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Species composition, elevation, and former management type affect browsing pressure on forest regeneration in the Tatra National Park

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Abstract. Effects of ungulate pressure on the development of young generation of trees is one of the most important issues in ecology and forestry. Ungulate pressure influence on the development of natural regeneration has been also reported from several national parks. Our study on the effects of ungulate browsing on the young generation of trees was conducted on more than 500 sample plots controlled during one growing season.

The overall browsing pressure ranged from 7.6% in seedlings to 20.3% in low saplings. The pressure of ungulates on the regeneration of *Picea abies*, the dominant species in the Tatra National Park, was by and large below 1%. Broadleaved species were browsed more frequently. The relationship between the plot altitudes and browsing intensity was statistically significant for seedlings and low saplings; at the higher altitudes, the browsing pressure was greater. There was also observed a statistically significant relationship between the type of former management and the browsing degree in seedlings; in the areas subjected to "landscape protection", the intensity of browsing was higher when compared to strictly protected areas. Pressure exerted by ungulates on tree regeneration was very unevenly distributed, i.e. some plots were heavily browsed and many others - not browsed at all. The most affected tree species were *Salix caprea* and *Sorbus aucuparia*, although the percentage of browsed individuals rarely exceeded 50%. Other species favored by ungulates was *Acer pseudoplatanus*; despite the high browsing pressure, this species was present among seedlings and tall saplings, suggesting that it would be able to recruit to the tree layer. *Abies alba* was browsed less frequently than the deciduous trees; however, among the tall saplings it was the third most browsed species.

Keywords: natural regeneration, montane forests, permanent sampling plots, ungulates, Western Carpathians

1. Introduction

Ungulates have an enormous impact on forest dynamics, primarily by browsing on the shoots of young tree specimens, which leads to a reduced growth rate, the death of more damaged individuals and changes in the species composition of forest regeneration in favour of the less intensely browsed species (Frelich and Lorimer 1985; Kujiper et al. 2010, White 2012). The population size of ungulates in temperate forests has been steadily increasing for a long time from North America (Horsley and others 2003) through Europe (Milner et al. 2006) to Japan (Takatsuki 2009). The majority of ungulates living in these forests feed mainly on shoots. In many forests, the shoots of young trees are the only available food. Browsing on the regeneration has, therefore, become a serious problem for forestry (Ammer 1996, Reimoser and Gossow 1996, White 2012). The number of ungulates is also increasing in the forests of Poland. Since the middle of the past century, the red deer population has increased from 30,000 to more than 200,000 individuals. The number of roe deer in the country is about 860,000, which is an increase of approximately 270,000 individuals from the beginning of the century (Górecki et al. 2016). In some regions, this has been a problem for many decades, but recently, it has also expanded to areas where there were few ungulates

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a dozen years ago. This is linked to increased damage to forest trees, mainly as the result of browsing. In managed forests, damage caused by ungulates changes the species composition by simplifying it and reducing the quality of the obtained wood raw material. A widespread response to the pressure of herbivores is the fencing of forest crops. Even larger areas of natural regeneration are protected (Łukaszewicz et al. 2017) by fences.

The problem of increased deer pressure on forest regeneration also affects national parks (Jamrozy and Brewczyński 1998, Skrzydłowski 2009, Miścicki and Żurek 2015), especially those where tree stands are being reconstructed. As a result, population reductions also take place in most national parks. For example, in 2015, ungulates were hunted in 19 out of 23 national parks, and a total of 9 elks, 336 red deer, 117 roe deer and 1899 wild boar were shot (GUS 2016). However, information about the pressure of ungulates on tree regeneration is insufficient. It is collected using various methods and, to a large extent, relies on subjective estimates. Permanent monitoring areas (Miścicki and Żurek 2015) provide the opportunity to collect objective data on the impact of ungulates on tree regeneration. Such areas have been established in national parks since the 1970s (Dziewolski 1972), enabling repeated measurements to be taken in the same places using the same methods, making it possible to objectively assess ungulate pressure on the regeneration and changes to this phenomenon over time.

In the first years of the existence of the Tatra National Park (TNP), the pressure of wild ungulates on the forest regeneration was not as significant as the pressure of sheep and cattle grazing in the Tatras. According to Fabijanowski (1962), the main difficulty in reconstructing tree stands and afforestation was easements, which covered a significant part of the TNP forests, but he did not mention that game animals negatively affected the regeneration. The first information about fencing tree plantings is from the TNP archives of 1967, and then in 1972, information about their protection against animals appeared. The actual level of ungulate pressure on regeneration, both artificial and natural, was never the subject of more detailed research in the TNP and was limited only to selected fragments of the High Tatras (Brągiel 1976). The first studies on this topic have appeared only recently (Skrzydłowski 2009; Stopka, Skrzydłowski 2014).

The aim of this study was to analyze the level of browsing on forest regeneration depending on the species of tree, elevation above sea level and the area's type of protection status caused by ungulates in the western part of the TNP. Thanks to the decision of the Park authorities to establish a regularly spaced network of permanent research areas, it was possible to present a picture of the spatial variability of browsing over a large area, based on a large sample collected in a short time in a methodically uniform and objective manner. Such a network was established in the TNP for the first time and is intended for multifaceted research.

