soil moisture (Bellemare et al. 2002; Fischer & Lindner 2002; Bolte & Villanueva 2006). If these assumptions are not synchronized at the appropriate moment, full seeding does not occur, and the effect of natural regeneration loses its significance. This phenomenon is also exacerbated by the occurrence of the herbaceous and moss layer, which significantly reduces or eliminates the survival of seedlings on strongly infested soils (Kühne & Bartsch 2003; Jaloviar 2005; Collt & Chenost 2006; Provendier & Balandier 2008). The microrelief also plays an important role if the successful growth of natural regeneration, affecting water retention and the amount of available nutrients (Vacek et al. 2015b, 2017b).

In the area of interest, the Krušné hory Mts., European beech (*Fagus sylvatica* L.) forms the main part of forest stands on the mid- and lower elevation sites, where it has its production optimum (Plíva & Průša 1969; Neuhäuslová et al. 1998; Burda 2016). This tree species accounts for 5.3% in the Czech part and for 4.2% in the German part of Krušné hory Mts., however natural tree species composition was significantly higher (ÚHÚL 2019; SEKUL 2020). In the Czech Republic, the natural species composition reached 40. %, while the current tree species composition is only 8.8% (Ministry of Agriculture 2020). Both ecologically and economically, it is the most important and widespread deciduous tree in Europe (Bolte et al. 2007; Štefančík et al. 2018; Sharma et al. 2019a; Šimůnek et al. 2021). Due to its ecological plasticity, it is able to grow even in relatively heavily shaded and weed-infested places, and subsequently respond well to the release of canopy (Ellenberg et al. 1992; Bulušek et al. 2016). This predisposition predestines it to be the ideal tree species for regeneration by border felling, shelterwood system, or selection system (Kantor 2001; Poleno et al. 2009; Podrázský et al. 2019). These methods are suitable for optimal beech growth in conditions where there is no risk of damage by drought, sun exposure or late frost (Ningre & Colin 2007; Gallo et al. 2014), to which beech shows high vulnerability (Gallo et al. 2017; Šimůnek et al. 2019). The highest amounts of natural beech regeneration can be found on lush, mineral-rich soils (Musil & Möllerová 2005). Beech can form ideal vegetation mixtures with various deciduous trees (ash, maple, hornbeam, birch, rowan, cherry, linden), or conifers (spruce,

larch, fir, Douglas fir, pine) (Dittmar et al. 2003; Wagner et al. 2003, 2010; Podrázský et al. 2014; Králíček et al. 2017; Vacek et al. 2019a). In addition, in mixed stands, beech can achieve higher production potential, stability and resistance to extreme weather fluctuations, drought and climate change (Schäfer et al. 2017; Pretzsch et al. 2021; Vacek et al. 2021). In later stages of growth, tending has a great importance from the silvicultural point of view (Remeš et al. 2015; Štefančík 2017, 2019; Sharma et al. 2019b). In the submontane and mountain areas forest regeneration is often damaged by ungulates – browsing, bark stripping and fraying (Rooney 2001; Vacek et al. 2018; Cukor et al. 2019; Gallo et al. 2020b; Prokūpková et al. 2020; Vacek et al. 2020a). Growth is strongly negatively affected mainly by the browsing of terminal buds (Schulze et al. 2014). This damage limits terminal bud growth, individual height, vitality, and ability to survive in subsequent years (Ammer 1996; Vacek et al. 2014). This preference of ungulates for the tree species mainly results in a change of species composition, especially to the detriment of interspersed and admixed deciduous trees and firs attractive to game (Motta 2003; Konôpka & Pajtík 2015; Vacek et al. 2015a; Slanař et al. 2017). Suppression of species diversity by game or humans leads to unification of the tree layer (Poleno et al. 2009). This reduction in species diversity in turn brings about a change in the stability and vitality of the forest ecosystem. Heterogeneous ecosystems have higher productivity at a later stage of development compared to monocultures (Pretzsch et al. 2010; Dănescu et al. 2016; Zeller & Pretzsch 2019; Gallo et al. 2020c). In addition, mixed and largely structured forests are more resilient to ongoing climate change that is manifested by higher mean annual temperatures, uneven precipitation distribution and more frequent climatic extremes (Pretzsch et al. 2013; Seidl 2017; Ammer 2019; Vacek et al. 2020b).

