Cent. Eur. For. J. 70 (2024) 222–234 sciendo DOI: 10.2478/forj-2024-0015

CENTRAL EUROPEAN Forestry Journal

ORIGINAL PAPER

Assessing the influence of ruminating ungulates on forest regeneration and young stands in Slovakia: results from the National Forest Inventory

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Abstract

Our analyses utilized data from the latest National Forest Inventory conducted in Slovak forests in 2015–2016. Specifically, we included data on approximately 21,737 trees grown on forest land and 3,342 trees on non-forest land, all with a height of up to 1.3 meters. Browsing emerged as the second most frequent limiting factor for regeneration on forest land, following light deficiency, whereas on non-forest land, it ranked third after ground vegetation and light deficiency. Our results revealed the highest browsing rates on goat willow (47.8%), silver fir (39.3%), and rowan (35.1%). Conversely, certain commercial tree species exhibited relatively low browsing rates, notably Norway spruce (13.9%), European beech (8.1%), and oaks (6.2%). Among abiotic factors, exposition and slope were found to be significant, the south aspect was associated with the highest browsing rates, while browsing rates decreased with increasing slope steepness. Planted trees were more frequently browsed than those of natural origin. At the same time, higher trees (height between 0.5 m and 1.3 m) were browsed more frequently than small trees (under 0.5 m). Furthermore, significant differences in browsing frequency were observed among specific territories (hunting sub-regions), with the heaviest browsing occurring in the southwestern and northeastern parts of Slovakia, as well as in the Rimavská Sobota district. Given that reducing browsing pressure primarily relies on hunting activities, which are outside the forestry sector, close collaboration between foresters and hunters is essential. Additionally, hunting strategies in the near future must consider also the needs of other sectors such as forestry, agriculture, and nature conservation.

Key words: limiting factors in regeneration; browsing rate; forest and non-forest land; tree species; hunting region

Editor: Pavol Hlaváč

1. Introduction

Although animals such as ungulates are an inseparable and irreplaceable part of forest ecosystems, their influence on other segments, especially vegetation, can often be very intense and not always desirable. Ungulates impact forest ecosystems in a variety of ways, mostly via trampling, defecation, and urination, but mainly through consumption of plant parts, i.e. browsing (Forbes et al. 2018). Practically, whether the influence of ungulates on forest ecosystems from a management perspective is positive or negative depends predominantly on their population density (Maron et al. 2006). Simply put, their overabundance brings a lot of problems to forests in the form of damaging or even total destruction of tree components or whole trees.

According to a literature review published by Forbes et al. (2018), it was shown that wild large herbivores (an essential part of ungulates) are declining worldwide. Simultaneously, oppositional situations have been reported in most European countries. The works have manifested an increasing tendency in population densities, with some regions experiencing an extraordinary rate of ungulate growth, particularly in the population of red deer (*Cervus elaphus* L.; see e.g., Speed et al. 2019; Valente et al. 2020; Balčiauskas & Kawata 2022). Recently, this overabundance has also been observed in Slovakia, where since the beginning of the millennium, the population of red deer has nearly doubled, and densities of other ungulates have increased considerably as well (Bučko et al. 2010; Konôpka et al. 2022). Consequently, damage to

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forest stands by ungulates, especially by red deer and roe deer (*Capreolus capreolus* L.), and locally also fallow deer (*Dama dama* L.) and European mouflon (*Ovis aries musimon* Pallas), has become increasingly severe (Kunca et al. 2015; 2019). The mentioned ungulates represent a group of ruminants, which browse on tree parts, especially on shoots and stem bark (Červený et al. 2010). In addition to them, some damage in forests can also be caused by wild boar (*Sus scrofa* L.), which is an omnivore. This animal usually destroys the seeds of trees, such as beech mast and acorns, or the roots of seedlings (Tarvydas & Belova 2022).

Forest regeneration, natural, artificial or combined, is a crucial stage of forests since it determines their future existence and functionality. Since forest biodiversity is of principal importance to maintain healthy forests and provision of large range of ecosystem services (e.g., Felipe-Lucia et al. 2018), rich species composition of trees must be established from very early stage of forest. At the same time, ungulates browsing on seedlings and saplings can reduce tree species composition (Konôpka et al. 2021) since they prefer for nutrition palatable trees species than unpalatable ones (Borowski et al. 2021). It means that some palatable tree species can be damaged intensively and might miss in elder growth stages. For instance, our newest work (Konôpka et al. 2024) showed that browsing fully eliminated silver fir (*Abies alba* Mill.), reduced occurrence of some palatable tree species, and dramatically decreased aboveground biomass of trees in forest regeneration.

In fact, quantifying the impact of browsing on forest regeneration is very difficult. Some seedlings are fully consumed by ruminating ungulates; therefore, they are simply missing and cannot be discovered at the time of measurements. Here, only rough estimates or educated guesses can be made regarding which factors (e.g., browsing, weeds, lack of light, etc.) have been limiting forest regeneration. Estimations based on slightly larger trees are more feasible since these trees are still present and show visible damage in the form of bitten-off shoots (Akashi et al. 2022) or stripped/wounded bark on the stem (Candaele et al. 2020).

The National Forest Inventory (NFI) is a program widespread in most European countries (Gschwantner et al. 2022). Since the 20th century, the main motivations for introducing sample-based NFIs have been concerns about the danger of overexploitation and, in parallel, the lack of information about the status of forests, related to the need to plan the sustainable utilization of forest resources (e.g., Breidenbach et al. 2020). Practically, the volume of growing stock is considered one of the most important forest characteristics estimated by NFIs to quantify the status and temporal change of wood resources. At the same time, in addition to growing stock estimates, NFIs provide a variety of outputs on a regular basis to meet national and international information requirements (Vidal et al. 2016). Regarding Slovakia, two cycles of NFI have been performed, specifically in the years 2005–2006 and 2015–2016 (Šebeň 2017). The Slovak NFI offers, besides other information, data on forest damage, including visual or assessable marks of browsing. Such data were collected in all sampling plots, encompassing any tree mixture, ages, ownerships etc., not only for forest lands but also for non-forest lands (mostly former agricultural fields covered by forest trees; Šebeň 2017).

