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Modelling forage potential for red deer: A case study in post-disturbance young stands of rowan

J. Pajtík, B. Konôpka, M. Bošel'a, V. Šebeň, P. Kaštier

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Abstract. Recently, the red deer (*Cervus elaphus*) population has increased considerably and caused serious damage in forest stands in Slovakia as well as in other Central-European countries. Rowan (*Sorbus aucuparia* L.) is the tree species that is most intensively browsed and stripped by deer, especially during young stages of tree development. Our research focuses on estimating rowan mass consumption by red deer in young stands which developed after large-scale wind disturbance that occurred in the Tatra National Park in 2004. New models were developed for estimating the mass of tree components that are potentially edible by red deer using tree-base diameter as an independent variable. The results showed that the mass contribution of particular tree components to accessible deer forage depended on tree size (tree-base diameter). At stand level, total forage potential increased with an increase in tree size. However, whereas the quantity of bark available for stripping increased with tree size, the total mass accessible for browsing (leader shoot and branches with foliage) decreased. For instance, the contribution of stem bark to total forage potential in stands with a mean tree-base diameter of 20 mm and 50 mm was 15% and 50%, respectively. Theoretically, if all tree mass potential is consumed by red deer, young rowan stands (considering tree coverage of 50%) growing within an area of 100 m^2 might provide sufficient forage for one adult deer for ca. 10 days. It is suggested that rowan species should not be removed from forest stands in territories with a high deer population in order to decrease the potential damage of other, commercially important, tree species.
Keywords *Cervus elaphus, Sorbus aucuparia,* browsing, bark stripping, feed potential.

Authors. Jozef Pajtík, Bohdan Konôpka (bkonopka@nlcsk.org), Michal Bošeľa - National Forest Centre, Forest Research Institute Zvolen, T. G. Masaryka 22, 960 92 Zvolen, Slovak Republic; Czech University of Life Sciences Prague, Faculty of Forestry and Wood Sciences, Kamýcká 176, 165 21 Praha 6 - Suchdol, Czech Republic; Vladimír Šebeň, Peter Kaštier - National Forest Centre, Forest Research Institute Zvolen, T. G. Masaryka 22, 960 92 Zvolen, Slovak Republic.
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Introduction

In general, the presence of red deer (*Cervus elaphus*) as one of the most common, large-intermediate feeding herbivores in forested areas cause conflicts between forestry interests and wildlife management because the species produce intensive damage to forest stands due to browsing and bark stripping (Gill 1992). For instance in Slovakia, the degree of forests damaged by game is significant and can be attributed to red deer over-population. Estimates of the red deer population in 2000 was approximately 33,000, whereas the estimated population in 2010 was as high as 51,000 (Bučko et al. 2011). Repeated selective browsing by red dear not only delays forest regeneration, but also dramatically alters tree species composition (e.g. Motta 2003). Bark stripping causes a reduction in stem increment (Vasiliasukas 2001) and often results in biological damage, since de-barked stems are highly susceptible to pathogenic fungi (Kiffner et al. 2008).

In addition to browsing woody vegetation - i.e. foliage, small twigs and bark, red deer graze grasslands. The proportion of these two forage resources, browsing and grazing, depend, on the properties of the habitat (Trdan & Vidrih 2008). Renaud et al. (2003) suggested that the red deer is a selective herbivore for which food selection is determined not only by preferences associated with quality and taste, but also by the cost or effort of obtaining forage. For red deer grasses and low lying branches are the most easily accessible forage components. Therefore, it is assumed that young forest stands distributed over large-scale post-disturbance areas would be considered very attractive sites for obtaining forage, the young trees with branches situated close to the ground, easily accessible to red deer with patches of grass for resting and comfort behaviour (e.g. lying, ruminating and self-grooming). Such conditions exist in the marginal foothills of the High Tatra Mountains within the protective zone of the Tatra National Park, Slovakia. On the 19th of November 2004 a storm destroyed large areas of spruce-dominated forest in this region. In the subsequent two or three consecutive years, broken and uprooted trees were harvested and both natural regeneration and artificial reforestation occurred simultaneously. In addition to Norway spruce (*Picea abies*), prevailingly pioneer tree species such as rowan (*Sorbus aucuparia)*, white birch (*Betula pendula*), and sallow (*Salix caprea*) regenerated naturally within the affected area. In fact, Šebeň (2010) showed that nearly 21% of natural regeneration (expressed as the number of tree bases) in the post-disturbance area was comprised of rowan. Recently, serious game derived forest damage caused by red deer in young rowan stands in the Tatra National Park was reported (Kaštier & Bučko 2011).

Rowan is a native species distributed throughout Europe with the exception of southern Europe. According to the Atlas of Woody Plants (Pagan & Randuška 1987), rowan is a relatively rare tree species within Slovakia but however, it is present almost throughout the entire country (ranging from an altitude of 300 m to the tree line located ca 1,600 m and in a few isolated cases, up to 2,010 m a.s.l.). Rowan is a pioneer species and does not usually form typical even-aged and homogeneous stands. For example, the species is a stable component of mountain spruce complexes of *Sorbeto-Piceetum*, a forest type determined by Zlatník (1976), which is predominantly located at altitudes of between 1,250 and 1,550 m a.s.l. The commercial importance of rowan wood is low because of its growth characteristics (i.e. stem shape, stem forking, multi-stem growth and other wood properties). An ecological advantage of this species are the modest demands for nutrients and water, which make it able to colonise unfavourable sites, where the foliage litter of rowan subsequently improves soil properties (Myking et al. 2013). Even though the species is somewhat rare, a high abundance can be found in young stands of mixed coniferous-broadleaves species. Usually, multiple rowan trees develop post-disturbance events due to its rapid regeneration and growth; in such cases, the species can spread over large areas with rowan fruits widely distributed by birds (Paulsen & Högstedt 2002).

In terms of the intensity of game derived forest damage, rowan is one of the most frequently affected tree species. This is supported by data from the Slovak National Forest Inventory (NFI 2005-2006, unpubl. data), which indicates that more than 15% of rowan trees, expressed per unit area, were damaged due to game browsing (the mean intensity of game damage for all tree species was 2.8%). The most intensively damaged rowan trees were recorded at young growth stages, where nearly half of the trees were browsed or stripped. Similarly, Myking et al. (2013) showed that rowan and sallow were the preferred winter forage of red deer and moose in the Scandinavian Peninsula. In Germany, Eiberle & Bucher (1989) identified that rowan is an attractive food species for game and its local presence reduced browsing damage to commercial trees such as *Fagus sylvatica, Picea abies* and *Abies alba*. Thus, rowan is a suitable species to control game derived forest damage in young forest stands (see also Čermák et al. 2009). On the other hand, breakage of rowan by red deer can severely decrease the regeneration capacity of forest stands in *Sorbeto-Piceetum* stands (Heroldová et al. 2003).

