SZENT ISTVÁN UNIVERSITY

DOCTORAL SCHOOL OF ANIMAL SCIENCE

THE EFFECTS OF FOREST MANAGEMENT TECHNIQUES ON UNGULATE IMPACT AND FOREST HABITAT QUALITY

Theses of Ph. D. dissertation

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1. INTRODUCTION AND OBJECTIVES OF THE STUDY

Ungulates as main parts of the forest ecosystem can exert various impact on their habitat, and shape the structural and compositional attributes of the forest. They have a significant effect on vegetation diversity through selective browsing (BOULANGER et al. 2009), debarking (FEHÉR et al. 2016) and grubbing; furthermore their facilitating (FAGIANI et al. 2014) or interfering effects (e.g. LOZANO et al. 2007, MUÑOZ et al. 2009) were also revealed on several plant and animal species. These impacts can alter soil nutrient cycles in many ways (HOBBS 1996). Long-term cascading effects also occur in the vegetation structure and composition during the complete absence of ungulates (NEWMAN et al. 2014, PEKIN et al. 2014). Therefore the relationship between ungulate herbivores and plant species is a dynamic interaction which exerts many indirect effects towards other coexisting species of the ecosystem and vice versa (SKARPE & HESTER 2008). The strength and pattern of ungulate impact play a key role in habitat changes, therefore ungulates - especially large game herbivores - can act as „ecosystem engineers" or „environmental engineers". Ungulates have both positive and negative effects at the same time, depending on their relation with other coexisting species and the scale of the observed ecological level.

Due to their simultaneous positive and negative impact, stakeholders (forest management, wildlife management and nature conservation) have various opinions about ungulates. Failing forest regeneration and renewal is common phenomenon in temperate forests (BLEIER et al. 2010) equally at local and regional scale. This environmental problem is mostly associated with the "overabundance" of ungulate species and considered as primarily source of the problem. On the other hand, vulnerability issues of forest stands to tolerate negative ungulate impacts are often neglected (REIMOSER & GOSSOW 1996). Furthermore, tree saplings show a wide

range of reactions to ungulate browsing determined by abiotic conditions, plant competition intensity and specific adaptiveness. The pattern, intensity, timing and recurrence of browsing are just key factors in the plant's response.

This complexity renders ungulate impact to a controversial phenomenon: when differing human interests overwrite the ecosystem-based approach of sustainable forest use, the plant-herbivore interactions turn into a forest-ungulate conflict. In this case, population reduction of ungulates seems the only useful tool, but many other factors need to be considered (e.g. forest predisposition, food supply, conservation aims) for an efficient long-term solution.

The main aims of my dissertation are 1) to reveal the ecological background of ungulate impact, 2) to specify the ecosystem services of ungulates, 3) to implement a new method for the adaptive prevention and management of negative ungulate impacts.

The phrase "forest techniques" as it mentioned in the title above consists all type of intervention which modifies forest habitat structure and shapes the pattern and intensity of ungulate impact. In this context, my study focused on how forestry operations influence habitat quality and ungulate impact in both direct and indirect ways.

I studied the ungulate-vegetation relationship from a multiscale perspective: from leaf to landscape view. At the scale of tree saplings simulated browsing surveys were implemented; botanical survey methods were used to monitor vegetational responses to ungulate impacts at the scale of forest patches. On the other hand, the ungulate impact monitoring protocol was used to determine how do vegetation attributes influence each specific ungulate impact and vice versa at the scale of the forest community. I raised five main questions (I. to V.), which guided my study.

I. **Can ungulate browsing significantly reduce the growth and vitality of black locust *(Robinia pseudoacacia)* saplings? How does the browsing affect the nutritional quality of locust shoots?**

    a) Can browsing hinder the growth of black locust?

    b) Can browsing hinder the shoot establishment of black locust?

    c) Can browsing hinder the leaf production of black locust?

    d) Can spine production of black locust triggered by browsing?

    e) Does browsing have a negative effect on the nutritional quality of black locust shoots for ungulates?

    f) Is there any significant difference in the mortality between browsed and unbrowsed locust saplings?

II. **Can black locust affect the development and survival of oak saplings? How can the browsing on locust influence this interspecific competition?**

    a) Can locust saplings nearby hinder the growth of sessile oak *(Quercus pertraea)* and Turkey oak *(Quercus cerris)* saplings?

    b) Can locust saplings nearby hinder the shoot establishment of sessile and Turkey oak saplings?

    c) Can locust saplings nearby hinder the leaf production of sessile and Turkey oak saplings?

    d) How does the presence of black locust alter the mortality rate of sessile and Turkey oak saplings?

III. Does black locust generates unfavourable soil conditions for oak saplings?

    a) Is there a significant difference in the soil nitrogen level between the vegetation patches with and without black locust?

IV. Could an ungulate exclosure fence favor woody plant diversity or mitigate woody species richness through the invasion of black locust?

    a) Does black locust presence have a significant hindering effect on the frequency of other woody species?

    b) Does black locust presence have a significant hindering effect on the density of other woody species?

    c) Can black locust reduce woody plant diversity when ungulates are excluded?

    d) Can black locust reduce herbaceous plant diversity when ungulates are excluded?

    e) How does ungulate exclosure influence the woody vegetation dynamics in a short-term period?

V. How do the patterns and intensity of ungulate impact change among the main forest types in Mátra Mountains (beech; oak-hornbeam; Turkey oak - sessile oak; mixed and ravine forests)?

    a) Is there any difference in the selective feeding of ungulates among the main forest types?

    b) How do sapling density and browsing patterns change among the main forest types?

    c) What is the difference in the selective tree stem utilization of ungulates among the main forest types?

d) Do main characteristics of wild boar grubbings change in the different forest types of Mátra Mountains?

e) Do ungulate impacts hinder forest regeneration at a local or regional scale in Mátra Mountains?

f) How do the changes in food and trunk supply influence ungulate impacts in the different forest types of Mátra Mountains?

Several field surveys were used to find answers to these questions by collecting field data and different samples for laboratory tests. With these results the ecological aspects of ungulate impact can be better explained, just as the ecosystem services of ungulate game species.

2. MATERIALS AND METHODS

The multiscale data collection required different methods to implement, which can be sorted to three main groups (Table 1). The plant-sided aspects of ungulate-plant relationship were observed by the simulated browsing experiments and botanical surveys, while the results of ungulate impact monitoring revealed the responses of ungulate species.

Table 1: Scale and attributes of the implemented methods

Method	Scale	Measured variable	Application
Simulated browsing	Plant individuals (tree saplings)	➤ height change ➤ shoot density ➤ leaf density ➤ thorn density (b. locust)	Monitoring plant responses to different levels of ungulate browsing
Botanical surveys and descriptive soil analysis	Plant patches (forest patches)	➤ Woody plant species • frequency • density • diversity ➤ soil physical and chemical properties	Analyzing compositional shifts and plant competition intensity in the vegetation related to soil properties
Ungulate impact monitoring	Forest community (forest stands, associations)	• woody plant supply • browsing - • trunk utilization - • habitat use of ungulates • wild boar grubbing intensity	Evaluating ecological impact of ungulates in forest dynamics

2.1. Introduction of the study areas

Simulated browsing and botanical field surveys took place in a 40 years old managed Turkey oak – sessile oak forest *(Quercetum petraeae-cerris)* in the forest compartment '17A' of Apc town in Heves county, Hungary (N 47°49'0.2"; E 19°42'59") at the SW side of Mátra Mountains. Black locust occupies an increasing area in the understory at the western side

of this 3.9ha large oak stand, where the 420 m^2 large and 1.8m high exclosure was created before the beginning of field experiments in March 2014. The site was partitioned to 1 m^2 large sampling plots (N=412) to get detailed information about vegetation dynamics in a high spatial resolution and locate tree saplings correctly. Fencing had two main purposes: 1) to exclude interfering effects of ungulate herbivory; and 2) observe the vegetational changes in absence of ungulates.