Successful growth of natural as well as artificial regeneration requires individual or areal protection, most often in the form of deer enclosure fencing (Švestka et al. 1996; Jurásek 1998; Sage et al. 2003; Baumhauer et al. 2005; Olesen & Madsen 2008; Hanophy 2009). Maintaining the regulated numbers of game individuals as biological protection seems to be a difficult task in the long run (Švarc 1981; Poleno et al. 2009). The use of repellents in the form of chemical protection is not very effective (Cislerová 2001). Regular reinstatement of repellents is laborious and the efficiency does not achieve lasting effects (Vosátka 2007).

The aim of this research was to determine the effect of game on the natural regeneration of beech stands in the German and Czech part of the Krušné hory Mts. and the subsequent proposal of appropriate silvicultural measures to reduce damage by game to natural regeneration. The specific objectives were to i) evaluate the quantity, silvicultural quality and structure of natural regeneration in 10 permanent research plots (PRPs), ii) compare species composition and diversity of natural regeneration and

tree layer, iii) determine the effect of browsing damage on dynamics and species composition of natural regeneration and iv) to assess interactions between natural regeneration, tree layer, habitat and the influence of wildlife.

2. Material and methods

2.1. Study area

The area of interest, located in the central part of the Krušné hory Mts. at an altitude of 635–804 m a.s.l., was composed of 5 forest stands, and 2 PRPs were established in each stand. Four stands were located in the Czech Republic and 1 stand in Germany (Fig. 1). The average monthly temperature was around 5.9 °C and the total annual precipitation reached 780 mm. The temperature reached a maximum in July (15.2 °C), while the lowest temperature was in January (−3.4 °C). The minimum and maximum precipitation was in February (49 mm) and June (87 mm) (1961–2019 CHMI). The study area was

qualified as a humid continental climate zone, characterized by warm to hot, humid summers and cold to severely cold winters (Dfb) as defined by the Köppen climate classification (Köppen 1931). The predominant soil type was modal Cambisol and the bedrock was mainly formed by crystalline shales (schists) and granites. The slope ranged from 5 to 23 degrees.

Data collection was performed in 5 stands with dominant European beech (its share was over 75%) aged over 120 years and stocking less than 0.8 (Table 1). Other tree species occurring in the upper storey included Norway spruce (*Picea abies* [L.] Karst), silver birch (*Betula pendula* Roth.), sycamore maple (*Acer pseudoplatanus* L.) and sessile oak (*Quercus petraea* [Matt.] Liebl.). From a typological point of view, it was a habitat of the *series trophicum*, specifically *categoria mesotrophica* (*Fagetum mesotrophicum*, *Abieto-Fagetum mesotrophicum*, *Piceeto-Fagetum mesotrophicum*) and *categoria subxerothermica* (*Fagetum subxerothermicum*) (Viewegh et al. 2003).

Fig. 1. Localization of European beech stands on permanent research plots in the Krušné hory Mts. and mean monthly climatic values (1960–2020); the map was created in ArcGIS 10 software (Esri).

Table 1. Overview of basic site and stand parameters of permanent research plots 1–10 in the Krušné hory Mts. according to Forest Management Plan.

PRP	GPS coordinates	Country	Altitude [m a.s.l.]	Exposure	Slope [%]	Forest site type	Stand volume [m ³ ha ⁻¹]	Age [y]	Stocking
1	50°38'37.1"N, 13°39'44.0"E	Czechia	804	E	23	6S	280	171	0.7
2	50°38'34.3"N, 13°39'45.5"E	Czechia	800	E	20	6S	280	166	0.7
3	50°35'50.5"N, 13°30'01.6"E	Czechia	682	SW	12	6S	337	166	0.7
4	50°35'50.2"N, 13°30'02.2"E	Czechia	679	W	10	6S	337	166	0.7
5	50°21'31.7"N, 13°02'55.3"E	Czechia	672	SW	5	4C	64	130	0.3
6	50°21'31.4"N, 13°02'54.4"E	Czechia	668	SW	5	4C	64	168	0.3
7	50°35'19.3"N, 13°30'12.2"E	Czechia	633	NW	8	5S	396	168	0.8
8	50°35'21.2"N, 13°30'16.1"E	Czechia	637	NW	5	5S	396	149	0.8
9	50°39'03.3"N, 13°17'46.6"E	Germany	662	SW	7	4S	247	149	0.7
10	50°39'03.6"N, 13°17'45.0"E	Germany	665	S	6	4S	247	149	0.7