The general aim of the paper is to analyse the red deer feeding and forage potential in rowan trees. Research was conducted im post-disturbance areas from the protected zone of the Tatra National Park. The specific objectives of this study were: (i) to quantify consumed tree biomass (leader shoot, branch, foliage browsing and bark) and (ii) to estimate the amount of forage potential for game, mainly red deer, in young rowan stands, at the branch, tree and stand level. To fulfil the aims, a procedure was developed to estimate consumed and potentially edible rowan biomass by red deer. The procedure is novel without having any analogy in the existing scientific papers. Also we consider that the procedure can be used in other forest tree species, in any region, with red deer presence.

Material and methods

Overview of site conditions

The total area of the Tatra National Park is nearly 74,000 ha, of which almost 21,000 ha is protected. The mountains show unique glacier features and the largest number of endemic species in the Carpathians. Moreover, the Tatra Mountains contain the highest summits of the Carpathian range, with 17 peaks over 2,500 m a.s.l. The prevailing forest soils are cambisols and podzols and the bedrock is predominantly formed of granodiorit. The climate is characterised 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 National Park 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 National Park, ranging from the low altitudes, adjacent to agricultural land, to the tree line, dominated by dwarf pine (*Pinus mugo*) (Vološčuk et al. 1994).

This study focuses on post-disturbance sites that were created during a significant, intense storm in 19 November 2004, wich destroyed a total of 12,000 ha of Norway spruce dominated forest within the Tatra National Park (Koreň 2005). The storm mostly affected intermediate and lower altitudes forests of the National Park, including the foothills and basin of the High Tatra Mountains. Approximately 10,000 ha of the destroyed area represented a relatively uninterrupted forest belt that extended 35 km long and 5 km wide, situated at an altitudinal range between approximately 700 and 1,400 m a.s.l. (Šebeň 2010). This storm event created some of the most significant forest damage in the history of Slovakia and was certainly the most destructive storm disaster documented within the Tatra National Park.

To quantify game consumption (almost exclusively by red deer) and forage-potential in rowan stands, field data was collected during the growing season in 2012. During that year, the post-disturbance areas were covered by young forest stands that originated mostly from natural regeneration with some areas artificially reforested between 2006 and 2008. Open areas among the young forest stands were dominated by grasses, herbs and shrubs, with a predominance of *Epilobium angustifolium, Calamagrostis* sp., *Avenella flexuosa*, *Luzula luzoloides, Senecio nemorensis, Rubus idaeus, Vaccinium myrtillus* mixed with other species (Máliš et al. 2013).

Data collection

Rowan stands were randomly selected from forest management plans (FMP) database in post-disturbance areas in the High Tatra region and young stands with minimum rowan tree species composition of 30% were identified. Field survey in the Tatra National Park within the target area (around 3.000 ha) with high proportions of rowan indicated more or less four different sub-areas typical with certain prevailing mean heights of stands. To cover entire range of tree heights of young rowan stands, 5 tree clusters in each sub-area were randomly selected (subareas A, B, C, D hereinafter). Further, 20 circle plots were established for detailed rowan measurements. The radius of the plots varied between 1.0–3.0 m depending on the stand density and included a minimum of 30 individual rowan trees. The plots were established among groups of trees where rowans dominated (90% of the tree species composition). Each tree in the plot was measured for height (h), stem diameter at 130 cm from the ground (dbh) and stem base diameter at ground level (diameter d_0 hereafter). In addition, game browsing, defined as leader shoot, branch with foliage browsing or bark stripping, was recorded. For leader shoot and branch browsing, the diameter at the browsing point and its distance from the ground were recorded. For bark stripping, the size (area) and upper and lower distance from the ground was recorded. In total, we measured over 800 rowan trees in all the plots. On each plot, canopy coverage (based on rowan tree crown projection) was estimated visually.

In addition to the circular plots, 90 sample trees with a diameter d_0 between 5 and 80 mm were selected to proportionally represent the entire range of stem diameters observed in the study area. The entire above-ground biomass was harvested and transported to the laboratory, where tree height and diameter (dbh and diameter d_0) were measured. Particular tree components (foliage, branches, bark and under-bark stem) were separated and packed into paper bags. Simultaneously, foliage and branches were divided into two groups: those that could potentially be consumed by red deer (within 0–200 cm from ground level and with a diameter of branches up to 1.0 cm) (Konôpka et al. 2012) and the rest, which was not accessible to red deer. For bark-stripping potential, the same 90 sample trees were used. All bark on the stems was considered from ground level to a height of 180 cm (e.g. Konôpka et al. 2012).

The samples were dried to constant weight in an oven at 95°C and were weighed to the nearest 0.05 g. The data was used to construct allometric equations for tree component masses using tree height and diameter d_0 as independent variables. A detailed description of the construction of models for tree components using allometric equations has previously been documented (Pajtík et al. 2008, Konôpka et al. 2010).

To obtain empiric material for constructing regression relationships between consumed dry mass (branch without foliage and branch with foliage) and diameter of the branch base, approximately 100 samples of excised branches with a base diameter up to 10 mm were randomly selected and used for modelling constraints.

Data analysis

Estimates of tree biomass were performed at three levels: branch level (BL), tree level (TL) and stand level (SL).

Edible mass *(B_e)* at the BL was estimated separately for two categories: branch without foliage (B_{eb}) and branches with foliage (B_{eb+ef}), using the diameter of branch at the broken point using the equations:

$$B_{eb}(BL) = b_1 d_b^{b_2} \quad (1a)$$

$$B_{eb+ef}(BL) = b_1 d_b^{b_2} \quad (1b)$$

where: d_b - the branch diameter at the point of breakage (independent variable); b_1, b_2 - regression coefficients to be estimated.

A regression equation of the same type was also used to estimate the specific surface mass of bark (w_s) based on the diameter d_0:

$$w_s = b_1 d_0^{b_2} \quad (2)$$

Allometric equations for the calculation of the dry mass of specific tree components were constructed for two independent variables: diameter d_0 and/or tree height (*h*). Since the tree diameter d_0 is not a conventional characteristic in growth modelling studies, curves were constructed to convert diameter d_0 to *dbh* and tree height.

Then, equations including diameter d_0 in the following form were used for the construction of models for all tree components, specifically stem *(B_s),* branches *(B_b)*, and foliage (B_f):

$$B(TL) = e^{(b_1 + b_2 \ln d_0)} \cdot \lambda \quad (3)$$

where: b_1, b_2 - regression coefficients; λ - correction coefficient.

Edible dry mass *(B_e)* at the TL was quantified separately for the particular components; branches, foliage, leader shoot and stem bark. The potential edible branch mass (B_{eb}) and foliage mass (B_{ef}) was calculated following the allometric equation related to branch mass (B_b) and foliage mass (B_f), the following equation was used:

$$B_e(TL) = B \cdot r \quad (4)$$

where: *r* (r_b and r_f) is the proportion of edible branch and foliage mass related to the total branch and foliage mass.

This proportion was calculated from the dry mass weight of both edible and non-edible branch fractions for each sampled tree.