The main aim of this work is to assess the impact of game browsing on forest regeneration and very young forest stands, defined as all trees with a maximum height of 130 cm. We included trees in both forest and non-forest land. A further aim was to quantify the main environmental and stand characteristics affecting the intensity of browsing damage. Moreover, we attempted to make interspecific comparisons between tree species based on browsing frequency, reflecting their palatability for ruminating ungulates.

2. Material and methods

2.1. Sampling design and data collection

We utilized data gathered during the second cycle of the Slovak National Forest Inventory (NFI) in 2015–2016 (Šebeň 2017). The NFI represents a relatively new approach to gathering information on forest status in Slovakia, as comparing to traditional data collection methods employed in the development of Forest Management Plans. It relies on representative data collection through permanent sample inventory plots (IPs), where detailed measurements are conducted. IPs were systematically distributed across the entire country in a 4 × 4 km grid, with each plot surveyed and monitored for all forest elements such as mature trees, small trees, deadwood, etc. At the national level, Slovakia has a total of 3,069 IPs spots, of which approximately 45% met the criteria for forest classification, and field data was collected accordingly (Table 1; Fig. 1). Each IP had a circular size of 500 m^2, with a radius of 12.62 m. Within the center of each IP, designated “regeneration circles” (RC) were established to monitor the state and development of forest regeneration (centroid), and all regeneration individuals were recorded within these circles.

Table 1. Basic characteristics of inventory plots and assessed trees (height ≤ 1.3 m).

Characteristic of plot / trees	Forest land	Non-forest land	Together
Total number of plots	1,104	186	1,290
Total number of trees	21,737	3,342	25,079
Total number of tree species	48	41	52
Mean number of trees*	18.4	15.6	18.1
Mean number of tree species*	2.41	2.73	2.49

Explanatory note: *expressed on a plot level.

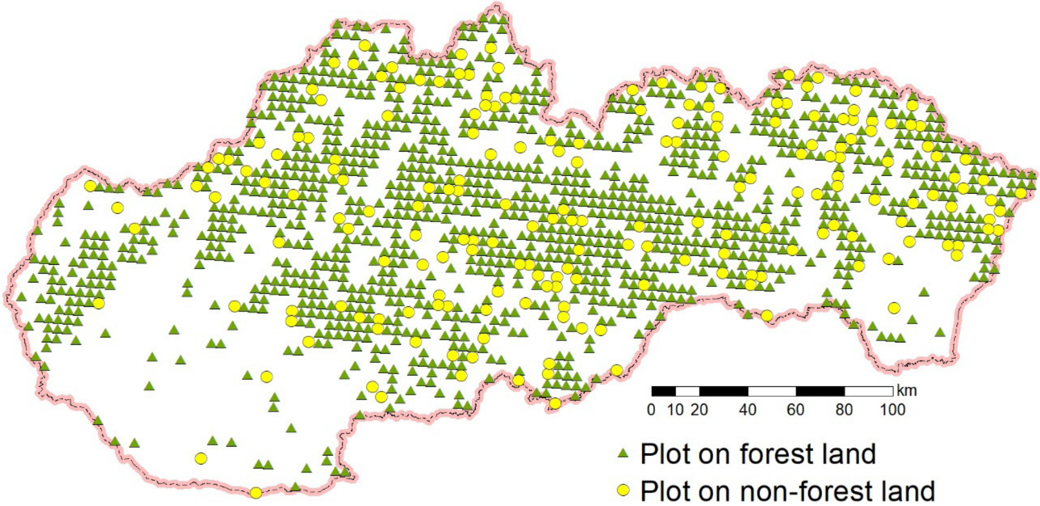

Fig. 1. Distribution of the inventory plots covered by forest vegetation in Slovakia (National Forest Inventory, second cycle; n = 1,443) with respect to forest land and non-forest land (i.e. former agriculture lands currently occupied by trees).

The data were collected at the country level by five inventory groups, with a control group responsible for verifying their correctness at 5% of all IPs. Field data collection utilized Field-map technology (IFER), employing a combination of measuring instruments such as rangefinders, compasses, and hypsometers, along with a Field computer (Šebeň 2017).

2.2. Measurements of trees in forest regeneration

The term "regeneration" refers to saplings ranging from a height of 10 cm (excluding current year seedlings) to a 7 cm in diameter at breast height (Šebeň et al. 2015). In this study, our focus was not on the entire regeneration but rather on a significant portion, specifically individuals up to 1.3 m of height. The size of the RC varied and was determined to ensure a minimum of 30 trees per RC. The minimum size was set at a radius of 1.0 min dense stands, and in cases where trees were sparse, it was increased to 2, 3, or 4 m until at least 30 saplings were recorded. If this number was not reached within a maximum radius of 4 meters, the actual situation was noted at 4 meters. Due to the wide variability in regeneration counts, the majority (50%) of RCs had the largest radius of 4 meters, while those with the densest regeneration (1 m radius) constituted only a tenth. Approximately only 10% of RC in the Slovak NFI did not contain small trees. By each small tree (≤ 130 cm height) were consider tree species, origin type (artificial, natural) and measured tree height by height-gauge in 10-cm interval.

2.3. Damage detection and recording

Negative factors impacting the condition and growth of forest stands were evaluated. This assessment was subjectively classified at the level of the entire IP. Signs indicating the presence of the following factors were examined: light deficiency due to overshadowing by mature stands, lack of seed resources, browsing by game, competitive effects of ground vegetation, and other negative factors (such as unfavorable micro-climatic or soil conditions, presence of insects, pathogens, mechanical damage, etc.). In cases where no signs of detrimental factors were observed, the inventory plot was classified from a damage perspective as "None."

In addition to the subjective assessment (or better to say expert estimate), damage at the level of individual trees was recorded. Each recorded individual of regeneration was assessed and classified into the following categories: undamaged, damaged by game, damaged by other agents (such as insects, fungi, weeds, abiotic factors, and others). Of particular interest to us was damage caused by game. By analyzing the proportions of injured and undamaged individuals within RCs, the browsing ratio for the entire IP was calculated.

2.4. Damage detection and recording

The data collected at the level of IP (plot level) or RC (tree level) were subsequently aggregated for larger units. The data from variable-sized RC were standardized to a common base size to enable comparison between IP. The mean number of trees and the mean number of tree species per IP were calculated. Subsequently, a browsing rate was determined as the proportion of game-damaged individuals to all individuals. The browsing rate was then analyzed separately based on terrain characteristics, including slope, aspect, altitude, (see also Table 2) and the tree height as well as origin of the tree.

