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Quantifying edible biomass on young Salix caprea and Sorbus aucuparia trees for Cervus elaphus: estimates by regression models

Quantifizierung der Biomasse von jungen Salweiden (Salix caprea) und Ebereschen (Sorbus aucuparia) die für Cervus elaphus genießbar ist: eine Bestimmung durch Regressionsmodelle

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Keywords: Red deer, Browsing, Forage potential, Goat willow, Rowan, Tree components

Schlagworte: Rothirsch, Verbiss, Äsungspotential, Salweide, Eberesche, Baumbestandteile

Abstract

Goat willow (*Salix caprea*) and rowan (*Sorbus aucuparia*) species are the preferred forage for large herbivores including red deer (*Cervus elaphus*). Both species could be considered as suitable biological control for mitigating damage to commercial tree species. Research activities focused on a post-disturbance area that originated after an intensive windstorm in the Tatra National Park (Slovakia). We estimated edible biomass specifically; leader shoot, branches, foliage and stem bark in young trees of willow and rowan. Regression models of edible biomass on a tree level were

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constructed. They covered forage by particular tree components as well as forage by groups of components associated with forage availability for deer in the winter and growing season. In willow, the maximum feed potential (251 g and 361 g for winter and growing season, respectively) were found for individuals with diameter at stem base d_0 of 41 mm. In rowan, the maximum feed potential (315 g and 322 g for winter and growing season, respectively) occurred for individuals with d_0 of 80 mm. The feed potential was lower in rowan than in willow for trees with d_0 up to 50 mm, and the opposite situation occurred in larger trees. In future, feed potential modelling could be implemented in evaluating the carrying capacity of biotopes for red deer.

Zusammenfassung

Sal-Weiden (*Salix caprea*) und Eberschen (*Sorbus aucuparia*) sind bevorzugte Äsungspflanzen für Großherbivoren einschließlich des Rothirsches (*Cervus elaphus*). Beide Baumarten können als geeignete biologische Kontrolle für die Verminderung von Wildschäden an kommerziellen Baumarten berücksichtigt werden. Die Forschungsaktivitäten fokussierten sich auf eine Schadfläche die durch einem intensiven Sturm im Nationalpark Tatra (Slowakei) entstanden ist. Wir bestimmten die vom Rothirsch verwertbare Biomasse, speziell Haupttriebe, Zweige, Belaubung und Stammrinde von jungen Salweiden und Ebereschen. Die Regressionmodelle für die vom Rothirsch verwertbare Biomasse wurden aufbauend auf ein Einzelbaumlevel erstellt. Sie berücksichtigten Äsungspflanzen durch einzelne Baumbestandteile ebenso wie Äsungspflanzen von Gruppen der Komponenten verbunden mit der Verfügbarkeit von Äsungspflanzen für Rothirsche im Winter und in der Wachstumsperiode. Für die Salweide betrug das maximale Äsungspotenzial 251 g im Winter und 361 g in der Wachstumsperiode für Individuen mit einem Durchmesser an der Stammbasis d_0 von 41 mm. Für die Eberesche war das maximale Äsungspotential 315 g im Winter und 322 g in der Wachstumsperiode für Individuen mit einem d_0 von 80 mm. Das Äsungspotential war geringer für Eberesche als für Salweide für Bäume mit einem d_0 kleiner als 50 mm, und das Gegenteil trat für größere Bäume ein. Zukünftig kann die Modellierung des Äsungspotenzials in die Auswertung der Tragfähigkeit von Biotopen für Rothirsche einfließen.

1. Introduction

Both goat willow (*Salix caprea*) and rowan (*Sorbus aucuparia*) are not considered important for commercial purposes due to their stem characteristics, especially their irregular shape, frequent forking, multi-stem formation and wood properties. However, they are common species types with modest ecological demands that allow them to occupy less desirable sites such as post-disturbance areas. Their presence improves soil conditions and micro-climate properties creating favorable conditions that promote the establishment of other tree species (Myking et al., 2013).

In Slovakia, the distribution of goat willow ranges from the lowlands to the mountainous regions, up to altitudes of between 1300 and 1400 m a.s.l. In contrast, rowan is also distributed from lowlands, up to very high altitudes of nearly 2,000 m a.s.l. (Pagan and Randuška, 1987). It is well documented (e.g. Shipley et al., 1998; Månson et al., 2007; Jager and Pastor, 2010; Finďo and Petráš, 2011; Myking et al., 2013) that goat willow and rowan together with aspen (*Populus tremula*) are tree species identified as the preferred forage for large herbivores including red deer (*Cervus elaphus*). Thus, as species identified as attractive for large herbivores (i.e. ungulate ruminating game), with good regeneration capacity and are fast growing; they can increase the carrying capacity of biotopes (hunting grounds). Therefore, their presence might reduce damage by ungulate ruminating game (biological control) to commercial trees (e.g. Čermák et al., 2009).

In European temperate forests, red deer is a largest herbivore with high forage (tree biomass) requirements for food, including leader shoot, branches, foliage and bark. Hell et al. (2000) showed that red deer consumed daily between 1.2 kg (calf) and 3.0 kg (adult) of biomass expressed as dry matter. Contribution of tree biomass depends on landscape characteristics. For example, Finďo et al. (1993) showed that for mountainous areas in Central Slovakia (specifically the Poľana Mts. and Sitno Mts.), biomass of forest trees represented as much as 79% of total forage. Similarly, Prokešová (2004) calculated that tree biomass contributed to 71% of total red deer feed in wetland forests in the southern part of Moravia (Czech Republic). For other region of the Czech Republic, Fišer and Lochman (1969) estimated a much lower share (between 6% and 29%) of red deer forage was allocated to tree biomass. However, this data came from landscapes with low proportions of forest covers. Composition of red deer feed also changes relative to seasonally and availability of particular forage, e.g. wood plants from 40% of total forage during the growing season to nearly 90% of total forage during the winter season (Jamrozy, 1980; Homolka, 1990).

Red deer can cause extensive damage to forest stands including damage to leader shoots (terminal part of stem), branch and foliage browsing and bark stripping (e.g. Heroldová et al., 2003; Kiffner et al., 2008; Čermák et al., 2009; Iszkulo et al., 2014 and others). However, there are not any studies detailing potential edible tree biomass by red deer using tree biomass models constructed by components for young (small) trees (such biomass models can be found in Wirth et al., 2004; Pajtík et al., 2008 and few others). So far, perhaps only one study by Konôpka et al. (2012) estimates forage resources in young trees, specifically in European ash (*Fraxinus excelsior*). This is a problem because there is an increase in red deer population in most of the countries in Central Europe (Milner et al., 2007). Red deer browsing in the forest creates not only economic loss but also, in some regions, ecological loss by threatening the biodiversity of biotopes (Schulze et al., 2014).