Beta regression (Ferrari & Cribari-Neto 2004) was used to model the proportion of the tree mass consumed by red deer, with the diameter d_0 used as an independent variable. This type of regression is used for modelling continuous variables and assumes that values are in standard unit intervals e.g. rates, proportions or concentration indices. The beta regression model is defined as:

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

where $\beta = (\beta_1, ..., \beta_k)^{\mathrm{T}}$ is a k x 1 vector of unknown regression parameters; $x_i = (x_{i1}, ..., x_{ik})^{\mathrm{T}}$ are independent variables or covariates and η_i is a linear predictor (i.e. $\eta_i = \beta_1 x_{i1} + ... + \beta_k x_{ik}$), and finally $g(.): (0,1)$ is a link function. In this study, the following link functions were tested: logit $\exp(X \cdot \beta)/[1 + \exp(X \cdot \beta)]$, complementary loglog: $1 - \exp[-\exp(X \cdot \beta)]$, log: $\exp(X \cdot \beta)$ and Cauchy: $1/2 + \mathrm{atan}(X \cdot \beta)/\mathrm{pi}$.

To identify the link function that best explains the variability and shape of data distribution, the AIC criterion (Akaike 1974) was used. From this comparison, complementary loglog was identified as the best for these data and was subsequently selected for modelling:

$$r = 1\text{-}exp(\text{-}exp(b_1 + b_2 \cdot d_0)) \quad (5)$$

where r is the proportion of edible mass previously defined in equation (4). To model the edible part of the stem (i.e. leader shoot), it was assumed that the maximum distance from ground level for browsing is 200 cm and the maximum diameter d_0 is 1.0 cm after measurements for European ash (*Fraxinus excelsior)* and rowan plots (Konôpka et al. 2012). This means that for trees with a diameter d_0 lower than 1.0 cm, the entire dry stem mass can be consumed by red deer. Thus, in such trees, edible stem potential equates to the dry stem mass calculated using the allometric equation. Alternatively, if the diameter d_0 is greater than 1.0 cm, the amount of edible dry stem mass does not increase with stem diameter d_0. It is assumed that stem volume for trees with d_0 equal to 1.0 cm is approximately the same as the volume of leader shoot with the same diameter at the point of breakage by a red deer i.e.:

$$B_{es}(TL) = B_s(TL) \quad (6)$$

for $d_0 \leq 10$ mm

or $B_{es}(TL) = B_{s(10)}(TL) = 21.17$ g, (7)

where $B_{s(10)}$ is the dry stem mass from a thickness of 10 mm to the top for $10 < d_0 < 16.4$ mm (this diameter is approximately equivalent to a tree height of around 2 m).

To model the edible dry mass of tree bark, it is assumed that red deer do not strip trees with a diameter d_0 under 2.0 cm and that the maximum height of bark stripping is 180 cm from the ground as in the previous measurements in *F. excelsior* and rowan plots (Konôpka et al. 2012). First, the specific surface mass of bark (w_s) was estimated based on the diameter d_0 using equation (2).

The dry mass of edible stem bark (B_{ebark}) was then calculated for the individual sampled trees as:

$$B_{ebark}(TL) = S \cdot w_s \quad (8)$$

where: S - the area of edible bark; w_s - specific surface area of bark.

To calculate S, the equation for expressing the surface area of a blunted cone (frustum) with a radius of base $r_{0.0}$, radius of upper side $r_{1.8}$ and height of 180 cm was implemented. Edible dry mass of bark for each sample was calculated using equation (8). A point cloud, created by pairing the diameter d_0 with the dry mass of each sample, was fitted by the regression function (1), where the only independent variable is diameter d_0:

$$B_{ebark}(TL) = b_1 d_0^{b_2} \text{ , for } d_0 \geq 20 \text{ mm} \quad (9)$$

where b_1, b_2 are regression coefficients.

Equation (9) was used to estimate potential edible dry mass of bark only. In the case of estimating the currently consumed dry mass of bark equation (8) is used, in which S denotes the surface of the browsed area of bark.

The models were implemented for the 20 research plots to calculate the dry mass for leader shoot, branches, foliage, bark and all combined components actually consumed by red deer. Moreover, the models were used to estimate the forage potential or edible biomass of leader shoot, branches, foliage, bark and all combined components on the SL. Both actual forage consumed and forage potential per 100 m^2 were calculated, considering consistent rowan coverage (canopy projection) of 50%. For this model, a regression function (using method of least squares) that accurately approximate the empiric values measured for the plots was identified and from amongst the functions that were tested, the following functions were best suited:

For dry mass of edible foliage:

$$B_{ef}(SL) = b_1 d_{m0}^2 + b_2 d_{m0} \quad (10)$$

For dry mass of edible branches:

$$B_{eb}(SL) = \frac{d_{m0}^2}{b_1 d_{m0}^2 + b_2 d_{m0} + b_3} \quad (11)$$

For dry mass of edible leader shoot (modified from Warren 1980, Warren & MacWilliam 1981):

$$B_{es}(SL) = d_{m0}^{b_1} e^{b_2 d_{m0}} \quad (12)$$

For dry mass of edible bark:

$$B_{ebark}(SL) = b_1 d_{m0} + b_2 \quad (13)$$

For dry mass of all edible parts:

$$B_{etot}(SL) = b_1 d_{m0}^{b_2} \quad (14)$$

Schematic explanations of procedures for the estimation of consumed biomass and the construction of models to estimate edible biomass in rowan trees and stands are available in Supp. Info. I, II.

Regression models were constructed and all statistical analyses were performed in the Statistica 10.0 program and R program (R Development Core Team, 2012). The regression functions with parameter estimates and goodness-of-fit are expressed by the coefficient of determination (R^2) and are presented for each model.

Results

The mean tree diameter d_{m0} of the measured rowan stands varied between 5.1 and 45.5 mm and the mean tree height varied between 31 and 467 cm (Table 1). A high variability amongst the plots was also recorded for number of trees per hectare, approximately 11,000 to 66,000 individuals. Most plots with a high mean diameter (especially plot numbers 11–20) were composed not only of trees close to the mean size (i.e. height over 300 cm) but also by much smaller individuals. This means that there is the potential for trees within plots to be suitable for both branch browsing (small trees)

Table 1 Characteristics of the research plots in the rowan stands (average values ± standard deviation)