Finally, we categorized hunting sub-regions (Hell et al. 2004) based on tree harm caused by game browsing. We implemented two criteria within each hunting sub-region: the proportion of IP with browsing as a limiting factor (with a threshold value of 40%) and the mean browsing rate calculated from all assessed trees within each separate hunting sub-region (with a threshold value of 20%). Then, the hunting sub-regions were classified into three groups:

a) Mild damage (potentially mild endangerment of young forest stands by ruminating ungulates) – both indicators had assessed values lower than the threshold values;
b) Medium damage (moderate endangerment) – one of the indicators exceeded the threshold value;
c) Heavy damage (severe endangerment) – both indicators exceeded the threshold values.

Following this analysis, the data were surveyed, archived, and processed in the MsAccess geodatabase.

3. Results

Certain limiting factors for forest regeneration exhibited very similar intensity in both forest land and non-forest land, while others differed between these two types of lands (Fig. 2). Comparable ranges were observed in both forest land and non-forest land for the impact of light deficiency (on approximately 38% of IP) and browsing by game (over 31% of IP). Ground vegetation competition and lack of seed resources showed approximately double the differences. Ground vegetation was the most frequent limiting factor in non-forest land IP (57.5%), whereas light deficiency (38.4%) was the most common factor in forest land. Browsing was the second most frequent factor in forest land and the third most frequent factor in non-forest land. No limiting factor was found in 23.6% and 15.5% of IP within forest land and non-forest land, respectively. It's important to note that more than one limiting factor might be recorded within individual IP.

We observed differences in tree species composition between the IP in forest land and non-forest land (Table 3). The five most common tree species on forest land were European beech (36.8%), maples (17.8%), oaks (9.3%), ashes (7.2%), and common hornbeam (7.0%), whereas on non-forest land, the order was maples (25.8%), European beech (15.6%), ashes (11.2%), com-

Table 2. Number of inventory plots and assessed trees (height ≤ 1.3 m) based on specific categories of abiotic factors.

Factor	Category vs numbers (plots / trees)			
Altitude (m a.s.l.)	up to 300	301–600	601–900	over 900
Number of plots / trees	441 / 9,088	494 / 9,896	256 / 4,858	84 / 1,237
Exposition (N, E, S, W)	North	East	South	West
Number of plots / trees	370 / 6,852	323 / 6,354	301 / 5,790	281 / 6,083
Slope (%)	up to 10	11–30	31–50	over 50
Number of plots / trees	192 / 3,817	494 / 9,683	364 / 7,312	225 / 4,267

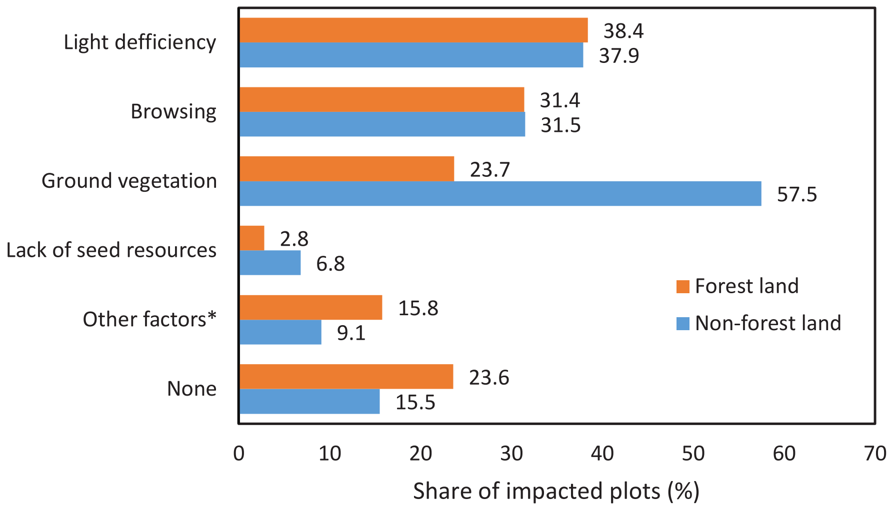

Fig. 2. Share of inventory plots with identified factors limiting forest regeneration. Note that a single plot may be impacted by multiple factors simultaneously.
Explanatory note: *other factors were prevailingly: unfavorable micro-climatic or soil conditions, insects, pathogens, mechanical damage (harvest, snow), etc.

Table 3. Number and share of assessed trees by species for forest and non-forest land.

Forest land			Non-forest land			Together		
tree species	number	share (%)	tree species	number	share (%)	tree species	number	share (%)
European beech	8,003	36.8	Maples	861	25.8	European beech	8,523	34.0
Maples	3,866	17.8	European beech	520	15.6	Maples	4,727	18.8
Oaks	2,032	9.3	Ashes	373	11.2	Oaks	2,231	8.9
Ashes	1,562	7.2	Common hornbeam	368	11.0	Ashes	1,935	7.7
Common hornbeam	1,521	7.0	Oaks	199	6.0	Common hornbeam	1,889	7.5
Norway spruce	1,364	6.3	Norway spruce	157	4.7	Norway spruce	1,521	6.1
Rowan	997	4.6	Rowan	142	4.2	Rowan	1,139	4.5
Silver fir	558	2.6	Trembling poplar	116	3.5	Silver fir	598	2.4
Lime trees	259	1.2	Goat willow	56	1.7	Goat willow	275	1.1
Goat willow	219	1.0	Silver fir	40	1.2	Lime tree	297	1.2
Others	1,356	6.2	Others	510	15.3	Others	1,944	7.8
Together	21,737	100.0	Together	3,342	100.0	Together	25,079	100.0

mon hornbeam (11.0%), and oaks (6.0%). Our analyses primarily focused on interspecific differences in browsing rates for the ten most common species, pooling plots from both forest land and non-forest land (Fig. 3). The results indicated that the highest browsing rate was found for goat willow (47.8%) and the lowest for oaks (6.2%). By categorizing the tree species based on browsing rates, we divided them into three groups: extensively browsed species (browsing rate over 35%), moderately browsed species (browsing rate between 15–35%), and lightly browsed species (under 15%). The extensively browsed tree species included goat willow, silver fir, and rowan; the moderately browsed species were maples, lime trees, ashes, and common hornbeam; while the lightly browsed species were Norway spruce, European beech, and oaks. This suggests that silver fir is the most heavily browsed among the commercially significant tree species.