The aim of this paper is to construct models for the estimation of edible tree biomass (leader shoot, branches, foliage and bark) by red deer in young goat willow and rowan using regression models. Also, to analyze inert-specific differences in forage resources between goat willow and rowan and to compare these results to other broadleaved species in young growth stages.

2. Material and Methods

2.1. Site description

Research activities focused on a post-disturbance area that originated after an intensive windstorm on 19th November 2004 in the Tatra National Park (TNP, hereinafter). The disturbance affected approximately 12,000 ha of Norway spruce (*Picea abies*) dominated forest in the TNP (Koreň, 2005). The storm mostly damaged forests between low and intermediate altitudes (between 700 and 1,400 m a.s.l.) in the TNP with over 80% of all damaged trees located in a continual belt, approximately 35 km long and 5 km wide, oriented in a west-east direction (Šebeň, 2010). The forest soils consist mainly of cambisols and podzols and the bedrock is predominantly formed of granodiorit. The climate is characterized by low mean annual temperatures (around 4.0°C), high precipitation (nearly 1,000 mm) and 140 days of snow cover (Vološčuk et al. 1994). The fauna in the TNP is abundant, particularly the diversity of birds and mammals. The red deer is the most frequent ungulate species and inhabits almost the entire area of the TNP, ranging from the low altitudes, adjacent to agricultural land, to the tree line (Vološčuk et al. 1994). In 2014, density of red deer in the TNP was 16 per 1000 hectares. This means the population density has doubled during the last fifteen years (Dr. Peter Kaštier – pers. comm.).

During 2012 and 2013 (the eighth and ninth growing seasons post-disturbance), the areas were prevailingly covered by young forest that originated from both natural regeneration and planting. Pioneer broadleaved tree species such as goat willow, rowan and aspen natural regeneration prevailed over few coniferous species e.g. Norway spruce, Scots pine (*Pinus sylvestris*), European larch (*Larix decidua*) and silver fir (*Abies alba*; Šebeň, 2010). However, plantations of conifer species, including sycamore maple (*Acer pseudoplatanus*) were common. Open areas among the young forest stands were covered by grasses (e.g. *Calamagrostis* sp., *Avenella flexuosa*, *Luzula* *luzuloides*), herbs (e.g. *Epilobium angustifolium, Senecio nemoralis*) and shrubs (mostly *Rubus idaeus, Vaccinium myrtillus*).

2.2. Field and laboratory work

Filed work was performed in the territories of Smokovce, Tatranské Matliare and Vyšné Hagy which are all Protective Units and belong to the State Forests of the TNP. Preliminary, young forest stands were identified for potential sampling and were chosen in collaboration with employees at the State Forests of the TNP. Individual trees (100 trees of each species) of different dimensions covering height interval from cca 0.5 m to approx. 4.5 m were selected. The trees were selected from 14 forest stands with both willow and rowan trees present. The forest stands were located within the post-disturbance area between an altitudinal range of approx. 820 and 1040 m a.s.l. Another criterion for the selection of sampled trees was none (or negligible) damage caused by red deer browsing. However, this was challenging as most of the willow and rowan trees (approx. two thirds of all trees) in the stands were affected by browsing.

Each tree was cut by handsaw at the ground level and a code number was marked on the stem base using permanent marker. Tree height and diameter d_0 (at stem base) were measured. Foliage and branches were divided into two groups: potentially edible biomass and inedible (or unreachable) biomass for red deer. These two groups were defined in accordance to previous results (see also Konôpka et al., 2012). Specifically, branches situated above 2.0 m from the ground level and/or with a diameter exceeding 10 mm were inedible (unreachable). Branches and foliage were identified, cut by garden shears and packed separately into paper bags. Similarly, stems were also packed into bags. The stems were defined as a main axis of trees, including range from the ground level to the terminal point. Trees with a clear main stem were included in the analysis and we avoided multiple-stem individuals. All bags were labeled by code number and component specification, i.e. edible foliage and branches, inedible foliage and branches, stem with bark.

The bags containing the samples were transported to the laboratory. The stems were divided into approximately 50 cm-long sections and if trees were under 150 cm in height they were divided into three equal sections. Three diameters were measured on each section; the middle and the diameter at both ends. These measurements were used to calculate the surface of stem sequences. Stems were debarked and both bark and stem were packed separately. After few days, when foliage dropped from the branches, for each tree we separated and identified the following sub-compartments: edible foliage, edible branches, inedible foliage, inedible branches, bark (from stem) and debarked stem. The samples were oven-dried at temperatures below 95°C for five days and weighed at a precision of 0.1 g.

2.3. Calculations and constructions of models

The data measured on sample trees were used to construct allometric equations for tree compartments using stem diameter d_0 as an independent variable. Constructions of models for quantification of biomass in tree components were based on allometric relationships which are described in e.g. Pajtík et al. (2008) and Konôpka et al. (2010). More details on the procedure followed for the calculations and the construction of the models, including formulas 1-14, are given in Appendix 1.

Regression models were constructed and statistical analyses were performed in Statistica 10.0 and R (R Development Core Team 2012). The regression functions with parameter estimates and goodness of fit are expressed by the coefficient of determination and are presented for each model.

3. Results and discussion

Diameter d_0 of sampled goat willows is between 3.7 and 68.7 mm with a height ranges from 0.49 to 4.50 m (Table 1). As for rowan trees, diameters d_0 are between 5.0 and 81.0 mm and the height ranges from 0.41 up to 4.86 m (Table 2). Consumable biomass in willow ranges between 0.4 and 249 g for branches and from 0.8 to 186 g for foliage. Consumable biomass in rowan is between 0 and 325 g for branches and between 1.6 and 244 g for foliage. Since all allometric models are based on diameter d_0 (considered the best predictor for biomass estimates but not a common characteristic in forestry), the relationship between the diameter and tree height was expressed (Fig. 1a and 1b). The inter-specific comparison shows that rowan trees were slightly taller than willow trees with the same stem thickness (diameter d_0).