Field surveys of ungulate impact monitoring were implemented on the Special Areas of Conservation (SAC) belonging to the Natura 2000 network in Mátra Mountains (N=7) with an area of 4786 hectares. All of them located within the operational area of Bükk National Park, furthermore 6 sites out of 7 belong to the Special Protection Area (SPA) of migratory and threatened bird species and 3 sites are part of the Mátra Landscape Protection Area. The traditional even-aged forestry system was implemented on more than 80% of the full forested area, but transitions to uneven-aged forests through group selection have an increasing importance.

Each site was represented by three transects where field measures were conducted on 100 sampling points per transect line (300 sampling points per SAC). The collected data were pooled separately by the actual forest type, such as: beech forests (BF) N=501; sessile oak-hornbeam forests (SHF) N=297; Turkey oak-sessile oak forests (TSF) N=707; mixed and ravine forests (MRF) N=595. The total number of sampling points was 2100.

2.2. The methods of simulated browsing

Direct clipping was focused on black locust saplings within the exclosure where three types of vegetation patches (Figure 1) were designated: **1)** plots with clipped locust saplings and unharmed oak saplings nearby (<1m) (N=100); **2)** plots with control locust saplings and oak saplings nearby (N=126); **3)** plots where only oak saplings are available (N=69).
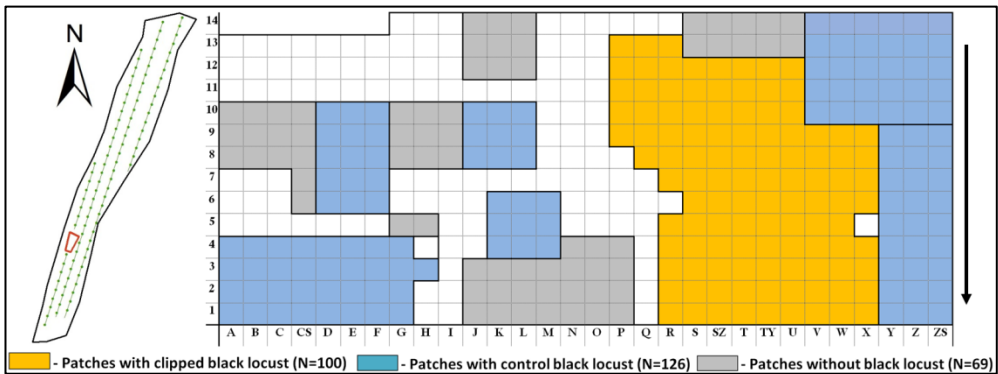
Figure 1: The location of the exclosure and the outer sampling points in the forest stand '17/A'(left); and the distribution of vegetation patches inside the exclosure (center). The right arrow indicates the direction of the slope.

Simulated browsing treatments were conducted twice: in September 2014 and 2015. The leader shoot and 50% of lateral shoots of locust saplings were clipped. I collected the removed shoots for further feed analyses (Weendee analysis, detergent fiber analysis and tannin content evaluation), and registered the biometric data of treated locust saplings and control saplings (locust, sessile oak and Turkey oak) seasonally such as: sapling height and stem length, basal diameter, shoot density, leaf density, spine density. Additionally, the seasonal mortality of locust and oak saplings were registered.

The aim of the monitoring was the descriptive observation of biometrical changes on the saplings; therefore the mean differences of relevant variables were calculated by subtractions and reported seasonally for every vegetation patch. Leaf density and spine density of locust saplings were reported in the ratio of shoot density. Actual and cumulated mortality rates were distinguished from each other. I used various statistical tests and analyses depending whether sampling groups are paired or not; and follow Gaussian distributions or not.

2.3. The methods of botanical surveys

The botanical surveys were focused on woody plant dynamics and implemented in every spring and autumn from 2014 to 2016. I measured the density of all woody species in every sampling plot (N=412) to monitor horizontal dynamics, and classified them into five height categories to monitor vertical dynamics: **1)** seedling: h=0-25 cm; **2)** sapling: h=26-50 cm; **3)** older sapling: h=51-200 cm; **4)** young tree: h>200 cm, DBH<5cm; **5)** mature tree: h>200cm, DBH>5cm. Simultaneously, the percent cover of herbaceous flora was assessed.

The same fieldwork was implemented outside the exclosure on 100 sampling points placed along transects in May 2015 and 2016.

By these collected data, I was able to evaluate the spatial and temporal changes in frequency and density of the vegetation at both sides of the exclosure. I also evaluated plant diversity by calculating the evenness (E), Shannon-Wiener (H) and Simpson-Yule (D) indices of woody vegetation.

We used a Pürckhauer-type core sampler for soil profile description (N=13) and toke soil samples from the upper 25cm layer of the soil for laboratory tests (N=17) within the exclosure in autumn 2014. Laboratory tests included measurements regarding to major nutrient (N, P, K) and organic matter (humus and total organic carbon) content and soil pH. The results were grouped by vegetation patches.

2.4. The methods of ungulate impact monitoring

The monitoring protocol contained five main types of field research (FEHÉR et al. 2014) mostly implemented on sampling points.

- **Available woody plant supply and its browsing intensity by ungulates in the understory:** To investigate the actual status of the vegetation, we use a special frame as a sampling tool with the dimensions of 50x50x30 cm (height x width x length). This tool helps us to count the number of all available and browsed woody shoots (as "food units" for large herbivores) up to 2m height on all sampling points.

- **Tree sapling density and their browsing patterns by ungulates:** Browsing patterns were measured on the sapling indivuals of main tree species in a circular area of $4m^2$ on every sampling point. The patterns and intensity of browsing was described by categorization of saplings such as: "unbrowsed", "only leader shoot browsed", "only side shoots browsed", "both leader and side shoots browsed", or "deformed".

- **Tree stem-availability and utilization by ungulates:** We traced out a circular area of $10 \ m^2$ with a 1.78 m long stick in each sampling point. There the number of available stems counted and girth at breast height of every woody species were measured if their height was above 1.3 m (available for ungulate debarking). When either new or old debarking was revealed, the type of the injury was specified and categorized into three groups: **1)** bark stripping; **2)** antler rubbing; **3)** bark rubbing. The vertical and horizontal extensions of the wounded area were also registered.

- **Wild boar grubbing intensity:** Intensity of rootings was reported by their depth and extension in a circular area of $10 \ m^2$ on every sampling point. Depth of grubbing was evaluated by ordinal scales: **1)** litter layer grubbed; **2)** topsoil surface grubbed; **3)** topsoil deeply grubbed. While the

extension was assessed in the percent cover of the sampling area (0%; 1-25%; 26-50%; 51-75%; 76-100%).

- **Intensity of area use of ungulates:** The density of laying beds and droppings of ungulate species (red deer – *Cervus elaphus*, roe deer – *Capreolus capreolus*, mouflon – *Ovis musimon*, wild boar – *Sus scrofa*) were measured simultaneously along transects with a simple distance sampling method.

We created portable field guides for the proper identification of ungulate signs and for the field surveys of ungulate impact monitoring (KATONA et al. 2013a, 2013b). Ungulate impact monitoring courses are available online at *Webuni.hu* (SZEMETHY et al. 2016).

Smart forms were created in Microsoft Excel to evaluate more than 70.000 monitoring data by combining mathematical, statistical and logical functions. This way I can analyze the food supply of tree and shrub species; the relative availability of woody plant supply; the browsing patterns and intensity on specific plants etc. Among statistical tests, I implemented Chi-square goodness of fit test with Bonferroni Z test (BYERS et al. 1984) to decide, whether a given woody species or stem perimeter category was preferred or avoided in the actual forest type. To quantify ungulate selectivity, Jacobs' preference index (JACOBS 1974) was calculated.

3. RESULTS

3.1. Can ungulate browsing significantly reduce the growth and vitality of black locust saplings? How does the browsing affect the nutritional quality of locust shoots?