In terms of environmental conditions (Fig. 4), we observed that the highest browsing rate occurred within altitudes ranging from 601 to 900 meters above sea level (m a.s.l.), while the lowest rate was recorded in sites over 900 m a.s.l. Regarding exposition, the highest browsing rate was observed on southern orientations (i.e. between 315 and 45 degrees), whereas other orientations (from 46 to 314 degrees) had browsing rates ranging from 15.1% to 18.6%. Additionally, browsing rates exhibited a decreasing tendency with slope; sites with slopes up to 10° had a browsing rate of 29.5%, whereas those on slopes over 50° had a rate of only 12.7%.

Furthermore, we found that browsing rates were influenced by the origin of young stands and their growth stage (Fig. 5). Trees from natural regeneration were browsed less frequently than those from artificial regeneration (planted). This trend was observed for both groups of trees, those with a height of up to 0.5 m and those ranging from 0.5 to 1.3 m in height. Additionally, smaller trees (up to 0.5 m) were browsed less often than taller trees (0.5–1.3 m).

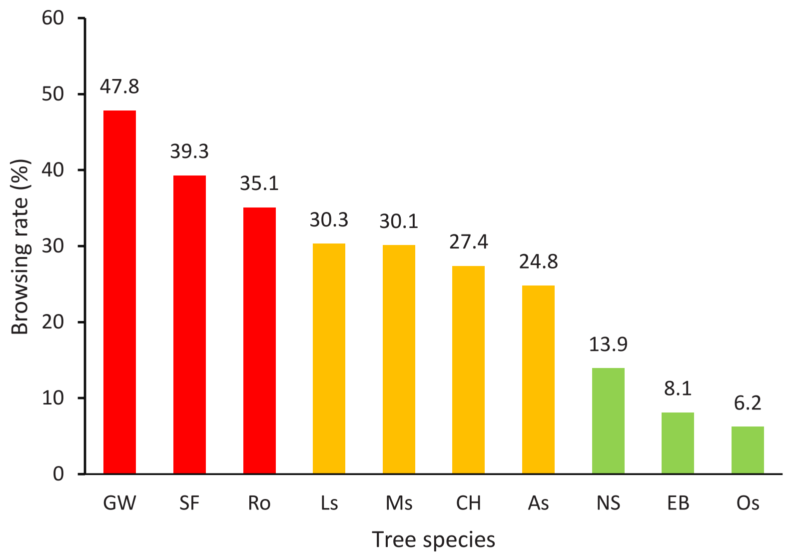

Fig. 3. Share of trees browsed by ruminating ungulates (browsing rate) by tree species (≤ 130 cm). Abbreviations: GW – goat willow, SF – silver fir, Ro – rowan, Ls – lime trees, Ms – maples, CH – common hornbeam, As – ashes, NS – Norway spruce, EB – European beech, Os – oaks.
Explanatory note: red columns represent tree species extensively browsed (over 35%), orange represents species moderately browsed (15–35%), and green represents species lightly browsed (under 15%).