2. Materials and methods

2.1. Study area

The research covered the forests and mountain pine *Pinus mugo* thickets in the western part of the TNP. This area is bordered on the west by the Polish-Slovak border (above the Chochołowska Valley), from the south by the upper boundary of dense patches of mountain pine (to a maximum elevation of 1,773 m a.s.l.) to the Liliowe Pass region and from there down along the Sucha Woda Stream to Murzasichle and then along the northern border of the TNP (a minimum elevation of 816 m a.s.l.).

The northern and central part of this area is built of sedimentary rocks, mainly limestones and dolomites, on which various types of rendzina soils developed. The southern part, called the crystalline core of the Tatras, is made up of gneisses, granodiorites and granites covered with podzols and, in the higher areas, also with various types of rankers (Passendorfer 1996; Piotrowska et al. 2015; Skiba et al. 2015). The border between these two tectonic units is a belt of quartz sandstones, shales and conglomerates extending from west to east (Piotrowska et al. 2015). In addition, a significant area of the valley floors are covered with moraine deposits, which at the eastern end of the study area reach almost to the mouths of the valleys, covering the local sedimentary rocks with a layer of granite boulders and podzolic soils (Piotrowska et al. 2015, Skiba et al. 2015).

The lowest areas of the TNP are located in the lower montane zone, characterised by a moderately cool climate (average temperature, +5°C; average precipitation, approximately 1,100 mm). The upper montane zone starts from about 1,250 m a.s.l., where the climate is cool (average temperature, +3°C; average rainfall, about 1,400 mm). The mountain pine zone starts above 1,550 m a.s.l. to the upper limit of the study area and has a very cool climate (annual average temperature, +1°C; average rainfall, about 1,700 mm) (Hess 1996; Ustrnul et al. 2015; Żmudzka et al. 2015). The lowest areas are mainly occupied by the fertile Carpathian beech forest, *Dentario glandulosae-Fagetum*, transformed into artificial spruce stands over significant areas. In slightly poorer habitats, *Galio-Abietetum* fir forests developed. In addition, on the sun-exposed limestone rocks, relic pine forests *Vario-Pinetum* and fragments of thermophilic beech forests in the fir *Carici albae-Fagetum abietetosum* subassociation can be found, whilst Carpathian alder *Alnetum incanae* occurs in the mouths of the valleys, along streams. In turn, on the moister, steep slopes, fragments of sycamore forests *Sorbo-Aceretum s.l.* have been preserved (Pięknaoś-Mirkowa, Mirek 1996). On the eastern edges of the study area, assemblages of lower montane spruce *Abieti-Piceetum montanum* and mountain spruce bog *Sphagno-Piceetum* (Mirek et al. 2013) forest communities have developed on the moraines, which are extremely rare in the Polish Carpathians.

The upper montane zone is the domain of spruce forests. The dominant forest association here is the West Carpathian high-mountain spruce forest *Plagiothecio-Piceetum*, whilst on more fertile fragments built of limestone rocks, the calcareous upper montane spruce forest *Polysticho-Piceetum* has developed (Piękoś-Mirkowa, Mirek 1996; Mirek et al. 2013). The areas located above the upper boundary of the forest are covered with mountain pine thickets - poor *Pinetum mughi carpaticum silicicolum* and the floristically richer *P.m.c. calcicolum* (Piękna-Mirkowa, Mirek 1996; Mirek et al. 2013).

2.2. Data collection methods in the field

The research was conducted in 509 permanent test plots established in a spacing of 500 m × 500 m in a system referenced to the AtPol geobotanical grid. The range of variability of the permanent test plots in the elevation gradient ranged from 816 to 2,062 m a.s.l. The distribution of the test plots in terms of type of protection is presented in Figure 5. In order to determine the density of the regeneration, at each test plot, we measured 30 specimens closest to the centre but at a distance not exceeding a radius of 12.62 m, which determined the borders of the sample plots in which the stand structure was studied. Regeneration was measured by specifying the species, measuring height, distance from the centre of the plot and azimuth. The regeneration was assigned to three classes: seedlings ($h < 0.5$ m), short saplings ($0.5 < h < 1.3$ m) and tall saplings ($h > 1.3$ m and DBH < 7 cm). Each specimen of the sample was subjected to a detailed inspection for the occurrence of damage from ungulate browsing.

2.3. Statistical methods of data analysis

To analyze the relationship between the extent of browsing and elevation above sea level, the entire test area was divided into elevation bands: below 1,000, from 1,001 to 1,200, from 1,201 to 1,400, from 1,401 to 1,600 and above 1,600 m. Data was analysed in two ways: first, the frequency of browsing the regeneration of a given species and a given size category (seedlings, low and tall saplings) was determined in relation to the number of individuals recorded in the study area. Some of the analyses were conducted at the sample plot level, that is, these quantities were calculated as the features of the plots. This is also why two types of estimates for browsing intensity are presented in the results, which sometimes quite clearly differ from each other: the first is based on the number of browsed individuals in relation to their total number; the second is based on the frequency of the sample plots in which a given species was browsed. Both were quantitative data based on the percentage of shares or frequency of the plots. Statistical analyses were performed by verifying whether the measurement results of a given feature for a particular species were characterised by normal distributions using the Kolmogorov–Smirnov test with the Lilliefors correction. Consequently, all subsequent hypotheses were tested using nonparametric methods: the Spearman test and the Kruskal–Wallis test. All analyses were performed in the STATISTICA program (ver. 12 StatSoft).