Although clipping treatments influenced the growth of locust saplings; significant difference was not revealed neither after the first nor the second treatment. The reduction in growth intensity was higher at control saplings during the period from March to June 2015 (Figure 2). These results can be explained by the effective compensatory ability of the clipped locust saplings. Only the repeated clipping treatment was able to significantly hinder the height growth of locust saplings temporarily in November 2015. In conclusion, treated and control groups have not differed significantly in the total period of the experiment (Welch: t=0.7, p=0.49).
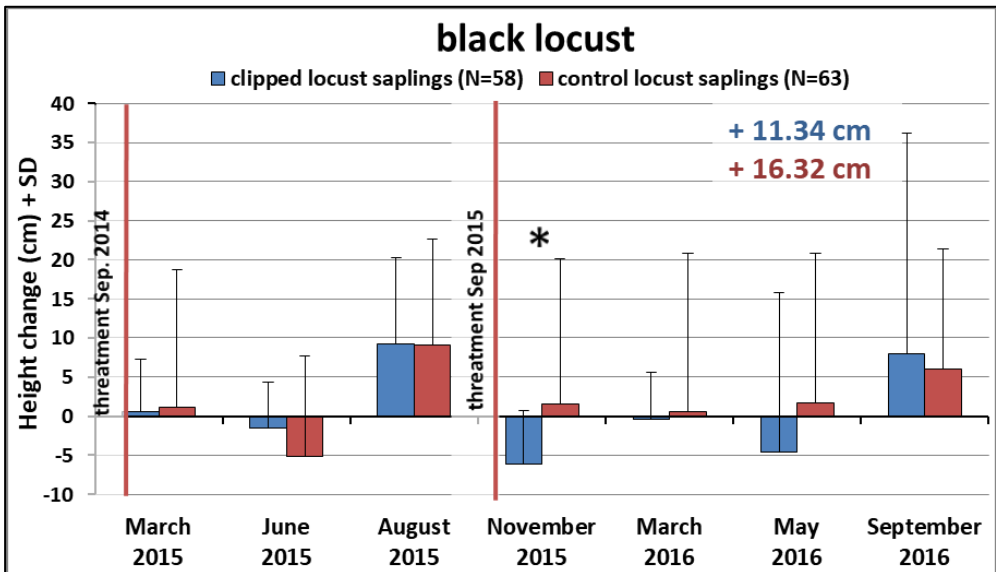
Figure 2: The average height change of the clipped and control black locust saplings. Blue and red coloured numbers show the average full time change of the saplings. * means significant difference (p≤0.05).

Similar results occurred at the shoot development of the clipped locust saplings (Figure 3), where the negative effects of clipping only appeared

14

after the second treatment. Despite of simulated browsing, the loss of shoot density was significantly higher in control saplings than in treated ones in September 2016 (Welch: t=3.12, p=0.003). Still, their full time balance remained higher (+7.91) than the clipped saplings' (+4.79). In sum, simulated browsing treatments did not hinder the shoot development of the locust saplings significantly.
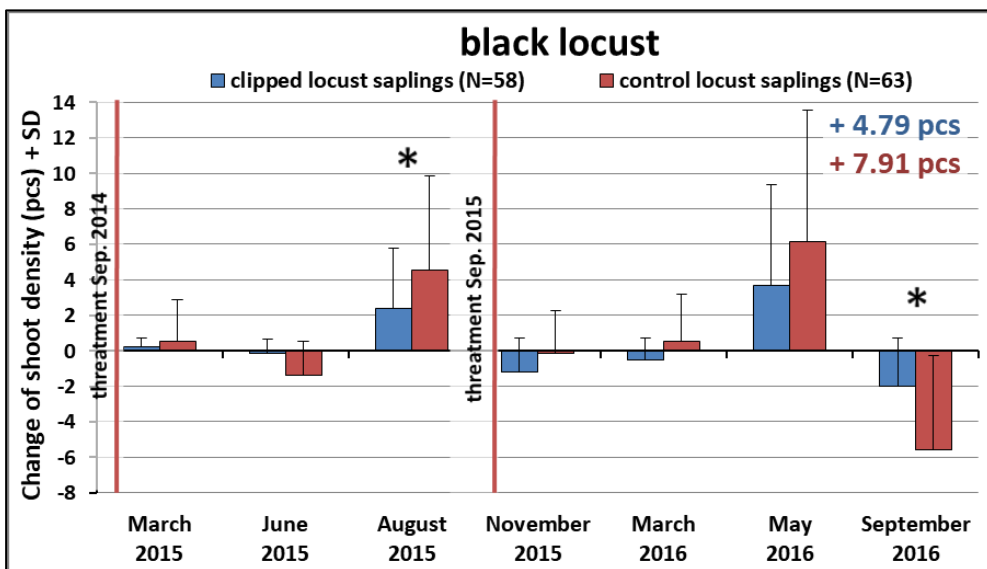

Fig. 3: Average shoot density change of clipped and control locust saplings

The variance of leaf density change was high during the full time of the experiment at both groups. After the first treatment clipped saplings grew more leaves than controls until June 2015. But due to severe drought in summer 2015, leaf loss reached an extreme level in both groups, especially at clipped saplings.

Apart from the temporary water stress, the threated group did not show any significant reduction in leaf density compared to control individuals. Therefore abiotic stress factors just as summer droughts could have a bigger negative impact on leaf density than the simulated browsing itself; but their additive impact should not be underestimated.

15

The clipped saplings did not develop more spines after the treatments. Moreover, their density significantly decreased in the treated group (Wilcoxon: W=156, p=0.0001). This change was not significant in comparison to control saplings due to their high variance (Mann-Whitney: U=275, U'=333, p=0.57), because the majority of saplings (70%) did not have any spines at all from the beginning.

The absolute values of mortality were always higher at clipped locust samplings than controls, but statistical difference was not revealed between them at any time. Mortality rates reached a significant level in both groups by the end of September 2016: 67% of clipped saplings (39 out of 58 individuals) and 51% of control saplings (32 out of 63 individuals) were died. This massive dieback also points out the importance of other contributing factors in black locust's survival.

Table 2: The nutritional quality of browsed and unbrowsed black locust shoots.

Feed component		Before browsing (Aug. 2014)	Browsed (Sep. 2015)	Control (Sep. 2015)	METHOD
dry weight	(g/kg)	333.4	329.8	325.7	MSZ ISO 6496:1993
crude protein	(g/kg)	211	219.5	226.6	MSZ 6830-4:1981
crude lipid	(g/kg)	43.8	44.7	39.9	MSZ 6830-6:1984
crude fiber	(g/kg)	176.1	216.2	214.2	MSZ 6830-7
ash	(g/kg)	103	94.7	96.6	MSZ ISO 5984
N-free extracts	(g/kg)	466.1	424.9	422.8	calculated
NDF	(g/kg)	339.5	419.7	418.1	Van Soest, 1963
ADF	(g/kg)	231.7	253	235.4	Van Soest, 1963
ADL	(g/kg)	78.2	82.4	71	Van Soest, 1963
Tannin	% (m/m)	0.99	0.84	1.33	MSZ ISO 9648:1994

One year after the first treatment, a slight increase in fiber content was revealed by the detergent fiber analysis (Table 2). Levels of hemicellulose (+58.9 g/kg), cellulose (+ 17.1 g/kg) and lignin (+4.2 g/kg) were also increased; though these changes were not significant compared to control

results. Simultaneous increase in fiber and decrease in Nitrogen-free extract (incl. carbohydrates) levels indicate a deteriorating nutritive value for ungulate herbivores. Especially the relative high tannin concentrations (around 1% m/m) in both groups can escalate this negative effect.

3.2. Can black locust affect the development and survival of oak saplings? How can the browsing on locust influence this interspecific competition?