Table 1: Descriptive statistics for characteristics measured on the sample trees for goat willow

Characteristics	Mean	Median	Min.	Max.	Lower quartile	Upper quartile	Standard deviation	Standard error	Skewness
Diameter d_0 (mm)	25.0	22.6	3.7	68.7	14.6	33.3	13.2	1.3	1.023
Tree height (m)	2.04	2.03	0.49	4.50	1.38	2.37	0.85	0.08	0.806
Branch biomass (g)	106	43	0.4	1186	13	120	173	17	3.526
Biomass of edible branches (g)	55	38	0.4	249	13	74	54	5	1.367
Foliage biomass (g)	78	47	0.8	467	20	110	87	9	2.175
Biomass of edible foliage (g)	47	39	0.8	186	17	63	40	4	1.492
Biomass of stem underbark (g)	153	75	0.7	1258	20	160	240	24	3.100
Bark biomass on stem (g)	45	27	0.5	265	9	54	54	5	2.365

Table 2: Descriptive statistics for characteristics measured on the sample trees for rowan

Characteristics	Mean	Median	Min.	Max.	Lower quartile	Upper quartile	Standard deviation	Standard error	Skewness
Diameter d_0 (mm)	36.7	33.2	5.0	81.0	17.6	53.7	21.4	2.2	0.337
Tree height (m)	2.82	2.74	0.41	4.86	1.78	3.99	1.21	0.12	-0.116
Branch biomass (g)	293	103	0.5	2715	10	374	478	52	2.812
Biomass of edible branches (g)	51	30	0.0	325	7	82	62	6	2.299
Foliage biomass (g)	170	70	1.6	916	19	283	202	21	1.622
Biomass of edible foliage (g)	27	18	1.6	244	9	32	33	3	3.805
Biomass of stem underbark (g)	626	319	1.9	2749	59	1003	690	72	1.132
Bark biomass on stem (g)	117	74	1.3	419	23	190	111	11	0.908

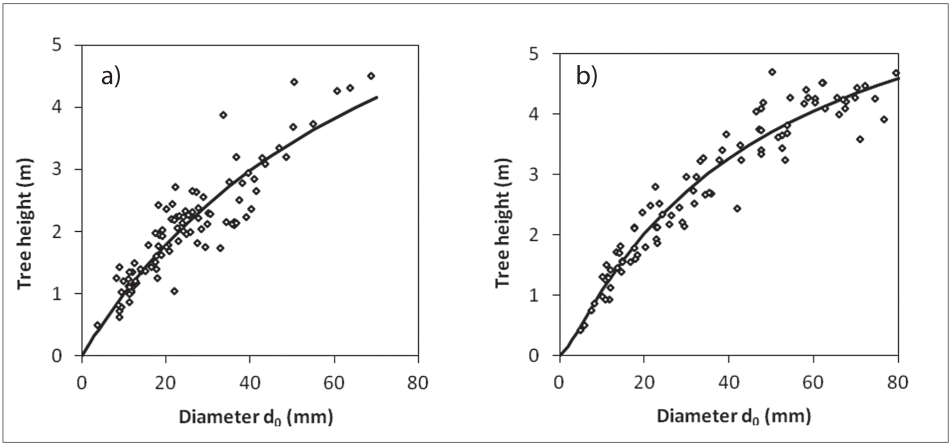

Fig. 1: Relationship between diameter d_0 and tree height in (a) goat willow and (b) rowan

The inter-specific differences between biomass of the specific tree components were relatively small (Fig. 2a and 2b, Table 3 and 4). The largest differences occurred for stems (without bark) e.g. trees with diameter d_0 of 60 mm recorded biomass values of 913 g in willow and 1369 g in rowan. For bark, trees with diameter d_0 of 60 mm, bark biomass of 222 g was recorded in willow and 239 g in rowan. At the same time, 60-mm-thick trees recorded branch biomass of 699 g and 629 g in willow and rowan, respectively, and further, retained 365 g of foliage on willow and 338 g of foliage on rowan. The willow and rowan trees show very similar bark biomass relative to similar stem surface and/or similar bark thickness. Our analyses suggest that bark thickness, or biomass quantity per stem surface unit did not differ considerably between the species (Fig. 3a versus Fig. 3b). For instance, specific surface masses of bark in trees with diameter d_0 of 60 mm were 6.7 $g.dm^{-2}$ and 6.4 $g.dm^{-2}$ in willow and rowan, respectively.

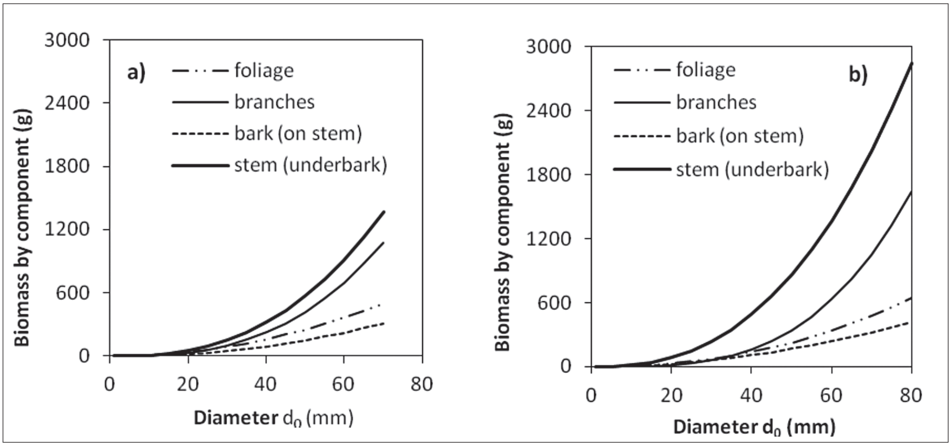

Fig. 2: Biomass by tree components against diameter d_0 in (a) goat willow and (b) rowan