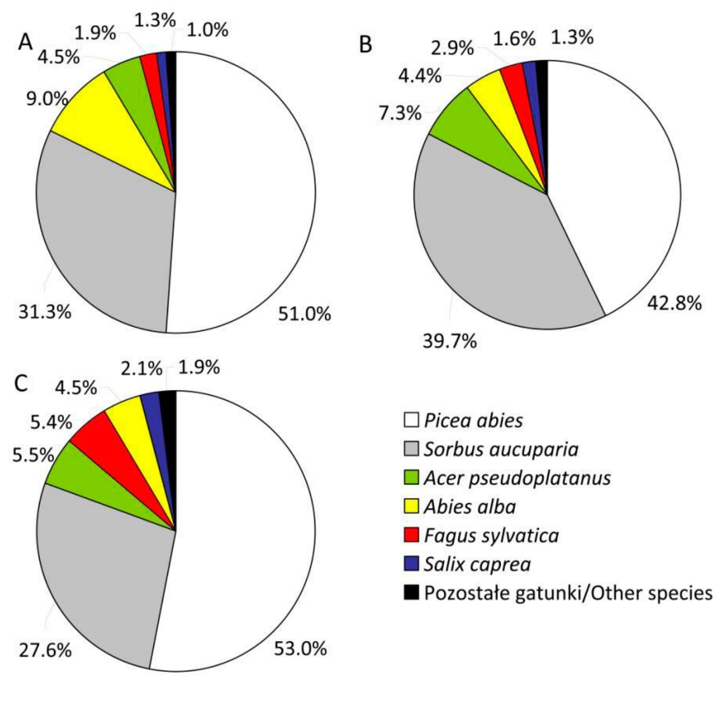

Figure 1. Species composition of the regeneration in permanent sample plots: (a) seedlings, (b) short saplings and (c) tall saplings.

3. Results

The occurrence of seedlings of trees species was found in 433 sample plots (a total of 10,867 specimens), whilst short saplings (8313 specimens) and tall saplings (7353 specimens) were found in 409 and 348 plots, respectively. A total of 22 tree species were represented in the regeneration, including 15 species in the seedling category, 17 species of short saplings and 18 species of tall saplings. The species composition of the regeneration in individual height classes is shown in Figure 1. The most abundant species were the same in each of the three analysed height classes of the regeneration.

The average level of browsing ranged from 7.6% for seedlings to 20.3% for short saplings. Tall saplings were browsed at 10.4%. There were large differences between species. Practically no spruce regeneration was browsed. Only in the case of short saplings, that is, the most vulnerable category, the level of spruce browsing was 1%, whilst in the other classes, it was a fraction of a percent. Beech was also very rarely browsed - the level of browsing in its case ranged from 1.9% for seedlings to 4.1% for short saplings. The most browsed species was *Salix caprea*, which had the highest percentage of browsing amongst seedlings (27.1%) and tall saplings (26.6%), whereas amongst short saplings, it was placed third (33.6% of browsing). The second most browsed species was *Sorbus aucuparia*, which had the highest percentage of browsing in the class of short saplings (38.5%), whilst among seedlings (18.3%) and tall saplings (25.1%), it was in third place. The next species in the ranking of browsing intensity were both sycamore and ash. The former was relatively strongly browsed in the category of short saplings (35.5%), and the latter amongst the seedlings (10%). However, ash has an insignificant share in the regeneration of the western part of the TNP, which is why this species was not included in the statistical analyses and figures. Fir was only in fifth place; in the case of this species, the relatively high level of browsing amongst tall saplings (25.9%) deserves attention. In this category, fir only gave way to pussy willows. However, the level of fir browsing amongst the seedlings (7.8%) was only slightly higher than the average for all species.

In terms of the frequency of the monitored plots where the seedlings of a given species were browsed, rowan was in first place (almost 18%) followed by pussy willow (17%), sycamore (12%), fir (6%) and beech (3%). The analysis using the Kruskal–Wallis test showed that the difference in browsing frequency at the monitored plots between rowan on one side and beech and fir on the other was statistically significant ($H = 30.00$, $p < 0.001$). However, there were no significant differences were found between rowan, on one side, and sycamore and willow, on the other, or between beech and fir.

In the group of short saplings, the highest percentage of plots with browsed specimens was found for sycamore (41%), which was followed by rowan (38%) and willow (26%). In the case of fir, the percentage of monitored plots with browsed short saplings reached 24%, and that for beech reached 6%. The Kruskal–Wallis test showed that the differences between beech, on the one hand, and rowan, sycamore and fir, on the other hand, were statistically significant ($H = 44.69$, $p < 0.001$). The difference between beech and willow was not statistically significant because of the smaller number of sample plots in which willow occurred.

