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What have we learnt from the stand level estimates on stem bark browsing by large wild herbivores?

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Abstract

Damage on forests by large wild herbivores, especially by red deer (*Cervus elaphus* L.) has been increasing in Central Europe including Slovakia. Therefore, we attempted to estimate the forage potential, i.e. potentially available bark for consumption by large wild herbivores and actually consumed bark of common rowan (*Sorbus aucuparia* L.) and goat willow (*Salix caprea* L.). For these purposes, we measured basic tree characteristics and dimensions (length and width) of wounds due to bark browsing at 15 plots located in a young mixed forest stand (Javorníky Mts; Slovakia). Browsing was recorded separately for four stem sections: 0–50, 51–100, 101–150, and 151–200 cm measured from the ground level. Three stem bark browsing metrics were implemented: browsed bark area (cm^2), browsed bark mass (g) and portion of browsed bark mass to total stem bark mass representing potential forage for game expressed in percent. We proved that while common rowan and goat willow were browsed in a great extent, nearly no damage occurred on stems of Norway spruce (*Picea abies* [L.] Karst.) and silver birch (*Betula pendula* Roth.). Our estimates showed that the total forage potential of stem bark at common rowan and goat willow was about 13.4 kg per 100 m^2 of a forest stand. We learnt from our estimates for instance that the total available stem bark at 100 m^2 of our young mixed forest might suffice (if theoretically entire potential was exploited) for red deer, fallow deer (*Dama dama* L.) and mouflon (*Ovis aries musimon* L.) for one, two and nearly four weeks, respectively. At the same, that during four years, large wild herbivores browsed nearly 2.6 kg of bark per 100 m^2 area, i.e. about 1/5 of the available potential on rowans and willows. It seems like common rowan and goat willow might generate important resources of forage for large wild herbivores and would be treated as a part of biological protection of target tree species against bark browsing.

Key words: bark stripping; *Cervus elaphus*; *Dama dama*; forage potential; Western Carpathians; young mixed stand

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1. Introduction

Although large wild herbivores are important and very probably also irreplaceable elements in a variety of ecosystems including forests, the complexity of their effects to ecosystem functioning is still not known to its full extent (Koerner et al. 2018). In theoretical and empirical literature, all herb-consuming animals with a body weight exceeding 5 kg are considered large wild herbivores (McNaughton 1979). Large wild herbivores influence forest ecosystems in a variety of ways, mainly by trampling, defection and urination, but most severely by biomass consumption (Forbes at el. 2018). Some authors stated that large wild herbivores are keystone species in "ecosystem engineering" because through browsing they often shape the structure and dynamics of entire ecosystems (e.g. Waller & Alverson 1997; Rooney 2001). Obviously, the intensity of large wild herbivore impact on ecosystems is related to their body size, population density as well as site fertility (Ramirez et al. 2019).

A literature review by Forbes et al. (2018) showed that large wild herbivores are declining worldwide. However, the opposing situation has been reported from a variety of European countries, where especially the population of red deer (*Cervus elaphus* L.) manifested an increasing tendency, in some regions even at an extraordinary rate (e.g. Milner et al. 2007; Burbaité & Csányi 2010; Speed et al. 2019; Valente et al. 2020). This trend is typical also for Slovakia where the population of red deer has nearly doubled within the last two decades (Bučko et al. 2010; Konôpka et al. 2022b). Therefore, the damage on forests by large wild herbivores, especially by red deer, fallow

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deer (*Dama dama* L.) and roe deer (*Capreolus capreolus* L.) has been increasing (Kunca et al. 2019).

In the countries of Central Europe, red deer are the largest herbivores and cause the most damage to forest ecosystems by bark browsing (Valente et al. 2020). Since the weight of fallow deer is approximately three times lower than that of red deer in this territory, fallow deer cause less damage in forest stands (Finďo & Petráš 2007). Both red deer and fallow deer consume a variety of plant species. Although they obviously prefer grasses, a substantial part of their diet, especially in winter seasons, is composed of tree components as well as of woody shrubs (Spitzer et al. 2020). To maximize the input of energy and nutrients, the deer select the most nutritious and at the same time the most palatable plant species and their best digestible parts (Gordon & Prins 2003). However, when their population density is too high and/or forage sources are insufficient, deer consume also forages of lower quality or less palatable ones (Borowski et al. 2021).

According to the Slovak National Forest Inventory, the most intensive damage to forest trees occurred in young growth stages (approximately up to 20 years), and on soft broadleaved species (Šebeň 2017). While roe deer browse exclusively foliage and shoots, red deer, fallow deer and partly also mouflon (*Ovis aries musimon* L.) browse often bark, especially on stems (Finďo & Petráš 2007). Stem bark browsing decreases the quality of timber production either directly by causing wood deformations (Kiffner et al. 2008) or indirectly by fungal infestation through wounds and subsequent wood rotting (Jelonek et al. 2022). In other cases, individual trees or even entire stands subjected to stem rotting often perish (Wang et al. 2021) or get easily broken due to the mechanical pressure of snow or wind (Konôpka et al. 2016). This often remarkably lowers timber production (Vacek et al. 2020) and reduces economic gain from forests as such wood can be utilized only for low-cost goods, for instance as fuel or for energy production (Reimoser et al. 1999).