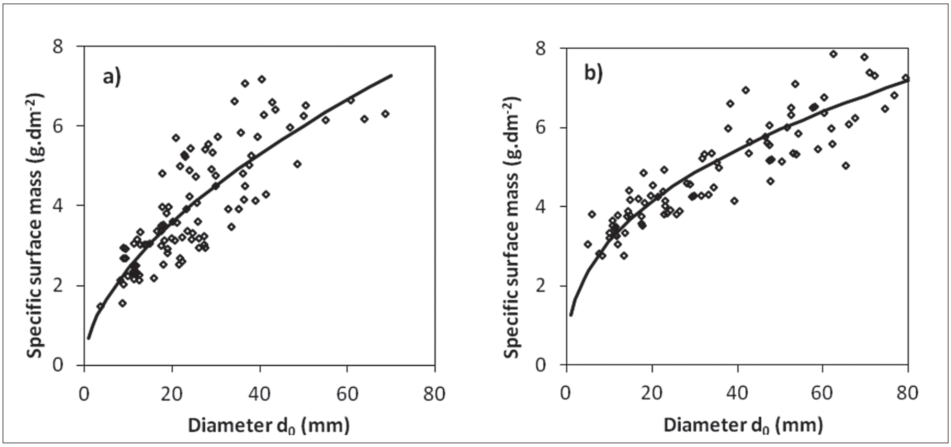

Fig. 3: Specific surface mass of bark against diameter d_0 in (a) goat willow and (b) rowan

Not all tree biomass is available as forage for red deer. Some parts of the trees can not be consumed by red deer because of branch thickness (branches and stem terminal thicker than 10 mm) or inaccessibility (usually for branch browsing over 2.0 m and for bark stripping over 1.8 m from the ground level; see for instance Konôpka et al., 2012). Fig. 4a and Fig. 4b demonstrate models describing the share of edible branches (foliage) to total tree biomass of branches (foliage) in both willow and rowan. While trees with diameter d_0 up to cca 30 mm provide nearly 100% of branches and foliage for red deer forage, consumable branch and foliage biomass sharply decreases with increasing diameter. Thus, in trees with diameter d_0 of 60 mm, the theoretically edible proportions of branches were 17.2% and 9.7% in willow and rowan, respectively. Similarly, theoretically edible proportions of foliage in trees with diameter d_0 of 60 mm were 11.0% and 9.9% in willow and rowan, respectively. These models show that in trees with diameter d_0 of 80 mm, the share of edible branches and foliage is only approximately 3 - 4% of total component biomass.

Table 3: Regression models for B_s – stem biomass; B_b – branch biomass; B_f – foliage biomass; r_b – proportion of edible branch biomass to total branch biomass; r_f - proportion of edible foliage biomass to total foliage biomass; $d_{1.8}$ – stem diameter located 1.8 m from ground level; h_{10} – distance from ground level to spot where stem diameter equals 10 mm; w_s – specific surface area of bark; B_{ebark}- biomass of edible bark in goat willow. All variables are expressed on diameter d_0 as an independent variable.

Eq.	Dependent variable	b_1 (S. E.) P	b_2 (S. E.) P	R^2	MSE	λ	S. D.
(1)	B_s	-3.178 (0.189) <0.001	2.479 (0.061) <0.001	0.945	0.107	1.048	0.306
	B_b	-5.018 (0.236) <0.001	2.807 (0.075) <0.001	0.935	0.166	1.078	0.403
	B_f	-2.409 (0.206) <0.001	2.015 (0.066) <0.001	0.906	0.127	1.061	0.360
(3)	r_b	8.848 (1.207) <0.001	-0.200 (0.029) <0.001	0.524	0.017	–-	–-
	r_f	8.461 (1.259) <0.001	-0.193 (0.030) <0.001	0.452	0.023	–-	–-
(10)	$d_{1.8}$	-8.103 (1.273) <0.001	0.542 (0.037) <0.001	0.791	11.287	–-	–-
(12)	h_{10}	-0.421 (0.078) <0.001	0.063 (0.003) <0.001	0.863	0.103	–-	–-
(13)	w_s	0.675 (0.093) <0.001	0.559 (0.041) <0.001	0.679	0.663	–-	–-
(14)	B_{ebark}	-66.085 (1.164) <0.001	3.706 (0.034) <0.001	0.995	8.700	–-	–-

Note: abbreviations in the table captions means; b_1, b_2 - coefficients, R^2 - coefficient of determination, MSE - mean square error, λ - logarithmic transformation bias, and SD - its standard deviation.

In fact, while inter-specific comparisons between willow and rowan indicate little difference in biomass of specific tree components, differences occurred in their availability for red deer. Smaller inter-specific differences were found for branches (Fig. 4a) compared to foliage (Fig. 4b). Thus, there is a difference in biomass between theoretically edible branches and foliage in willows and rowans (Fig. 5a versus Fig. 5b). Biomass of edible branches in willow shows a steep increase with diameter d_0 compared to rowan. On the other hand, after reaching a peak, edible branch biomass decreases quicker in willow than in rowan. While maximum edible branch biomass (163 g) was found for willows with diameter d_0 of 41 mm, in rowan the maximum value (108 g) occurred at d_0 55 mm. Similarly, biomass of edible foliage in willow manifests a steeper increase in diameter d_0 compared to rowan. Then, after reaching a peak, the decrease of edible foliage biomass is steeper in willow than it is in rowan. Maximum edible foliage biomass (113 g) was found with diameter d_0 of 40 mm for willow while in rowan the maximum value (55 g) occurred for diameter d_0 of 39 mm.

While the amount and course of edible branches and foliage differs between species, edible leader shoot were similar in both species (Fig. 5a versus Fig. 5b). The figures clearly show that tree dimensions influence the proportions of biomass available for browsing (leader shoot, branches and foliage) and bark stripping. In both species, contribution of bark (possibly consumable for red deer stripping) ranges from negligible values in small trees to 60 – 70% in the largest trees.

Table 4: Regression models for B_s – stem biomass; B_b – branch biomass; B_f – foliage biomass; r_b – proportion of edible branch biomass to total branch biomass; r_f - proportion of edible foliage biomass to total foliage biomass; $d_{1.8}$ – stem diameter located 1.8 m from ground level; h_{10} – distance from ground level to spot where stem diameter equals 10 mm; w_s – specific surface area of bark; B_{ebark}- biomass of edible bark in rowan. All variables are expressed on diameter d_0 as an independent variable.