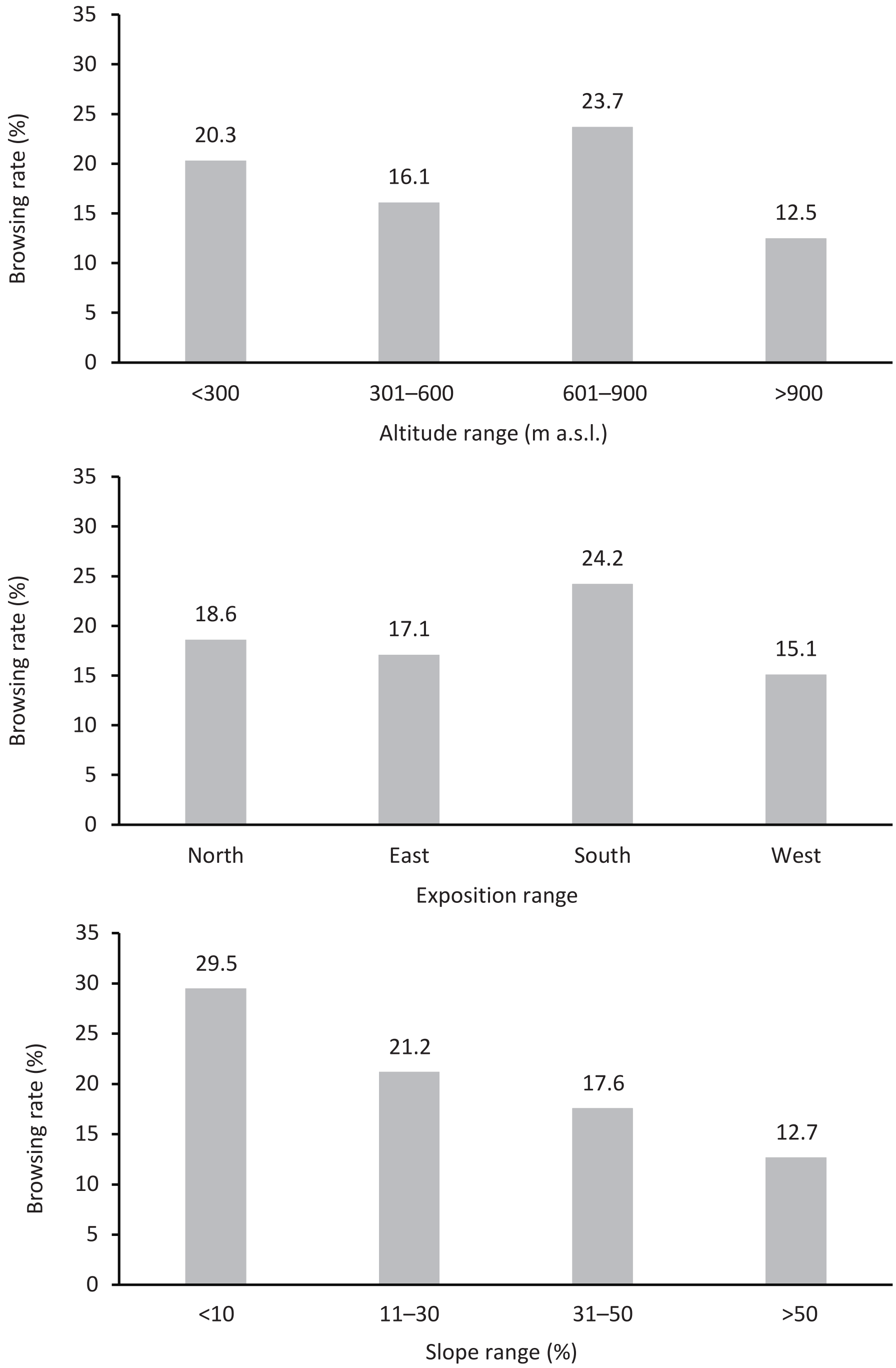

Fig. 4. Browsing rate on trees (all inventory plots, n = 1,443) categorized by altitude range (upper graph), exposition range (middle graph; North: 316–45 degrees, East: 46–135 degrees, South: 136–225 degrees, and West: 226–315 degrees), and slope range (lower graph).

Combined analysis of game browsing as a limiting factor in reforestation (Fig. 6 – upper plate) and browsing rates (Fig. 6 – lower plate) on trees with a height of up to 1.3 meters revealed spatial differences in the endangerment of young forests by ruminating ungulates across hunting sub-regions in Slovakia (see Table A1 in Attachment and Fig. 7). The results indicate heavy damage by ruminating ungulates in ten hunting sub-regions primarily located in southwestern and northeastern Slovakia. When considering orographic units, heavy damage in southwest Slovakia was notably observed in the Malé Karpaty Mts., Borska Lowland, the southern part of the Biele Karpaty Mts., and the Strazovske vrchy Mts. In the cluster exhibiting heavy damage in northeastern Slovakia, it was predominantly observed in the Ľubovnianska vrchovina Mts., Levočské vrchy Mts., Spišská Magura Mts., and Branisko Mts. Additionally, heavy damage due to browsing was recorded in one hunting sub-region situated in the southern part of Central Slovakia, roughly within the Rimavskosobotská

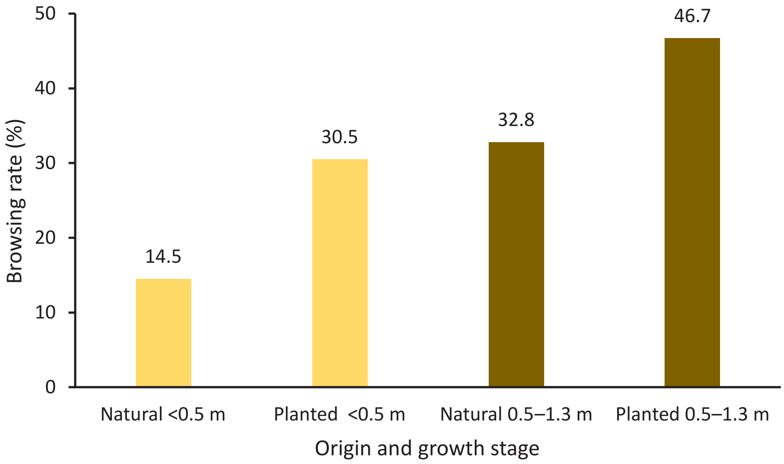

Fig. 5. Browsing rate on trees of different origins (natural vs. planted) with respect to two growth stages.

Lowland. Conversely, the majority of territory experiencing mild damage from ruminating ungulates was found in beech-dominant forests in Eastern Slovakia and oak-dominant forests in the southernmost part of Western Slovakia, specifically in the Podunajská Wold and Podunajská Lowland.

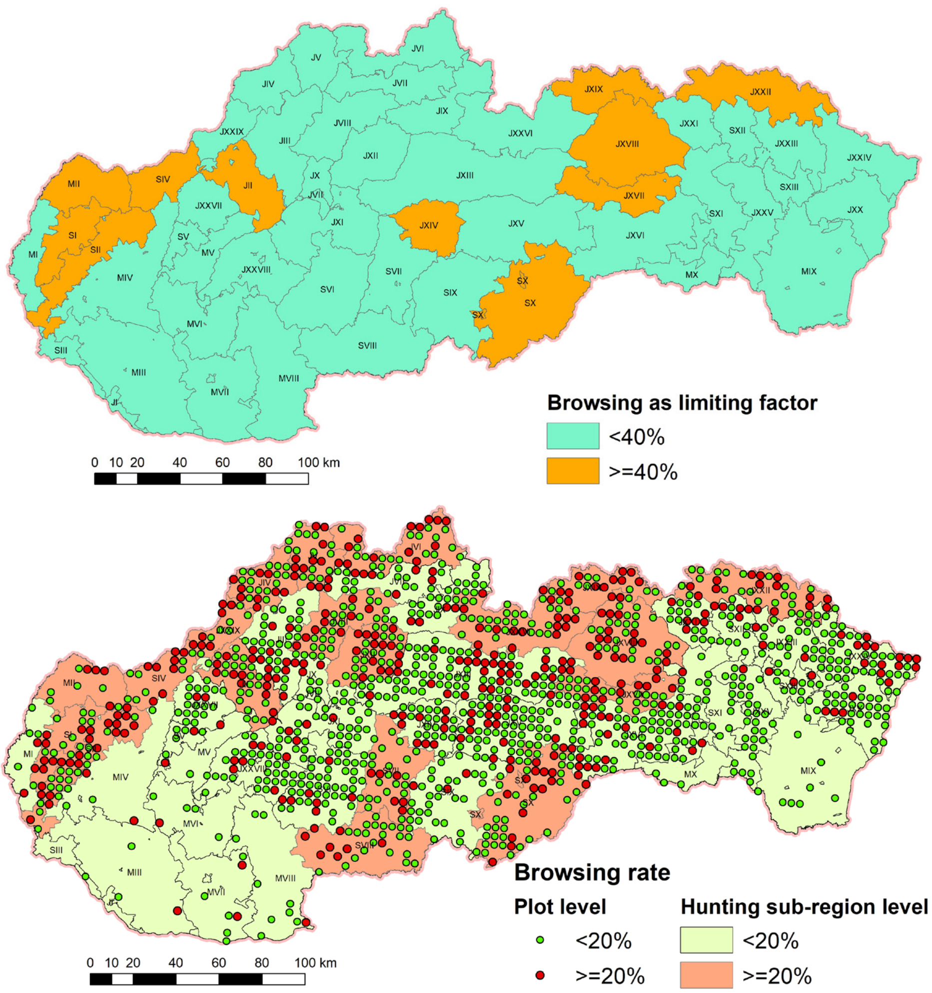

Fig. 6. Hunting sub-regions divided into two groups with respect to share of plots with browsing as limiting factor for forest regeneration, i.e. under 40% and ≥ 40 (upper plate). In addition, the inventory plots (National Forest Inventory, second cycle; n = 1,290) and alternatively sub-regions are divided into two groups regarding browsing rate with limit of 20% (lower plate). See Table A1 in the Attachment for the specific codes of hunting sub-regions.

