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Positive impact of large wild herbivore exclusion on silver fir regeneration: A case study from the Poľana Mountains, Central Slovakia

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Abstract

In forest ecosystems, the browsing activity of large wild herbivores (LWH) often leads to reduced tree and plant diversity, diminished biomass production, and challenges in achieving forest management objectives. Our case study focuses on assessing the impact of LWH browsing during the initial stages of forest growth by comparing fenced plots (F plots) with excluded LWH and control plots (C plots) with the presence of LWH. The experiment took place at the Hukavský Grúň research site in the Poľana Mts., characterized by a high red deer (*Cervus elaphus* L.) population. Fifteen F plots and fifteen C plots, all situated within mixed maternal forests, were established in the 2023 growing season. Thus, circular plots with a radius of 2.5 m were utilized, and comprehensive data were collected on young trees (excluding those under 10 cm in height), covering tree species, positions, heights, and stem diameters. Species-specific allometric relations were employed to calculate the aboveground biomass of each tree, contributing to the overall biomass stock on a plot basis. A comparison between F and C plots revealed a prevalence of silver fir (*Abies alba* Mill.) in F plots, while European beech (*Fagus sylvatica* L.) dominated C plots. F plots exhibited higher tree species diversity (4.5 species), contrasting with the lower diversity (2.0 species) and absence of silver fir in C plots. The F plots also demonstrated greater tree density and sizes, resulting in substantial differences in aboveground biomass stocks. Browsing in C plots predominantly affected tree height rather than stem diameter, leading to a bigger height-to-diameter ratio in F plots compared to C plots. We suggest that fencing as a method to exclude LWH might be economically expensive and provide a temporary solution limited by the functionality of the fence. Therefore, the primary strategy for safeguarding the future of silver fir may lie in regulating LWH populations to a reasonable threshold.

Key words: *Abies alba* Mill.; shoot browsing; fenced area; mixed maternal forest; red deer; Western Carpathians

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1. Introduction

Several European studies, including Carpio et al. (2020), Valente et al. (2020), and Balčiauskas & Kawata (2022), have consistently reported a rising population of large wild herbivores (LWH; in our case also synonym to ruminating ungulates), with a particular focus on red deer (*Cervus elaphus* L.). In Slovakia, for example, the red deer population has exhibited significant growth, estimated at 33,000 in 2000, escalating to 51,000 by 2010 (Bučko et al. 2010), 65,000 in 2015, and a substantial 75,000 in 2020 (IBULH 2021). This surpasses the sustainable levels projected by Finďo & Petráš (2007). The overpopulation of LWH, especially red deer, poses a multitude of challenges, including heightened demands for forage and living space. This surge has resulted in various issues across sectors, notably influencing agriculture (e.g., Drimaj et al. 2023) and forestry (e.g., Cukor et al. 2019). The increasing pressure on available resources due to LWH overpopulation underscores the urgency of addressing these ecological imbalances and finding sustainable solutions for coexistence.

In the forestry sector, the impact of LWH on forests is profound, leading to diminished tree and plant diversity (Schäfer et al. 2019), decreased timber production (White 2012), and worsened wood quality (Kiffner et al. 2008). Central European forests, inhabited by red deer and other LWH, witness a diverse diet that includes

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a broad array of plant species. While these herbivores exhibit a preference for grasses, they also consume significant quantities of leaves, stems, and tree bark (Červený et al. 2010), selecting the most nutritious plants and plant parts available (Finďo & Petráš 2007). The intense trophic pressure exerted by LWH manifests in various effects on tree species, stemming from both direct damage through consumption (Kamler et al. 2010) and indirect impacts mediated by their influence on interspecific competition among trees (e.g., Vacek 2017; Konôpka et al. 2021). While roe deer (*Capreolus capreolus* L.) primarily focus on browsing foliage and shoots, red deer, fallow deer (*Dama dama* L.), and partially mouflon (*Ovis aries musimon* L.) often target bark, particularly on stems (Gill et al. 1992). Browsing on stem bark poses a threat to timber production quality, directly leading to wood deformations (Kiffner et al. 2008) or indirectly facilitating fungal infestation through wounds, resulting in wood rots, which varies robustly among tree species (Jelonek et al. 2022). This damage significantly diminishes timber production (Vacek et al. 2020) and undermines economic gains from wood of certain tree species (Reimoser et al. 1999). Addressing these challenges requires a comprehensive understanding of the interactions between LWH and forest ecosystems to implement effective and sustainable management strategies.

The findings from the Slovak National Forest Inventory reveal that the most severe damage to forest trees occurs during their early growth stages, typically within the first 20 years (Šebeň 2017). Notably, the impacted trees are not confined to soft broadleaved species (Konôpka et al. 2023) of low economic significance; but also commercial species, such as the silver fir (*Abies alba* Mill.), are significantly affected. The silver fir, a species of notable economic and ecological importance, faces intensive damage by LWH during its initial growth stages, often resulting in a substantial decrease in species composition or complete disappearance. Studies by Senn & Suter (2003) and Häsler & Senn (2012) emphasize that the silver fir is the most heavily browsed among important tree species in montane forests of central and south-eastern Europe. They noted that, consistent with widespread reports, silver fir regeneration has been consistently poor or has even failed for decades, with browsing LWH identified as the primary negative factor. As early as the 1980s, Ott et al. (1989) raised concerns about the significant threat posed by LWH to the regional long-term survival of the silver fir. Despite these challenges, the silver fir holds great importance from both production and ecological perspectives in the Carpathian Arch (Barbu & Barbu 2005) and numerous Eurasian regions (San-Miguel-Ayanz et al. 2016). In mixed forest stands, the silver fir contributes to wood productivity (Mina et al. 2018), enhances species biodiversity (Dobrowolska et al. 2017), and improves soil conditions (Třeštík & Podrázský 2017). Consequently, active support for the species through suitable forest management (Vacek et al. 2015) and potentially game management, even if it involves reducing LWH population density (Bödeker et al. 2023), is crucial for the conservation and sustainable utilization of the silver fir.

In fact, quantifying the effect of LWH in tree stands can be challenging because recent signs of damage, such as bark peeling and branch bites, are easier to detect and measure (e.g., Konôpka et al. 2022) than that occurred in the past. Therefore, one of the most effective methods for quantifying the effects of LWH on plants is through the use of herbivores exclusion, typically achieved by means of fences and comparing with adjacent control areas (e.g., Konôpka et al. 2021; Bödeker et al. 2023; Iijima & Oka 2023). This comparative method has allowed researchers to examine the effects of LWH not only on forest tree characteristics, but also on understory shrubs and herbs (e.g., Schäfer et al. 2019) and even on some animals, especially small mammals (Bernes et al. 2018). On the other hand, creating and maintaining LWH exclusion over appropriate spatial and temporal scales to study their effects can be challenging, as it can be rather time- and labor-consuming. Therefore, existing infrastructure, such as fenced areas in forests, especially those maintained for extended periods, could be advantageous and utilizable for scientific purposes.