On the basis of the percentage of browsed individuals, we found that amongst the tall saplings, rowan was the most frequently browsed species (25%), which was followed by sycamore (22%) and fir (20%). Pussy willow was in fourth place (13%) and beech in fifth place (4%). According to the Kruskal–Wallis test, the differences between beech and rowan and between sycamore and fir were statistically significant ($H = 34.12$, $p < 0.001$), whilst the difference between beech and willow, as with all of the remaining differences not listed above, turned out to be not significant.

On the basis of the obtained results, the hypothesis about the conformity of the empirical distribution with the theoretical normal distribution was rejected; therefore, nonparametric tests were used. Because the p values obtained were below 0.05, the hypothesis about the equality of all medians was rejected. The median test showed that the percentage of browsed specimens was statistically significantly associated with the elevation above sea level for seedlings (Chi-square = 29.5, $p < 0.001$) and short saplings (Chi-square = 24.3, $p = 0.0001$); in both cases, specimens growing at higher elevations were more often browsed. On the other hand, in the case of tall saplings, there was no significant relationship between the browsing rate and elevation above sea level of the band (Chi-square = 4.7, $p = 0.3232$).

The relationship between the percentage of browsed specimens and the type of protection status analysed with the Chi-square test turned out to be statistically significant only in the case of seedlings (Chi-square = 13.7, $p = 0.001$). The analysis conducted with the Kruskal–Wallis test showed significant differences between landscape protection and strict protection ($H = 12.5$, $p = 0.002$). The remaining differences between the types of protection were not statistically significant.

In strict protection areas up to 1,000 m a.s.l., seedling browsing was sporadic. In the elevation band from 1,001 to 1,200 m, seedling browsing was slightly more than 5%, with the most severely browsed species being rowan (19%) and pussy willow (11%). In the range of 1,201 to 1,400 m, the level of seedling browsing was similar, but the most browsed species was sycamore (16%) followed by rowan (13%). From 1,401 to 1,600 m a.s.l., the average seedling browsing level was 7%, and the most severely browsed species was rowan (13%). Above 1,600 m, seedling browsing was slightly more intense (13%), and the most severely browsed was pussy willow (85%) followed by rowan (18%). Silver

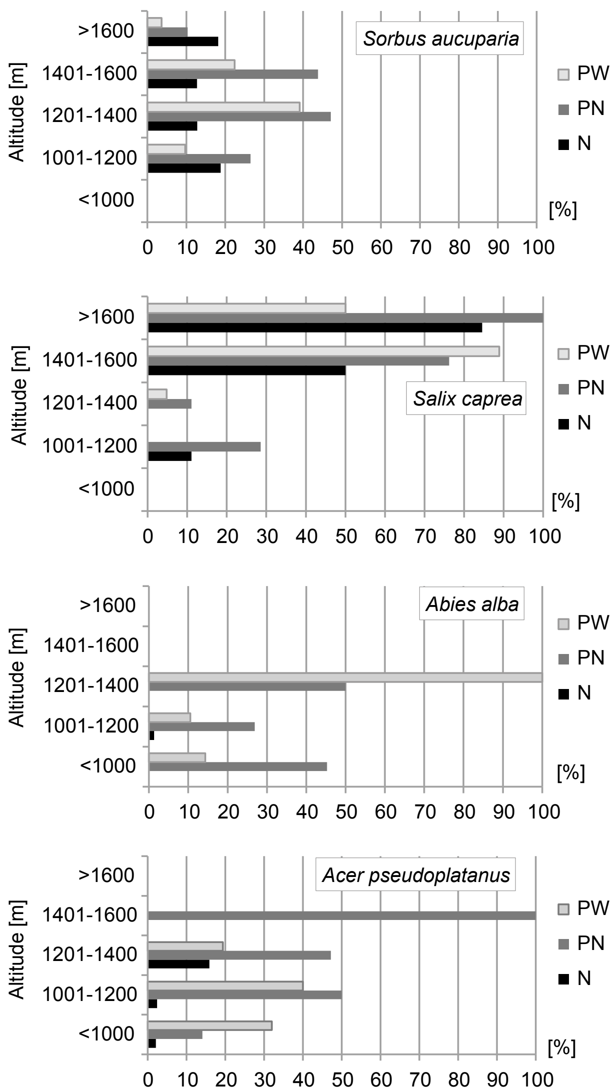

Figure 2. Intensity of browsing of the natural regeneration in different elevation bands in the strictly protected area.
Explanations: N, seedlings; PN, short saplings; PW, tall saplings.

fir, which occurred most frequently amongst all seedlings in the elevation band of up to 1,000 m a.s.l., was not browsed at all, and between 1,001 and 1,200 m, just barely more than 1% of the specimens were browsed (Figure 2).

In the active management zone, seedling browsing in areas located below 1000 m a.s.l. was negligible (2%), and the only heavily browsed species was European ash (30%).