Notes: 4S – nutrient-medium beech site (*Fagetum mesotrophicum*), 4C – water-deficient beech site (*Fagetum subxerothermicum*), 5S – nutrient-medium fir-beech site (*Abieto-Fagetum mesotrophicum*), 6S – nutrient-medium spruce-beech (*Piceeto-Fagetum mesotrophicum*; Viewegh et al. 2003).

2.2. Data collection

A total of 10 PRPs of 3×30 m in size were established along the slope using a steel diameter tape. The PRPs were randomly selected by the coordinates using the RNG function. The boundaries of the area were marked at least 10 m from the edge of the stand. All corners of the PRPs were stabilized. Subsequently, the PRPs were delineated and divided into 10 square transects (3×3 m). Natural regeneration was recorded in each of the squares, i.e. individual seedlings (recruits) from 10 cm in height up to 4 cm of diameter at breast height (DBH) were measured. In addition, the following data were recorded for each individual: identification numbers of transects (1–10), numbers of recruits, tree species, height, silvicultural quality (evaluated only in individuals over 1 m in height on a scale of 1–4), browsing status (old, new, repeated, no damage) and type of damage (terminal, lateral, both, no damage). The height was measured with a lath to the nearest 1 cm.

The evaluation of the silvicultural quality of recruits was performed according to the following scale:

1. a straight vital individual without forking showing good height growth and representing the future basic element of the stand,
2. a slightly curved individual or individual with slight branching, which, if necessary, can still replace an individual with quality 1, good growth again,
3. a crooked branched individual unsuitable for future growth from the silvicultural point of view, shows irregular or poor growth,
4. a severely deformed or highly forked individual showing minimal to zero growth or dying individual with the typical “bonsai appearance”.

2.3. Data analysis

In terms of species diversity, indices of species richness (Margalef 1958; Menhinick 1964), species heterogeneity (Shannon 1948; Simpson 1949) and species evenness (Hill 1973; Pielou 1975) were calculated for individual PRPs (Table 2). The vertical structure was evaluated according to the Gini index (Gini 1921) and the spatial distribution according to the index of cluster size (David & Moore 1954). The equations of diversity indices are given in Vacek et al. (2020c).

Microsoft Excel was used for basic data analysis and creation of graphs, especially species composition and height distribution. Statistica 13 (StatSoft, Tulsa) was used for statistical analyses. The nonparametric Kruskal-Wallis test was used to evaluate the differences between heights in relation to tree species and tree damage by game browsing, because the data did not meet the normality according to the Shapiro-Wilks test. In the graphical outputs, the error bars show the standard error.

Principal component analysis (PCA) was performed in CANOCO 5 (Ter Braak, Šmilauer 2012) to evaluate the relationships between stand structure (stocking, stand volume, height, diameter, age), natural regeneration (density, height), tree damage by game browsing and habitat conditions (slope, altitude). Data were logarithmized and standardized prior to analysis. The results of multidimensional PCA analysis were visualized in the form of an ordination diagram. The overview map was created in ArcGIS 10 (Esri).

3. Results

3.1. Density and tree species of natural regeneration

Sufficient potential of natural regeneration was found on the PRPs, ranging from 23,300 recruits ha^{-1} (on PRP 2) to 114,100 recruits ha^{-1} (on PRP 9; Fig. 2). European beech was dominant on all PRPs, accounting for 75–100%. On most PRPs (1, 2 and 5 to 10) mixed species composition of sycamore, black alder, silver birch, rowan, sessile oak and Norway spruce was recorded, always up to 10%. The exclusive occurrence of natural beech regeneration was recorded on two PRPs (3 and 4). The average number of beech recruits was around 63,900 recruits ha^{-1} . The most numerous admixtures included silver birch (on average 3,600 recruits ha^{-1}) and rowan (1,700 recruits ha^{-1}). The maximum number of recruits was observed in European beech on PRP 8 and 9 (93,200 recruits ha^{-1} and 92,700 recruits ha^{-1} , respectively). The minimum number of beech recruits was recorded on PRP 2 (19,300 recruits ha^{-1}). The highest number of species was found on PRP 8 and 9, where, in addition to European beech (84%), also Norway spruce (10%), sessile oak (1%) and silver birch (5%) were present.