The principal objective of this case study is to elucidate the impact of LWH, particularly red deer, on forest regeneration, with a specific emphasis on silver fir. Our methodology revolves around a comparative analysis of forest regeneration in the presence and absence of LWH, achieved by analysing disparities between areas outside (control) and inside (LWH exclusion) fence. Key indicators employed for gauging these distinctions encompass species composition, as well as the abundance and dimensions of trees, both at the level of individual species and the all species. Additionally, we have integrated allometric relationships to calculate aboveground biomass stock, providing insights into carbon sequestration with regard to tree components, among other interpretative purposes. This comprehensive approach aims to enhance our understanding of the intricate dynamics between LWH, particularly red deer, The aims were linked to our hypothesis, which focused on the effects of LWH on forest regeneration: (i) exclusion increases current tree density (number of trees per square unit), (ii) exclusion supports productivity, resulting in current tree aboveground biomass stock, (iii) the presence of LWH has different impacts among tree species (attractive tree species, such as silver fir, are more influenced by browsing than those which are less attractive, e.g., European beech), (iv) consequently, the presence of LWH decreases species diversity (mean number of species per plot).

2. Material and methods

2.1. Site and stand characteristics

The study site is situated within the Poľana Mountains, characterized by volcanic origin and andesite bedrock. With an altitude of approximately 850 meters above sea level, this region boasts Mesotropic cambisoils, placing it in the fertile site, which ensures high forest productivity. The vegetation zone corresponds to the fifth zone, i.e. fir-beech, indicating a natural tree species composition dominated by European beech (*Fagus sylvatica* L.) and silver fir. The local climate is defined by an annual precipitation sum of nearly 1,000 mm and a mean annual temperature of 5.5 °C. The coldest period occurs in January, with temperatures dropping to –4.9 °C, while the warmest period is in July, reaching 15.4 °C. The region experiences a snow cover duration of approximately 90 days.

In 1991, the staff of the Forest Research Institute in Zvolen, specifically the Department of Forest Ecology, established the Hukavský Grúň permanent research site. The site's detailed description can be found in the work by Pavlenda & Čaboun (2016). The primary focus of their research encompasses various components of the forest environment and ecosystem, including soil, air, and all types of vegetation. The investigations delve into the intricate relationships within the ecosystem, such as the influence of the atmosphere on vegetation, element and substance cycles (e.g., soil nutrient status, litter, biochemical processes), physiological processes, tree growth, vitality, ecological stability, and biophysical phenomena. At the initiation of research activities, a forest complex covering an area of 0.575 hectares was enclosed by a fence. The fence, with nearly 2.5 meters, was built to safeguard the trees within from LWH. Notably, this region is characterized by an overabundance of red deer population, a factor that significantly impacts forest regeneration, as documented by Bučko et al. (2010). In addition to red deer, occasional sightings of roe deer, fallow deer, and mouflon are also possible in this area.

The maternal forest stand at the Hukavský Grúň research site is predominantly composed of European beech, representing approximately 70% of the trees (year 2023). Norway spruce (*Picea abies* [L.] Karst.) made up 17%, while silver fir accounts for nearly 4%. The remaining tree species included maples (*Acer pseudoplatanus* L. and *Acer platanoides* L.) and common ashes (*Fraxinus excelsior* L.). The trees in the main canopy boast a mean age of approximately 120 years, with heights ranging between 32 and 40 meters. According to measurements performed in the autumn 2022, the basal area of the stand was 52.1 m^2 per hectare, and the growing stock (represents stem wood under bark) was 821 m^3 per hectare. This forest stand originated from natural regeneration, and the influence of any previous forest management on the present trees is deemed negligible.

Long-term measurements conducted since 2000 reveal a gradual decline in the number of trees, attributed to competitive processes and disturbances. Among all the species, disturbances have particularly impacted spruce, primarily due to strong winds causing uprooting and subsequent bark beetle outbreaks leading to tree mortality. Over the span of two decades, the total number of trees has decreased by 20%, declining from 570 to 450 trees per hectare. Noteworthy declines were observed in the years 2004 and 2020, during which gaps in the stand canopy emerged, potentially creating favorable conditions for forest regeneration. These disturbances, while contributing to the reduction in overall tree numbers, presented an opportunity for ecological renewal and the establishment of new vegetation within the forest ecosystem. The records from the local hunting association showed that the population density in the hunting ground was 26 red deer and 14 roe deer per 1,000 hectares, as counted in early spring (before parturition) in 2023. The occurrence of other ruminating ungulates, i.e. fallow deer and mouflon, is occasional here. In fact, no individuals were recorded in spring 2023, but a few pieces were rarely seen in the previous years.

In the second part of the growing season 2023, we established a total of 30 plots, with 15 situated inside the fenced area denoting LWH exclusion (referred to as F plots), and 15 located outside the fenced area serving as controls (referred to as C plots; see also Fig. 1). Plot locations were strategically chosen to maintain a minimum distance of one meter from the fence, mitigating potential "edge effects". Simultaneously, we aimed to minimize differences between the growth conditions of the F and C plots. While we could not adhere to an exact schematic design, such as organizing the plots in precise lines with constant spacing, we prioritized avoiding existing paths and steering clear of microsites with installed devices or previously established plots within the areas, where strict exclusion of human influences was essential.

2.2. Tree measurements, calculations, and analyses

Each of our 30 plots was configured in a circle-like shape with a radius of 2.5 meters, and the central points were fixed by iron tubes hammered into the soil. The trees within the 30 plots underwent our comprehensive measurements. Specifically, only trees with a height exceeding 10 cm were included in the study, as smaller seedlings, primarily emerging in the current year, often do not persist for subsequent years. Our measurements encompassed the diameter at the stem base (diameter d_0), using a digital caliper with an accuracy of ±0.01 mm. Additionally, tree height was measured using a wooden measure with an accuracy of ±1.0 cm. Recording not only the species but also the precise position of individual