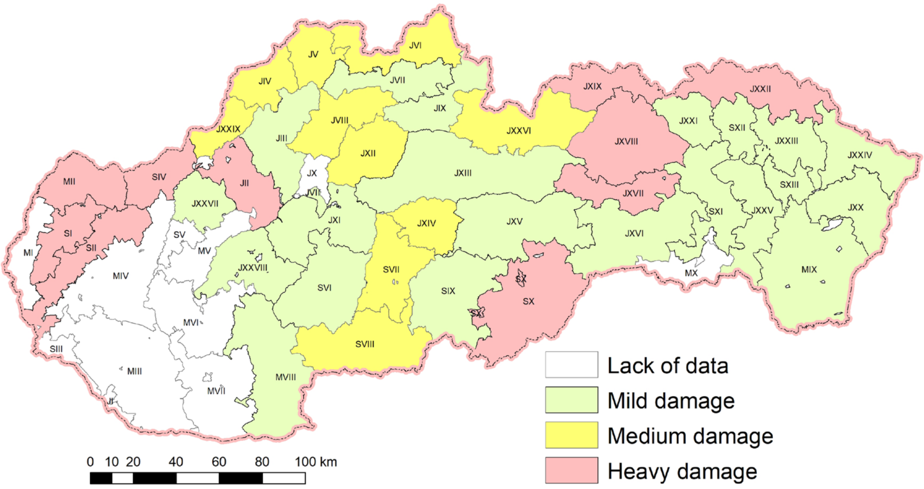

Fig. 7. Final categorization of hunting sub-regions: “mild”, “medium” and “heavy” damage synthesizing both indicators, i.e. browsing as limiting factor (plot level; see Fig. 6 upper plate) and browsing rate (tree level within sub-region; see also Fig. 6 lower plate). Table A1 in the Attachment shows the specific codes of hunting sub-regions.

4. Discussion

4.1 Factors limiting reforestation

Our results suggest that factors limiting forest regeneration differ between forest and non-forest lands. In forest lands, light deficiency was the most frequent limiting factor, whereas ground vegetation competition pressure was the most common factor in non-forest lands. These findings are logical, as light intensity is a decisive factor for seedling emergence and the early growth of trees in forests (Chen et al. 2023). Additionally, sufficient light availability can be influenced not only by the canopy density of the maternal stand but also by ground vegetation density, especially in trees with a height of up to 0.5 m (Kanjevic et al. 2021). Therefore, these two factors can often coexist within the same forest stand. Pressure from ground vegetation as a limiting factor for forest regeneration would be more significant on non-forest (former agricultural) land than on forest land, since grasses, herbs, and bushes are more prevalent due to past development, as well as the absence of forest management measures (e.g., pruning, weed removal) in non-forest areas. Browsing was identified as a limiting factor on nearly one-third of plots in both forest and non-forest lands. However, objectively identifying browsing in the initial growth stages is challenging, as ruminating ungulates can consume entire seedlings, resulting in the absence of trees, thus, the real impact of browsing is not visually observed during inventory.

Actually, browsing has been recognized as an extremely serious problem for regeneration in a variety of European countries (e.g., Partl et al. 2002; D’Aprile et al. 2020; Konôpka & Šebeň 2024). Here, we must point out that some limiting factors such as light deficiency, ground vegetation, and lack of seed resources can be mitigated or fully eliminated by implementing forestry measures. However, browsing as a harmful factor can be ruled by forest management only to a limited extent. The primary responsibility for addressing problems caused by game, especially ruminating ungulates, lies with hunters. Therefore, collaboration between foresters and hunters is a necessary step for creating favorable conditions for forest regeneration.

In Austria, Gschwantner et al. (2024) showed that the most frequent limiting factor for forest regeneration was competition from ground vegetation, followed by light deficiency and game browsing. While light deficiency was the most relevant limiting factor at altitudes between 300–600 m a.s.l., browsing was most intensive at altitudes up to 300 m a.s.l. Simultaneously, ground vegetation was most significant at the lowest, and at the same time, in very high altitudes.

4.2 Interspecific differences in browsing rate

We found large interspecific differences in browsing rates, ranging from 6.2% (in oaks) to 47.8% (in goat willow). Based on the obtained results, we categorized the tree species into three groups: extensively damaged, with browsing rates over 35% (including goat willow, silver fir, and rowan); moderately browsed species, with browsing rates between 15% and 35% (maples, lime trees, ashes, and common hornbeam); and lightly browsed species, with rates under 15% (Norway spruce, European beech, and oaks). This means that among commercial tree species, silver fir is the most extensively browsed species. As early as the 1980s, Ott et al. (1989) mentioned the serious threat posed by browsing to the long-term survival of silver fir in various European regions. Similarly, later work by Häsler & Senn (2012) demonstrated that silver fir is the most heavily browsed among the common tree species, especially in the middle and high altitudes of central and south-eastern European forests. Moreover, they stated, in consistency with many other reports, that silver fir regeneration has long been scarce or even nonexistent due to browsing being the principal limiting factor. The high susceptibility of certain tree species, especially silver fir during initial growth stages, to browsing has been highlighted in numerous previous studies (e.g., Vacek et al. 2015; Bernard et al. 2017; Csilléry et al. 2022). In response to the current critical situation in several European countries, many authors (e.g., Bödeker et al. 2023; Griesberger et al. 2023) have recommended the prompt reduction of ruminating ungulate populations as the most effective measure for reducing damage in forest stands and preserving plant biodiversity.