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

Criterion	Quantifiers	Label	Reference	Evaluation
Species diversity	Species richness	D ₁ (Mai)	Margalef 1958	minimum D = 0, higher D = higher values
		D ₂ (Mei)	Menhinick 1964	
	Species heterogeneity	λ (Sii)	Simpson 1949	range 0–1; minimum λ = 0, maximum λ = 1
		H' (Shi)	Shannon 1948	
Vertical diversity	Species evenness	E ₁ (Pii)	Pielou 1975	range 0–1; minimum E = 0, maximum E = 1
		E ₂ (Hi)	Hill 1973	
Horizontal structure	Gini index	G (Gi)	Gini 1921	range 0–1; low G < 0.3, very high differentiation G > 0.7
	Index of cluster size	CS (D&Mi)	David & Moore 1954	mean value CS = 0, aggregation CS > 0, regularity CS < 0

Fig. 2. Density of natural regeneration on permanent research plots 1–10 differentiated according to tree species composition of European beech and other tree species in 2020.

The proportion of European beech in natural regeneration was by 2% lower (88%) in comparison with the tree layer (90%; Fig. 3). In the mature stand, European beech reached 100% representation on six PRPs (3 to 8), while in the regeneration it was only on two PRPs (3 and 4). On PRP 1 and 2, there was an admixture of sycamore in the mature stand (up to 5%). In addition to European beech, PRP 9 also included rowans and Norway spruce (up to 10%). In addition to beech, sessile oak and Norway spruce were present on PRP 10, both up to 5%. The average stand volume of the mature stand was around 300 m³ ha⁻¹ (269 m³ ha⁻¹ for beech).

3.2. Height structure and quality of natural regeneration

The highest mean height of natural regeneration was registered on PRP 9 (144 cm), on the contrary, the lowest mean height was found on PRP 3 (43 cm). The deter-

mined heights of natural regeneration were divided into individual height classes using a 20-cm interval (Fig. 4). On all PRPs, beech was most common in the height class of 40 to 60 cm (11,800 recruits ha⁻¹), then in the height class of 60 to 80 cm (11,700 recruits ha⁻¹) and subsequently in the height class of 80 to 100 cm (9,500 recruits ha⁻¹). The height of the beech was significantly greater than that of the other tree species, individuals with a height over 300 cm were recorded. At higher heights, the number of beech recruits gradually decreases. The smallest representation of beech was in the height class up to 20 cm (1,500 recruits ha⁻¹). The height competition consists mainly of silver birch in the height class of 80 to 100 cm (700 recruits ha⁻¹) and also of rowan in the height class of 60 to 80 cm (400 recruits ha⁻¹). The greatest frequency of admixed tree species in natural regeneration was in the height class from 60 to 80 cm (14,900 recruits ha⁻¹). On the contrary, it was the smallest in the height class from 0 to 20 cm (1,700 recruits ha⁻¹).

The significant difference between tree species was found in the mean height of recruits (Kruskal-Wallis test, Chi-square = 166.0, df = 6, $p < 0.001$; Fig. 5). Sessile oak (113 cm), Norway spruce (108 cm) and silver birch (103 cm) had significantly ($p < 0.05$) higher mean height. On the other hand, significantly ($p < 0.05$) lower height was observed in maple (48 cm), alder (49 cm) and rowan (69 cm). European beech reached the mean height of 88 cm across all PRPs.

For silvicultural quality of natural regeneration, quality 2 was the most frequent with 49% (35,600 recruits ha⁻¹). It was followed by quality 1 with 32% (23,200 recruits ha⁻¹) and quality 3 with 18% (13,100 recruits ha⁻¹). The worst quality 4 was represented by 1% (700 recruits ha⁻¹).

Fig. 3. Tree species composition of a) natural regeneration (according to numbers) and b) mature stand (according to stand volume) for all permanent research plots in 2020.