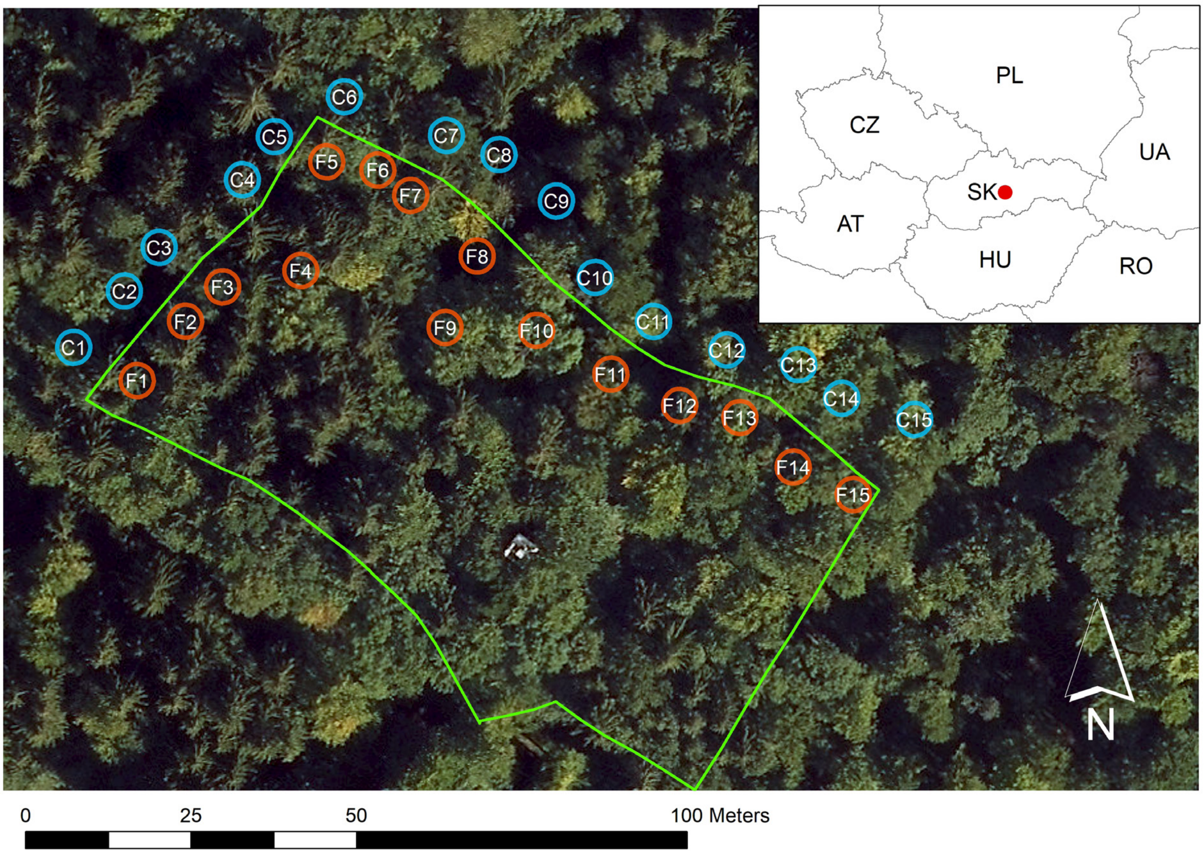

Fig. 1. The Hukavský Grúň research site's location and the positions of the plots where forest regeneration tree measurements were conducted. The red circles denote the fenced (F) plots, while the blue circles represent the control (C) plots. The plot orders range from F1 to F15 and from C1 to C15, arranged from left to right, the codes correspond to the layout depicted in Fig. 7.

trees was accomplished through the Field-Map system and its corresponding device (refer to https://www.field-map.cz/ for details).

Following the measurements, we derived basic characteristics for tree groups within each plot. Subsequently, mean values and standard errors were calculated for the sets of the F and C plots. Specifically, the following plot characteristics were computed: the number of trees, the number of species, Lorey's tree height (as described by West 2009), and the mean diameter d_0. These metrics provide a comprehensive overview of the composition and structural attributes of the tree populations within the respective plots. To enhance the visualization and spatial understanding of tree positions within each plot,

Table 1. The regression coefficients (b_0, b_1, and b_2), as well as the logarithmic transformation bias (λ) or random intercept (u) for Equation 1 or Equation 2 (refer to subsection 2.2 for the formulas), express the biomass of aboveground tree components in kilograms.

Tree species	Tree component	b_0	b_1	b_2	λ [u]
Silver fir	foliage	–3.690	1.208	1.140	[0]
	branches	–4.226	1.544	1.000	[0]
	stem	–3.433	0.444	2.285	[0.418]
European beech	foliage	–3.286	2.188	0.188	1.100
	branches	–4.768	2.630	0.423	1.130
	stem	–1.530	1.848	1.015	1.026
Maples (both species)	foliage	–3.107	2.158	–0.231	1.118
	branches	–5.755	2.638	0.186	1.222
	stem	–1.223	1.736	0.966	1.006
Common ash	foliage	–2.219	1.717	0.531	1.075
	branches	–6.807	2.830	0.795	1.244
	stem	–0.906	1.667	1.052	1.038
Other species (formula for rowan was implemented)	foliage	–3.389	2.240	–0.004	1.047
	branches	–6.976	3.162	0.244	1.137
	stem	–1.317	1.857	0.749	1.008

we conducted visualizations using the ArcMap 10.6.1 software.

Finally, we calculated aboveground biomass for each individual tree present at the plots. For that purpose, we implemented allometric relations adopted from the works of Jagodzinski et al. (2019) and Pajtík et al. (2018). The formula for silver (but see also Table 1) is:

$$B_i = e^{(b_0 + b_1 \cdot \ln d_0 + b_2 \cdot \ln h + u)} \quad [1]$$

where B_i is biomass (in kg) of i^{th} tree component (i.e. foliage, branches, stem or aboveground part together), d_0 is diameter at stem base (mm), h is tree height (m), and b_0, b_1 and b_2 are equation coefficients, u is random intercept (see Jagodzinski et al. 2019). Then, the formula for all other species is:

$$B_i = e^{(b_0 + b_1 \cdot \ln d_0 + b_2 \cdot \ln h)} \cdot \lambda \quad [2]$$

where B_i is biomass of i^{th} tree component, d_0 is diameter at stem base, h is tree height, and b_0, b_1 and b_2 are equation coefficients, λ is correction factor (see also Pajtík et al. 2018). It means that the allometric relations involved diameter (d_0) and tree height as independent variables. Consequently, the total aboveground biomass of trees for each plot, as a sum of the biomasses from trees present at a single plot, was calculated (e.g., Pajtík et al. 2022).

Differences in tree characteristics between the F plots and the C plots were tested using Student's t-test ($p < 0.001$). All statistical analyses were performed in the Statistica 10.0 program (StatSoft, Tulsa, OK, USA).

3. Results

The differences in forest regeneration status between the exclosure and the ambient area were visually well recognizable (Fig. 2). In total, 994 trees were recorded on the F plots, and 223 individuals on the C plots. This indicates nearly a 4.5 times higher tree density in the area with LWH exclusion than in the area with the presence of LWH (see also Table 2). While the F plots were characterized by the dominance of silver fir (48%), regeneration in the C plots was primarily represented by European beech (87% of all trees). No silver fir was recorded in the C plots. In terms of the F plots, the species with the greatest mean height was silver fir (Lorey's height equaling 1.69 m), closely followed by European beech (1.54 m). When comparing heights within European beeches, individuals inside the fence were three times as high as those outside the fence. Examining another indicator that combines tree height and diameter d_0 (data illustrated in Fig. 3b and Fig. 3c), known as the "slenderness ratio", clear dif-

Fig. 2. Illustration depicting the contrasting situations outside (left part of the photograph) and inside (right part) the fence.

Table 2. The basic stand characteristics in the fenced and control plots (Hukavský Grúň research site, Poľana Mts., Central Slovakia).

