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Why was browsing by red deer more frequent but represented less consumed mass in young maple than in ash trees?!

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ABSTRACT: European ash (*Fraxinus excelsior*) and sycamore maple (*Acer pseudoplatanus*) are considered amongst tree species as some of the most attractive forage for red deer (*Cervus elaphus*). The aim of this paper is to estimate branch and foliage mass browsing by red deer in young Sycamore maple and European ash in Central Slovakia and to analyze interspecific differences in browsing frequency and quantity. Altogether 665 ash trees and 701 maple trees were measured for height and stem diameter at the ground level. Red deer browsing, defined as leader shoot or lateral branch cropping, was recorded for all trees. A combination of the diameter of browsed branches and branch regression models allowed for the estimation of browsed (potentially consumed) mass by red deer. Results show that browsing occurred more frequently on maple (5 cases per tree) compared to ash (3 cases per tree); however, more total branch biomass was consumed in ash (10.7 g per tree) compared to maple (2.6 g per tree). This is because browsed branches were larger in ash than in maple. We assume that the difference in the size of browsed branches between ash and maple is relative to species-specific branch morphological and structural features.

Keywords: browsing; branch model; *Cervus elaphus*; *Fraxinus excelsior*; *Acer pseudoplatanus*

In general, most species of deer (*Cervidae*) are predominantly browsers with the exception of red deer (*Cervus elaphus*), North American elk (or wapiti, *C. canadenis*) and fallow deer (*Dama dama*), who obtain the greatest proportion of their summer diet from grass (Gebert, Verheyden-Tixier 2001). Browsers and mixed feeders (browsing and grazing) are more selective feeders than grazing ungulates (Gordon, Illius 1988) and red deer prefer certain tree species for forage. The nutritional value and digestibility of broadleaved trees, especially leaves, are highly preferred over most conifer species (Nelson, Leege 1982). In Europe, rowan (*Sorbus aucuparia*), goat willow (*Salix caprea*) and common aspen (*Populus tremula*) are considered as the most attractive feed sources for red deer (Myking et al. 2013) followed by ash (*Fraxinus*, usually *F. excelsior*) and maple (*Acer*, especially *A. pseudoplatanus*; see for instance Čermák, Grundmann 2006). However, while rowan, willow and aspen are of low commercial value (except for bio-energy), maple and ash are more valuable with a wider range of the environmental and economic potential. Hence, browsing on ash and maple can result in negative economic consequences. Recently, this has become an extremely serious problem since the population density of red deer has considerably increased in the last decades, not only in Slovakia (Bučko et al. 2011) but also in most European countries (Milner et al. 2006; Rurbaite, Csányi 2010).

The red deer preference to tree species for browsing is complex and not fully understood. Important aspects of attractiveness for red deer feed are palatability and morphological properties of the tree crown (Gordon, Prins 2003). Palatability is re-

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lated to the anatomical and biochemical properties of trees which determine taste and availability of proteins and carbohydrates. Morphological properties of the crown can affect both comfort and efficiency of feed gain. For example, large browsers often avoid biting short, thin stems branching at wide angles from which they can obtain little mass (Myers, Bazeley 1992). They prefer mostly woody plants that provide large leaves, thick and/or long annual shoots, and non-thorny plants such as willows that allow them to strip many leaves and in one bite (Shipley et al. 1998). In fact, the size of the bite an animal obtains depends on both the architecture of the plant and the size and morphology of its mouth (Gordon, Prins 2003).

European ash and Sycamore maple are amongst the tree species considered attractive for red deer forage. Both species, under favourable growth conditions, are very productive and often provide high-value timber. In addition, they have a positive effect on the soil, particularly on humus quality and topsoil chemistry (Weber-Blasckhe et al. 2008). In Slovakia, European ash and Sycamore maple usually create an admixture to main commercial tree species, especially to European beech (*Fagus sylvatica*), Pedunculate oak (*Quercus robur*), Sessile oak (*Q. petraea)* and Norway spruce (*Picea abies*). Rarely they form small patches of pure stands, mostly on moist humic or stony sites with accumulated humus layers, and are more important for ecological (especially enriching biodiversity) rather than commercial purposes (Pagan, Randuška 1987). The National Forest Inventory (NFI) in Slovakia performed in 2005–2006 (unpublished data) shows that Sycamore maple represented approx. 8.2% of the entire forest cover when considering the first age class (up to 20 years). However, this species made up only 3.0% and 1.5% in stands aged 40–80 years and over 100 years, respectively. Similarly, European ash accounted for about 3.2, 2.0 and 0.6% of the forest cover in stands with age structures between 0–20, 40–80, and over 100 years, respectively. The percentage cover of these tree species evidently decreases with stand age, probably as a result of interspecific competition, intentional forest management (thinning) and external factors such as ungulate browsing.