In the elevation band of 1,001 to 1,200 m, the average browsing level was less than 7%, and amongst the more numerous species found amongst the seedlings, primarily, sycamore (23% and rowan 11%) were browsed. In the elevation band of 1,200 to 1,400 m, seedling browsing reached a level of almost 24%, and the most severely browsed were pussy willow (73%), sycamore (44%) and rowan (40%).

Fir browsing, which was in third place in terms of numbers, was slightly higher than that in strictly protected areas (Figure 3). In landscape protection areas, the level of seedling browsing increased with elevation, from 6% below 1,000 m a.s.l. to almost 12% at the elevation of 1,201-1,400 m, then dropping sharply to 1.5% between 1,401 and 1,600 m and to 0% above 1,600 m. In the lowest zone (up to 1,000 m), only fir (27%) and sycamore (6%) were browsed. The pressure of ungulates in the next elevation band, between 1,001 and 1,200 m (Figure 4), was completely different. Here, the most browsed species was rowan (28%), which was followed by fir (11%) and sycamore (3%). In the most severely browsed elevation band - 1,201–1,400 m - the order was similar (Figure 3).

The browsing of short saplings in the strictly protected area, similar to the seedlings, increased with elevation: from 18% below 1,000 m through 19.5% between 1,001 and 1,200 m and 26% in the elevations of 1,201-1,400 m and 1,401-1,600 m a.s.l. The rapid decline in the browsing intensity on short saplings to less than 6% occurred only above 1,600 m. Below 1,000 m, the most browsed were the short saplings of fir (45%) and sycamore (14%), whilst the rowan was not browsed at all. Between 1,001 and 1,200 m a.s.l., the most intensely browsed species amongst the short saplings was sycamore (50%) followed by fir (27%) and rowan (26.5%). Between 1,201 and 1,400 m, a similarly high level of browsing (47%) occurred on rowan and sycamore saplings. Above 1,400 m, willow (76% of 21 individuals) and slightly fewer rowan (44%) were the most intensely browsed.

In the active management zone below 1,000 m a.s.l., the percentage of browsed specimens was very low (4%). Of the browsed species, the most preferred were rowan (9%) and ash (15% browsed from just 20 individuals). In the band of 1,001 and 1,200 m, the share of browsed short saplings was almost 20%, and the most browsed species were sycamore (40%), as well as rowan and willow (28% each). The remaining species growing in this zone were sporadically browsed. Above 1,200 m, the level of short sapling browsing was 30%, and the most browsed species were rowan (53%), sycamore (43%), willow (29%) and the rarely found grey alder (21%).

In the landscape protection area in the group of short saplings located up to 1,000 m a.s.l., amongst the more numerous occurring species, a large share of browsed individuals was recorded for fir (51%) and sycamore (42%), whilst rowan was moderately browsed (18%). In the elevation band of 1,001–1,200 m, the most intensely browsed species was the sycamore (86.5%), which was followed by rowan (37%) and fir (22%). Beech was also affected, of which 18% were browsed.

Above 1,200 m, rowan was extensively browsed (77%) and fir browsing was relatively high (13%). Above 1,400 m, the only strongly browsed species amongst the short saplings was the rowan (75%).

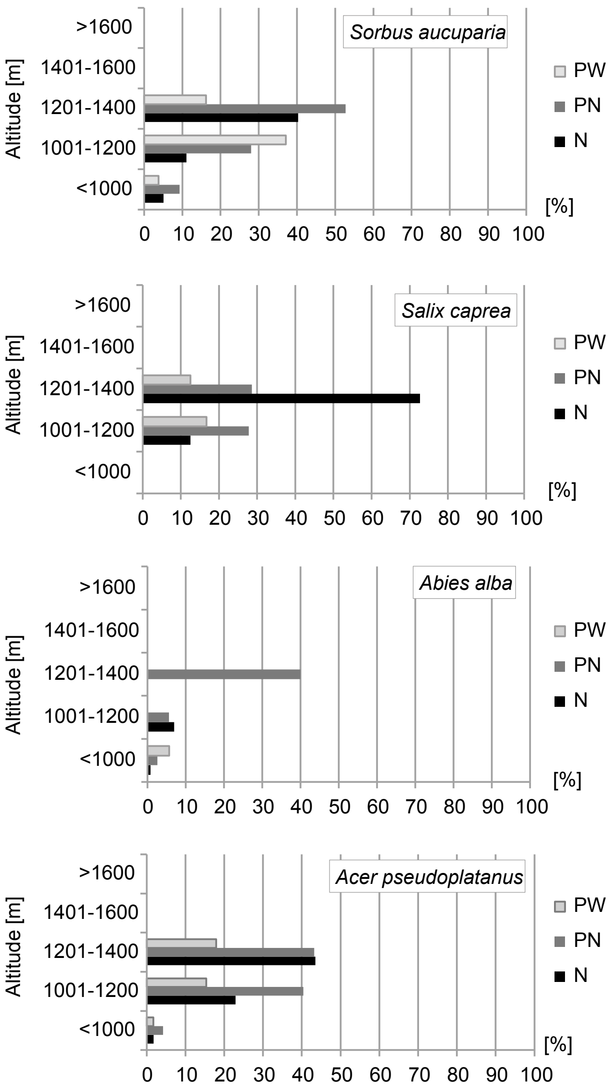

Figure 3. Intensity of browsing of the natural regeneration in different elevation bands in the strictly protected areas.
Explanations: as in Figure 2.