Fig. 4. Height structure of natural regeneration on permanent research plots differentiated according to tree species composition of European beech and other tree species in 2020.

Fig. 5. Mean height of natural regeneration on permanent research plots differentiated according to tree species in 2020; error bars indicate standard error; significantly (Kruskal-Wallis test, $p < 0.05$) different values are designated by different letters.

3.3. Diversity of natural regeneration

In view of species diversity, natural regeneration showed low species richness, similarly like species heterogeneity (Table 3). Only on PRP 1 and 9 the heterogeneity reached higher values (medium diversity). Higher variability between PRPs was in species evenness. According to the E_2 index, the evenness on all PRPs was high, except for PRPs 2 and 3, where there was only natural regeneration of beech. The species evenness was the highest on PRP 1, in the plot with the lowest share of beech (75%) of all monitored PRPs.

As for the structure of natural regeneration, the height diversity reached medium values except for PRPs 9 and 10, where the diversity was high due to the high number of advanced individuals. The horizontal structure was significantly ($p < 0.05$) aggregated on all PRPs, only PRP 2 showed the random distribution of recruits. The highest aggregation of recruits was in stands with the highest stocking (PRPs 7 and 8).

3.4. Effect of browsing on natural regeneration

Out of the total number of recruits, on average 78% of individuals were damaged by browsing. Thus, 22% of recorded individuals were without damage. The type of browsing showed that out of the total number of recruits on all PRPs, most individuals were damaged by both terminal and lateral browsing (33,400 recruits ha^{-1} , 51%), fewer individuals suffered from lateral browsing only (12,900 recruits ha^{-1} , 17%), and similarly from terminal browsing only (5,900 recruits ha^{-1} , 10%). The degree of damage indicated that natural regeneration was most frequently damaged by repeated browsing (41,800 recruits ha^{-1} , 58%), followed by old browsing (7,900 recruits ha^{-1} , 11%) and new browsing (6,900 recruits ha^{-1} , 9%).

The species preference of ungulates with respect to damage to natural regeneration is depicted in Fig. 6. The most frequently damaged individuals were sycamore maple (98%), black alder (97%) and rowan (94%). The least damage was recorded for sessile oak (50%) and Norway spruce (31%). Seventy-nine percent of Euro-

Table 3. Diversity of natural regeneration on permanent research plots 1–10 in 2020; the highest values are in bold and the lowest in italics.

PRP	D_1 (Mai)	D_2 (Mei)	λ (Sii)	H' (Shi)	E_1 (Pii)	E_2 (Hi)	G (Gi)	CS (D&Mi)
1	0.195	0.018	0.402	0.727	0.662	0.628	0.466	0.817*
2	0.199	0.020	0.289	0.235	0.493	0.564	0.427	0.639
3	<i>0.000</i>	<i>0.000</i>	<i>0.000</i>	<i>0.000</i>	<i>0.000</i>	<i>0.000</i>	0.399	1.720*
4	<i>0.000</i>	<i>0.000</i>	<i>0.000</i>	<i>0.000</i>	<i>0.000</i>	<i>0.000</i>	0.397	1.477*
5	0.088	0.007	0.205	0.156	0.517	0.597	0.405	2.414*
6	0.089	0.007	0.271	0.192	0.637	0.668	0.415	2.474*
7	0.088	0.007	0.168	0.134	0.445	0.559	0.460	3.310*
8	0.087	0.006	0.164	0.131	0.437	0.555	0.451	2.698*
9	0.258	0.012	0.328	0.295	0.490	0.501	0.506	1.690*
10	0.263	0.013	0.277	0.244	0.405	0.509	0.570	0.855*

Notes: D_1 and D_2 – indexes of species richness, λ and H' – indexes of species heterogeneity, E_1 and E_2 – indexes of species evenness; G – Gini index of vertical structure, CS – index of cluster size; *statistically significant (0.95 confidence interval) aggregated horizontal structure (CS indexes).

pean beech recruits were damaged, similarly like in silver birch (78%).

Fig. 6. Proportion of tree damage caused by game browsing (terminal, lateral, both) of natural regeneration on permanent research plots differentiated according to tree species in 2020.