Subarea (A-D)	Plot number	Radius (m)	Coverage (%)	Tree density (10^3 pcs.ha^{-1})	Mean diameter d_{m0} (mm)	Mean height (cm)	Top height (cm)
A	1	3.0	10	20.5	5.1 ± 2.1	31.1 ± 12.6	40.4
	2	3.0	10	19.6	8.9 ± 3.7	72.9 ± 30.0	91.6
	3	2.0	35	66.0	10.6 ± 4.2	132.7 ± 58.4	168.8
	4	2.0	35	50.1	14.2 ± 4.8	152.3 ± 46.7	183.6
	5	2.0	20	29.4	15.4 ± 4.4	123.0 ± 39.4	154.7
B	6	1.4	75	60.1	21.8 ± 8.3	297.4 ± 76.1	340.7
	7	2.0	30	33.4	22.4 ± 11.8	274.3 ± 129.9	315.6
	8	1.5	35	43.9	22.5 ± 11.8	290.2 ± 111.4	313.3
	9	1.5	50	60.8	23.9 ± 15.1	306.6 ± 192.6	334.2
	10	2.0	75	45.4	23.6 ± 8.9	318.4 ± 90.7	375.5
C	11	1.2	85	75.2	23.1 ± 11.0	362.2 ± 153.5	406.4
	12	1.5	80	59.4	27.2 ± 12.3	369.9 ± 115.0	411.3
	13	1.5	50	35.4	27.6 ± 16.8	373.2 ± 176.7	402.0
	14	2.0	65	34.2	27.7 ± 10.1	365.3 ± 101.3	424.4
	15	3.0	20	11.3	36.7 ± 13.8	410.1 ± 103.4	456.7
D	16	1.3	85	52.7	36.0 ± 18.2	439.6 ± 199.7	506.7
	17	2.0	80	32.6	37.7 ± 14.8	464.3 ± 112.8	523.1
	18	2.0	60	23.1	40.6 ± 14.3	466.6 ± 108.9	525.8
	19	1.5	50	21.2	44.6 ± 14.8	430.7 ± 78.3	480.0
	20	1.0	75	25.5	45.5 ± 11.9	441.7 ± 59.7	475.0

Note. Top height represents the mean value from the 20% of the tallest trees in the stands.

and bark stripping (large trees).

Regression modelling on BL showed a high correlation between diameter at branch base and dry branch mass (Fig. 1a and Table 2), and eventually branches including foliage mass (Fig. 1b, Table 2). This indicates that the models are suitable for estimating missing or browsed branches via measurements of diameter at the browsing point. The sum of browsed branches provides a reasonable estimate for consumed dry mass of branches (winter season) or branches with foliage (growing season). At the same time, the models indicated that dry mass of branches prevailed slightly over that of foliage in young rowan trees. A close relation ship was also found between specific surface mass and diameter d_0 (Fig. 2). Here, the specific surface mass of bark of the

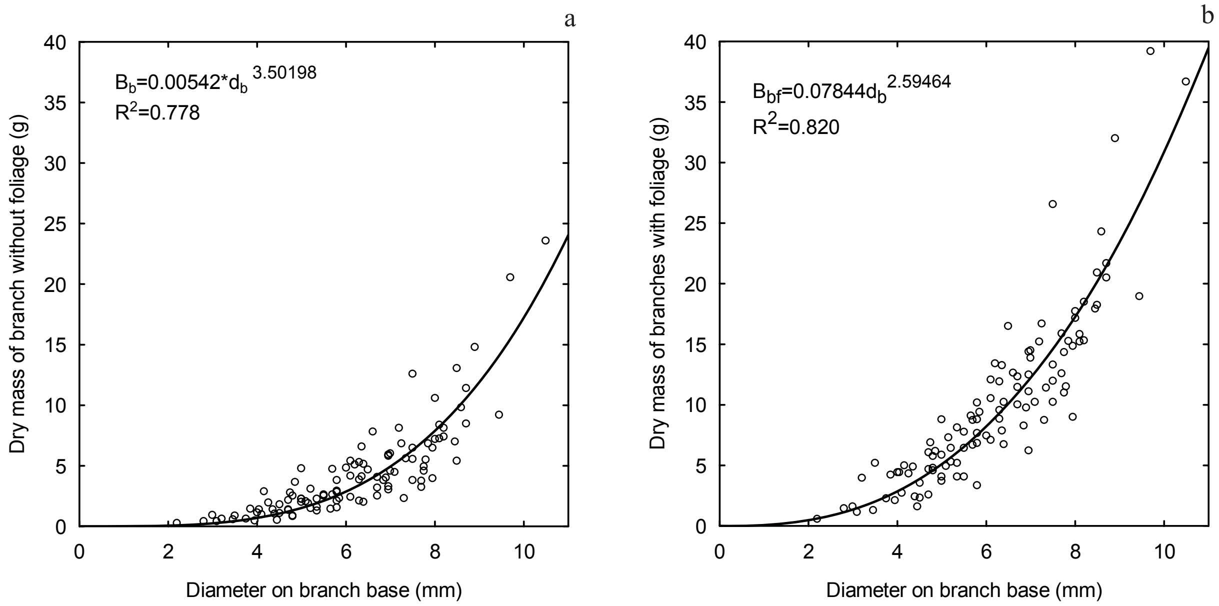


Figure 1 Dry mass of branches (a) without foliage and (b) with foliage compared to diameter at branch base

Table 2 Regression models for edible dry mass of branches (B_{eb}) and edible dry mass of branches with foliages (B_{eb+ef}) expressed on the branch level (*BL*), further, surface mass of bark (w_s), stem mass (B_s), branch mass (B_f), conversion coefficient for edible branch (r_b), conversion coefficient for edible foliage (r_f) and edible bark dry mass (B_{ebark}) expressed on the tree level (*TL*)

Eq.	Dependent variable	b_1 (SE) P	b_2 (SE) P	R^2	*MSE*	λ	*SD*
(1a)	B_{eb} (BL)	0.005 (0.002) <0.017	3.502 (0.195) <0.001	0.778	3.284		
(1b)	B_{eb+ef} (BL)	0.078 (0.021) <0.001	2.595 (0.132) <0.001	0.820	9.027		
(2)	w_s (TL)	1.253 (0.110) <0.001	0.398 (0.023) <0.001	0.789	0.439		
(3)	B_s (TL)	-2.515 (0.088) <0.001	2.412 (0.025) <0.001	0.990	0.028	1.014	0.171
	B_b (TL)	-7.336 (0.312) <0.001	3.334 (0.090) <0.001	0.943	0.280	1.138	0.596
	B_f (TL)	-3.383 (0.161) <0.001	2.237 (0.046) <0.001	0.962	0.096	1.047	0.322
(5)	r_b (TL)	2.411 (0.181) <0.001	-0.068 (0.005) <0.001	0.772	0.141		
	r_f (TL)	2.288 (0.226) <0.001	-0.073 (0.006) <0.001	0.635	0.163		
(9)	B_{ebark} (TL)	0.249 (0.066) <0.001	1.585 (0.064) <0.001	0.938	286.6		

Note. Abbreviations in the table captions means; b_1, b_2 - coefficients, *SE* - their standard errors, *P* - p-value, R^2 - coefficient of determination, *MSE* - mean square error, λ - logarithmic transformation bias, and *SD* - its standard deviation.