Our previous study conducted in the Western Carpathians indicated that red deer browsed soft broadleaved tree species much more frequently and intensely than the economically important species such as Norway spruce (*Picea abies* [L.] Karst.; Konôpka et al. 2021). Hence, the presence of economically unimportant softwood broadleaved tree species can protect other tree species valuable in the timber processing industry from browsing. Moreover, our results (Pajtík et al. 2015; Konôpka et al. 2018) as well as findings from other European works (see Motta 2003; Myking et al. 2013; Edenius & Ericsson 2015) proved that from all soft broadleaved species, common rowan (*Sorbus aucuparia* L.), and goat willow (*Salix caprea* L.) are extraordinarily attractive for red deer and possibly for some other large wild herbivores.

To understand how these species could serve as a biological protection of commercial tree species, e.g. Norway spruce, silver fir (*Abies alba* Mill.), European beech (*Fagus sylvatica* L.) and oaks (*Quercus* spp.), it is required to quantify their forage potential for some large wild herbivores, especially their stem bark biomass. Moreover, the quantification of tree biomass consumed by large wild herbivores at tree- and stand levels considering the current population density of these animals would be a great basis for making correct decisions about future game management. As for stem bark browsing, previous studies focused on a rather simple quantification such as the rate of browsed trees at a stand level (Wam et al. 2021) or the area of browsed stem bark at a single tree level (Hahn & Vospernik 2022). The main difficulty in predicting bark biomass available for browsing (edible potential) and the actually consumed bark by large wild herbivores is the absence of bark models allowing such estimates. However, our recent work offers bark mass models for some broadleaved tree species (Konôpka et al. 2022a). The models may be implemented to derive tree level estimates, and in combination with basic stand characteristics also for stand level calculations.

The main aim of this work was to quantify stem bark browsing in common rowan and goat willow by implementing the novel bark models (Konôpka et al. 2022a) in a young mixed forest stand located in Javorníky Mts. (western part of Carpathians), Slovakia. Since both basic stand characteristics and browsed bark areas on individual trees were measured, these data together with the bark models might be used to estimate the forage potential (available bark mass) and the actually consumed bark mass of common rowan and goat willow. At the same time, we were able to estimate the browsing intensity as a percentage of the browsed bark mass to total bark mass representing the potential forage for game. Another goal of the work was to analyse the relationship between the stem base diameter as well as the bark position along the vertical stem profile and the intensity of bark browsing.

Here it must be explained that the term "bark browsing" is used in the entire subsequent text. Actually, another similar term is "bark stripping", however this usually express peeling a bark by large wild herbivores within the growing season when bark is easily detached without any substantial resistance to animals' teeth (see also the Discussion section for further information).

2. Material and methods

2.1. Site and stand characteristics

Our field study was conducted at a study area called "Husárik". The area is a part of the Javorníky Mts. in the Kysuce region, i.e. located in the north-western Slovakia (Šebeň & Kulla 2011). The climatic conditions are characterized with rather cold and humid weather, an average July temperature close to 16 °C and less than –5 °C in January (Hlásny et al. 2010). The mean annual temperature is 6 °C, the annual precipitation is about 1,100 mm, the

duration of snow cover is nearly 100 days a year. A substantial part of bedrock in the Javorníky Mts. is formed by clay-stones and shales while the soil is prevailingly modally acidic, mostly clayey. The Husárik study area belongs to *Abieto-Fagetum* forest type (see the quantification of forest types by Hančinský 1972), i.e. the natural forest vegetation was composed of European beech and silver fir.

At the Husárik study area, similarly like at many other sites of the Javorníky Mts., secondary spruce dominated monocultures have been declining, especially since the beginning of the current century (Hlásny et al. 2010). The decline has been mostly caused by climatic extremes (e.g., the extremely dry year of 2003) and the subsequent bark beetle outbreaks. Hence, in 2010 the mature stands at the Husárik study area were harvested during the "incidental felling", removing already perished, dying, weakened or insect- and fungi-infested trees.

The Husárik study area is a part of nearly 3,000 ha hunting ground consisting of 2,000 ha of forest and 1,000 ha of fields and grasslands. Records from the local hunting association indicated 15 red deer, 60 roe deer, 50 mouflons, and 50 fallow deer within the hunting ground in the early spring (before parturition) of 2010. In the spring of 2020, as many as 35 red deer, 50 roe deer, 30 mouflons and 60 fallow deer were counted in form of field observation by the members local hunting association (information obtained via personal communication with the members).