Tree species	Fenced plots				Control plots			
	Number of trees (pieces)	Lorey's height (m)	Diameter d_0 (mm)	Tree density (pieces per 10 m^2)	Number of trees (pieces)	Lorey's height (m)	Diameter d_0 (mm)	Tree density (pieces per 10 m^2)
Silver fir	477	1.69	12.15	25.31	0	none	none	none
European beech	81	1.54	6.70	4.30	195	0.57	5.51	10.35
Sycamore maple	93	0.81	5.79	4.93	1	0.21	3.99	0.05
Norway maple	27	1.16	6.66	1.43	5	0.22	3.39	0.27
Common ash	86	0.42	4.17	4.56	20	0.25	4.25	1.06
Other species	7	0.46	5.04	0.08	2	0.38	4.44	0.15

ferences between the F plots and C plots can be observed. Specifically, while the mean value of the slenderness ratio in the F plots was 149, the mean value in the C plots was 1.8-times smaller, i.e. 89. Even larger differences were found for European beech, a species that was present in both types of plots (as shown in Table 2). In this case, the differences were more than double, with mean values of slenderness ratios of 230 and 103 in the F plots and C plots, respectively.

When considering tree species together, all characteristics were significantly larger (Student's t-test; $p < 0.001$) in the F plots than in the C plots (Fig. 3). Thus, the numbers of trees calculated per 10 m^2 were 41 individuals and 12 individuals in the exclosure and adjacent area, respectively. Lorey's heights were 1.37 and 0.44 m, mean diameters (d_0) were 9.2 and 5.3 mm, and the numbers of species were 4.5 and 2.0 in the F plots and C plots, respectively. Comparisons among these indicators suggested

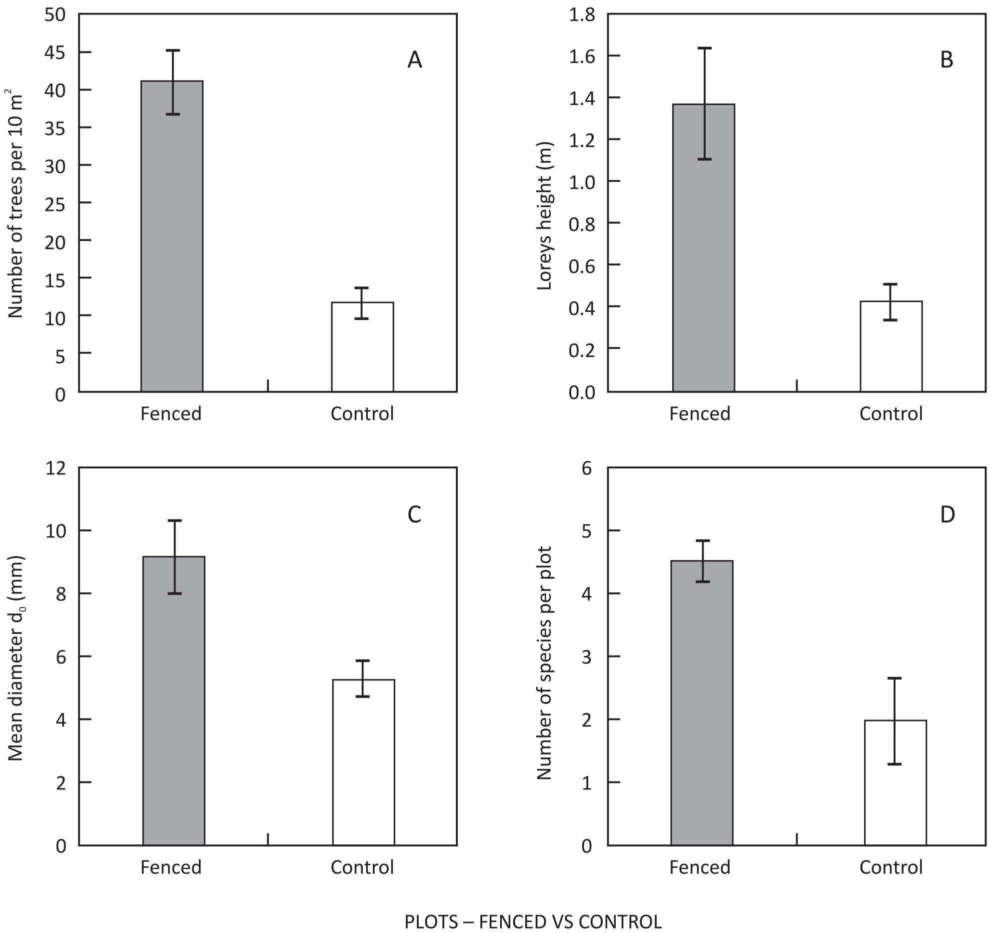

Fig. 3. Comparisons of tree numbers (graph A), Lorey's heights (graph B), mean stem diameter d_0 (graph C), and the number of tree species (graph D) between the fenced and control plots. The columns represent mean values, and error bars indicate standard errors calculated from 15 plots. In all cases, the differences between the fenced and control plots were statistically significant (Student's t-test; $p < 0.001$).

that the largest difference between the F plots and C plots was in the case of stand density (number of individuals per unit of area), specifically nearly fourfold in favour of the area with LWH exclusion.

Interesting insights arise from the comparison of the numbers of trees in different height classes between the F plots and the C plots (Fig. 4). The most meaningful comparison of tree heights (or height development) can be made for European beech since the species was quite common in regenerations in both types of plots. The frequency diagram demonstrated that beech trees were present in all height classes in the F plots. On the other hand, in the C plots, most beech trees were in the height class up to 0.5 m, some in the class 0.51–1.0 m,