Eq.	Dependent variable	b_1 (S. E.) P	b_2 (S. E.) P	b_3 (S. E.) P	R^2	MSE	λ	S. D.
(1)	B_s	-2.515 (0.088) <0.001	2.412 (0.025) <0.001	–-	0.990	0.028	1.014	0.171
	B_b	-7.336 (0.312) <0.001	3.334 (0.090) <0.001	–-	0.943	0.280	1.138	0.596
	B_f	-3.383 (0.161) <0.001	2.237 (0.046) <0.001	–-	0.962	0.096	1.047	0.322
(4)	r_b	2.411 (0.181) <0.001	-0.068 (0.005) <0.001	–-	0.772	0.026	–-	–-
	r_f	2.288 (0.226) <0.001	-0.073 (0.006) <0.001	–-	0.635	0.020	–-	–-
(10)	$d_{1.8}$	-5.660 (0.968) <0.001	0.592 (0.020) <0.001	–-	0.931	8.490	–-	–-
(11)	h_{10}	-0.0009 (0.0001) <0.001	0.130 (0.007) <0.001	-1.153 (0.129) <0.001	0.951	0.082	–-	–-
(13)	w_s	1.253 (0.110) <0.001	0.398 (0.023) <0.001	–-	0.789	0.439	–-	–-
(14)	B_{ebark}	-53.687 (1.445) <0.001	3.643 (0.029) <0.001	–-	0.996	15.900	–-	–-

Note: abbreviations in the table captions means; b_1, b_2, b_3 - coefficients, R^2 - coefficient of determination, MSE - mean square error, λ - logarithmic transformation bias, and SD - its standard deviation.

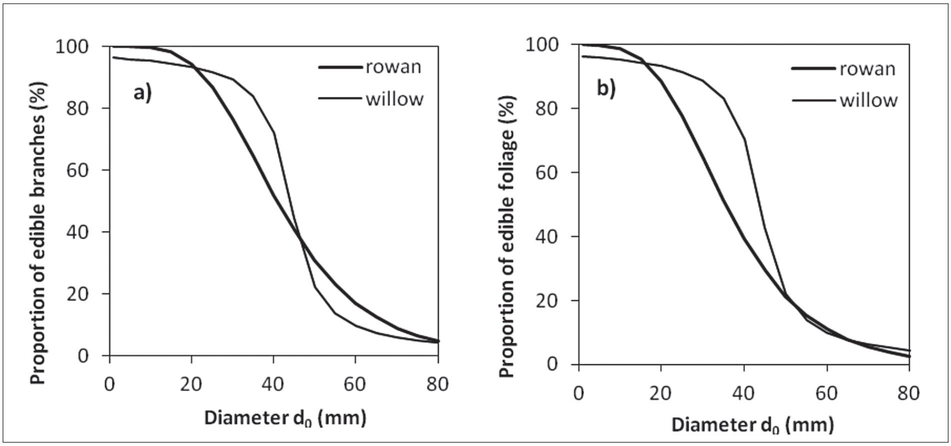

Fig. 4: Proportion of (a) edible branches to total branch biomass and (b) edible foliage to total foliage biomass in both goat willow and rowan

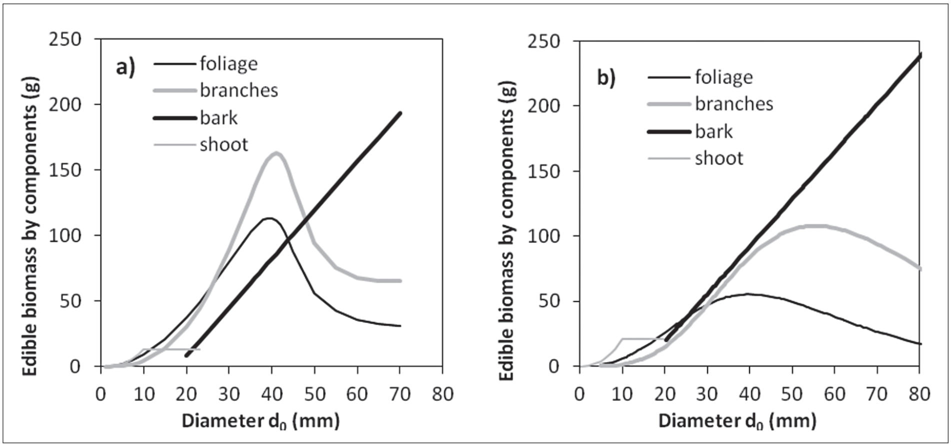

Fig. 5: Edible biomass for foliage, branches, bark (on stem) and leader shoot in (a) willow and (b) rowan

Forage potential on willow and rowan biomass was expressed for winter (includes edible leader shoot, branches and bark; Fig. 6a) and growing season (edible leader shoot, branches, foliage and bark; Fig. 6b). Inter-specific comparisons between willow and rowan show contrasting results for edible potential in both the winter and growing season. While in willow the maximum values (251 g and 361 g for winter and growing season, respectively) were found for individuals with diameter d_0 of 41 mm, in rowan the maximum (315 g and 322 g for winter and growing season, respectively) occurred for trees with a diameter d_0 of 80 mm. The results on total feed potential for the winter and growing seasons suggest that differences are small between willow and rowan. However, it is worth explaining that red deer usually exploit branch and foliage browsing more intensively than bark stripping. For instance, Konôpka et al. (2012) showed that in young stands of European ash, red deer consumed between 25% and 86% of branch and foliage edible potential, while bark striping only occurred on up to 4.2% of total available biomass. Hence, foliage and especially branches in young forest stands are more important for the carrying capacity of hunting ground than stem bark. As for seasonal changes in tree biomass (presence or absence of foliage in crown), branches are the most important feed resource, especially in winter time during periods of snow cover. For instance, Homolka (1990) showed that composition of red deer diet in forest environment fluctuated during the year. While woody plants contributed to 40% of total forage during the growing season, in winter this proportion was nearly 90%. If an average daily edible biomass of 3 kg per adult red deer is considered (see Hell et al., 2000), our model suggest that approx. 30 individuals of willow or rowan trees (in the case of 100%-exploitation of edible branches) with diameter d_0 around 50 mm might provide sufficient diet during the winter season. In reality, this "daily damage" to trees is very probably much higher (only some part of consumable potential on individual trees is eaten) especially if deer game does not have any other forage resources (e.g. during periods of snow cover without supplementary feeding). If we consider current red deer population density in the TNP, 16 individuals per 1000 hectares, "mean annual feed demand" of red deer might equal 17 kg of dry mass per hectare. Thus, this amount of dry mass represented as edible biomass (winter aspect) is approx. 170 trees of willow or rowan with diameter d_0 around 50 mm.