3.2.1. Sessile oak *(Quercus petraea)*

The growth of sessile oak saplings was independent from black locust presence during the full time of the experiment (one-way ANOVA: $F_{(2,84)}=0.36$, $p=0.7$). Only temporary differences occurred in growth intensity in May and September 2016 ($p<0.0001$) which arose from the different timing of growth between oaks with and without black locust (Figure 4). In a short term view, the typical 'slow growing' attribute of sessile oak seems to be the primary disadvantageous effect instead of black locust allelopathy.
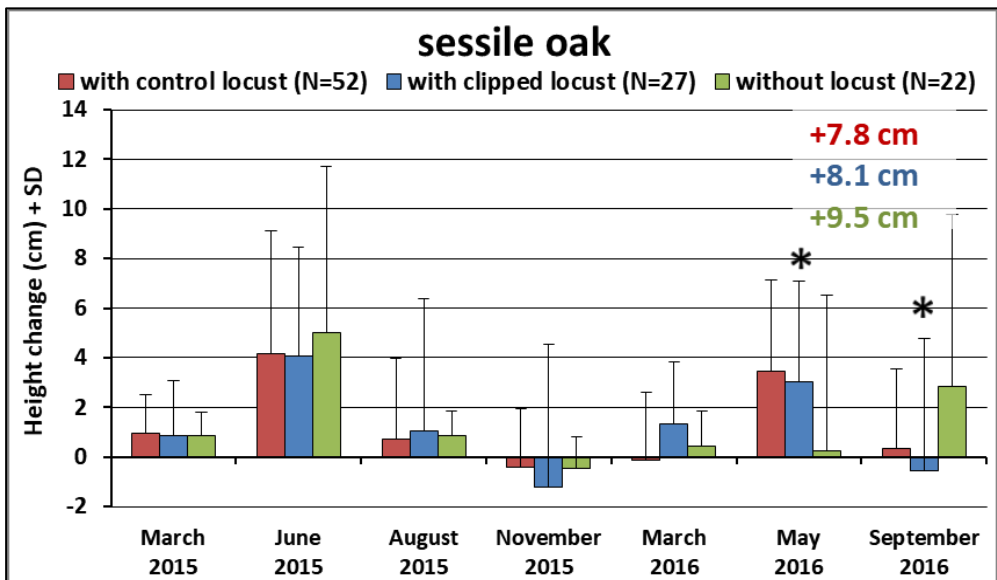

Figure 4: The average height change of sessile oak saplings.

The shoot development of sessile oak was quite low in all groups without exceptions (full time average change: with control locust= +0.55; with clipped locust= +1.82; without locust= +1.86). Therefore the seasonal shoot density increase of black locust saplings was much higher than sessile oaks' (oak +1.14 vs. locust +6.17), which could have an adverse effect on the competitive ability of oak saplings. Shoot density of sessile oaks was the lowest when untreated locusts were located nearby (+0.55), but no significant difference was found among the three groups.

Leaf density did not change significantly during the two years of the experiment (Kruskal-Wallis: KW=1.09, p=0.58) neither in oaks which coexist with locust nor without them. But positive full time balance of leaf density occurred only at oak saplings without any black locust (+0.11), while the other two groups with locust saplings gone through a slight decrease in leaf numbers (with control locust= -0.76; with clipped locust= -0.51).

The total mortality rate of sessile oak saplings was 17% (17 out of 101 individuals). Most of them died in groups where locust saplings located (16 individuals – 94% of total mortality) especially, when control locust saplings were nearby (11 individuals – 65% of total mortality and 21% of the actual group size). Mortality rates were low in the absence of black locust (only 1 oak sapling – 6% of total mortality and 5% of the actual group size). Despite of the various mortality rates, differences were not statistically significant among the groups (χ^2= 0.25 - 3.12, p=0.3 - 0.9).

3.2.2. **Turkey oak** *(Quercus cerris)*

Contrary to sessile oak, the height growth of Turkey oak saplings was the most intensive near to black locust saplings (Figure 5). However, the differences were not statistically significant (KW=1.82, p=0.4). The total height growth was the biggest in oaks surrounded by control locust saplings, their seasonal values were exceeded only once by the group of saplings without locust (in March 2016).
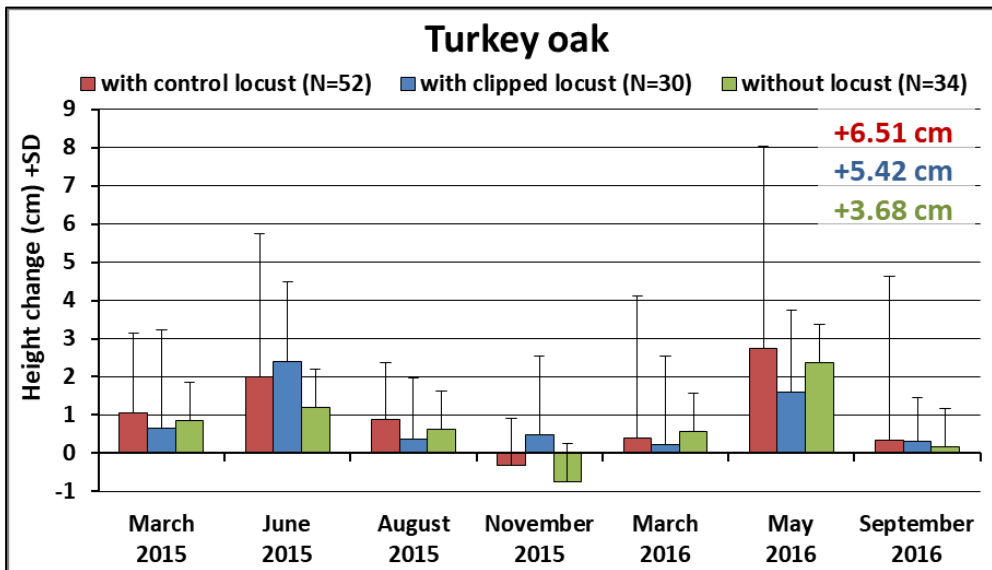

Figure 5: The average height change of Turkey oak saplings

Regarding the results, the potential interspecific competition between Turkey oak and sessile oak seems to be a more important issue for Turkey oak, than the direct proximity of black locust.

The presence of black locust did not hinder the shoot development of Turkey oak saplings, moreover, the absolute values of total shoot increase were the highest in these vegetation patches (full time average change: with control locust= +1.29; with clipped locust= +1.04; without locust= +0.67). The differences were not significant among groups (KW=0.677, p=0.71). Leaf density decreased in all groups, but not influenced by black locust.

The total mortality rate of Turkey oak saplings reached 19% (23 out of 121 individuals). Many of them died near to locust saplings (13 ind. – 56% of total mortality), but their mortality without black locust was similar (10 ind. – 44% of total mortality and 24% of actual group size). The majority of dieback occurred in the first year of the monitoring (2015) in patches without locust saplings, while it remained stable in the presence of black locust (1-2 fatalities seasonally) during the experiments. The total numbers of oak mortality were almost equal between groups with control locust (7 ind. – 30% of total mortality) and clipped locust saplings (6 ind. – 26% of total mortality). Significant difference was not revealed among the groups (χ^2= 1.2 - 3.5, p=0.17 - 0.54).

3.3. Does black locust generates unfavourable soil conditions for oaks?

The results of laboratory tests confirmed the strong acidity (mean pH 4.3±0.1) and the compaction of the topsoil layer prevailing uniformly in all vegetation patches (N=17). Moreover the topsoil was extremely shallow at some sampling points (especially in slope top: average= 11.2±11 cm), and eluvial layers were thick (43.8±33 cm). According to Arany-type plasticity index, the soil texture was identified as clay or clay-loam.

The very low pH and significant compaction represents disadvantageous soil conditions for black locust and oak saplings, which could be compensated by the satisfactory levels of humus (mainly over 5%) and total organic carbon (TOC) content, in all vegetation patch (KW=1.02, p=0.6). No major differences were found in soil ammonium and nitrate N concentrations (p>0.06) between vegetation patches with locust (NH_4^+-N: 5.4±2.3 mg/kg; NO_3^- -N: 16.6±4.7 mg/kg) and without locust (NH_4^+-N: 7.3±2 mg/kg; NO_3^- -N: 13.7±7.1 mg/kg). Potassium and Phosphorous levels were similar in the absence (K_2O: 192±117, P_2O_5: 35±4 mg/kg) and in the presence (K_2O: 149±75, P_2O_5: 43±11 mg/kg) of black locust as well.