Furthermore, we found that other commercially important tree species such as Norway spruce, European beech, and oaks showed slight browsing. However, we cannot conclude that these species are not problematic and that browsing on them is negligible. Damage by game to trees is related to a variety of factors, which in combination determine browsing rates (Spake et al. 2019). Probably, the most important factor is the population density of ruminating ungulates (Gaudry et al. 2022). For instance, results from Poland (Borowski et al. 2021) showed that red deer preferred foraging on silver fir and some broadleaved tree species over European beech. However, these foraging preferences decreased with increasing population density of red deer. Hence, keeping population density on certain "favorable" level would mitigate damage to both palatable and unpalatable tree species.

Previously, in Slovakia, Šebeň et al. (2011) utilized data from the first NFI (2005–2006) to estimate browsing damage to forest trees by species. Since they included trees with stem diameters up to 7 cm, the results may not be entirely comparable to our findings. Nevertheless, they demonstrated that while ashes, goat willow, maples, and rowan were browsed most frequently, European beech and Norway spruce were browsed rather rarely.

Here, we can state that the differences in palatability (browsing rate) among individual tree species also determine future species composition. In other words, more attractive tree species will continually decrease their contribution, while less attractive species will increase or remain stable in species composition. In our case, the most frequently occurred tree species on the inventory plots were European beech and maples, accounting for 34% and 19% respectively. However, according to the Slovak NFI (Šebeň 2017), the share of European beech across all forest age classes was approximately 30%, while that of maples was only 6%. This indicates that while the share of European beech would change negligibly, the contribution of maples may decrease by two thirds with forest development. Hence, we may assume that ruminating ungulates is one of the most important factors influencing tree species composition.

4.3 Factors of environment and stand features

Our analyses indicated that the browsing rate was highest at altitudes ranging from 301 to 600 m a.s.l., closely followed by altitudes up to 300 m a.s.l. Conversely, the least frequent browsing occurred at altitudes over 900 m a.s.l. Results from Austria (Gschwanter et al. 2024) showed that game browsing was most intensive at lower altitudes, specifically up to 300 m a.s.l. We might assume that population density as well as species richness of ruminating ungulates (such as red deer, roe deer, fallow deer, and mouflon) are highest at lower altitudes. Practically, low altitudes are characterized by favorable climatic conditions and robust forage potential, including forests, pastures, and crop fields (Hell et al. 2004).

Clear results emerged from the comparison of browsing rates among different aspects. South-facing slopes (ranging from southeast to southwest, i.e. from 135 to 225°) had a browsing rate approximately 30% higher than other aspects. This is attributed to the most favorable climatic conditions for the existence of game and indirectly to potentially richer plant communities due to sunlight exposure (Stolina et al. 1985). Browsing rates clearly decreased with increasing steepness. For instance, the browsing rate on sites with slopes up to 10° was 2.3 times higher than on those with slopes over 60°. These differences are likely related to the duration of residence of ruminating ungulates. We hypothesize that more comfortable conditions, including flat or mild slopes, result in longer durations of ungulate residence. Consequently, longer residence leads to more forage consumption in the area, hence, a higher browsing rate.

The planted trees were more frequently browsed than those from natural regeneration. This contrast might be related to the different number of trees between planted and naturally regenerated young stands. In the very initial stage (approximately 2–3 years after regeneration or reforestation), naturally regenerated stands may represent tens or even hundreds of thousands of trees per hectare (Pajtík et al. 2022), while plantations usually have only a few thousand trees (Repáč et al. 2017). Therefore, the forage potential is greater in naturally regenerated stands than in planted young stands, resulting in a higher proportion of trees without browsing. Another reason for the contrast is that in the case of combined reforestation (a combination of natural regeneration and planting), additional planting usually aims to enrich species composition. Ruminating ungulates often prefer species that are in the stand as a minority (Akashi et al. 2022). Anyway, ruminating ungulates nearly always prefer artificial plantations to naturally regenerated young stands (Barančeková et al. 2007).

Our results further showed that browsing rates were higher in larger trees (height between 0.5–1.3 m) than in smaller ones (under 0.5 m). There may be several reasons for this difference. The first factor is that the number of seedlings is much bigger than that of larger trees since tree density in the initial growth stages decreases inter-annually due to a variety of reasons, but prevailingly due to tree competition (Pajtík et al. 2022). Lower tree density would be reflected in a higher proportion of browsed trees. Another factor is related to the principles of probability. More specifically, older trees (0.5–1.3 m in height) are exposed to browsing threats for a longer time than younger trees (under 0.5 m), hence, probability of browsing is enhanced as time span increases.

4.4 Spatial distribution of browsing damage

Our analyses related to browsing as a limiting factor for forest regeneration and browsing rate generated three groups of regions: with mild damage, medium damage, and heavy damage. We considered hunting regions, and their lower level, i.e. hunting sub-regions (Hell et al. 2004), as these units would synthesize both natural conditions and hunting administration entities. Hence, the population status of ruminating ungulates reflected partly environmental conditions and previous hunting management. Here, we must explain that hunting regions are based on a complex of aspects, including the principal hunting game, specifically: red deer, roe deer, and small game. We found that there were no evident differences between these three sorts of hunting regions; therefore, our analyses had to be focused on hunting sub-regions (there are 64 in total, 30 of them are with the provenance of red deer, 21 for roe deer, and 13 for small game). In fact, the current situation in Slovakia is such that red deer is the most overpopulated hunting game and spread over the entire area of the country, at the expense of the distribution of other hunting game species (MARD 2021). Our calculations yielded outputs showing that the heavy damage to young stands by browsing was primarily in three "clusters": the southwestern part, northeastern part of Slovakia, and one sub-hunting region around the Rimavská Sobota town. The first and the second clusters. represent roe deer hunting sub-region, but this parts of Slovakia are also abundant with red deer, fallow deer, and mouflon (MARD 2021). The second cluster is typical with a huge prevalence of red deer.