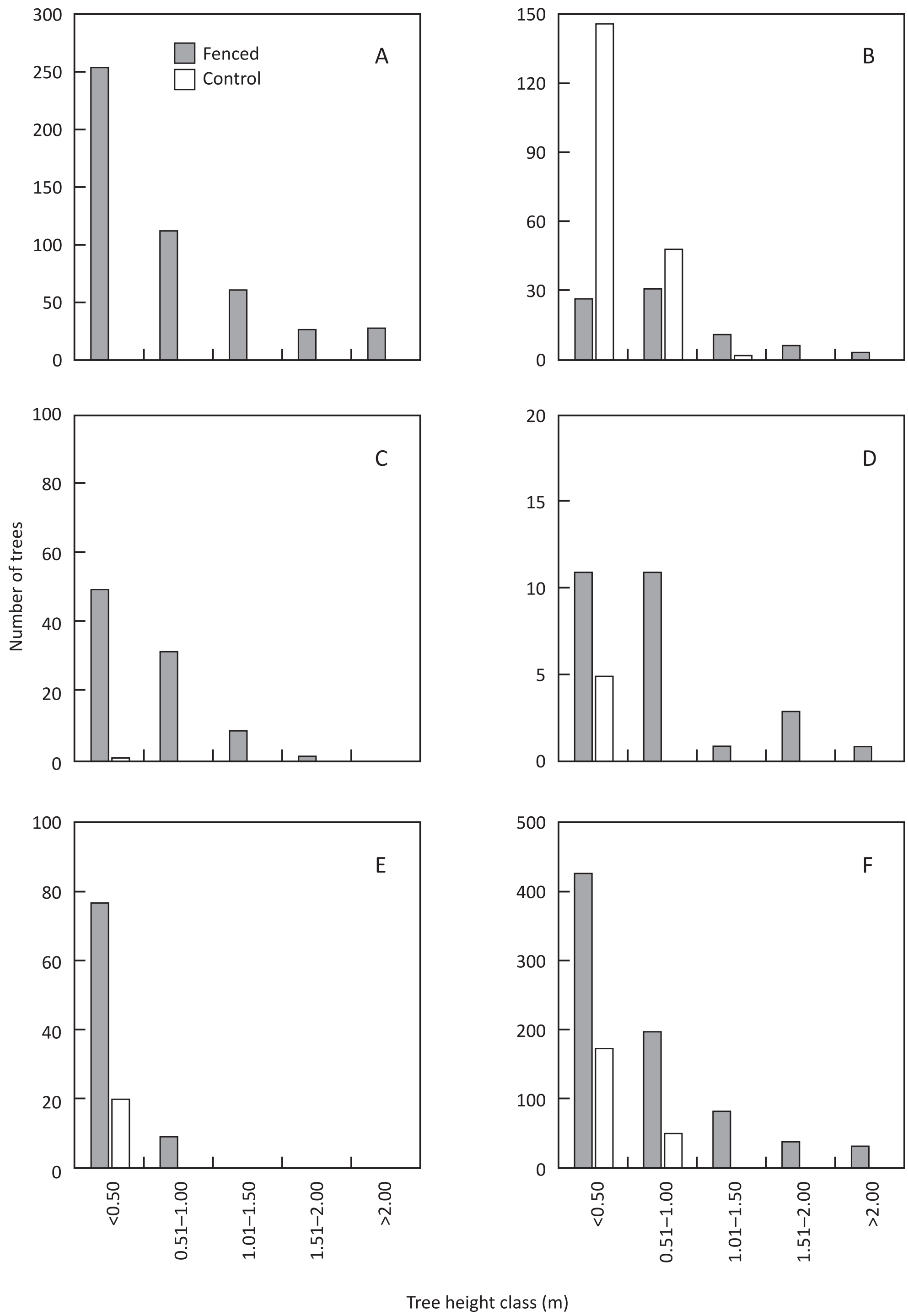

Fig. 4. Frequency diagrams depicting tree height classes in the fenced and control plots for various species: silver fir (A), European beech (B), sycamore maple (C), European maple (D), common ash (E), and all species together (F).

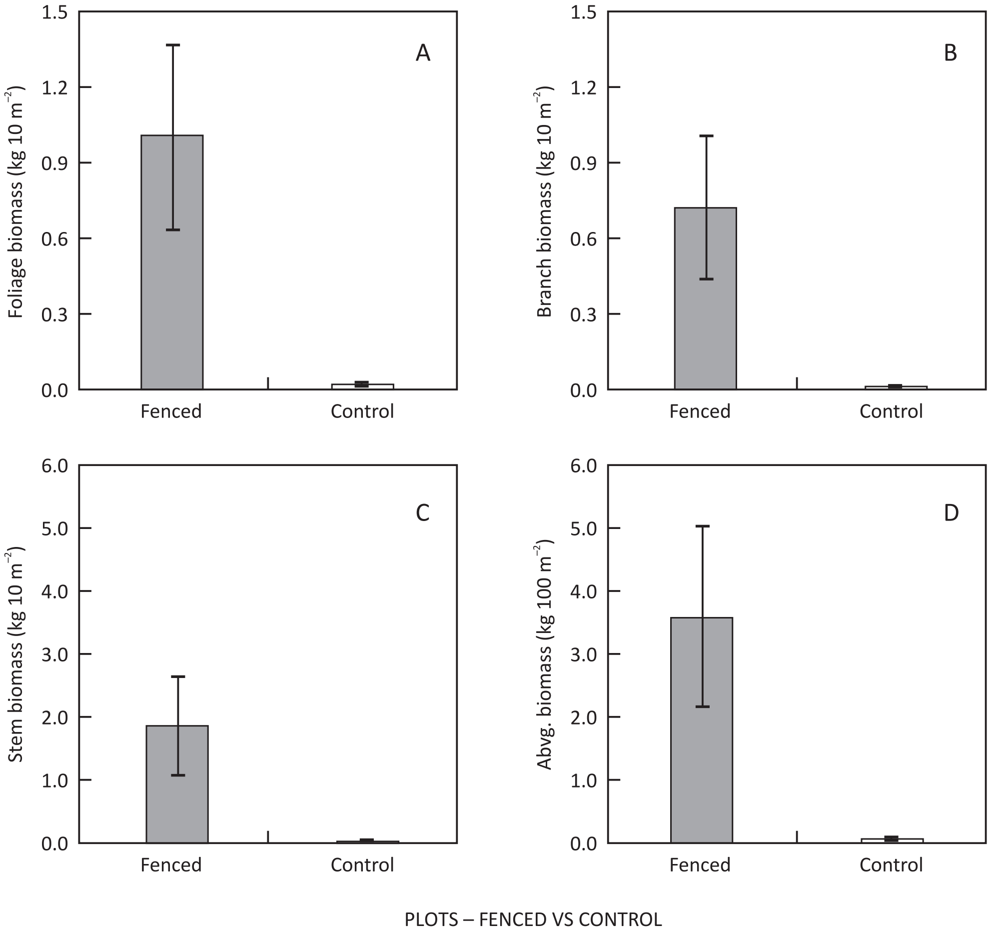

Fig. 5. Comparisons of foliage biomass (A), branch biomass (B), stem biomass (C), and aboveground biomass (D) stocks between the fenced and control plots. The columns represent mean values, and error bars indicate standard errors calculated from 15 plots. In all cases, the differences between the fenced plots and control plots were statistically significant (Student's t-test; $p < 0.001$).

very few individuals in 1.01–1.5 m, and no individuals in the classes over 1.5 m. Regarding both maples and European ash in the C plots, all trees were only within the height class up to 0.5 m.

The LWH exclusion also had a very positive effect on the biomass production of trees in the forest regeneration stage. While the actual standing aboveground biomass in the F plots was 3.6 kg per 10 m^2, its amount on the C plots was negligible, specifically about 0.06 kg per 10 m^2. Concerning the F plots, nearly 1/4 of the aboveground biomass (1.0 kg per 10 m^2) consisted of foliage, which is a component sequestering carbon for a short period (Fig. 5). The remaining 3/4 of the biomass quantity (2.6 kg per 10 m^2) was concentrated in woody parts, i.e. in the stem and branches.

Moreover, we expressed the contribution of tree species to aboveground biomass (Fig. 6). The situations between the F plots and C plots were contrasting. While silver fir made up about 95% of the aboveground biomass in the F plots, as much as 96% of the aboveground biomass in the C plots was formed by European beech. These proportions in the aboveground biomass were different from those in the number of trees (compare the two diagrams in Fig. 6). This comparison suggests that firs in the F plots and beeches in the C plots are more dominant in terms of tree biomass than in the number of trees. In other words, these dominant species (fir in the F plots and beech in the C plots) contained more aboveground biomass per tree than the other species.