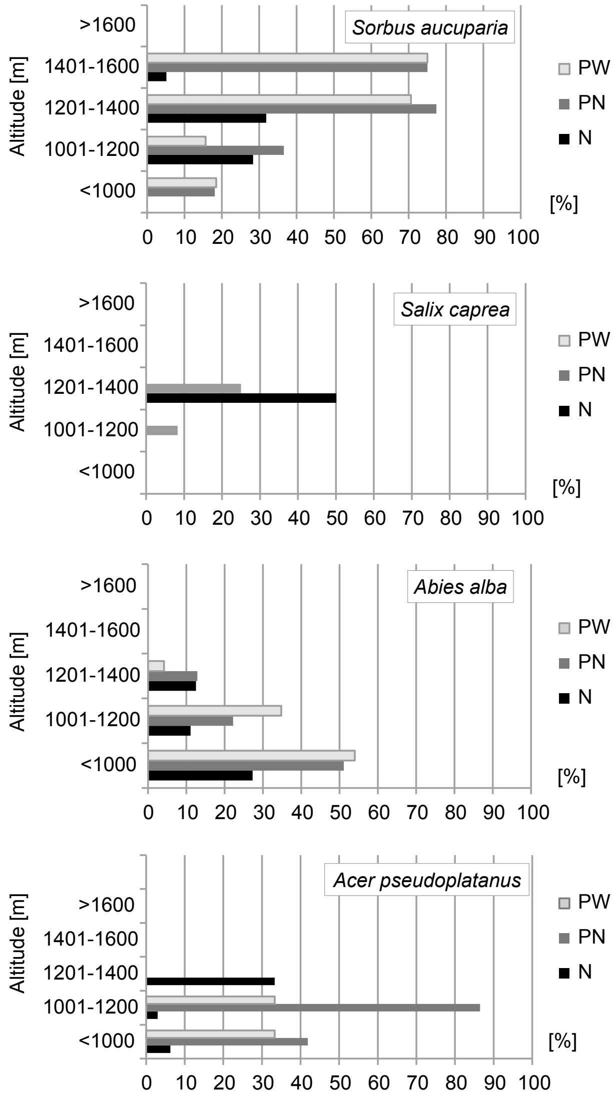

Figure 4. Intensity of browsing of the natural regeneration in different elevation bands in the strictly protected area.
Explanations: as in Figure 2

The tall saplings in the strict protection area were browsed with a frequency of more than 10% only in the upper elevation bands - from 1,201 to 1,600 m a.s.l.. However, below 1,200 m and above 1,600 m, the level of browsing did not exceed 10%. In the band up to 1,000 m, the most frequently browsed species was sycamore (32%), which was followed by fir (14%). Between 1,001 and 1,200 m, the overall level of browsing on tall saplings was around 7%. In this band, sycamore (40%), fir (10.5%) and rowan (10%) were the most intensely browsed. In the next elevation band – 1,201–1,400 m – the most abundant rowan (39%) was most intensely browsed, less so was sycamore (19%). In the band of 1,401–1,600 m, the only species found to have significant damage from browsing were pussy willow (89%) and rowan (22%). However, in the band above 1,600 m a.s.l., browsing was below 3%; the same species occurred many times less frequently and experienced less damaged (Figure 2).

In the active management area, the general scheme was similar. The strongest browsing of tall saplings (19%) occurred in the 1,001–1,200 m elevation band. Below 1,000 m, browsing was very low (<2%), whilst at above 1,200 m, it reached 7.5%. In the band below 1,000 m, a slightly higher level of browsing was recorded only for fir (<6%), rowan (4%) and ash (3%). Between 1,001 and 1,200 m, the strongest browsed species amongst the tall saplings was rowan (37%), which was followed by willow (17%) and sycamore (15%). Above 1,200 m, the most intensely browsed were sycamore (18%), which was followed by rowan (16%) and willow (12.5%). The details are presented in Figure 2.

In the landscape protection area, the highest level of browsing on tall saplings was observed in the lowest and highest elevation bands above sea level. Below 1,000 m, the most browsed species amongst the tall saplings was fir (54%), which was followed by sycamore (33%) and rowan (18.5%). Similarly, in the band of 1,001–1,200 m, the most intensely browsed species was fir (35%) followed by sycamore (33%), and the next species was beech (22%), whilst the level of rowan browsing was relatively low (16%). Between 1,201 and 1,400 m, 71% of browsing was recorded on the rowan (Figure 4). Of the 24 tall fir saplings found in this height zone, only one specimen was browsed. Above 1,400 m, only the tall rowan saplings were browsed (75%).