Variation in browsing intensities among hunting sub-regions is related to a variety of factors, especially browsing ungulate population densities and the carrying capacity of the area. Population density, in turn, is governed by a complex of factors (Bobek et al. 1984), but the decisive aspect is human activity, primarily the previous hunting regime (Tourani et al. 2023). On the other hand, Calkoen et al. (2023) demonstrated that the influence of large carnivores on ruminating ungulates is currently negligible across Europe. Regarding the carrying capacity of a certain area, this characteristic is influenced by a large set of conditions, primarily the availability of resources in crop fields, pastures, and tree species composition in forests (Hell et al. 2004). Some studies have shown that the carrying capacity of an area is usually enhanced by an increase in gaps in forests and/or the contribution of young stands (Kuijper et al. 2009).

Here, we would like to emphasize that ruminating ungulates have a significant impact on forest ecosystems across a wide range, making this relationship important, particularly in the context of climate change. Currently, potential interactions between ruminating ungulate populations and climate-adapted forest management are occasionally considered but are not adequately incorporated into adaptation strategies (Champagne et al. 2021). While more data and research findings would be beneficial, particularly regarding the interactive effects of climate variables and browsing on tree regeneration, further delay in implementing climate-adapted strategies could lead to future regeneration failures and increased pressure on forests (Champagne et al. 2021). According to Skonhoft et al. (2013), a bio-economic analysis of a red deer population within a forest sector should be conducted. This analysis must incorporate both the hunting value and browsing/grazing damage, and the optimal hunting composition should be planned and implemented. It appears that hunting strategies in the near future will need to consider numerous aspects, with involvement from other sectors such as forestry, agriculture, and nature conservation being essential.

5. Conclusion

Our analyses have revealed that forest regeneration and the early stages of forest growth in Slovakia are significantly influenced by browsing activity from ruminating ungulates. Browsing ranks as the second most important factor limiting forest regeneration, following light deficiency. While light levels can often be managed by foresters through canopy reduction in the maternal stand via tree felling, reducing browsing pressure primarily relies on hunting activities outside the forestry sector. Therefore, close collaboration between foresters and hunters is imperative.

Another noteworthy finding from our study pertains to the considerable variability in browsing damage among hunting sub-regions. This variability suggests that specific measures, particularly those aimed at reducing ruminating ungulate populations, should be prioritized in areas experiencing the most severe browsing damage. Furthermore, our findings regarding the differential attractiveness of tree species for game forage indicate a need for targeted protection against browsing in the forestry sector. This issue is not only crucial for forest productivity but also for preserving biodiversity in forest ecosystems.

Acknowledgements

This research was funded within the projects APVV-20-0168 and APVV-22-0056 from the Slovak Research and Development Agency. A part of research activities was conducted within fulfilling the goals of the project "Progressive methods of forest protection in changing ecological conditions (PROMOLES)": financed from the budget of the Ministry of Agriculture and Rural Development of the Slovak Republic (No. 08V0301), as well as within the LignoSilva project [Grant Agreement #101059552] under the Horizon Europe Teaming for Excellence action, funded by the European Commission.

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Attachment

Table A1. Basic information about number of inventory plots, assessed trees and browsing damage across the hunting sub-region in Slovakia. The first letter in the code of each specific hunting sub-region indicates the primary game species: J – red deer, S – roe deer, and M – small game.
The categorization of the hunting plots regarding to browsing damage is in the Fig. 7.

Hunting sub-region (code and name)	Number of plots (pieces)	Share of plots with browsing as limiting factor (%)	Number of trees (individuals)	Browsing rate on trees (%)
J I. Poddunajská	1	0.0	3	—
J II. Bebrava	31	64.5	782	22.9
J III. Strážovská hornatina	39	35.9	599	19.9
J IV. Javorníky I	23	21.7	332	21.7
J V. Javorníky II	23	8.7	379	41.4
J VI. Slovenské Beskydy	30	30.0	377	29.7
J VII. Oravská Magura	22	22.7	453	17.4
J VIII. Malá Fatra	30	30.0	414	24.9
J IX. Orava	25	28.0	397	7.1
J X. Žiar	7	28.6	94	11.7
J XI. Vtáčnik	40	22.5	1,069	8.5
J XII. Veľká Fatra	37	37.8	788	22.8
J XIII. Nízke Tatry	84	28.6	1,758	16.7
J XIV. Poľana	29	37.9	672	18.5
J XV. Muránska	67	31.3	1,289	13.7
J XVI. Smolník	64	20.3	1,150	11.0
J XVII. Slovenský Raj	31	58.1	480	26.9
J XVIII. Levočské pohorie	39	59.0	739	28.4
J XIX. Spšská Magura	20	55.0	304	31.2
J XX. Vihorlat	34	0.0	562	11.6
J XXI. Čergov	20	20.0	287	14.3
J XXII. Nízke Beskydy	37	45.9	799	23.8
J XXIII. Humenné	24	0.0	349	10.3
J XXIV. Poloninské Karpaty	48	0.0	842	18.5
J XXV. Slanské pohorie	30	10.0	564	0.7
J XXVI. Vysoké Tatry	38	28.9	456	27.0
J XXVII. Považský Inovec	18	27.8	452	10.0
J XXVIII. Tribeč	32	21.9	998	8.5
J XXIX. Biele Karpaty	13	38.5	246	35.8
M I. Záhorská nížina	4	50.0	55	41.8
M II. Senica	11	45.5	159	45.3
M III. Žitný ostrov	3	66.7	50	8.0
M IV. Trnavsko-piešťanská	7	71.4	155	37.4
M V. Horná Nitra	4	50.0	71	31
M VI. Nitra	4	75.0	119	15.1
M VII. Nové Zámky	7	28.6	87	13.8
M VIII. Pohronie	7	28.6	219	14.2
M IX. Zemplínska	8	12.5	85	—
M X. Južná	4	0.0	102	—
S I. Záhorie	17	52.9	225	39.1
S II. Malé Karpaty	33	75.8	656	45.3
S III. Bratislava	1	0.0	21	—
S IV. Stará Turá – Bošáca	16	75.0	276	37.7
S V. Marhat	7	28.6	207	12.1
S VI.Štiavnické pohorie	42	19.0	981	13.5
S VII. Zvolen	20	25.0	710	20.3
S VIII. Hontiansko-veľkokrtíšska	30	13.3	401	30.4
S IX. Tuhár	31	41.9	733	9.0
S X. Rimavská Sobota	55	56.4	1433	25.9
S XI. Prešovská	22	13.6	370	7.6
S XII. Toplianska	13	38.5	221	13.1
S XIII. Tovarné	8	0.0	119	11.8