3.4. Could an ungulate exclosure fence favor woody plant diversity or mitigate woody species richness through the invasion of black locust?

After two years of exclosure, minor changes occurred in the spatial frequency of tree species (Figure 6). The proportion of plots occupied by black locust has started to decrease significantly in May 2015 from 22.8% to 12.4% by October 2016 (χ^2=19.3, p=0.0002). Simultaneously, the density of black locust was declined by 58% (0.43 ±1.5 ind./m^2 → 0.18 ±0.7 ind./m^2). The new locust seedlings were died early and mortality occurred after the several diebacks on older saplings as well.

Both frequency (April 2014: 21.1% → October 2016: 22.3%) and density (0.34±0.9 ind./m^2 → 0.37±0.9 ind./m^2) data of sessile oak remained stable during the survey period. Turkey oak began to occupy new plots (October 2014: 10% → October 2016: 25%); the spreading was significant (χ^2=51.2, p<0.0001). The stabilized density reflects that died oak saplings were soon replaced by new oak seedlings on the occupied plots.
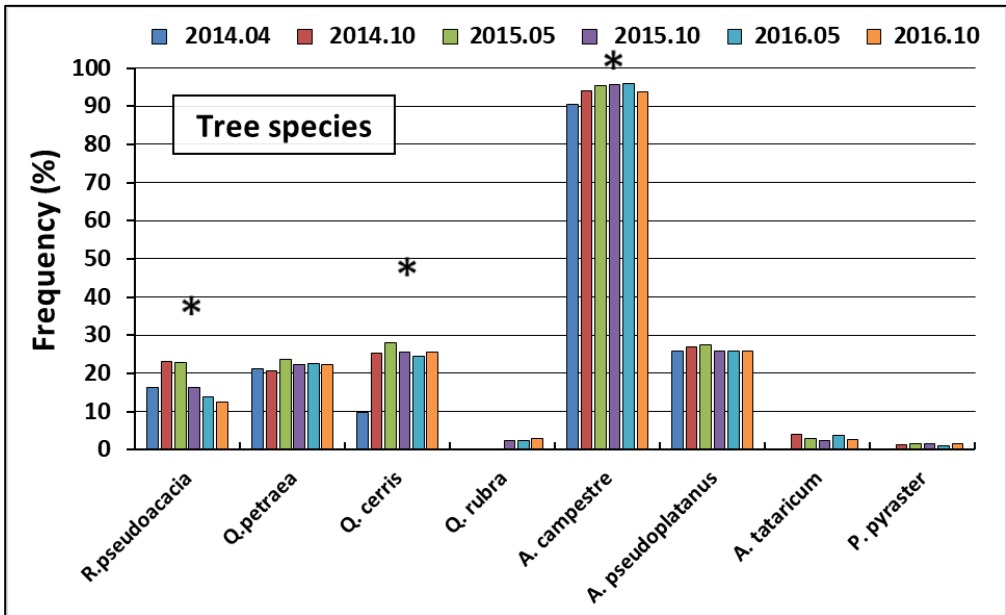

Figure 6: Frequency of tree species within the exclosure

The frequency of field maple was the highest above all woody species in the exclosure everytime ($\chi^2=15.1$, p=0.01) and still increased (91% → 96%).

Shrubs occupied plots more intensive than tree species (Figure 7). Especially blackthorn, dewberry and common spindle frequencies were increased significantly (p<0.0001). Dewberries (*Rubus caesius & Rubus fruticosus*) keep their dominance both in frequency and density among shrubs (Friedman test: Fr=379.9, p<0.0001). Shrub species occupied new plots more likely than tree species when their density increased; while the majority of new tree seedlings emerged next to their conspecifics.
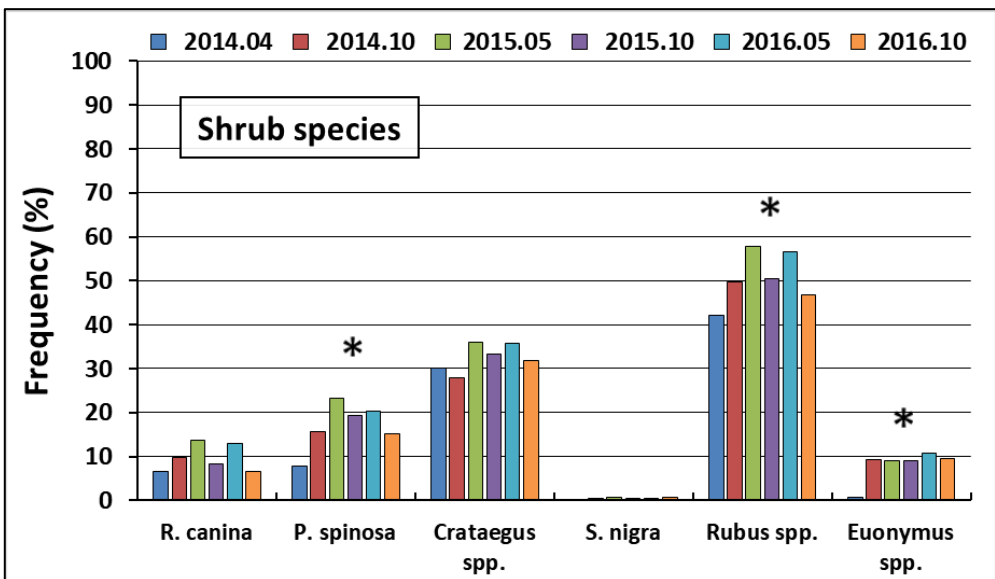

Figure 7: Frequency of shrub species within the exclosure

The most important result of ungulate exclosure was the significant height change of the understory (Figure 8): a dense and relatively high understory was developed. The density of 'seedlings' (under 25 cm in height) was gradually decreased during the two years (Fr=570, p<0.0001; Dunn post hoc test: p<0.05), followed by the significant increase of 'older saplings' (above 50cm in height), whose density exceeded all of the other height categories in May 2016 (Fr= 954, p<0.0001).

Field maple was dominant in the understory from the beginning, and started to overgrow other species. The density of maple seedlings decreased from 62% to 44% (Fr=301, p<0.0001; Dunn p<0.01), but more and more individuals occurred above 50cm height from 43% to 68% in the 'older sapling' category (Fr=859, p<0.0001; Dunn p<0.0001) during the study. Therefore field maple has strengthened its dominance and influence on interspecific competition in shaping vegetation dynamics.
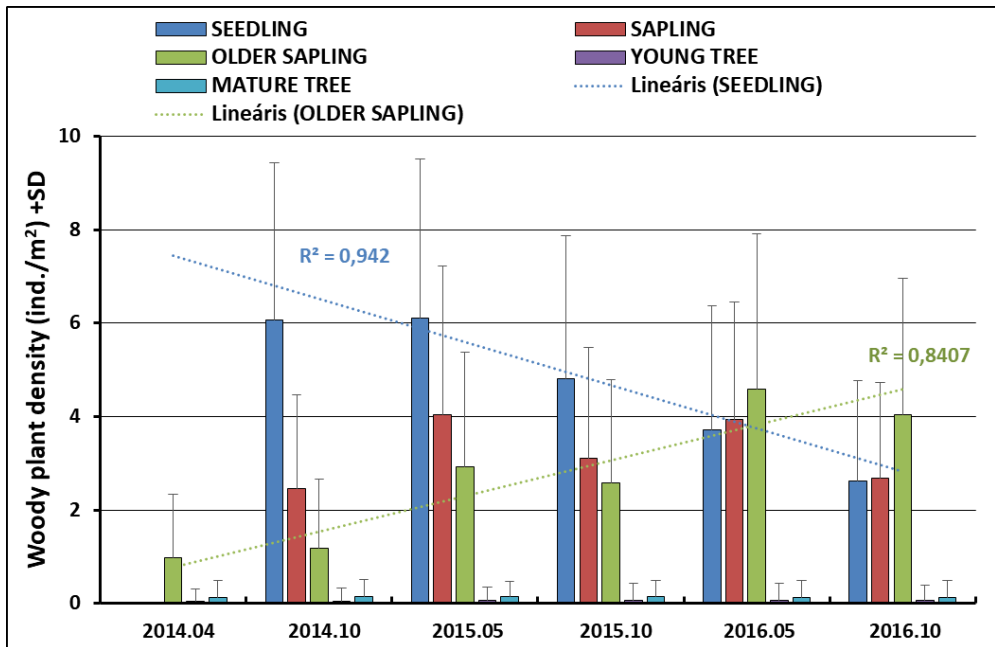

Figure 8: Density of woody species sorted by height categories within the exclosure.