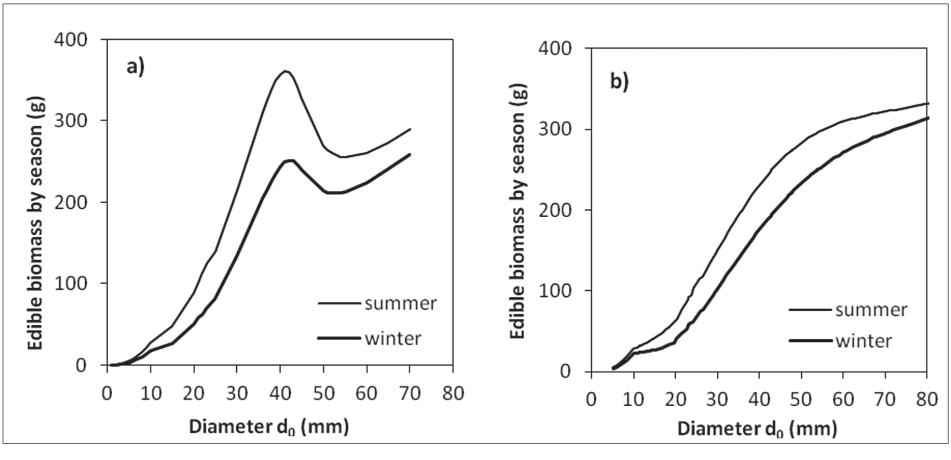

Fig. 6: Edible biomass by season, i.e. summer (growing season) and winter for (a) goat willow and for (b) rowan

The preference of willow and rowan biomass for red deer diet was identified by Kaštier and Bučko (2011) who surveyed damage by red deer browsing (specifically leader shoot and branches) to young post-disturbance stands in TNP. They showed a higher percentage of browsed trees in rowan (72.9%) compared to goat willow (50.7%) and silver fir (Abies alba; 50.6%). All other species (Norway spruce, European larch, Scots pine and silver birch) were less frequently damaged by browsing. To understand interactions between red deer and forest ecosystems, knowledge on attractiveness (quality) of different tree species for deer forage, as well as information about edible biomass (quantity) on specific tree species are necessary. Our previous studies (see Pajtík et al., 2011; Konôpka et al., 2015) focused on models for tree components in young trees of broadleaved species. These models for trees of certain dimensions can be implemented for inter-specific comparisons of edible biomass between goat willow, rowan, sycamore maple, European beech (*Fagus slyvatica*), European ash, and sessile oak (*Quercus petraea*). In summary, branch (Fig. 7a) and foliage (Fig. 7b) models were constructed for trees with height up to 2.0 m as nearly 100% of their biomass would be theoretically available for red deer diet. The results indicate that goat willow recorded the largest biomass of both branches and foliage in tree height between 1.5 and 2.0 m, while the lowest biomass was for braches in maple and for foliage in oak. Rowan ranked among the species with mean branch and foliage biomass.

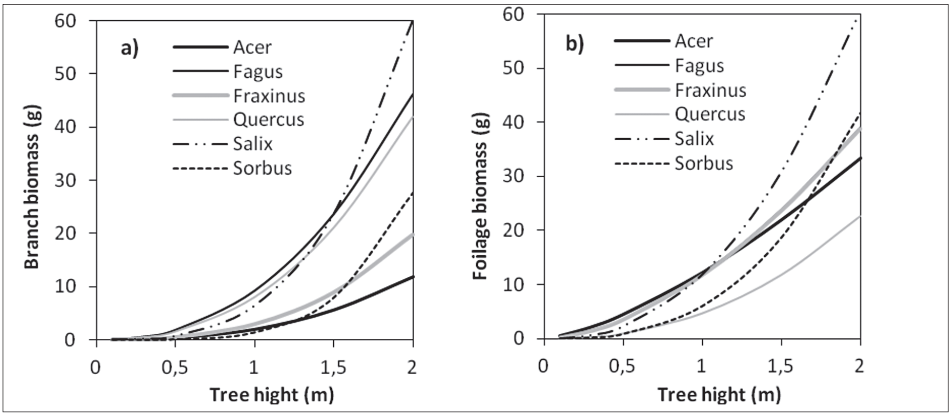

Fig. 7: Inter-specific comparison of (a) branch biomass, (b) foliage biomass for *Acer pseudoplatanus* (Konôpka et al., 2015), *Fagus sylvatica* (Pajtík et al., 2011), *Fraxinus excelsior* (Konôpka et al., 2015), *Quercus petraea* (Pajtík et al., 2011), *Salix caprea*, and *Sorbus aucuparia* against tree height

Feed potential modelling could be implemented to evaluate the carrying capacity of biotopes for red deer. However, to reach this aim, additional scientific knowledge is required. For instance, feed potential has to be quantified, not only for the main forest tree species (as we have done for willow and rowan in this paper) but also for other plants, i.e. shrubs, herbs and grasses co-existing in the areas that are edible for red deer. Further, more exact information relating to maximum branch browsing and bark stripping on commercial forest trees is required. Consequently, the knowledge would be utilized for decision-making on population density regulations of red deer game to avoid serious damage to forest stands (e.g. Augustine and McNaughton, 1998; Shipley et al., 1999).

4. Conclusions

Our results suggest that goat willow and rowan could enhance carrying capacity of forest biotopes for red deer. Both species are palatable for red deer, especially young goat willow provides above-average (compared to other broadleaved species) edible branch and foliage potential. Our estimates show that "winter" (leader shoot, branches and bark) and "summer" (leader shoot, branches, foliage and bark) feed potential was lower in rowan than for willow for small trees (up to diameter d_0 around 50 mm) with the opposite situation for larger trees. It is suggested that the traditional approach of foresters: the inclusion of willow and rowan in young stands, should be re-considered. In principal, both willow and rowan could be maintained within young stands in "reasonable" proportions alongside commercially important trees species. This is extremely important in the case of commercial species which are attractive for red deer browsing and stripping, e.g. silver fir, maple and ash in territories with a high population density of game. The presence of willow and rowan might present a suitable biological control for mitigating damage by red deer to commercial tree species.

Moreover, we suggest establishing and maintaining specific browsing plots to entice red deer away from threatened stands with commercially valuable trees, towards stands with a high proportion of willow and rowan trees. Combining these species ("two species are better than one") to establish browsing plots would create interspecific differences in development of edible potential with tree size and would also provide a diverse food resources. The browsing plots would preferably consist of individuals with variable dimensions to provide biomass for both browsing and bark stripping and fruit consumption from rowan.