In the spring of 2011, a variety of experiments were established at the Husárik study area to test different reforestation and silvicultural approaches, i.e. exclusive natural regeneration, planting, and their combinations with different shares of natural regeneration and planting, as well as combinations of tree species (Kulla & Sitková 2010). During 2011, a fence was built to protect a 5.12 ha area of the Husárik study area with artificial regeneration experiments (Šebeň & Kulla 2011). The 2.4 m high fence from 45 × 45 mm mesh completely prevented the inner area from the access of large wild herbivores. For our measurements, we selected a part of the exclosure outside the artificial restoration plots, i.e. within a sub-area covered by a young forest originating from natural regeneration, i.e. from seed dispersal of adjacent mature trees. The target forest complex was about 0.5 ha large.

Here we must explain the situation about the exclusion and the subsequent presence of large wild herbivores inside the fenced area. Some sections of the fence were damaged approximately 7 years after the fence was built, and a few individuals of red deer, fallow deer, roe deer and mouflons were occasionally seen inside the fence. Although the fence was repeatedly repaired in 2019 and 2021, other damages on the fence occurred between the years of 2019 and 2022. We assume that the upper part of the fence was damaged mostly by red deer and the lower part by wild boar (*Sus scrofa* L.). It looked like large wild herbivores noticed the differences in tree species composition between the stands outside - prevalence of less attractive species for nutrition, especially Norway spruce and silver birch (*Betula pendula* Roth.), and inside the fence – a high proportion of common rowan and goat willow. The local game, especially red deer and wild boar probably "learned" the way to destroy the fence and break inside. Hence, this new situation allowed us to quantify the stem bark browsing on young trees (7–10 years old) during a short period, i.e. 4 years, but under the high population pressure by large wild herbivores.

2.2. Tree and wound measurements

We established fifteen plots inside the fenced area, following a rule that they had to be at least 10 m apart. Each plot was circular with a constant radius of 2.0 m, i.e. it represented an area of 12.57 m^2. The centre of each plot was fixed with a metal tube hammered in the ground, all trees were marked with metal labels showing tree- and plot-specific codes. Measurements on the plots were performed at the end of 2022 growing season. Tree heights were measured with a hypsometer TruPulse 360° R (Laser Technology, Inc., Centennial, CO, USA) with a precision of ±0.1 m. At the same time, stem base diameters were measured with a digital caliper Masser BT (Masser Precision, Rovaniemi, Finland) with a precision of ±0.1 mm.

Then, the vertical profile of each stem was divided into 50 cm long sections delineated by white chalk. Diameters at lower and upper borders of the sections were measured with digital callipers at a precision of ±0.1 mm Each debarked (browsed) area was measured, specifically its height with digital callipers (precision of ±0.1 mm) in the vertical direction and its width with a rolling measure tape (±1.0 mm) in the horizontal direction. When the browsed area occurred across stem sections, it was divided between them proportionally. In total, about 500 trees were measured and recorded on the plots, out of which about 320 individuals of common rowan and goat willow were browsed by large wild herbivores (see also Table 1). Since spruces and birches were damaged very rarely (a couple of cases of shoot browsing but nearly none browsing on stem bark), we could not record and measure any injuries for these species at the plots.

Table 1. Basic stand characteristics based on measurements of 15 plots at the Husárik study area, Javorníky Mts.; Slovakia. Mean values and standard deviations are shown.

Tree species	Tree height [m]	Stem base diameter [mm]	Basal area [cm^2 per 100 m^2]	Tree density [individuals per 100 m^2]
Common rowan	4.58 (1.49)	34.0 (10.0)	17.4 (14.4)	154.9 (107.4)
Norway spruce	1.48 (0.32)	21.8 (5.0)	2.8 (2.2)	55.7 (34.5)
Goat willow	3.74 (1.41)	30.6 (12.3)	3.2 (5.9)	35.0 (55.5)
Silver birch	5.18 (1.68)	77.1 (40.8)	12.0 (8.9)	18.0 (15.8)
Together	3.68 (0.94)	32.6 (6.2)	35.6 (10.2)	279.6 (86.3)

2.3. Calculations and analyses

The total pre-browsed surface of stem bark was calculated for individual stem sections using the formula for the surface of the truncated cone omitting the areas of bottom and top cross-sections, i.e.:

$$S_b = \pi(r_1 + r_2)\sqrt{(r_1 - r_2)^2 + l_s^2}$$

where:
S_b is stem bark surface (cm^2),
r_1 is a radius of the bottom (cm),
r_2 is a radius of the top (cm),
l_s is the length of the section (i.e. 50 cm).