Seedling-sized woody plants remained dominant outside the fenced area on all occasions (June 2015: 4.8 ± 4.1 ind./m^2 → June 2016: 7 ± 5.9 ind./m^2), significant height changes were not occurred.

In 2015, the density of black locust was higher in the exclosure than outside of it (U=16648, U'=24552, p=0.003), however this difference was faded in 2016 (U=19967, U'=21234, p=0.63), due to their increased mortality in the exclosure. Sessile oak density was always higher in the exclosure (p=0.01), while Turkey oak had three times more saplings outside (p<0.0001).

Among shrubs, dewberries, common spindle and blackthorn had a significantly higher cover inside (χ^2=2.9-54.1, p=0.0001-0.05). Further increases can be expected in the density of dewberries, blackthorn and hawthorns.

Woody species diversity – which was represented by the actual species density per plot – was the highest in vegetation patches with locust saplings in the exclosure (min-max: 2.5±1.2 – 3.8±1.2 species/m^2). The average species density was always lower in patches where locust was absent from (min-max: 2.6±1.1 – 3.4±1.3 species/m^2). However, significant difference occurred only once (U=3528, U'=5167, p=0.03).

The values of evenness and Simson-Yule index varied between 0.4-0.5 in the exclosure. The results of Shannon-Wiener index reported low diversity values between 1.4-1.6 (ideal levels should be around 1.5-4.5 depending on habitat type). At the scale of vegetation patches, plots with control locust got the highest values (E: min= 0.55, max=0.62; H: min=1.5, max=1.65). The diversity outside was not differed significantly (E: 0.45-0.67; H: 1.31-1.82).

Herbaceous cover was fluctuated seasonally both inside and outside of the exclosure. The percentage cover was the highest in springtime on both area (inside: 44 ±27%; outside 22±28%), but their maximum values were significantly different (2016: U=8025, U'=33175, p<0.0001). Within the fenced area, herbaceous plants mostly concentrated on the vegetation patches with black locust in spring (min: 24 ±22 %/m^2; max: 68 ±20 %/m^2); while their cover was higher on patches without locust in autumn (min: 5.5 ±11%/m^2; max: 14 ±22 %/m^2).

3.5. How do the patterns and intensity of ungulate impact change among the main forest types in the Mátra Mountains?

Among main forest types, beech forests (BF) had the lowest woody plant diversity and food supply for ungulates. Only 8 woody species were found in those forests, but beech – as a major tree species – was highly overdominant in the food supply (98 ±285 thousand shoot/ha), however its frequency was quite low: beech occurred only at the 27% of the relevant sampling points. This result also implies that the food availability per sampling points was the lowest in BF (N=156 out of 501 sampling points) below all other forest type. Despite of beech was a significantly abundant feed source by the Bonferroni-test (p<0.05), the most browsed species were the minor broadleaved tree species as hornbeam (25 ±33%), ash (23 ±28%) and field maple (13 ±25%). Furthermore the shoots of ash (*Fraxinus excelsior* & *Fraxinus ornus*) were preferred feed by ungulates (Jacobs' index: D=0.84).

The available woody food supply in sessile oak-hornbeam forests (SHF) was twice as high as in BF (297 ±609K shoot/ha). The frequency of understory was 46% (N=137 out of 297 points) and 17 woody species were registered. Ungulate browsing was the highest on shrub species (33 ±30% in average), especially common privet (*Ligustrum vulgare*) and dogwood (*Cornus sanguinea*) were browsed (33 ±47% and 57 ±22% respectively). Among the major tree species, hornbeam was extremely abundant (125 ±369K shoot/ha) and significantly preferred by ungulates (28±35%, D=0.14).

Woody species density was the highest in Turkey oak – sessile oak forests (TSF= 0.72±0.8 species/sampling point, p<0.0001), the available food supply was also high and diverse (527 ±838K shoot/ha). Browsing occurred on all of the 22 registered woody plant species. Browsing intensity

was low on major tree species as sessile oak (18 ±31%) and Turkey oak (6 ±20%) which were significantly avoided by ungulates (p<0.05). The most browsed and preferred plants were shrubs: common dogwood (53 ±46%, D=0.41), common privet (27 ±35%, D=0.27) and hawthorn (*Prunus spinosa* - 30±32%, D=0.21).

Mixed and ravine forests (MRF) were similar to TSF in woody plant supply (568 ±982K shoot/ha), but minor tree species as manna ash, field maple and sycamore maple (*Acer pseudoplatanus*) were dominant in this forest type. Browsing pressure was the highest on hornbeam (41 ±39%, D=0.3) among all woody species in MRF. Oaks were less intensely browsed by ungulates (11-13%), while common privet (33 ±32%, D=0.21) and blackthorn (33 ±31%, D=0.18) were preferred. The total browsing intensity (23 ±29%) was not differed significantly from SHF (25 ±31%) and TSF (21 ±29%) by Dunn's post hoc test (p>0.05).
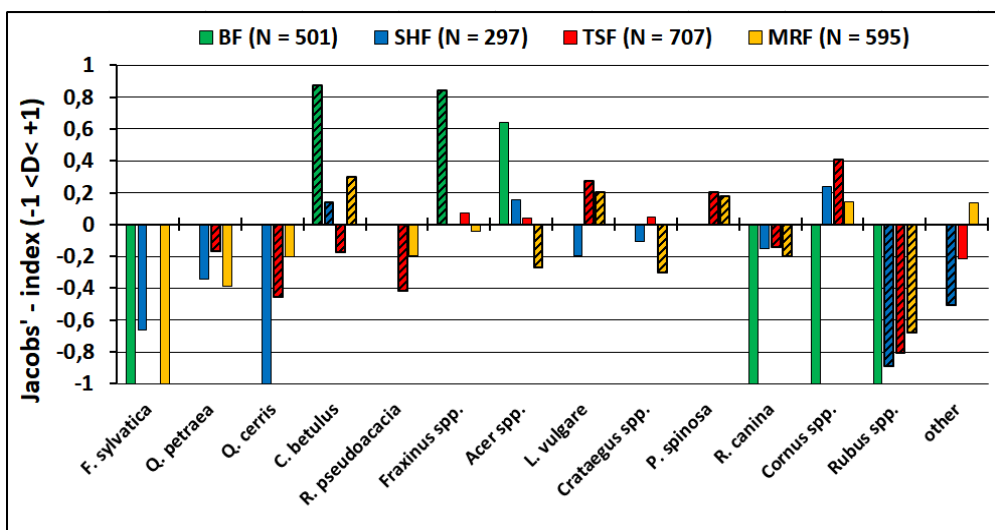

Figure 9: Jacobs' preference index values of available woody plants in the main forest types of Mátra Mountains. Striped bars indicate the significantly preferred (positive values) or avoided (negative values) plants by ungulates (Bonferroni-test, p<0.05).

Many woody species can be sorted to 'generally preferred' or 'generally avoided' groups by summarizing their local browsing intensity and preference data (Figure 9). Therefore, beech and oaks among major tree species; dewberries, dog rose (*Rosa canina*) and hawthorn (*Crataegus spp.*) among shrubs can considered as 'generally avoided' plants for ungulates (D= -0.16 – -1). (However, avoidance is not equal to non-utilization!) On the other hand, hornbeam among tree species; blackthorn, common privet and common dogwood among shrubs were generally preferred feed sources.