The game also had a significant (Kruskal-Wallis test, Chi-square = 576.0 df = 3, $p < 0.001$) effect on the height of natural regeneration in relation to the browsing status (Fig. 7). The significantly ($p < 0.05$) highest mean height was observed in natural regeneration without browsing damage (119 cm). In contrast, the significantly ($p < 0.05$) lowest recruits were those damaged by new (63 cm) and repeated browsing (79 cm). Individuals of natural regeneration damaged by old browsing reached a height of 95 cm. The mean height of natural regeneration significantly (Kruskal-Wallis test, Chi-square = 710.8, df = 3, $p < 0.001$) corresponded to the type of browsing. Terminal and combined browsing significantly ($p <$

0.05) limited the height of natural regeneration (71 cm and 73 cm, respectively). In contrast, individuals with lateral browsing and those without browsing damage reached the significantly ($p < 0.05$) highest mean heights (104 cm and 119 cm).

3.5. Interactions between natural regeneration, stand parameters, sites and tree damage

The results of the PCA expressing the interactions between natural regeneration, tree damage by game browsing, tree layer and habitat on 10 PRPs in the Krušné hory Mts. are presented in the form of an ordination diagram in Fig. 8. The first ordination axis explains 40.3% of data variability, the first two axes explain 72.8% and the four axes together explain 94.8% of data variability. The x-axis represents the height of natural regeneration and its species evenness. The y-axis represents the altitude and horizontal structure of natural regeneration. The quality of natural regeneration was negatively correlated with damage by game. The density of natural regeneration was negatively correlated with stand stocking, which was positively correlated with mean DBH, age and stand volume. The frequency of regeneration was also influenced by the slope and elevation. With increasing elevation, the number of recruits decreased and the horizontal structure tended more towards a regular spatial pattern (aggregated distribution decreased). The lowest explanatory parameter in the ordination diagram was the vertical structure. In terms of typology and forest types, habitats in a lower forest vegetation zone had a higher number and quality of recruits, while stands in higher vegetation zones were characterized by higher tree damage by game browsing. The lowest variability within the stands

Fig. 7. The status a) and type b) of game browsing in relation to the height of natural regeneration on all permanent research plots in 2020; error bars indicate standard error; significantly (Kruskal-Wallis test, $p < 0.05$) different values are designated by different letters.

was found in the stand where only European beech was present in species composition (PRPs 3 and 4).

Fig. 8. Ordination diagram showing the results of PCA of the relationships between mature stand (stocking, stand volume, height, diameter, age), natural regeneration (DENSITY, HEIGHT), tree damage by game browsing (DAMAGE), diversity of natural regeneration (see Table 2) and habitat characteristics (slope, altitude); ● symbols indicate the permanent research plots (1–10), ▲ the group of forest site types (see Table 1).

4. Discussion

4.1. Density and tree species of natural regeneration

The representation of different tree species was mainly based on the present mature stand, altitude, soil composition and precipitation total (Pretzsch et al. 2014; Vacek et al. 2017b). Because individual PRPs were located in beech stands, the share of European beech was dominant, ranging from 75% (PRP 1) to 100% (PRPs 3 and 4). Admixed individuals of sycamore, black alder, silver birch, rowan, sessile oak and Norway spruce always accounted for up to 10%. The average number of recruits in the central part of the Krušné hory Mts. reached 72,600 recruits ha^{-1} , i.e. it ranged from 23,300 to 114,100 recruits ha^{-1} . A high abundance of natural regeneration was documented in the beech-dominated stands also in other localities in the Czech Republic and in other countries, e.g. in the Orlické hory Mts. the natural regeneration reached 37,200 recruits ha^{-1} (Vacek et al. 2014), 41,700 recruits ha^{-1} in the Jizerské hory Mts. (Slanař et al. 2017), 76,700 recruits ha^{-1} in the Krkonoše Mts. (Vacek et al. 2017b), 100,200 recruits ha^{-1} in the Broumov region (Hájek et al. 2020) or 27,300 recruits ha^{-1} in Tworylczyk in Poland (Jaworski et al. 2002). Substantially lower numbers (3,200 recruits ha^{-1}) of recruits were reported

by Oheimb et al. (2005) from close-to-nature beech forests in north-eastern Germany. The admixture of silver birch and rowan recruits (3,600 and 1,700 recruits ha^{-1} , respectively) corresponds to their usual number in similar stand and habitat conditions (Van Hees et al. 1996; Żywiec & Ledwoń 2008). The number of recruits was in negative correlation with altitude, stand stocking and tree damage by game browsing. Canopy of the mature stand significantly affects the density of natural regeneration in beech stands (Vacek et al. 2017b). Ambrož et al. (2015) and Turczański et al. (2021) reported the high intensity of game pressure as a limiting factor for the occurrence and frequency of natural regeneration.