Finally, we created visualizations of tree positions considering species and three stem diameter (d_0) classes (i.e. < 2.0 cm, 2.0–3.5 cm, and > 3.5 cm) to better imagine the real situation in the individual plots (Fig. 7). These visualizations clearly illustrate a much denser cover of forest regeneration, a higher diversity of species, as well as larger trees (i.e. thicker stems) in the F plots than in the C plots. Additionally, the visualizations suggest that silver firs are dominant not only in abundance but also in size in the F plots.

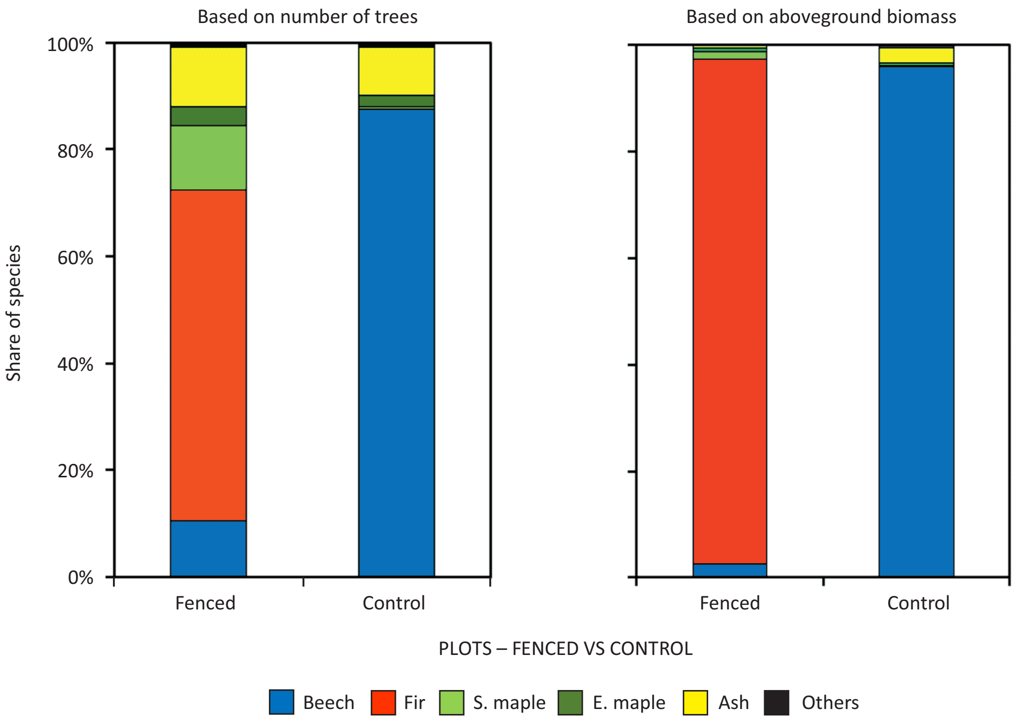

Fig. 6. Distribution of tree species in terms of the number of trees (left graph) and their contribution to aboveground biomass stock (right graph) in both the fenced and control plots.

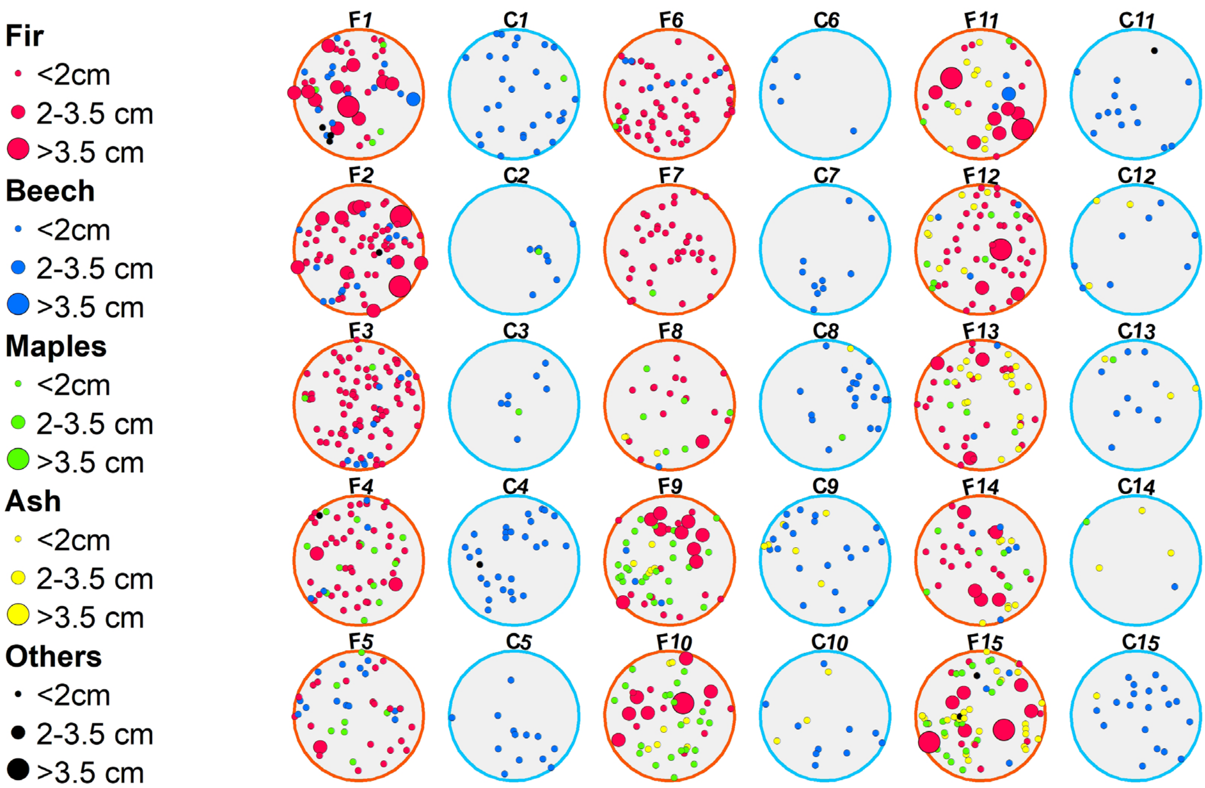

Fig. 7. Visualization of tree positions and sizes, expressed as three stem diameter classes, within individual fenced and control plots. The codes (F1–F15 and C1–C15) denote the placement of each plot within the research site (codes corresponding to those in Fig. 1).