The frequency of heavily browsed points (>50% of shoots browsed) was definitely low at regional scale (158 out of total 2100 sampling points – 7.5%). Furthermore, ungulate browsing occurred less than 21% of the total sampling points (N=450). Understory was completely absent from 55% of the total sampling points (N=1154), where no shoots of any woody species were found. The lacking understory could be a source of multiple problems: it can escalate negative browsing impact on isolated – still existing – feeding patches; and hinder forest regeneration by constraining ungulates to browse the non-preferred, but available tree saplings of economic importance.

Regarding the results of sapling density and browsing pattern surveys, the sapling density of major tree species showed a significant difference between beech (BF) and oak dominated forests (SHF, TSF, MRF). In BF the sapling density of beech exceeded 30K ind./ha; while the maximal density of sessile oak and Turkey oak saplings was around 3K ind./ha in SHF, TSF and MRF. The range of sapling density was higher in case of Turkey oak (min: 0.4±2.8K – max: 4.6±17K ind./ha) than sessile oak (min: 1.7±6.9K – max: 2.9±9.3K ind./ha). Hornbeam sapling density was far the highest in SHF (5.5±16K ind./ha) over BF (1.3±6.6K ind./ha), TSF (0.4±3K ind./ha) and MRF (0.2±1.3K ind./ha). The frequency of browsed saplings was the lowest in BF (below 5% on beech and hornbeam); 13 ±12% in TSF, 14 ±10% in

MRF and reached the maximal 18 ±11% in SHF. In the majority of cases (60-80%) both leader shoot and side shoots were browsed on the saplings. Hornbeam saplings were the most browsed ones (18 ±10%), which was followed by sessile oak (16 ±12%), Turkey oak (7 ±9%) and beech (5±7%) respectively.

In total, 3693 tree stems were registered and only 135 of them were debarked by ungulates (4%). Debarking intensity was the lowest in BF (0.2%) and highest in TSF (4.3%). Major tree species were less debarked (beech: 0.3%, sessile oak: 2%, Turkey oak: 2.2%) than minor trees as linden (20%), ash (13%) and maple (8.7%), which obtained the highest preference values (D= 0.34 – 0.76). Ash was significantly preferred by ungulates in TSF and MRF (Bonferroni-test: p<0.05).
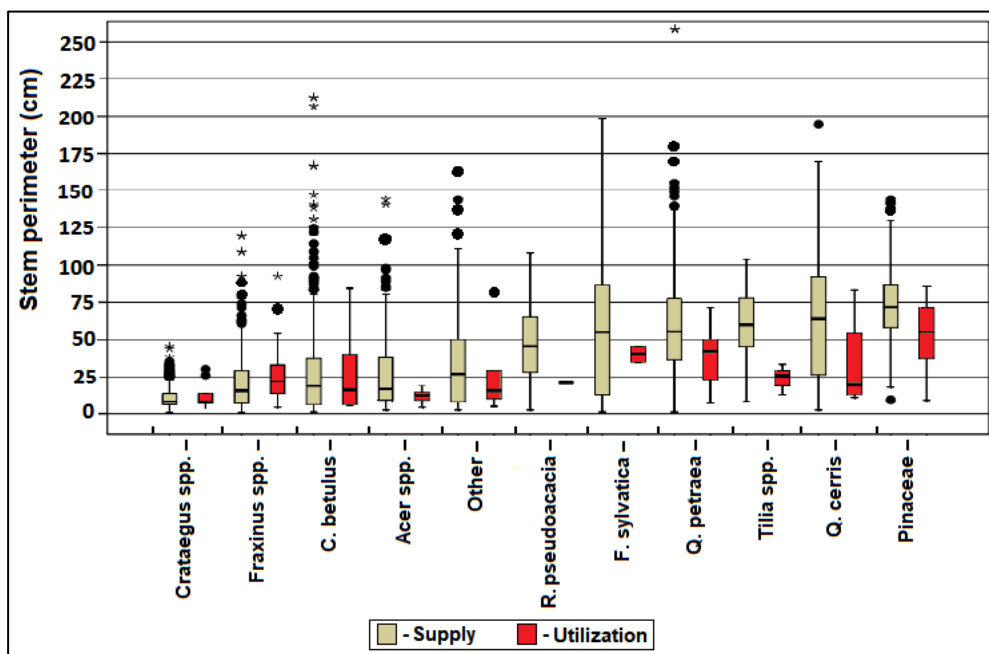

Figure 10: The median perimeter of available and utilized stems of woody species relevant to debarking by ungulates. Outliers are indicated with spots (out values) and asterisks (far out values).

Bark stripping was the most frequent type of the stem injuries (79% of 135 debarked stems). Antler rubbing by deer and bark rubbing by wild boar were relatively rare; we identified them at 13% and 7% of total debarked stems respectively. Stems with 3-22 cm girth were most susceptible to debarking (Figure 10). Ungulates used different sized stems for bark stripping ($\tilde{x}$: 18 cm; IQR: 14.8), antler rubbing ($\tilde{x}$: 37 cm; IQR: 14.6 cm) and bark rubbing ($\tilde{x}$: 51 cm; IQR: 19 cm). Bark stripped stems were significantly thinner than the others (KW= 22.11; Dunn's test: bark stripping vs. antler rubbing: $p<0.01$; bark stripping vs. bark rubbing: $p<0.001$).

Wild boar grubbings occurred more often in oak dominated forests than beech forests. Therefore the frequency and intensity of grubbings was quite low in BF, only litter layer or soil surface grubbings were detected on 7% of the relevant sampling points. In contrast, all the frequency, intensity and spatial extent results of grubbings were higher in SHF (19% of points; 10.1% of area - 299 m^2), in TSF (16% of points, 8.6% of area - 612 m^2) and MRF (13% of points, 5% of area - 277 m^2). In most cases, the grubbed area was below 2.5m^2 in extent and remained shallow on the relevant sampling points (N= 153 out of 284 occasions).

The intensity of ungulate browsing and stem utilization was highly correlated with the food availability and food supply of the understory. The probability of browsing (on saplings) and debarking was significantly increased by the rate of woody shoot supply available in the understory ($p<0.001$). These ungulate impacts could be more intensive in forests where understory has an aggregated distribution, because ungulate browsing could be damaging on vegetation and forest renewal in these fragmented feeding patches. Although browsing on saplings cannot be eliminated completely, its intensity can still be regulated by sustaining the continuous cover of the

understory. Furthermore, preferred shrub species over a significant density (~ 250-300K shoots/ha as reported in MRF) could exert a 'buffering effect' by reducing browsing intensity on oak and beech saplings.

The negative correlation between wild boar grubbing intensity and tree sapling survival was equivocal, because not even the heavily grubbed points had lower sapling density.

The density of laying beds was higher in forest types where dense understory was developed like MRF (7.4 bed/km) or TSF (6.6 bed/km) compared to BF (3.6 bed/km).

3.6. New scientific results

1. Ungulate browsing itself can not hinder the spread of black locust in temperate oak forests. Simulated browsing did not influence the mortality of black locust significantly. Saplings have compensated their loss in response of simulated browsing treatments.

2. Negative allelopathic effects of black locust saplings were not confirmed on the development and survival of oak saplings. Simulated browsing treatments did not influence the interspecific competition between black locust and oak species in a short term period.

3. Ungulate exclosure only ensured the height growth of the understory, but woody diversity remained unaffected in comparison with the outside area. Black locust had a decreasing, while field maple and dewberry had an increasing trend in frequency and density inside the fenced area. Exclosures can cause unwanted compositional shifts in the vegetation. Understory thinning could be required in the future, if ungulates remain excluded, thereby their selective browsing cannot take its regulating effect.

4. We developed, tested and implemented the complex method of ungulate impact monitoring for the first time in Hungary, which is able to evaluate the ecological impact of ungulates in temperate forests.