The representation of European beech in natural regeneration (88%) corresponds to its proportion in the parent stand (90%). Admixture of other tree species is based on dispersal of the seed material by wind from the surrounding stands (Suchockas 2002) and also on the introduction by game and birds (Karlsson 2001; Dobrovolný & Tesař 2010). In our case, these are tree species with scattered occurrence, such as silver birch (PRPs 5, 6) and rowan (PRPs 7, 8), which do not occur in the mature stand on PRPs. The increased share of these two pioneer tree species in natural regeneration was also documented for example by Slanař et al. (2017) from the Jizerské hory Mts. The average stand volume of the mature stand was around 300 $\text{m}^3 \text{ha}^{-1}$ (269 $\text{m}^3 \text{ha}^{-1}$ for beech), which corresponds to stands with reduced stocking (Condés 2013).

4.2. Height structure and quality of natural regeneration

The height of recruits ranged from 43 cm (PRP 3) to 144 cm (PRP 9), similarly like in the Krkonoše Mts. (Prokūpková et al. 2020). As for height structure, most beech recruits were in the height class from 40 to 60 cm (11,700 recruits ha^{-1}), on the contrary, the smallest number of recruits was in the height class up to 20 cm (1,700 recruits ha^{-1}). The dominance of European beech is partly competed by silver birch with 700 recruits ha^{-1} in the height class of 80 to 100 cm or rowan in the height class of 60 to 80 cm (400 recruits ha^{-1}). In beech forests in the Broumovské stěny National Nature Reserve, the average height of regeneration, depending on the microhabitat, ranged from 74 cm on the ridges to 121 cm in the depressions (Vacek et al. 2015). According to species, the largest mean height of recruits was found in sessile oak (113 cm), while the lowest mean height was recorded for sycamore (49 cm) in our study. Beech reached the mean height of 88 cm. Qualitatively, silvicultural quality 2 (49%) and quality 1 (32%) predominate on all PRPs. Quality 4 is represented by 1% only. Browsing of any type has a strong impact on quality, as documented by Olesen & Madsen (2008) and Madsen & Hahn (2008). The silvicultural quality of natural regeneration can also be significantly influenced by management methods and by the edge effect of the stand (Bílek et al. 2018).

4.3. Diversity of natural regeneration

Considering the species diversity, natural regeneration showed low species richness and species heterogeneity. Similarly, low values of diversity were documented by Vacek et al. (2015b) in beech stands in the Broumovsko Protected Landscape Area, while significantly higher species diversity was found in mixed beech stands (Slanař et al. 2017; Hájek et al. 2021). On the contrary, the species evenness was mostly high on all PRPs, where there were more tree species. The species evenness was the highest on PRP 1, in the area with the lowest share of beech (75%) of all monitored PRPs. The largest number of species was found on PRPs 8 and 9, where, in addition to European beech (84%), there was also Norway spruce (10%), silver birch (5%) and sessile oak (1%). The spatial distribution of regeneration was strongly aggregated in most cases. The clustered horizontal structure of regeneration was also reported by other researchers from dominant beech stands from other parts of the Czech Republic (Vacek et al. 2014; Ambrož et al. 2015; Slanař et al. 2017), and also from Slovenia (Nagel et al. 2006) and Poland (Paluch 2007). The aggregation of recruits increased with the increasing number of individuals. This positive correlation was also found in the mature stand in beech forests (Vacek et al. 2015c; Bulušek et al. 2016).