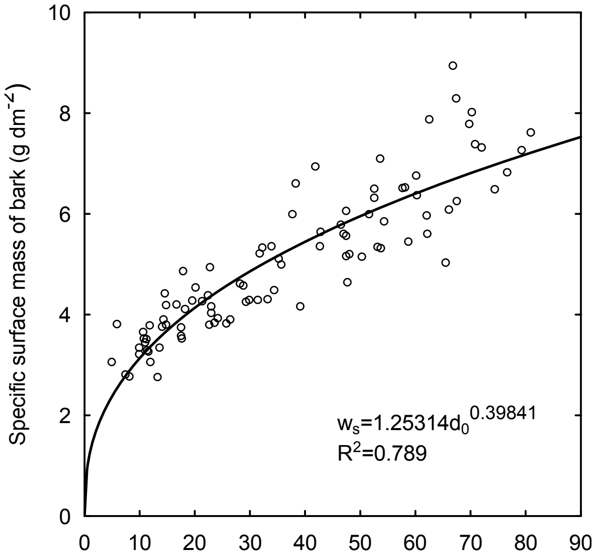


Figure 2 Specific surface mass of bark compared to tree diameter at stem base

largest observed trees was more than two times larger than that of the smallest trees. Since tree diameter d_0 is not a conventional tree characteristic used in growth studies, regression functions are included to convert the diameter d_0 to dbh and tree height (Fig. 3a, b).

The inventory of deer browsing on the 20 plots showed that whereas branch browsing was considered very frequent, bark stripping occurred sporadically (Table 3). In fact, all cases of bark stripping only occurred on plots with large trees, i.e. at plots located on the sub-areas C and D. The mean percentage of trees subjected to browsing when considering all plots was 80% (±18%). Here, both branches and leader shoot browsing were included in the analysis and this was typical for trees up to

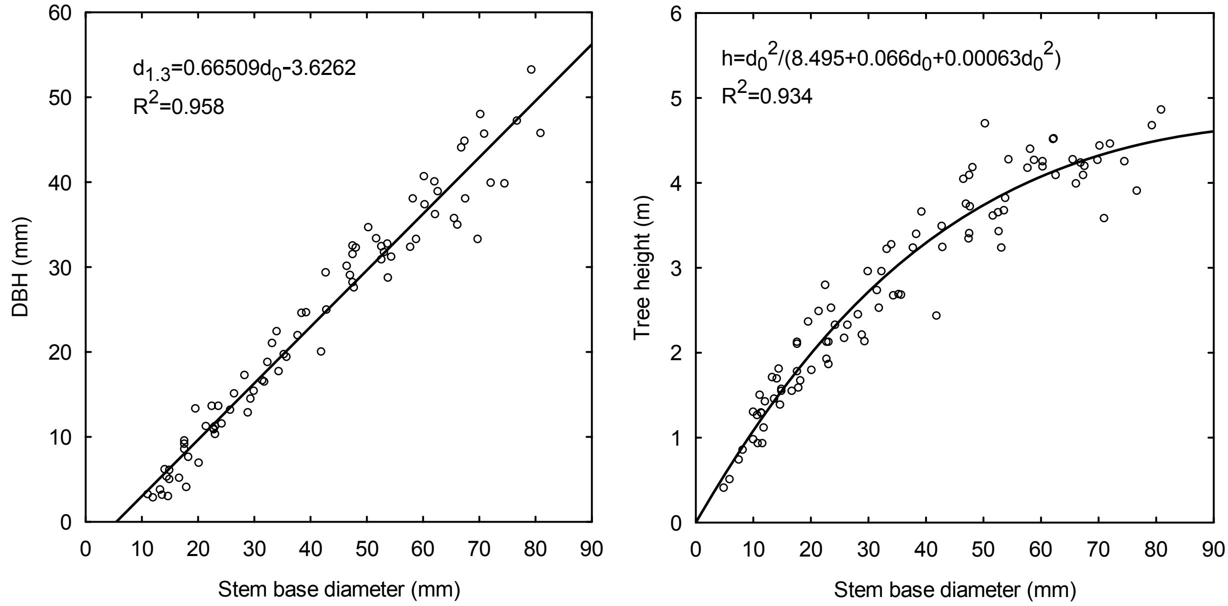


Figure 3 Estimations of tree diameter at breast height (a) and tree height (b) using tree base diameter as independent variable

Table 3 Characteristics of red deer browsing on rowan trees in the research plots. Data for branch browsing (including leader shoot) are in the white cells and for bark stripping in the grey cells.

Characteristics of tree damage by red deer	Mean	Standard deviation
Number of browsed branches per 100 m^2	1,323.0	1,219.0
Mean diameter of bases on browsed branches (mm)	3.3	0.5
Percentage of trees with browsing	80.0	18.0
Number of stripped areas per 100 m^2	19.0	31.0
Mean size of stripped areas (cm^2)	96.0	92.0
Percentage of trees with bark stripping	7.0	16.0

200 cm in height. As for bark stripping the percentage was 7% (±16%). These results might indicate that if the forest stand is composed of both small and large trees, red deer prefer easily accessible branches for browsing, instead of bark stripping.

For branch and leader shoot browsing, all cases identified were recorded from between 0 cm to nearly 270 cm from the ground (Fig. 4a). However, the maximum occurrence of the browsing was between 121 and 130 cm from the ground and browsing was considered frequent up to 200 cm from the ground but rarely at higher positions. Bark stripping occurred from the ground level to a height of ca 180 cm (Fig. 4b). Since bark stripping is characterized by one or more areas on the stem surface, the frequency of the lower and higher points are shown. The lowest point of stem de-barking was most frequent at a height between 41 and 60 cm from ground level, with the highest positions occurred between 101 and 120 cm.

A combination of models for branch with foliage (Fig. 1b) and bark dry mass and measurements on the plots relating to game browsing (Table 3) allowed an estimation of the dry mass of rowan trees consumed by red deer by browsing and bark stripping (Table 4). The results show that the average amount of branch dry mass consumed by deer was 2,931 g (±2,658 g) per 100 m^2. The average amount of bark stripped by deer was 101 g (±214 g) per