5. I confirmed that major tree species of economic importance as beech, sessile oak and Turkey oak are not primary feed sources for ungulate herbivores. Browsing on them can reach high intensity levels only, when their saplings form homogenous vegetation in regenerating areas, or understory is lacking in primarily preferred alternative food sources. I proved the selective stem utilization of ungulates: different tree species were used in specific girth intervals by ungulates for bark stripping, antler rubbing and bark rubbing.

6. The results of ungulate impact monitoring have not confirmed any presumption that ungulates caused serious regional problems in the forests of Mátra Mountains. However, the local extent of browsing, debarking or grubbing can be critical in forests with aggregated understory, which can hinder sapling growth in nearby regeneration areas.

4.   CONCLUSIONS AND SUGGESTIONS

4.1. The combined effects of ungulate browsing and soil conditions on the development and competitive ability of black locust saplings

1) Soil conditions were the primary limiting factors in the development of black locust saplings instead of simulated browsing. The low soil pH, soil compaction and steepness are all disadvantageous (VÍTKOVÁ et al. 2015) but still prevalent factors for saplings in the fenced area. Additionally, the frequent summer drought periods can aggravate this situation.

2) Extreme weather conditions as summer heat waves and long drought periods pose a greater threat to black locust than to oak saplings. Locust saplings take more risk by their intensive height growth and shoot development (see Fig. 2 and 3) and higher investment also means higher potential losses in bad years compared to oak saplings. Furthermore, the resource acquisition is limited under the current soil conditions: the pH below 4.5 represents an extremely acidic soil, where nutrient uptake decreases significantly. Soil aluminium and iron become soluble in their ionic (Al^{3+}, Fe^{3+}) forms (STEFANOVITS 1992), which are toxic to plants.

3) Black locust saplings were not able to express their competitive ability in this short period of time. Allelopathic effects and soil nitrogen enrichment by black locust could not be significant at the sapling life stage, due to unsatisfactory leaf development, which plays an important role in allelopathic potential of the species through releasing allelopathic compounds by fallen leaves (NASIR et al. 2005).

4) The primary competitive advantage of black locust saplings arise from their fast growth instead of their allelopathy in the early life stages. This trait makes them able to overgrow other plants under favorable circumstances.

The high variance in height growth and shoot density data indicates a significant variability in the individual development of black locust saplings. The local patterns of light, water availability and competition intensity may influence each sapling differently, therefore their response towards abiotic stress and simulated browsing was diverse.

The increase in fiber content after browsing treatments led to decreasing protein/fiber ratio in black locust saplings (see Table 2). This declining quality of nutrient content can reduce the chance of further browsing on black locust, thereby enhancing their survival in the future.

Both oak species had higher mortality rates in total near to black locust saplings. Therefore negative effects of black locust presence could be hypothesized; however, significant difference was not confirmed anytime.

4.2. The effects of ungulate exclosure on woody vegetation dynamics and species diversity

Despite expectations, the frequency and density of black locust have significantly decreased in the exclosure, primarily due to summer drought. On the other hand, shade tolerant species as field maple and sycamore could have better conditions for survival at 80% canopy closure than shade intolerant black locust saplings.

Field maple has a very wide ecological range and tolerates extreme temperatures (ZECCHIN et al. 2016). Also grows well on heavy clay and is able to subsist on soils with a pH lower than 6 (NAGY & DUCCI 2004). As a stress tolerant-ruderal species (BRZEZIECKI & KIENAST 1994) field maple can overgrow other saplings in the exclosure. The moderate shade under the relatively closed canopy and ungulate exclosure are both supporting field maple predominance. It seems that ungulate absence plays a key role in field maple overgrowth.

Regarding to oak, the increase of sapling density also depends on periodic mast production especially at sessile oak. Furthermore, soil compaction and increasing concurrence of field maple reduce successful sprouting and growth. The contrasting density of Turkey oak saplings inside vs. outside the exclosure has indicated this effect.

The secondary woody species as northern red oak (*Quercus rubra*), common spindle and elderberry (*Sambucus nigra*) have stabilized their density at a higher level after exclosure: ungulate browsing might regulated the development of these species before fencing. More and more saplings of field maple and sycamore maple occurred first in 'older sapling' then in 'young tree' height categories (above 2m), similar to dewberry in the 'older sapling' category, which suggests that ungulates have suppressed their growth previously. The winners of this interspecific competition will be those, which can adapt to the complete absence of ungulate disturbances in a relative short period of time, producing intensive height growth despite of moderate shade. Field maple could be the (only) one of them in the future, tends to homogenize the vegetation composition. This phenomenon was partly confirmed by the stable values of diversity indices registered in the exclosure.

4.3. Monitoring and managing ungulate impact in Mátra Mountains

The primary browse species of ungulates were shrubs in all forest type inasmuch as their shoots were sufficiently available in the understory. Browsing impact seems almost certain on every woody species whose density exceeds the amount of 2K shoots/ha independent of ungulate preferences based on our results. This could be the minimal level which ensures the opportunity of being found by ungulates. Thereby a limited amount of browsing shall occur even on plants avoided by ungulate herbivores.

Our results confirmed this phenomenon: ungulates browsed the shoots and saplings of beech, sessile oak and Turkey oak at various levels of intensity in each forest type. However, this impact was nowhere serious, because more than 75% of their saplings still remained intact in accordance with their low preference results! The overall low sapling density could raise much bigger problems in forest renewal, which has many counteracting factors beyond browsing impact though. Potential browsing damage can mostly occur at the local scale of homogenous regenerating areas, where ungulates can hinder sapling development through repeated leader shoot and side shoot browsing.

On the other hand, the regulating effect of ungulate browsing needs to be considered as an ecosystem service in case of specific tree consociations (e.g. hornbeam or ash). Hornbeam was preferred feed for ungulates at several times (Fig. 9). This status is important where hornbeam reaches extreme high density as it was registered in SHF. At this point, ungulate browsing and debarking can express a significant pressure to regulate hornbeam overgrowth and to reduce its competition with oak and beech. The same effect could be also prevalent in MRF, where manna ash became predominant.

Low understory cover and availability (below 50% in frequency) was one of the most critical issues what was revealed by the monitoring. Lacking understory can be problematic in at least two ways: on the one hand it results insufficient feed supply for ungulate species, because all ungulate herbivores which common in Hungary obtain their food mainly by browsing (including mouflon as well). On the other hand the still remaining foraging patches can concentrate ungulates and also their negative impacts, especially when the preferred shrub species are absent. This could lead to a far-reaching environmental problem and failing forest regeneration.

Many biotic and abiotic factors can aggravate or mitigate the negative effects of browsing, debarking and wild boar grubbing. However, the results of the ungulate impact monitoring showed that these impacts have not posed a regional threat to the environment at the full scale of Mátra Mountains. Furthermore, the temporal and spatial patterns of negative ungulate impacts greatly depend on the quantity and quality of feed sources and forest stand structure; therefore it cannot be explained by high ungulate density only (GERHARDT et al. 2013) and culling itself is not an adequate solution to manage ungulate impacts.

Grubbings by wild boar were mainly shallow and patchy. This impact is mostly associated with the acorn predation of wild boars, but these grubbings can also function as germination niches for other plants (SANDOM et al. 2013). Based on our results, we did not find negative correlations between 1) sapling frequency and grubbing frequency; 2) sapling density and extent of grubbing, moreover the completely grubbed (100%) points had significantly higher sapling density!

Browsing, grubbing or debarking will result diverse effects in different habitats and their consequences can vary under different environmental conditions. Positive and negative impacts occur simultaneously, but damages are always conspicuous. The ideal levels of ungulate impact are needed to be assigned which can contribute to sustain natural habitats through their positive effects. The methods of our ungulate impact monitoring offer a useful tool to understand the control mechanisms and create intervention plans based on the bioindicators of ungulate effects. Moreover the potential negative effects can also be forecasted and managed.

5. PUBLICATIONS RELATED TO THE TOPIC OF THE DISSERTATION

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<u>Fehér Ádám</u>, Szemethy László, Katona Krisztián (2016): Selective debarking by ungulates in temperate deciduous forests: preference towards tree species and stem girth. European Journal of Forest Research 135(6): 1131-1143. p.

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