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References

Akaike, H., 1974. A new look at the statistical model identification. IEEE Transactions on Automatic Control, 19, 716-723.

Augustine, D.J., McNaughton, S.J., 1998. Ungulate effects on the functional species composition of plant communities: herbivore selectivity and plant tolerance. Journal of Wildlife Management, 62, 1165-1183.

Cribari-Neto, F., Zeileis, A., 2010. Beta Regression in R. Journal of Statistical Software, 34, 1–24.

Čermák, P., Horsák, P., Spiřík, M., Mrkva, V., 2009. Relationship between browsing damage and woody species dominance. Journal of Forest Science, 55, 23-31.

Ferrari, S.L.P., Cribari-Neto, F., 2004. Beta Regression for Modelling Rates and Proportions. Journal of Applied Statistics, 31, 799-815.

Finďo, S., Farkaš, J., Hell, P., Katreniak, J., Žilinec, M., Stanovský, M., Hartl, G., 1993. Destabilizačné vplyvy jelenej zveri na les a zlepšenie jej obhospodarovania v CHKO Poľana. Zvolen, LVÚ.

Finďo, S., Petráš, R., 2011. Ekologické základy ochrany lesa proti poškodzovaniu zverou. Zvolen, NLC.

Fišer, Z., Lochman, J. 1969. Výsledky studia přirozené potravy jelení a srnčí zvěře. Sborník celostátní konference Myslivost – spárkatá zvěř, České Budějovice, pp 17 – 31.

Hell, P., Gašparík, J., Kartusek, V., Paule, L., Slamečka, J., 2000. Špeciálny chov zveri. Zvolen, TU vo Zvolene.

Heroldová, M., Homolka, M., Kramer, J., 2003. Breakage of rowan caused by red deer – an important factor for Sorbeto – Piceetum stand regeneration? Forest Ecology and Management, 181, 131-138.

Homolka, M., 1990. Food of *Cervus elaphus* in the course of the year in the mixed forest habitat of the Drahanská vrchovina Highlands. Folia Zoologica, 39, 1-13.

Iszkulo, G., Nowak-Dyjeta, K., Sekiewicz, M., 2014. Influence of initial light intensity and deer browsing on Taxus baccata saplings: a six years of field study. Dendrobiology, 71, 93-99.

Jager, N.R., Pastor, J., 2010. Effects of simulated moose *Alces alces* browsing on the morphology of rowan *Sorbus aucuparia*. Wildlife Biology, 16, 301-307.

Jamrozy, G. 1980. Winter food resources and food preferences of red deer in Carpathian forests. Acta Theriologica, 25, 221-238.

Kaštier, P., Bučko, J., 2011. Vplyv raticovej zveri na tatranské lesné ekosystémy poškodené veternou kalamitou. Zborník z medzinárodnej konferencie konanej 28. – 29. apríla 2011 v Novom Smokovci, pp 114-118.

Kiffner, C., Rössiger, E., Trisl, O., Schulz, R., Rühe, F., 2008. Probability of recent bark stripping damage by red deer (*Cervus elaphus*) on Norway spruce (*Picea abies*) in a low mountain range in Germany – a preliminary analysis. Silva Fennica, 42, 125-134.

Konôpka, B., Pajtík, J., Moravčík, M., Lukac, M., 2010. Biomass partitioning and growth efficiency in four naturally regenerated forest tree species. Basic and Applied Ecology, 11, 234-243.

Konôpka, B., Pajtík, J., Kaštier, P., Šebeň, V., 2012. Stanovenie dendromasy mladých jaseňov zožratej zverou pomocou alometrických modelov. Reports of Forest Research, 57, 283-294.

Konôpka, B., Pajtík, J., Šebeň, V., 2015. Biomass functions and expansion factors for young trees of European ash and Sycamore maple in the Inner Western Carpathians. Austrian Journal of Forest Sciences, 132, 1-26.

Koreň, M., 2005. Život nezanikne, iba sa zmení forma jeho prejavu. Slovenské lesokruhy, 4, 6-9.

Månson, J., Kalen, C., Kjellander, P., Andren, H., Smith, H., 2007. Quantitative estimates of tree species selectivity by moose (*Alces alces*) in a forest landscape. Scandinavian Journal of Forest Research, 22, 407-414.

Milner, J.M., Nilsen, E.B., Andreassen, H.P., 2007. Demographic side effects of selective hunting in ungulates and carnivores. Conservation Biology, 21, 35-47.

Myking, T., Solberg, E.J., Austrheim, G., Speed, J.D.M., Bohler, F., Astrup, R., Eriksen, R., 2013. Browsing of sallow (*Salix caprea* L.) and rowan (*Sorbus aucuparia* L.) in the context of life history strategies: a literature review. European Journal of Forest Research, 132, 399-409.

Pagan, J., Randuška, D., 1987. Atlas drevín (Pôvodné dreviny). Obzor, Bratislava.

Pajtík, J., Konôpka, B., Lukac, M., 2008. Biomass functions and expansion factors in young Norway spruce (*Picea abies* [L.] Karst) trees. Forest Ecology and Management, 256, 1096-1103.

Pajtík, J., Konôpka, B., Lukac, M., 2011. Individual biomass factor for beech, oak and pine in Slovakia: a comparative study in young naturally regenerated stands. Trees, 25, 277-288.

Prokešová, J., 2004. Red deer in the floodplain forests: the browse specialist? Folia Zoologica, 53, 293-302.

R Development Core Team, 2012. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL http://www.R-project.org/.

Shipley, L.A., Blomquist, S., Danell, K., 1998. Diet choices made by free-ranging moose in northern Sweden in relation to plant distribution, chemistry, and morphology. Canadian Journal of Zoology, 73, 1722-1733.

Shipley, L.A., Illius, A.W., Danell, K., Hobbs, N.T., Spalinger, D.E., 1999. Predicting bite size selection of mammalian herbivores: a test of a general model of diet optimization. Oikos, 84, 55-68.

Schulze, E.D., Bouriad, O., Wäldchen, J., Eisenhauer, N., Walentowski, H., Seele, C., Heinze, E., Pruschitzki, G., Danila, G., Marin, D., Hessenmöller, L., Bouriaud, L., Teodosiu, M., 2014. Ungulate browsing causes species loss in deciduous forests independent of community dynamics and silviculture management in Central and Southern Europe. Annals of Forest Research, 57, 267-288.