a b

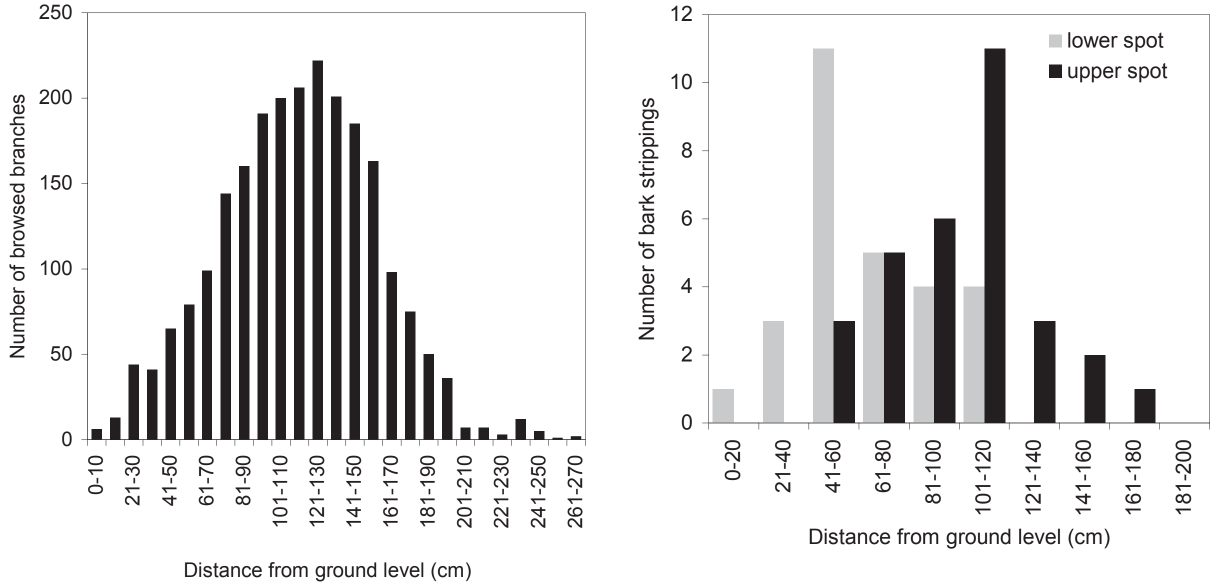


Figure 4 The number of browsed branches (a) and bark strippings (b) with regards to distance from the ground

Table 4 Summary of rowan tree dry mass consumed by red deer

Characteristics of dry mass consumed by red deer	Mean ± standard deviation	Minimum and maximum among plots
Total dry mass of branch browsing (g per 100 m^2) [A]	2,931 ± 2,658	93-10,617
Total dry mass of bark stripping (g per 100 m^2) [B]	101 ± 214	0-750
Sum of consumed dry mass (g per 100 m^2) [C = A + B]	3,033 ± 2,668	93-10,621
Percentage ratio of browsed branch dry mass to consumed dry mass [A/C]	96 ± 9	61-100

100 m². Thus, much more dry mass was consumed in form of branch browsing than bark stripping.

Models concerning rowan dry mass potentially edible by deer constructed on the TL showed specific tendencies for each tree component regarding tree size (Fig. 5 and Table 5. The edible dry mass of leader shoot increased concomitantly with tree size up to a diameter d_0 of ca. 10 mm and subsequently stabilised at a constant level (about 20 g) once a diameter of 20 mm (equal to a tree height of about 180 cm) was reached. Larger trees were not obviously damaged by red deer by browsing of the leader shoot. A significantly different result was found for bark, where no browsing was expected for trees with a diameter d_0 less than 20 mm. The result for potentially edible branches and foliage was similar; first increasing but later declining with increasing tree diameter. The maximum edible forage resource for red deer was trees with a diameter between about 35 mm and 50 mm for foliage and branches, respectively.

Modelling potential forage resources by tree components (at TL) on the 20 plots served as the basis for the construction of models on the SL, based on a rowan tree coverage (canopy projection) of 50% (Fig. 6 a–d) and the mean stand diameter d_0. The amount of edible dry mass varied between the particular components; while the modelled dry mass of branches and bark accessible to red deer increased together with mean stand diameter d_{m0}, it first increased then decreased for foliage and stem. The maximum estimates of dry mass of branch and bark was found for the largest rowan stand and reached about 17 and 23 kg per 100 m², respectively. In turn, the maximum estimated foliage dry mass of 11 kg per 100 m² and maximum leader shoot dry mass of 13 kg per 100 m² was observed for stands with a mean diameter d_{m0} of 27 mm and 10 mm, respectively.

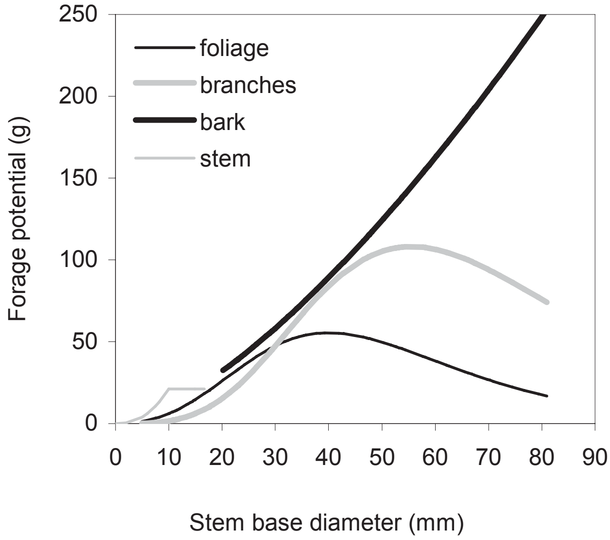


Figure 5 Dry mass of potential browsed items for red deer by tree components with respect to the diameter at stem base

The largest forage potential was estimated for bark and the smallest for foliage. However, in reality, bark is clearly not completely

Table 5 Regression models for edible dry mass of: foliages (B_{ef}), branches (B_{eb}), leader shoot (B_{es}), bark (B_{ebark}) and all parts together (B_{etot}) expressed on the stand level (SL)

Eq.	Dependent variable	b_1 (SE) P	b_2 (*SE*) P	b_3 (*SE*) *P*	R^2	*MSE*
(10)	B_{ef}(SL)	-0.014 (0.001) <0.001	0.790 (0.048) <0.001	-	0.607	2.500
(11)	B_{eb}(SL)	0.065 (0.033) 0.063	-1.261 (2.023) 0.541	48.952 (29.419) 0.114	0.902	2.934
(12)	B_{es} (SL)	2.075 (0.077) <0.001	-0.220 (0.014) <0.001	-	0.917	1.734
(13)	B_{ebark} (SL)	0.637 (0.055) <0.001	-8.925 (1.750) <0.001	-	0.912	3.097
(14)	B_{etot}(SL)	6.182 (1.574) <0.001	0.515 (0.075) <0.001	-	0.773	20.850

Note. Abbreviations in the table captions means; b_1, b_2 - coefficients, *SE* - their standard errors, *P* - p-value, R^2 - coefficient of determination, and *MSE* - mean square error.