4. Discussion

4.1. Large wild herbivores exclusion experiments

Before further discussion, we would like to emphasize that our study utilized existing infrastructure, i.e. the fenced area of the research site, originally dedicated to the long-term monitoring of forest status, development, processes, and various related factors (Pavlenda & Čaboun 2016). We took advantage of this site's fencing, which divided the forest stand into two mezzo-sites with very similar maternal stand status, as well as climatic and soil conditions, differing only in the presence or exclusion of LWH. In general, experiments based on LWH exclusions are widely respected worldwide (e.g., Forbes et al. 2019) and have been implemented in various types of ecosystems, with many focusing on forests (e.g., Hester et al. 2000; Leonardsson et al. 2015; Royo & Carson 2022; Iijima & Oka 2023). Forbes et al. (2019) recently conducted a comprehensive review of LWH exclusion experiments, concluding that the sizes of fenced areas varied between 25 m^2 and 128 km^2 (median size 400 m^2). In some countries of Central Europe, LWH exclusion was performed through a series of plots with a size of 6 × 6 m and a 1-m broad buffer zone to avoid "edge effects" along the fence (Finďo & Petráš 2007; Schäfer et al. 2019; Griesberger et al. 2023). Most of the experiments were relatively short-term, with durations up to 10 years (e.g., Leonardsson et al. 2015). The review by Forbes et al. (2019) also noted that only a portion of exclusion experiments could be considered as "well-studied ecosystem functions", as most of them focused exclusively on effects on vegetation cover. Similarly, our study considered only trees as the dominant part of vegetation cover on the site. When comparing our experiment with others, we find certain advantages in our design, especially the long-term existence of the fence (over three decades) and the relatively large area of exclosure (nearly 0.6 ha), which provided the opportunity to implement a large number of replicates, specifically fifteen plots.

Our study, based on long-term LWH exclusion, suggests the following main impacts of LWH on forest regeneration: (i) a reduction in tree density, (ii) an inhibitory influence on tree size (more pronounced in tree height than in stem diameter), consequently leading to (iii) a dramatic reduction in tree biomass stock, further resulting in (iv) a reduction in tree species diversity, and (v) fatal effects (extermination) on silver fir. Additionally, we observed severe impacts of LWH browsing on two maple species as well as common ash. In the following subsections, we discuss and compare these aspects of LWH browsing with results from other studies.

4.2. Main impacts of large wild herbivores on forest stands

Number of trees

Our experiment demonstrated a significant influence of LWH browsing on stand density (the number of trees per area unit). Specifically, there were about four times more trees in the F plots than in the C plots. The smallest difference, approximately 2.5-times more trees in the F plots than in the C plots, was found in European beech trees. This likely indicates that beech might be the least attractive tree species as forage for LWH among all other present tree species. For instance, Borowski et al. (2021) demonstrated that red deer showed a preference for foraging on silver fir and also certain broadleaved tree species (such as sycamore, hornbeam, and oaks) over European beech. However, these preferences diminished with an increasing population of red deer. Contrastingly to our current work, the previous study (Konôpka et al. 2021) showed relatively small differences in stand density between the F plots (28 individuals per 10 m^2) compared to the C plots (25 per 10 m^2). At the same time, this previous work revealed that silver birch (*Betula pendula* Roth) was slightly less abundant in the F plots than in the C plots. This suggests that birch may not be attractive to LWH, and this species might benefit from the reduced number of other tree species resulting from browsing, creating a freed competition space. In Sweden, a significant reduction of seedlings and saplings in mixed forest regeneration using LWH exclusion plots was found by Leonardsson et al. (2015). For instance, they demonstrated that the number of oaks (*Quercus* spp.) was reduced by approximately two-thirds. Similarly, in Denmark, Hester et al. (2000) showed a significantly reduced number of seedlings due to browsing by red deer and roe deer, not only in pedunculated oak (*Quercus robur* L.) but also in common rowan (*Sorbus aucuparia* L.), Scots pine (*Pinus sylvestris* L.), and even in birches (*Betula pubescens* Ehrh. and *Betula pendula* Roth; in contrast to the findings of Konôpka et al. 2021). Results from Royo & Carson (2022), obtained for white-tailed deer (*Odocoileus virginianus* Zimmerman) in a North American mixed forest, showed nearly no influence exclusion on the number of trees in regeneration. However, they stated that, beyond tree density, the species composition in forest regeneration was evidently modified.

In fact, a variety of factors are involved in the browsing phenomenon, which can be expressed as the "browsing ratio" (i.e. the ratio of browsed seedlings per year to the total number of seedlings (Akashi et al. 2022). Browsing depends especially on the population density of ruminating ungulates (Borowski et al. 2021; Zoltán et al. 2024) and their species composition (Hester et al. 2000), the availability of ground vegetation (Uno et al. 2019), food shortage (Häsler & Senn 2012), or, conversely, supplementary feed (Felton et al. 2022), climate conditions

(Salisbury et al. 2023), and landscape structure (Szwagrzyk et al. 2020), as well as a combination of some of the mentioned factors (Spake et al. 2019).

The review by Forbes et al. (2019) concluded that the influence of browsing mostly had a negative impact on the number of trees in regeneration, although some studies showed mild (e.g., Konôpka et al. 2021) or nearly no impacts (Royo & Carson 2022). The impact of LWH browsing on the number of trees in forest regeneration is related to a variety of factors, besides others also the population density of LWH and the abundance of understory vegetation (i.e. flora besides tree species; Spitzer et al. 2020). From a practical standpoint, particularly in the forestry sector, the quality of trees in forest regeneration, such as species composition, health status, and size, is very likely more important than just the number of trees per unit of area.

Tree size and biomass stock

Our experiment clearly showed that the presence of LWH not only reduced the number of trees per unit of area but also affected their sizes, including heights and stem diameters. Considering all trees, the heights of the trees in the F plots were approximately three times those in the C plots. Simultaneously, stem diameters (d_0) of the trees in the F plots were double those in the C plots. This indicates that tree height was more influenced by LWH browsing than stem diameter. This phenomenon is especially evident for European beech, a species that was common in both types of plots. Differences in height-to-diameter ratios were more than double. In the case of terminal browsing, height is immediately reduced, and often further growth is stopped at a certain distance from the ground level. On the other hand, diameter increment on the stem continues, although it might decrease due to the reduced amount of foliage – an organ performing photosynthesis. Analyses concerning tree frequency in particular height classes showed that browsing of shoots did not allow trees to exceed a height of approximately 1.0 m in beech and 0.5 m in both maple species and common ash.

Our previous studies on common ash (Konôpka et al. 2012) and common rowan (Pajtík et al. 2015) revealed that browsing of shoots was recorded from a lower height of 20 cm, with significant intensity from approximately 50 cm. This explains why some trees in the C plots approached 50 cm, and very few of them slightly exceeded this "critical" threshold. A certain exception was found for beech trees, as some individuals grew over 50 cm. In contrast, no individual silver fir was found in the C plots. Summarizing these findings, we can conclude that among the studied tree species, silver fir is the most palatable tree, followed by common ash, European maple, and sycamore maple, with European beech being the least palatable. This statement is in accordance with many studies highlighting silver fir as the most attractive commercial species for browsing (Senn & Suter 2003; Heuze et al. 2005; Häsler & Senn 2012; Vacek et al. 2015; among others).

The combination of tree density and tree size results in tree biomass stock. In a simplified way, we can state that one large tree contains more biomass than a group of small trees, as there is an exponential relationship between stem diameter and/or tree height and aboveground biomass (e.g., West 2009). In our experiment, the F plots, in comparison with the C plots, had both more individuals and bigger sizes (especially in height) of the trees. The multiplied result of these two characteristics resulted in much larger biomass in the F plots than in the C plots. It is essential to note that for carbon sequestration, woody parts are more important than foliage because of their contrasting turnover. In fact, nearly 1/4 of the aboveground biomass in the F plots consisted of foliage, a component sequestering carbon for a short period. The remaining about 3/4 of the biomass was in woody parts, i.e. in stems and branches, the organs that store carbon as long as the trees survive. Considering a hectare base (upscaling approach), the quantity of aboveground biomass in the exclosure was about 3.6 tons compared to only 0.06 tons in the adjacent area.