4.4. Effect of browsing on natural regeneration

Out of the total natural regeneration, 78% of recruits were damaged by browsing. Similarly, the negative influence of browsing on species composition and the future dynamics of forest in the Czech Republic was documented by Vacek (2017) from the Orlické hory Mts., Slanař et al. (2017) from the Jizerské hory Mts., Vacek et al. (2019) from Broumovsko and Prokūpková et al. (2020) from the Krkonoše Mts. The extremely high game damage is caused by its disproportionately large population in relation to forest stands or agricultural land, which is constantly rapidly increasing in the Czech Republic. Deer game has increased by 146% and wild boar even by 8,526% in the last 53 years (Hunting records of ÚHÚL).

In the area of interest, sycamore (98%) and black alder (97%) were the tree species most affected by game browsing. On the other hand, the least frequent damage was recorded in Norway spruce (31%). Seventy-nine percent of European beech recruits were damaged. In contrast to the study of Baran (2015), the species preference is different in the Orlické hory Mts.; the browsing of rowan prevails amounting to 44%, spruce 37% and only then beech 20% with a similar representation of beech in the species composition. Similarly, Vacek (2017) described the preference of some tree species in the Orlické hory Mts., where the highest level of damage occurred on fir (100%), rowan (94%), beech (56%) and the lowest damage was observed on spruce (18%). The preference of

some tree species, especially less represented broadleaves or firs, was also mentioned by foreign researchers from Germany (Ammer 1996), Italy (Motta 1996; D'Aprile et al. 2021), Slovakia (Konôpka & Pajtík 2015) and France (Bernard et al. 2017).

Damage by game not only affected the abundance, growing quality and species composition, but also the mean height and growth of natural regeneration. The mean height significantly corresponds to browsing (Ammer 1996; Vacek et al. 2014). Natural regeneration without damage had a significantly higher mean height (119 cm). On the contrary, individuals damaged by new browsing reached half the mean height (63 cm), due to severe damage of young and low-height regeneration. This was followed by repeated browsing with the recruit height of 79 cm. Recruits suffering from old browsing reached an average value of 95 cm and showed then vitality of natural regeneration and its subsequent growth, similarly like it was reported by Rozas (2003). Repeated browsing was registered as the most common damage to natural regeneration (58%). Taking into account the type of browsing, lateral browsing did not distinctly affect the height of recruits (height reduction by 12%, 104 cm). Terminal and combined browsing reduced the mean height (71 and 73 cm) of natural regeneration by 40% compared to regeneration without damage. Natural regeneration was most often damaged by the combined browsing of terminal and lateral buds (52%). The destruction of terminal buds causes a significant reduction in height increment (Dittmar 2003). This fact is also confirmed by repeated browsing, which not only reduces the increment, but also the vitality of individuals (Reimoser & Gossow 1996).

5. Conclusion

In the area of interest of the Krušné hory Mts., natural regeneration in European beech stands shows a high potential (72,600 recruits ha⁻¹). The species composition of natural regeneration, like other parameters, is linked to the character of the tree layer. On all permanent research plots, in the mature stands there was a dominant proportion of beech (90%) with a minimum admixture of other tree species. The natural regeneration of beech accounted for 88% with an admixture of other species, especially silver birch and rowan. This expansion of pioneer trees, which do not occur in the mature stand, is mainly due to seeding from the surrounding stands. Among the most damaged tree species by browsing were scattered broadleaves such as sycamore (98%), black alder (97%) and rowan (94%). Norway spruce (31%) and sessile oak (50%) were the least frequently damaged tree species. In total, 79% of beech recruits were damaged. In addition to the change in species composition, game had a significant negative effect on the silvicultural quality and extent of regeneration. The largest damage was caused by

terminal browsing (height reduction by 40%). Due to the high number of damaged individuals, it is necessary to protect the young stands with fences and reduce the high numbers of ungulates to an ecologically acceptable level. In view of hunting management, in addition to regulating the ungulate population levels, it is important to optimize the sex ratio and age structure of the population. As an alternative, it is possible to include individual mechanical fencing of valuable admixed tree species and support the natural predators of ungulates. The ever-increasing numbers of wolves (*Canis lupus*) could also contribute to limiting the number of ungulates in future. Another possible way to reduce the ungulate damage to stands is to increase the number of overwintering game enclosures and food fields for game. Overall, however, there is a need to harmonize hunting management and forest management with emphasis on silvicultural practices to support admixed trees and the creation of diversified forests. These mixed forests are characterized by high stability and sustainable productivity in the time of ongoing climate change.

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