Afterwards, the total surface of stem bark along the entire targeted profile, i.e. up to the height of 200 cm was calculated as a sum of surfaces in 50 cm long consecutive sections (i.e. 0–50 cm, 51–100 cm, 101–150 cm and 151–200 cm from the ground level).

Then, three stem bark browsing metrics were implemented: browsed bark area (cm^2), browsed bark mass (g) and proportion of the browsed bark mass to the total bark mass representing the potential forage for game expressed in % (browsed bark to total bark potential; hereinafter). Areas of browsing at a stem section level and along the entire stem profile were converted to bark mass using the specific surface mass. This indicator expresses the quantity of bark mass per unit area and was adopted from the models published in Konôpka et al. (2022a). Finally, we calculated the browsed bark to total potential as a proportion of the browsed bark mass to the total (pre-browsed) bark mass at the stem section level and the entire stem profile considering the maximum distance from the ground level of 200 cm.

All the mentioned calculations were done first at a plot level, obtaining 15 values. Then we expressed the overall situation in the target forest stand as an average value calculated from the plot-specific numbers. Finally, relationships between stem base diameter and browsed bark to total bark potential at a tree level separating species of common rowan and goat willow were expressed by linear fittings. Data archiving and analyses were performed in Excel and Access programs.

3. Results

We found that while stems of common rowan and goat willow were robustly damaged by game browsing, trees of Norway spruce and silver birch were nearly without any wounds on their stems. Therefore, further measurements were focused exclusively on common rowans and goat willows. Hence, all further results and text are dedicated to these tree species.

As we have mentioned in the Material and methods section, the models adopted from Konôpka et al. (2022a) were implemented in this paper. The models (see visualizations in Fig. 1) indicate that the bark mass increases with the stem base diameter and decreases with the distance from the ground level. Moreover, the visualizations proved that while goat willow had a greater bark mass than common rowan at the lowest stem section, the opposite situation was found for the other stem sections. As for the specific surface mass (Fig. 2), its values increased

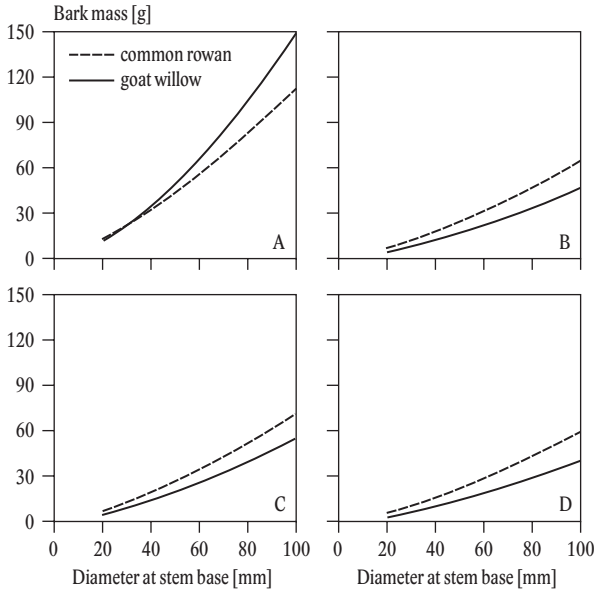

Fig. 1. Relationships between stem base diameter and bark mass for common rowan and goat willow in the sections 0–50 cm (chart A), 51–100 cm (chart B), 101–150 cm (chart C), and 151–200 cm (chart D). The models adopted from Konôpka et al. (2022a).

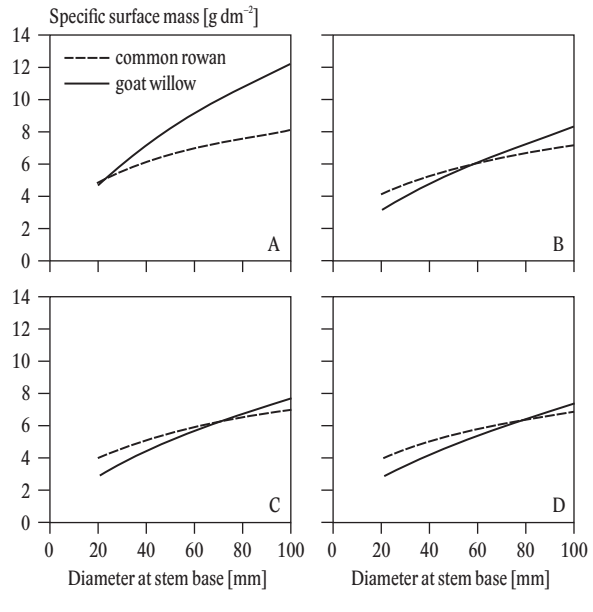

Fig. 2. Relationships between stem base diameter and specific surface mass of stem bark for common rowan and goat willow in the sections 0–50 cm (chart A), 51–100 cm (chart B), 101–150 cm (chart C), and 151–200 cm (chart D). The models adopted from Konôpka et al. (2022a).

with the stem base diameter. At the same time, a steeper increase of the specific surface mass with the stem base diameter was observed for goat willow than for common rowan in all stem sections. On the other hand, while at the lowest stem section, the specific surface mass of bark was greater in the case of goat willow than common rowan, interspecific differences in the other stem sections were minimal.