Forbes et al. (2019) summarized that some studies based on LWH exclusion focused on primary productivity in ecosystems. They mentioned that previous research primarily dealt with grass and grass/shrub-dominated landscapes. The results showed variable effects, ranging from positive to negative, which, among other factors, were related to the population density of LWH. Surprisingly, we found no studies quantifying the effects of LWH browsing on primary productivity or, at the very least, the current biomass stock in forest ecosystems. The only exception could be our previous experiment (Konôpka et al. 2021), which revealed that tree aboveground biomass stock in the F plots was only 10% higher than that in the C plots. In this case, less attractive tree species, specifically silver birch and partly Norway spruce, took advantage of the freed growth space caused by browsing on other species such as common rowan, trembling aspen (*Populus tremula* L.), and willows (*Salix* spp.). Since both birch and spruce were very productive in the site, losses due to browsing on some tree species were partly compensated by the stimulated increment of these two less palatable tree species.

We believe that research on the impact of LWH browsing on biomass stock/carbon sequestration should be a focus of future studies, especially those conducted in forests, as knowledge for this type of ecosystem is currently lacking. Additionally, we assume that this impact could be more severe than one might imagine, especially under the conditions typical of most European countries, i.e. regions characterized by an overabundance of LWH.

Tree species diversity

The results of our experiment indicated that LWH exclusion supported tree species diversity. Specifically, the mean number of tree species per plot was over twice as high in the exclosure compared to the adjacent area. Browsing by LWH decreased the abundance of most tree species, including beech, but predominantly ash and maples. One species, fir, was entirely exterminated. This selective effect of browsing on different tree species confirms the forage preference of LWH. The LWH selects the most palatable and nutritionally valuable species (see also Gill 1992). The review by Forbes et al. (2019) confirmed that most studies showed a negative impact of LWH on the biodiversity of flora. This kind of negative influence is typical in regions with an overabundance of LWH, such as in Europe. For example, in spruce-dominant forests in Czechia, intensive LWH pressure led to decreased diversity, especially in young stands (Merganič et al. 2009). Browsing of admixed tree species can decrease tree species diversity and sometimes may even lead to species loss (Martin & Daufresne 1999). However, in rare situations, LWH by browsing the most abundant tree species in regeneration may release other tree species, and in a few cases, increase the diversity of trees (Gill 1992).

4.3. Large wild herbivores and silver fir

Our experiment demonstrated that silver fir is extremely attractive as forage for LWH and may be reduced or even eliminated (if LWH is overabundant) in the very initial growth stage. The exclosure plots revealed that the regeneration of fir could be highly successful, and this species might dominate in tree species composition. As the site was covered by the maternal forest stand with a few openings in the canopy, resulting in relatively low light intensity under the crown layer, this condition was favourable for shade-tolerant species. For instance, Stancioiu & O'Hara (2006) and Kučeravá et al. (2013) identified silver fir as the most shade-tolerant commercial tree species in Europe, and the tolerance increased with site fertility. Therefore, this species often experiences successful regeneration under the maternal forest stand and requires a continuous increase in light intensity through the slow reduction of the canopy (Dobrowolska et al. 2017). Our results further showed that under suitable conditions (especially light, climate, soil properties, and available seed sources), fir can successfully compete with other species. This was observed in our case when silver fir constituted just an admixture in the maternal stand dominated by beech.

This experiment highlighted that the presence of LWH, especially in their state of overabundance, is a limiting or even fatal factor for silver fir regeneration. The vulnerability of silver fir in its initial growth stages to LWH browsing has been previously demonstrated in various studies (e.g., Senn & Suter 2003; Heuze et al. 2005; Häsler & Senn 2012; Vacek et al. 2015; Bernard et al. 2017; Csilléry et al. 2021). In response to the current critical situation in Europe, some authors (e.g., Carpio et al. 2020; Valente et al. 2020; Bödeker et al. 2023; Griesberger et al. 2023) have suggested intensive hunting of LWH as the only solution for the protection of certain tree species, especially silver fir. Excluding LWH by fences is, in fact, a rather expensive method and only addresses the problem for a limited time – essentially within the duration of the fence's full functionality. Šebeň (2017) demonstrated for Slovak conditions that the average time for silver fir to reach a height of 2.0 m is nearly 15 years. Since browsing on terminal by red deer can occur slightly above 2 m from the ground level, the duration of a fence must be approximately 20 years. After this period, group protection by means of a fence must be replaced by any method of individual protection, as silver fir is often damaged in the form of bark stripping (Pusz et al. 2021). Moreover, fences themselves do not provide perfect protection for trees, as their effectiveness is often reduced by deep snow cover and in conditions of steep slope terrain (Iijima & Oka 2023). In addition, the rate of fence protection may increase damage to unfenced stands, especially in the vicinity. Therefore, the reduction of ruminating ungulate populations in regions with their overabundance is the most efficient measure (e.g., Kamler et al. 2010; Candaele et al. 2020).

In summary of our results and findings from other studies, we can assert that the main opportunity for preserving silver fir for the future lies in the regulation of LWH populations to reach a reasonable threshold. The necessity to maintain silver fir in European forests is supported by findings that this species exhibits good ecological properties, especially in light of ongoing climate change (Lindner et al. 2010; Bosela et al. 2018). The species can enhance diversity, among other forest types, beech and/or spruce-dominated forests located in the middle altitudes of the Carpathian Arch.

5. Conclusions

Our case study clearly demonstrated that silver fir thrives under favourable conditions for regeneration in its ecological optimum, which is the fir-beech vegetation degree, particularly occurring in altitudes between 900 and 1,150 meters above sea level in Slovakia. The observations suggested that successful regeneration can occur even in forest stands with a low proportion of fir in the maternal stand and under relatively low light intensity, with small openings in the canopy. The key condition for this success is the exclusion or at least dramatic suppression of the existing population of LWH, especially red deer. The situation in the C plots suggests that LWH browsing may lead to the complete extermination of fir seedlings. Simultaneously, while maples and common ash are hardly impacted by LWH, beech appears to be the least attractive as forage. However, the height development of beech was also severely affected by browsing.

The primary practical implication of this experiment underscores the importance of maintaining the population of LWH at a sustainable level. Without doing so, foresters will struggle to establish diverse mixed forest stands. Constructing and maintaining fences are costly measures that only address the issue in the initial growth stages of the forest. Once the trees grow large and/or the fence is removed, individual protection of certain species (mainly silver fir, common ash, maples, etc.) becomes necessary. Implementing this kind of long-term protection from LWH is neither technically nor financially feasible on a large scale. Moreover, fencing also has certain vulnerabilities related to terrain relief, especially slopes, and climatic conditions such as deep snow cover. Therefore, regulating the LWH population appears to be the most efficient measure for reducing the negative impacts of browsing in forests.

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