Regeneration browsing was very strongly differentiated spatially. There were decidedly more sample plots on which damage to the regeneration of a given species was confirmed (Figure 5), but often next to them were found either plots with no browsing or those where the frequency of regeneration browsing of a given species approached 100%. To some extent, this can be explained by the abundance of the regeneration. Even though there were cases in which in a given sample plot, individuals of those species occurring there in very small numbers were browsed, the only statistically significant relationships between the density of a given species' regeneration and the frequency of their having been browsed were positive, that is, more intense browsing usually occurred in those places where there were a large number of regenerating trees of a given species.

The significant relationship between the density of the regeneration and the percentage of browsing in the case of rowan seedlings was confirmed using Spearman's rank correlation (rho = 0.176, p = 0.002) and Kendall's tau correlation (tau = 0.126, p = 0.001). Similarly, in the case of fir seedlings, this relationship proved to be positive and statistically significant in the case of both the rank correlation (R = 0.329, p = 0.0005) as well as the Kendall tau correlation (tau = 0.260, p < 0.001). A positive relationship was found for the pussy willow using Kendall's tau analysis (tau = 0.241, p = 0.04), whilst Spearman's correlation did not show a signifi-

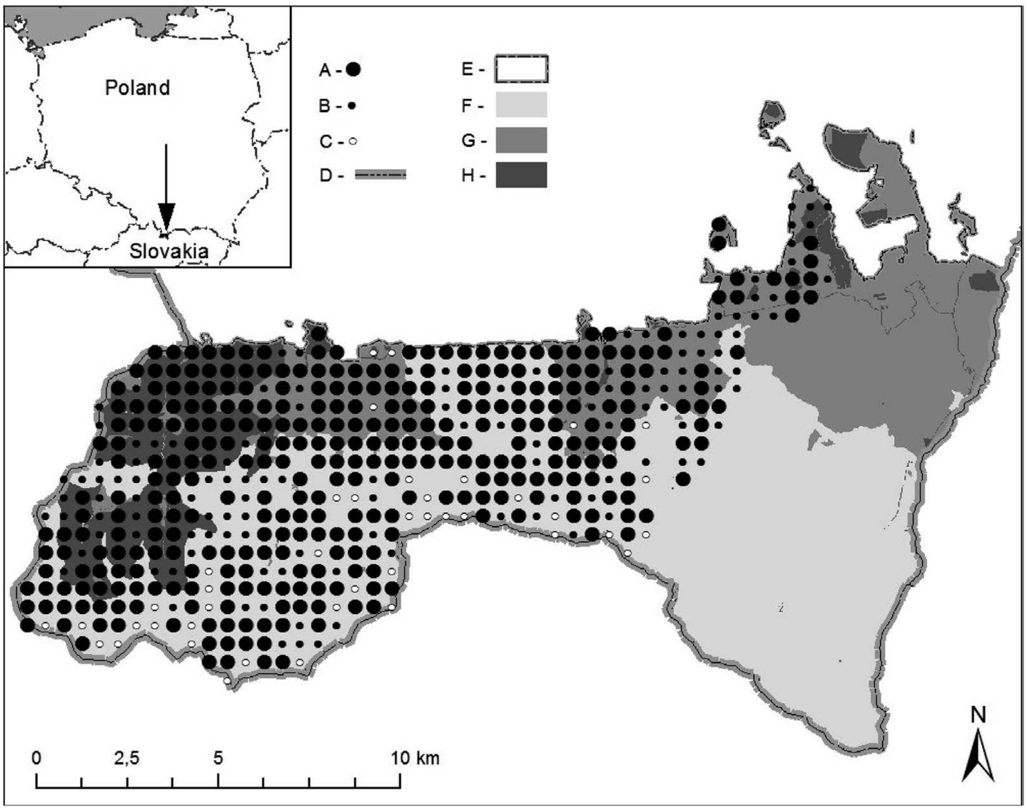

Figure 5. Distribution of the natural regeneration in the sample plots against the background of type of protection status in the Tatra National Park.

Explanations: A, plots with regeneration present and browsed; B, plots with regeneration present, but not browsed; C, plots without regeneration; D, national border; E, borders of the Tatra National Park; F, strictly protected areas; G, zone of active management; H, zone of landscape protection.

cant relationship (R = 0.285, p = 0.10). However, the percentage of browsing of sycamore and beech seedlings was not significantly related to their density.

Amongst the short fir saplings, the relationship between density and share of browsed trees was positive and statistically significant, both in the case of Spearman's rank correlation (R = 0.259, p = 0.028) and Kendall's tau correlation (0.203, p = 0.012). On the other hand, in terms of short rowan saplings, a positive relationship between density and percentage of browsed specimens was found not to be statistically significant, with the use of both Spearman's rank correlation and Kendall's tau correlation. No significant relationship between density and the browsing of short saplings was also found for the other species.

In the case of tall saplings, none of the species showed a statistically significant relationship between the percentage of browsed individuals and their density in the sample plots.

4. Discussion

The level of browsing on the trees in the TNP is relatively low if we compared it to the pressure of deer on the regeneration in national parks such as the Babia Góra National Park or the Magura National Park (Jamrozy and Brewczyński 1998). Our research shows that the relatively low intensity of browsing on the regeneration in the Tatras is affected by the fact that the most numerous tree species in the forests of the western part of the TNP is spruce (89%), which also has the largest share (45%) in the regeneration. Ungulates did not practically browse on spruce in the Tatras. The ungulate pressure was, therefore, focused on other species, mainly on broadleaved trees and fir. Despite this, only in exceptional cases, the percentage of browsed individuals was greater than 50% and the average values were decidedly lower.