Šebeň, V., 2010. Prirodzená obnova po kalamite z novembra 2004 vo Vysokých Tatrách. In: Výskum smrečín destabilizovaných škodlivými činiteľmi. Zvolen, NLC, pp. 297-308.

Vološčuk, I. et al., 1994. Tatranský národný park. Gradus, Martin.

Wirth, C., Schumacher, J., Schluze, E.D., 2004. Generic biomass functions for Norway spruce in Central Europe – a meta-analyses approach toward prediction and uncertainty estimation. Tree Physiology, 24, 121-139.

Appendix 1. Procedure for constructions of models

A particular model was constructed to estimate the specific surface mass of bark (i.e. weight of bark from 1 dm² of stem surface). Specific surface mass of bark originated from data based on total bark biomass of the entire surface of stem. Allometric equations for biomass of tree components were based on the form:

$$B = e^{\left(b_1 + b_2 \ln d_0\right)} \lambda \quad (1)$$

where b_1, b_2 are coefficients and λ is logarithmic transformation bias.

Edible biomass on a tree level was quantified specifically for each tree components, i.e. leader shoot, branches, foliage, and stem bark. As for potentially edible branch biomass (B_{eb}) a relationship based on total biomass of branches (B_b) was implemented:

$$B_{eb} = B_b * r_b \quad (2)$$

where rb is the proportion of edible biomass of branches to the total biomass of branches. The proportion was calculated using data that originated from sample trees referring to branch biomass (both edible and total). Beta regression, proposed by Ferrari and Cribari-Neto (2004) was used to model the proportion of the part of a tree biomass eaten by a deer species. This type of regression is used for modelling continuous variables that assume values are in the standard unit interval, e.g. rates, proportions, or concentration indices. The model is based on the assumption that a response variable is beta-distributed. Moreover, the motivation to use beta regression lies in the flexibility delivered by the assumed beta law. The beta density can assume a number of different shapes depending on the combination of parameter values, including left- and right-skewed or the flat shape of the uniform density (Cribari-Neto and Zeileis, 2010).

The beta regression model is defined as:

$$g(\mu_i) = x_i^T \beta = \eta_i$$

where $\beta = (\beta_1, \ldots, \beta_k)^T$ is a $k \times 1$ vector of unknown regression parameters, $x_i = (x_{i1}, \ldots, x_{ik})^T$

are independent variables or co-variates and η_i is a linear predictor (i.e. $\eta_i = \beta_0 x_{i1} + ... + \beta_k x_{ik}$), and finally, *g(.): (0,1)* is a link function. In this study we tested the following link functions:

logit : exp(X * *β*)/[1 + exp(X * *β*)]; complementary loglog: 1 - exp[-exp(X * *β*)]; log: exp(X * *β*); and Cauchy: 1/2 + ATAN(X * *β*)/pi

To select the link function that best explain the variability and the shape of data distribution we employed the AIC method (Akaike, 1974).

A similar procedure was used for the edible biomass of foliage. However, the most suitable method for calculating proportion of edible branch (rb) and foliage biomass to total biomass of the components in goat willow is Cauchy function therefore this was implemented:

$$r_b(r_f) = \frac{\frac{1}{2} + arctg(b_1 + b_2 d_0)}{\pi} \qquad (3)$$

and for rowan loglog function:

$$r_b(r_f) = 1 - \exp(-\exp(b_1 + b_2 d_0)) \qquad (4)$$

To model edible biomass of leader shoot, it was assumed that browsing is limited by maximum distance 2.0 m from the ground level and stem diameter of 10 mm. This means that if a tree has diameter d_0 of up to 10 mm, theoretically the whole stem can be consumed by red deer. Therefore, the edible biomass of the leader shoot is equal to the total biomass of the stem (expressed by allometric equation). On the other hand, if diameter d_0 is large than 10 mm quantity of edible biomass of leader shoot does not increase but remains constant under the condition that volume of stem with diameter d_0 is conform with volume of leader shoot at the point of browsing equaling 10 mm:

$$B_{es} = B_s \qquad (5)$$

for $d_0 \leq 10$ mm ,

eventually $B_{es} = B_{s(10)}$ (6)

for d_0 >10 mm and $d_0 \leq d_{h=2}$, where $d_{h=2}$ is diameter conforming with spot on stem situated 2.0 m from the ground level.

As for modeling edible bark on stem, it is anticipated that red deer brows trees with minimum diameter d_0 of 20 mm and at the same time, bark browsing can reach a height up to the point where stem diameter (d_k) equals 10 mm and is a maximum distance up to 1.8 m from the ground level (see Konôpka et al., 2012). Biomass of edible stem bark (B_{ebark}) was calculated for individual sample trees using the formula:

$$B_{ebark} = S * w_s \tag{7}$$

where S is area of edible bark and w_s is specific surface mass of bark.

The area (S) was calculated using the formula for surface of truncated cone with radius of lower base $r_{0.0}$, radius of upper base r_k and height h_k:

$$S = \pi(r_{0.0} + r_k).s, \text{ where } s = \sqrt{h_k^2 + (r_{0.0} - r_k)^2} \tag{8}$$

If stem diameter at 1.8 m is more than 10 mm, then h_k=1.8 m and the related diameter is expressed as:

$$r_k = \frac{d_{1.8}}{2} \tag{9}$$

On the other hand, if stem diameter at 1.8 m is less than 10 mm, then r_k in the formula (8) is equal to 5 mm and $h_k = h_{10}$. The relationship between diameter $d_{1.8}$ and diameter d_0 in both trees species was established from data measured on the sample trees and expressed by means of linear function:

$$d_{1.8} = b_1 + b_2 d_0 \tag{10}$$

Height h_{10} where rowan stem reaches a thickness of 10 mm was for rowan calculated by quadratic relationship:

$$h_{10} = b_1 d_0^2 + b_2 d_0 + b_3 \tag{11}$$

and for willow by linear function:

$$h_{10} = b_1 + b_2 d_0 \tag{12}$$

To express the relationship between specific surface mass of bark w_s and diameter d_0 the following allometric equation was used:

$$w_s = b_1 d_0^{b_2} \tag{13}$$

Then, calculated values B_{ebark} in both tree species were fitted by linear function:

$$B_{ebark} = b_1 + b_2 d_0 \quad \text{, for } d_0 \geq 20 \text{ mm} \tag{14}$$.