Our estimates showed that the total stem bark mass representing the potential forage for game at the stand level was about 13,372 g of dry mass per 100 m^2 of stand area (Table 2). Naturally, the bark mass per stem surface unit decreases along the stem profile from the ground level upwards. Thus, the maximum bark mass (3,870 g per 100 m^2) was allocated at the lowest stem section (0–50 cm), and the minimum quantity (2,909 g per 100 m^2) at the stem section 151–200 cm. The stem bark mass of common rowan exceeded that of goat willow four times (10,692 versus 2,680 g per 100 m^2). Further we found out that as many as 92.4% of individuals of goat willow and 75.7% of common rowans were damaged by game browsing (Table 3). As for common rowan, browsing was more frequent in sections 51–100 cm and 101–150 cm than in 0–50 cm and especially than 151–200 cm. A rather different situation was found for goat willow, since as many as 3/4 of all individuals were browsed in the sections 0–50, 51–100 and 101–15 cm in parallel.

Table 2. Stem bark mass potential on common rowans and goat willows expressed in grams per 10^2 m^2 of forest stand at the Husárik study area, Javorníky Mts., Slovakia. Mean values and standard deviations are shown.

Stem section [cm]	Common rowan	Goat willow	Together
	[g per 100 m^2]		
0–50	3,116 (2,706)	754 (1,256)	3,870 (2,550)
51–100	2,717 (2,430)	689 (1,139)	3,405 (2,311)
101–150	2,534 (2,285)	653 (1,088)	3,187 (2,174)
151–200	2,325 (2,106)	584 (972)	2,909 (1,997)
Whole available profile (0–200)	10,692 (9,524)	2,680 (4,455)	13,372 (9,029)

Table 3. Share of trees damaged by stem bark browsing from all trees of common rowan and goat willow at the Husárik study area, Javorníky Mts., Slovakia.

Stem section [cm]	Common rowan	Goat willow	Together
	[%]		
0–50	39.4	72.3	46.1
51–100	47.9	75.8	53.1
101–150	44.5	74.2	50.0
151–200	27.7	31.8	28.5
Whole available profile (0–200)	75.7	92.4	78.8

Considering the browsed bark area, nearly 477 dm^2 of wounds per 100 m^2 of the forest stand were estimated (Table 4). For both tree species, the largest browsed areas were recorded at stem sections 51–100 and 101–150 cm. At the same time, our estimates showed that large wild herbivores browsed and consumed about 2,600 g of stem bark per 100 m^2 of the forest stand (Table 5). If we expressed the share of the browsed bark area and the share of the browsed bark mass to the total amount (area or mass) of the browsed bark along the full profile, we could see that the essential quantity was consumed from stem sections 50–100 and 101–150 cm (Fig. 3). Specifically, about 80% of the browsed bark area as well as of the bark mass was taken from the two mentioned sections.

Table 4. Browsed bark area (in dm^2 per 100 m^2 of forest stand) of common rowans and goat willows at the Husárik study area, Javorníky Mts., Slovakia. Mean values and standard deviations are shown.

Stem section [cm]	Common rowan	Goat willow	Together
	[dm^2 per 100 m^2]		
0–50	23.2 (37.9)	16.9 (37.9)	40.1 (38.4)
51–100	141.6 (84.2)	59.6 (84.2)	201.2 (105.0)
101–150	128.2 (69.5)	57.1 (69.5)	185.3 (123.2)
151–200	32.4 (20)	17.6 (20)	50.0 (36.7)
Whole available profile (0–200)	325.4 (206.0)	151.2 (176.0)	476.6 (288.3)

Table 5. Browsed stem bark mass (in g per 100 m^2 of forest stand) of common rowans and goat willows at the Husárik study area, Javorníky Mts., Slovakia. Mean values and standard deviations are shown.