The results obtained in the Tatras are similar to the results of monitoring deer damage in the Gorce National Park (Miścicki and Żurek 2015). The main difference is that in Gorce, the most browsed species was sycamore, whilst in the Tatras, it was pussy willow and rowan. The fact that the first two most frequently browsed trees are early successional species (Żywiec et al. 2013), whose share in most managed forests is usually minimal, deserves close attention. The share of willow (0.3%) and rowan (0.8%) in the stands of the western part of the TNP (Szwagrzyk et al. 2016) is now slightly higher than that in the forests of other national parks, not to mention the managed forests (Czerepko 2008). This is clearly reflected in the numerous occurrences of these species (and especially rowan) in the regeneration. This phenomenon is associated with the significant thinning of the tree stand canopy in large areas because of damage caused by hurricane-force winds and the bark beetle gradation (Sproull and others 2017) in the past dozen or so years. With such a high density of rowan and willow regeneration, the amount of food available for ungulates in the Tatra forests is relatively high in relation to the moderate densities of ungulates.

Another species subjected to relatively high ungulate pressure in the western part of the Tatras is sycamore, a species that is very intensely browsed almost everywhere it is found in the regeneration (Jamrozy and Brewczyński 1998; Misiśicki and Żurek 2015). It is worth noting, however, that the sycamore in the Tatras was relatively often recorded not only amongst the seedlings but also amongst the saplings. This proves that despite browsing pressure, the sycamore is able to progress to successive height classes, and in time, its share in the stands will most likely increase.

Fir in the Tatras is treated in a special way. In active management and landscape protection areas, it is planted under the upper canopy of the stand and higher concentrations of fir regeneration are sometimes protected by the construction of fences (Skrzydłowski 2009). In terms of browsing frequency, fir trees are only in fifth place; fir seedlings are browsed only to a level of a few percent, whilst noteworthy is the fact that tall fir saplings are under relatively high ungulate pressure. In this size class, only the regeneration of rowan and sycamore are browsed more often than fir, and in landscape protection areas, more than 50% of fir saplings are browsed in the elevation band of up to 1,000 m a.s.l. Similar results were also found in earlier studies conducted in the Chochołowska Valley region (Stopka and Skrzydłowski 2014). This proves that the browsing of fir regeneration can be a serious problem locally, although it is moderate in the stands of the western part of the TNP.

A very important aspect of our study is the disclosure of the large spatial differentiation of ungulate pressure on regeneration. The large number of regularly spaced sample plots made it possible to present this phenomenon in an objective manner. The distributions of the extent of regeneration browsing in the sample plots definitely differ from the normal distribution, and in some of the plots (10%), browsing was not found at all. However, in other plots, the regeneration was browsed very intensely, even 100%. The results obtained in this study clearly differ from the results obtained earlier from a smaller number of subjectively spaced sample plots (Stopka and Skrzydłowski 2014), which indicates a fundamental difficulty in studying the impact of ungulates on regeneration without establishing many regularly spaced study plots. The pressure exerted on the regeneration of trees by browsing increases with the elevation above sea level. This is related to the change in the species composition of trees as the elevation increases. Whilst the lower montane zone has more than a dozen species of trees, the upper montane zone and the upper boundary of the tree line have only a few, including the predominant spruce, which is practically not browsed by ungulates. The pressure of game animals in higher zones is concentrated on the relatively numerous rowan, although the percentage of browsing on the less numerous willow and sycamore in this zone is even higher. An increase in ungulate pressure on tree regeneration with increasing elevation was recorded in the Dinaric Alps of Slovenia in the case of fir (Cater and Kobler 2017), but the range of elevations analysed in that study corresponded only to our lower montane zone.

Current research on the effects of herbivores on plants is assuming a wider dimension. Researchers are attempting to learn not only about the direct impact of animals on specific plant species but also about the response of biocenoses to the environmental conditions modified by herbivores (Sabo et al. 2017). The study of the relationship between light conditions and browsing on the growth of young trees conducted in the Białowieża National Park (Churski 2015) showed that the impact of the game animals on slowing down the growth rate of the regeneration is very high in strongly shaded conditions, whereas the height increment of trees is reduced only moderately by browsing under conditions of high light intensity. It can be expected that with the current reduction of the crown density in the Tatra tree stands, the growth of the broadleaved species in the regeneration is not significantly hindered by the pressure of ungulates.

Conflict of interest

The authors declare that there are no conflicts of interest.

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Authors' contributions

JB – study concept, coordination of field data collection, writing and correcting the text, preparing the figures; TZ-K – field data collection, study concept, writing the text, preparing the figures; AG – statistical analysis of the data, writing and correcting the text; JSze – preparing the database; MF – writing the text; AZ – field data collection, writing and correcting the text; JSzwa – study concept, writing and correcting the text.

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