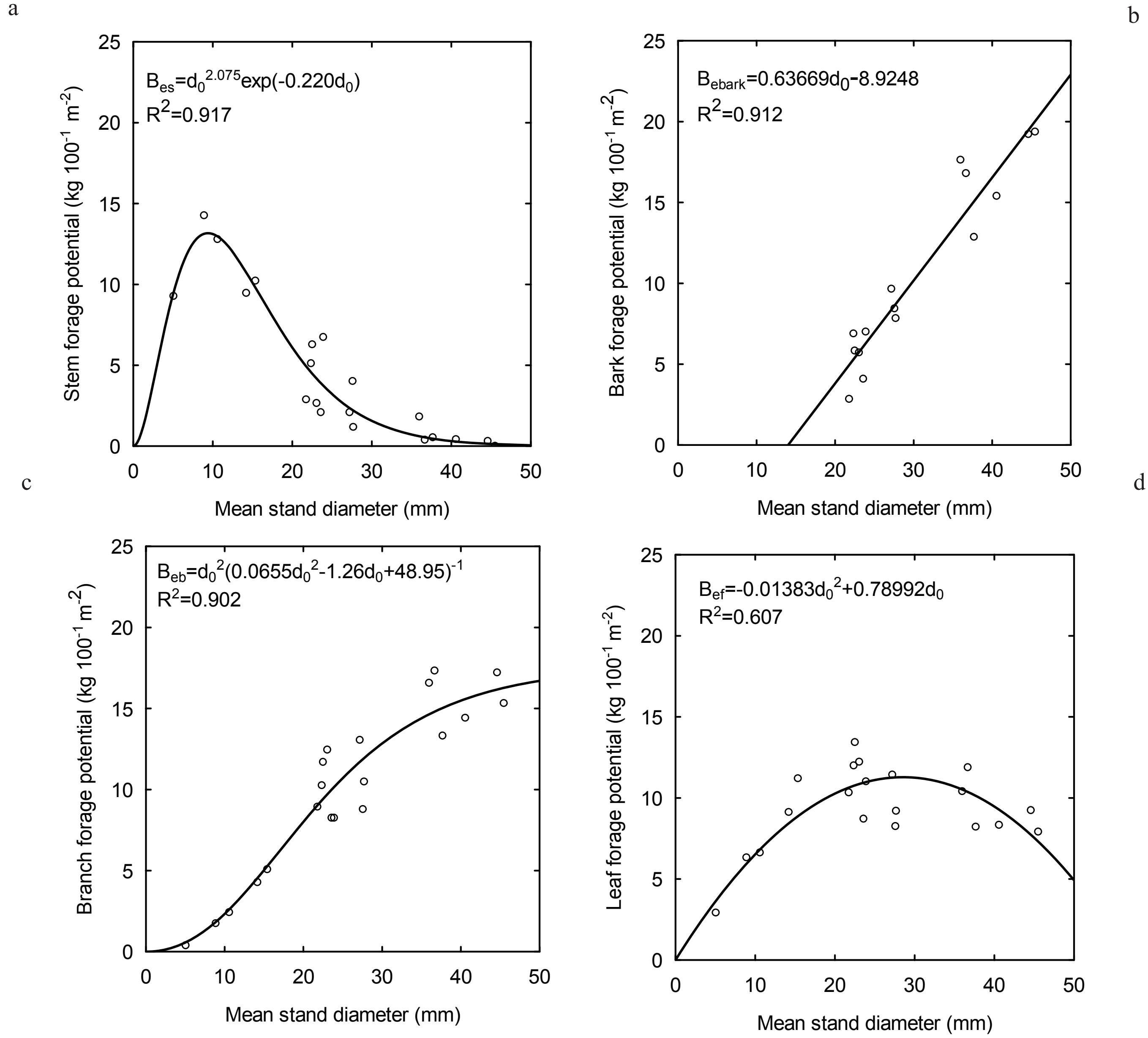
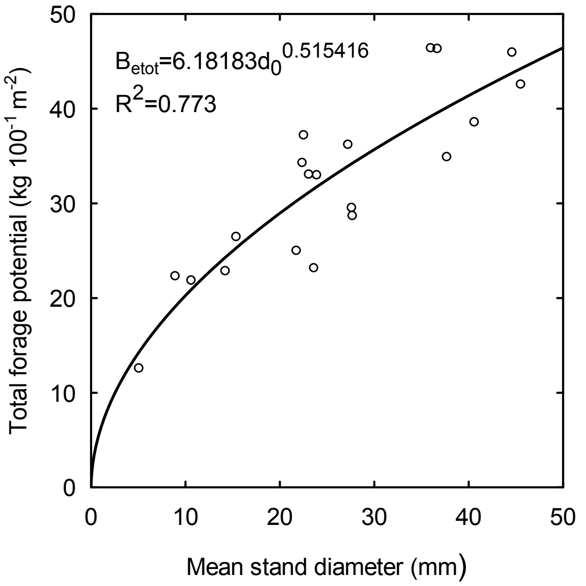


Figure 6 (a) Stem, (b) bark, (c) branch and (d) leaf forage potential for red deer with respect to mean stand diameter (measured on stem base). The model is constructed for rowan stands with a tree cover of 50%

surface-stripped by deer; therefore, the model probably overestimates the natural situation. Summing the models of all components resulted in a total forage potential on a rowan SL based on tree coverage of 50% (Fig. 7a). The model estimates ca. 45 kg of edible dry mass by red deer per 100 m^2 for a mean stand diameter d_{m0} of 50 mm. This figure is the maximum number which might be reached in exceptional conditions, for example, in a small isolated system such as a fenced area, without any other forage resources for the red deer. Our model shows that the contribution of the specific tree components to the total forage potential in a rowan stand depends on the mean stand diameter (Fig. 7b). The contribution of browsing potential decreased and the contribution of bark-stripping potential increased, with increasing stand size.

a

b



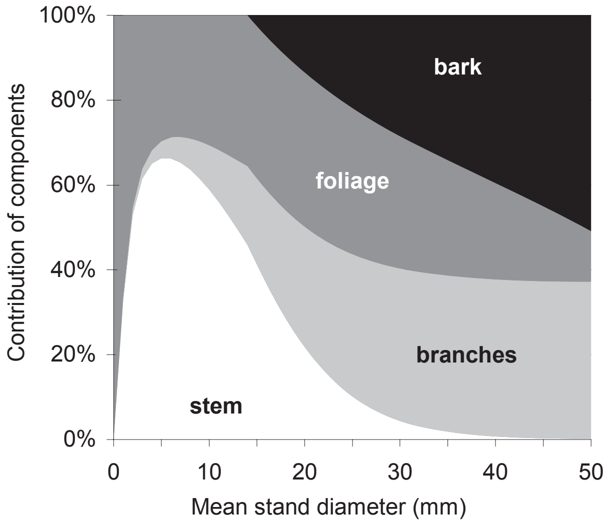


Figure 7 (a) Forage potential for red deer and (b) contribution of the particular tree components in rowan stands with respect to mean stand diameter (measured at the stem base). The model (a) is constructed for rowan stands with a tree cover of 50%

Discussion and conclusion

This survey of research plots indicates that a high proportion of rowan trees browsed by red deer in the form of leader shoot and branch browsing, so that in total, over three-quarters of individuals were affected. Conversely, bark stripping was found rare. It appears that red deer prefer rowan trees for forage, but for stands with a heterogeneous height structure, browsing small trees is preferred to bark stripping on larger trees. A study by Konôpka et al. (2012) performed on ash trees (*F. excelsior*), concluded that a higher proportion of stripped bark contributed to total tree biomass consumption compared to the results found for rowan in this study. However, the ash stands were more even-sized. Therefore, only a few branches in stands with a mean height over 4 m were accessible to the red deer. Konôpka et al. (2012) showed that whereas the dry mass of browsed branches predominated over that of stripped bark in ash trees with a diameter d_0 up to ca 50 mm, the opposite situation was observed for thicker trees.