Stem section [cm]	Common rowan	Goat willow	Together
	[%]		
0–50	158 (198)	122 (198)	280 (212)
51–100	806 (472)	280 (472)	1,086 (632)
101–150	727 (405)	257 (405)	984 (770)
151–200	17 (128)	82 (128)	259 (243)
Whole available profile (0–200)	1,868 (1,167)	741 (1,117)	2,609 (1,783)

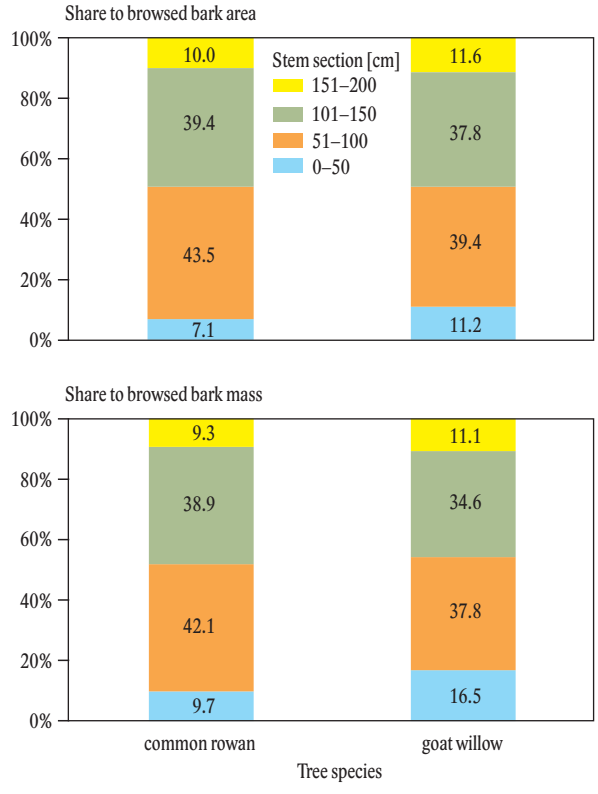

Fig. 3. Shares of browsed bark area (upper chart) and browsed bark mass (lower chart) in individual stem sections along the entire stem profile for common rowan and goat willow at the Husárik study area, Javorníky Mts., Slovakia.

Large wild herbivores browsed as much as 21.1% of available stem bark mass of rowans and willows in our stand, while more intense (26.0%) browsing was recorded on goat willow than on common rowan (17.1%; Table 6). The maximum proportion (40.6%) of browsed stem bark mass was found at stem section of 51–100 cm of the goat willow, and the minimum value (5.1%) was estimated for stem section 0–50 cm of common rowan.

Table 6. Percentage of browsed stem bark to total bark potential [%] on common rowans and goat willows at the Husárik study area, Javorníky Mts., Slovakia.

Stem section [cm]	Common rowan	Goat willow [%]	Together
0–50	5.1	13.5	8.1
51–100	29.8	40.6	33.2
101–150	28.7	39.4	34.3
151–200	7.6	14.1	9.8
Whole available profile (0–200)	17.1	26.0	21.1

Finally, we expressed the relationship between the stem base diameter of each wounded tree (those without the browsing damage were excluded) and the proportion of browsed bark mass from the total bark mass potential. For both species, clear ascending linear relationships with the same slopes were found with having large values in goat willow than common rowan (Fig. 4).

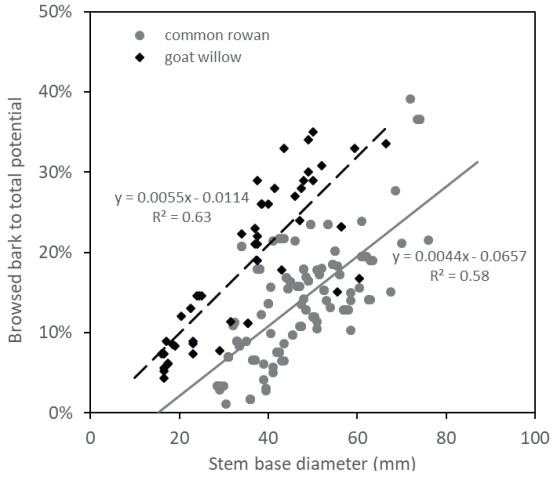

Fig. 4. Relationships between stem base diameter and the percentage of browsed bark mass to the total stem bark mass representing the potential forage for game in common rowan and goat willow at the Husárik study area, Javorníky Mts., Slovakia.

4. Discussion

4.1. Factors influencing bark browsing

Our results showed that during four years, large wild herbivores browsed almost 76% individuals of common rowan and over 92% of goat willow trees. At the same time, Norway spruces and silver birches were nearly without any browsing damage on stems. This finding supported an idea that large wild herbivores prefer certain plants in their nutrition based on taste properties (palatability) of individual species (see e.g. Augustine & McNaughton 1998). It seems that willow and rowan in young (and probably also in older) forests stands can attract the nutritional interest of large wild herbivores and protect Norway spruce, which is commercially an extremely important tree species in Central and Northern Europe. Therefore, these two deciduous broadleaved species can serve as a sort of biological control and practical protection of the target tree species, in Slovakia besides Norway spruce, also European beech, oaks, Scots pine (*Pinus sylvestris* L.) and silver fir.