However, browsing and stripping intensity highly depends on game density (Hörnberg 2001, Kiffner et al. 2008), the abundance of tree species and their nutrient content (e.g. Duncan et al. 1994, Čermák 1998), the site productivity of the biotope (Langbein 1997, Bergqvist 2014) as well as forest management (Bergqvist 2014, Edenius et al. 2014, Schulze et al. 2014). As for most areas of Slovakia, the High Tatra National Park has as a typically high population of red deer, due to its gradual increase in population size in the last decade; from approximatly 400 individuals in 2003 to nearly 700 in 2012 (Dr. Fleischer – personal communication). Regarding the abundance of rowan trees in the observed area, the species is one of the three most common species (together with *B. pendula* and *S. caprea*) in the naturally regenerated complexes (Šebeň 2010). For nutrient content in general, browsers prefers plants with a high nitrogen level and low fibre content (Danell et al. 1991). Unfortunately, no study that focused on the nutritional status in different components of rowan trees could be found although this type of analysis has previously been performed for foliage and branches of *F. excelsior* (Konôpka et al. 2012).

Previous studies (e.g. Padajga 1984) have shown that a high content of tree shoots in total red deer forage indicate that this tree component is sufficiently rich in nutrition and is often preferred to grasses. In habitats with frequently browsed tree species, woody plants form between about 40% (in the growing season) to ca. 90% (in the winter) of the red deer diet (Jamrozy 1980, Homolka 1990). In biotopes where woody plants were absent or rare, grasses predominated and composed of between 50% to 90% of the diet volume of red deer (Latham et al. 1999, Homolka & Heroldová 2001). In general, woody plants represent a significantly larger proportion of the red deer diet compared to other ungulate diets including that of roe deer (e.g. Prokešová 2004). If research had focused on nutritional conditions at the experimental sites, it might be assumed that red deer consume tree biomass more frequently than grazing. This is supported by the evidence observed over a relatively long period, nearly 5 months, of snow cover (Vološčuk et al. 1994). Moreover, in terms of light-tolerant herbs (especially *E. angustifolium* and *Calamagrostis* sp.), rapid growth occurs within post-disturbance areas, which are most probably not attractive for red deer grazing.

These results demonstrate that red deer browse branches of rowan from the ground level to a height of 200 cm and very rarely higher, with most frequent browsing occurring at heights of between 121 and 130 cm. Similar results were recorded for bark stripping, however, the maximum height was limited to 180 cm. Both browsing and bark stripping preferences of red deer probably relate to their body size. Red deer clearly browse shoots at the height of their shoulder (Renaud et al. 2001). For example, Hodge & Pepper (1998) observed that the most frequent browsing by red deer is up to a height of 180 cm. Konôpka et al. (2012) recorded frequent browsing on ash trees at heights of between 40 and 160 cm with an extreme upper limit of 260 cm. The same upper limit for bark stripping (ca 180 cm) as for rowan was also recorded for ash trees.

The results show that mean edible potential among all observed plots was 32 kg (composed of 10 kg of leader shoot, 12 kg of branches and 10 kg of foliage) per 100 m^2. The mean potential of strippable bark was about 3.0 kg per 100 m^2. Altogether, 35 kg of rowan dry mass per 100 m^2, potentially edible by red deer, was found in the studied area. Hell et al. (2000) showed that red deer require between 1.2 kg (calf) and 3.0 kg (adult) plant dry mass per day. Thus, 100 m^2 of young rowan stand can theoretically serve as a food resource for 10 days for one adult red deer, in case of the total browsing and stripping of all forage-potential. Thus, a single red deer requires seasonally minimum of 0.4 hectares of this type of forest stand (considering the standard tree crown coverage of 50%) for its diet. However, in our plot conditions, only 11.8% of edible dry mass (leader shoot, branches with foliage) and 1.2% of strippable dry mass (bark) was actually consumed by red deer.

Red deer can be considered as a selective consumer of tree biomass preferring rowan to other species which was supported by previous studies conducted in the territory of the Tatra National Park (Table 1 - Supp. Info III, modified data from Kaštier & Bučko 2011). Altogether nearly 4 000 young trees were inspected and categorised into five classes of game browsing: 0 – undamaged (no browsing), 1 – browsed branches, 2 – browsed stem, 3 – browsed branches and stem, 4 – whole tree intensively damaged by browsing. Rowan trees were the most frequently and also most intensively browsed species (Table 1 - Supp. Info. III). While only 5.0 % (± 1.0) of all spruce trees were damaged by game (all species together 29.2 %) as much as 72.9 % (± 2.6) of rowan trees were affected by browsing. Moreover, if we considered all damaged trees as a base, only 17.9 % (± 8.3) of spruce belonged to classes 3 and 4 (average for all species was 71.5 %). However, the proportion in rowan trees was as much as 83.1% (± 2.6) hence, the results clearly prove that rowan might represent a suitable biological control for mitigating forest damage by reducing browsing or economic damage to neighbouring commercial trees e.g. Norway spruce and Scots pine.

This study presents the initial step in achieving optimisation of different demands between interests of foresters and hunters (or wildlife management). We have shown that the novel procedure based on the regression models is applicable for quantification of consumed tree biomass as well as estimation of forage potential for game, mainly red deer, in young forest stands. In principle, this kind of modelling of forage potential would further serve for evaluation of carrying capacity of biotops for red deer and consequently for decision-making on regulation on population to avoid serious damage to commercial tree species in forest stands. However, to reach the final goal more specific, scientific knowledge is required. Specifically, forage potential has to be quantified, not only for main forest tree species (as we have done for rowan) but also for other plants, i.e. shrubs, grasses and herbs co-existing in the area. Moreover, exact information related to 'bearable' branch browsing and bark stripping on commercial forest trees does not yet exist. Therefore, currently a threshold of branch and bark reduction that does not endanger interests (sufficient number of undamaged trees in each stand growth stages without implementing inadequately high costs for protection measures against game) of forest owners is unknown.

On the other hand, these results indicated that rowan, especially in young growth stages, can play a considerable role in enhancing carrying capacity of forest biotops for red deer. Therefore, traditional attitudes of foresters to the presence of rowan in forest stands should be re-evaluated. Rowan trees should be maintained preferably as young stands together with commercial trees species, which are attractive for red deer barking and stripping, for instance, silver fir, maple and ash. This might represent a suitable biological control for mitigating commercial forest damage. Moreover, foresters or hunters could establish and maintain specific browsing plots to entice deer from threatened stands with commercially valuable trees to stands with a high proportion of rowan trees. Here, rowan trees would preferably consist of different size trees for both browsing (height under ca 3 m), bark stripping and perhaps also for fruit consumption (those over 3 m in height).

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Supporting Information

The online version of the article includes the Supp. Info.

Supp. Info. I: Schematic for the procedure of estimating

Supp. Info. II: Schematic for the construction of a model

Supp. Info. III: Proportion of damaged trees by game (browsing)