If we compare the attractiveness of rowan and willow, no definitive conclusion may be derived from our results on bark browsing. Higher frequency (considering the above-mentioned share of browsed trees to total number of trees) and also higher intensity (browsed bark to total bark potential: 26% versus 17%) observed on willow than on rowan does not need to be related exclusively to forage preference of large wild herbivores. It might be subjected to the lower proportion of willow in the stand, thus, willow might be more "interesting" for large wild herbivores than rowan. In general, large wild herbivores prefer the palatable tree species which are less abundant in stand (Finďo & Petráš 2007).

The measurements at the Husárik study area suggested that the intensity of bark browsing expressed as the proportion of the browsed bark mass to the total stem bark mass representing the potential forage for game was related to stem diameter of both common rowan and goat willow. Specifically, relationships between stem diameter and the intensity of bark browsing showed middle degree of association (R^2 equaled 0.63 and 0.58, in goat willow and common rowan, respectively). It indicates that the stem diameter is the most important factor for browsing intensity on a tree species level. We assume that the increasing stripping intensity with stem diameter might be related to: (i) better conditions for browsing and/or (ii) the "pragmatic" decision of large wild herbivores. The first expectation is subjected to the phenomenon that too thin stems are very flexible, due to which browsing might be difficult because large wild herbivores cannot press their teeth against the stem surface. This tendency does not to need to hold for larger trees than we measured. In fact, older trees might be unsuitable for browsing since they have thick and furrowed bark. This is typical mostly for the bark on the stem base of goat willow, where stem bark might protect the tree from herbivory browsing (see the chapter dealing with goat willow in Ayanz et al. 2006).

In fact, nearly all previous works focusing on stem browsing have been conducted on larger trees. For instance, Welch et al. (1988) observed that in stands with a mean diameter below 6.3 cm browsed trees were significantly larger than the plot mean tree (predominant and

dominant individuals), while in the range of mean diameters of 6.3–12.7 cm stripped trees had average diameters (dominant and codominant individuals), and in stands with a mean diameter above 12.7 cm browsed trees were significantly smaller (suppressed ones). A recent literature review (Hahn & Vospernik 2022) also indicated that the presence of stem bark browsing on trees is related to stem diameter. The extent of injury often decreases with stem diameter because small trees have more bark that is more digestible by large wild herbivores (Kiffner et al. 2008). Similarly, studies of wound areas from the Czech forests showed that injured trees had smaller stem diameters than healthy trees (Vacek et al., 2020). However, the wound size itself primarily increased with stem diameter because clearly larger wounds can only be inflicted on larger trees. The later decrease in wound size in older trees of the Austrian forests was interpreted as a tree recovery and the removal of most damaged individuals during the thinning of forest stands (Hahn & Vospernik 2022).

Our results clearly showed that bark of stem section situated at heights 51–150 cm from the ground level was browsed most. Browsing of stem sections 0–50 cm and 151–200 cm was about four and three times less intense than of the 51–150 cm. Here, we must add that stem bark browsing at heights over 200 cm was very rare, therefore, we did not show results. We would like to repeat that red deer were very probably the main browsing species, followed by fallow deer and slight browsing by mouflon might also be assumed (see also the information about large wild herbivore population density in the hunting ground). Our results support those reported by some other works. For instance, in Scotland, most wounds on stems caused by red deer browsing were between 51 to 150 cm (Welch et al. 1988). While in Slovakia the highest percentage of stem bark browsing on rowan was found between 101 and 150 cm with the upper limit at 200 cm (Konôpka et al. 2018), in Germany, red deer typically browsed stem bark at heights from 80 to 170 cm above the ground level (Prien 1997). These heights correspond with the height of a red deer's shoulder, which may vary among the regions (Renaud et al. 2003). The heights are connected to most comfortable positions of deer head during stem bark browsing. Considering our research stand, besides red deer, also browsing by fallow deer and a little bit by mouflon might be assumed. However, since the teeth prints on the stems were not well recognizable, we could not determine the species of browsing animal.

Besides other factors, stem surface orientation to relief characteristics can play a role in stem bark browsing (Han & Vospernik 2022). In principle, most wounds are found on the uphill side of the stem. Although we also visually noticed such a pattern in our stand, we did not record an exact orientation of wounds on stems with respect to the slope, and thus, a more detailed analysis was not possible. Very probably, a slope influences also vertical distribution (distance from the ground level) of bark browsing. On steeper slopes, browsing would shift to upper stem parts on the uphill side and the reverse situation might be expected on the downhill side of stems. As for browsing on the stem base, a lower occurrence of wounds in this part is driven by the thickness of snow cover which mechanically protects the stem base in winter (Hofmann 1978). On the other hand, the extent and the intensity of bark browsing in forest stands would increase with snow cover duration due to the lack of other available natural forage (Ligot et al. 2013).

4.2. Stem bark as forage potential

Our estimates showed that the total forage potential of stem bark of common rowan and goat willow was about 13.4 kg per 100 m^2 of forest stand. Within four years, large wild herbivores browsed nearly 2.4 kg of bark that represented approx. 21% of the available bark in rowans and willows. According to Hofmann (1978), red deer consumes daily about 2.0 kg of dry biomass, fallow deer about 0.8 kg, and mouflon about 0.5 kg. If we consider the total available bark in our stand, 100 m^2 of our forest might suffice for red deer, fallow deer and mouflon for one, two and nearly four weeks, respectively. However, the utilization of the full potential (i.e. 100% of available bark) by large wild herbivores is a very theoretical assumption and might be realistic only for the optimal stem zone, i.e. at heights between 51 and 150 cm from the ground. At the same time, the actually consumed bark (2.4 kg per 100 m^2) at the site could be eaten by red deer in 1.6 days, and by fallow deer, and mouflon in 3.0 and 5.8 days, respectively. These calculations are rather rough (obviously large wild herbivores combine a variety of forage sources at the same time) and might be close to reality only in the period of complete snow cover, i.e. without any possibilities in obtaining other forage.

According to Hahn & Vospernik (2022), "winter" and "summer" browsing may be visually distinguished. While the wounds caused by winter browsing are less regular and have clear teeth prints, the wounds that happened in a growing season are of a more regular shape, longer, without teeth prints suggesting that bark was stripped without any substantial resistance against peeling. Easier bark stripping in a growing season than in winter relates to contrasting water content in phloem as well as different mechanical properties of bark (e.g. Candaele et al. 2021). As for winter browsing, the main reason is obviously related to food insufficiency and occurs mostly in late winter when the phloem is richer in nutrients (White 2019). Summer browsing has a beneficial effect for the digestion of rumen thanks to the high content of tannins in bark (Mansson & Jarnemo 2013). Recent findings (Widén et al. 2022) suggested that the increased browsing intensity by red deer at the beginning of the growing season might be related to the increas-

ing concentration of starch in bark that is closely linked to the threshold temperature. As for our research plots, characteristics of wounds suggested that winter browsing robustly prevailed over summer browsing (exact data are not available, but see Fig. 1A in the Attachment).

Here we would like to point out that our results show cumulative values of stem bark browsing during four years. Unfortunately, we do not have data about bark browsing in each individual year, which might be related to characteristics of wounds (especially previous browsing), trees (e.g. actual stem diameter), and environment (climatic conditions). Moreover, additional data on biochemical properties, especially the nutritional value of bark would be very beneficial. Anyway, as a pilot study, the results suggest that while common rowan and goat willow are important for nutrition of large wild herbivores, silver birch is not. As we have mentioned, the supply of forage in the form of bark may be extremely important in winter when large wild herbivores could fully depend on this resource. In such a case, common rowan and goat willow, potentially also other softwood broadleaved species, can mitigate considerable damage by browsing on some commercially important tree species.

5. Conclusions

We learnt from our study that the total available bark at 100 m^2 of the young mixed stand might suffice for red deer, fallow deer and mouflon for one, two and nearly four weeks, respectively. At the same, that large wild herbivores browsed during four years about 1/5 of the available bark potential on rowans and willows. Although our estimates represent only a sort of case study, the results give some ideas about forage potential in stem bark on a stand level and also about real depletion rate of these resources by large wild herbivores. Moreover, the outputs indicate that common rowan and goat willow might provide important resources of forage for large wild herbivores and would be treated as a part of biological protection of target tree species against bark browsing.

In such context we recommend that a part of the softwood broadleaved species (except birches) be retained within "commercial" forest stands during cleanings, thinning and tending. While these tree species are attractive for stem bark browsing, foresters could leave enough individuals to provide sustainable forage and regeneration. On the other hand, competition effects of softwood species with economically relevant tree species (especially potential losses on wood production) would be intensively studied in near future. Another alternative to maintaining and managing softwood broadleaved species within economically important stands might in growing these species on dedicated plots with the primary mission of providing forage for large wild herbivores and luring them from economically valuable forest stands grown in the vicinity.

In general, wildlife habitat management has a central goal to increase the carrying capacity of a particular habitat by providing an appropriate plant species composition and sufficient water resources for animals throughout a year. Here, also softwood broadleaved species can play an important role. However, under the current situation in Slovakia characterized by an extremely high population density of large wild herbivores, their continuous reduction by hunting activities would be the most efficient way. This reduction of population would definitively decrease the damage on a variety of plants and mitigate economical loses in forestry and agricultural sectors.

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Attachment



Fig. A1. Examples of intense browsing of the stem section 51–100 cm on young trees of common rowan (left photo) and goat willow (right photo) by large wild herbivores; the Husárik research area; Javorníky Mts., Slovakia. These wounds were caused by winter browsing since teeth prints are well seen and the bark is not completely removed from wood.