There has been intensive research dealing with interspecific comparisons on damage by red deer among different tree species grown under identical conditions (e.g. Motta 2003; Čermák, Grundmann 2005; Schulze et al. 2014). However, there is still a lack of research quantifying browsed biomass consumption for individual tree species and consequently a lack of reasonable explanation for the observed differences in browsing preference. Therefore, the aim of this paper is to estimate branch and foliage mass browsed by red deer in young European ash and Sycamore maple and to analyze interspecific differences in browsed mass, especially with regard to the vertical distribution of red deer cropping and bite size.

MATERIAL AND METHODS

Site and stand description. Our research activities were focused on the territory of the Slovak Central Mountains, namely the subdivision of Javorie and Poľana mountains, which belongs to the sub-province of the Inner Western Carpathians. The mountains are volcanic in origin, made of andesitic bedrock covered by Cambisol. The forest composition is dominated by European beech with a mixture of other broadleaf species at lower altitudes such as Common hornbeam, European ash and Sycamore maple. At higher altitudes, coniferous species such as Norway spruce, Silver fir (*Abies alba*) and rarely European larch (*Larix decidua*) are present.

A preliminary screening of forest stands containing European ash or Sycamore maple was conducted using a forest database (Programs of Forest Management by Stand Units in Slovakia). Tree species composition and age class were used for screening. The main criteria for the final selection of forest stands were the minimum composition of 80% of target tree species (ash or maple) and stand age up to 15 years. The final selection of forest stands was identified as exclusively natural regeneration. The altitudinal range of the stands was between 710 and 950 m a.s.l. for ash and 700–980 m a.s.l. for maple forest stands. Thus, the area belonged to two altitudinal vegetation zones categorised by the native dominant forest tree species; beech and fir-beech. In this region the total mean annual precipitations is 950 mm and average annual temperature nearly 6°C.

Tree measurements and sampling. In the selected forest stands, 29 circular research plots (14 for ash and 15 for maple; Fig. 1) with the radius between 1 and 2 m were established in spring and summer 2013. The size (radius) of the particular plot was chosen with respect to stand density to include at least 40 trees for additional measurements. Hence, altogether 665 ash trees and 701 maple trees were included. Each tree within the plot was measured for height and stem diameter at the ground level (diameter d_0 hereafter). In addition, red deer browsing, defined as leader shoot or lat-

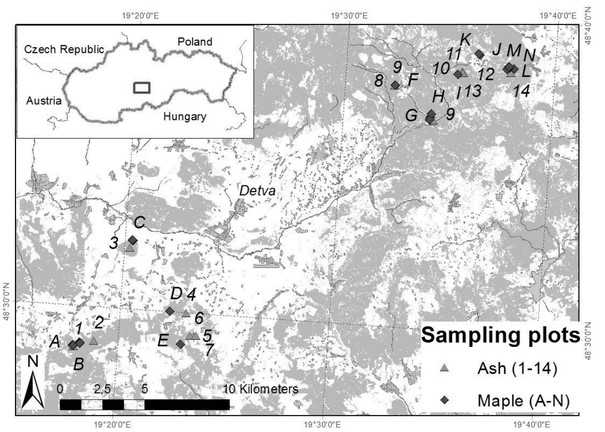

Fig. 1. Localization of the research plots

eral branch cropping, was recorded for all trees. For leader shoot and branch browsing, the diameter at the browsing point and its distance from the ground were measured. To obtain empirical material for constructing regression relationships between the branch and foliage mass and the diameter of the branch base, 300 samples of removed branches (170 ash samples and 130 maple samples) with a base diameter up to 12 mm were randomly selected and used for modelling constraints. The branch samples were divided into two groups: ramified (both current- and last-year shoots) and non-ramified (exclusively current-year shoots). The diameter at the branch base was measured at two perpendicular directions. The foliage was separated from branches, both tree components were oven-dried at 95°C for 48 hours and weighed to the nearest 0.1 g.

Model construction and estimates. Information related to height, number of browsed branches, diameter of browsed branches and their distance from the ground was used to analyze features of red deer browsing at a tree level. Moreover, the combination of diameter at browsed branches and branch regression models allowed estimations of browsed (potentially consumed) mass by red deer. For more details see Pajtík et al. (2015). Interspecific differences in browsing intensity (number of bites per tree) and its features (diameter or distance from the ground of snapped branches, quantity of browsed branches and foliage) were analysed by a two-way ANOVA test considering tree height classes as a factor. Differences between the mean values (ash versus maple) in the particular height classes were proved by Tukey's test. Statistical significance was defined as $P < 0.05$.

Regression models were constructed and all statistical analyses were performed in the STATISTICA 10.0 (SPSS, Tulsa, USA) 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 AND DISCUSSION

The mean tree height (167 cm and 170 cm in ash and maple, respectively) and diameter d_0 (19.9 mm and 19.0 mm in ash and maple, respectively) were similar in both sets of trees (Table 1). Frequency distribution of tree heights and diameter d_0 (right-tailed pattern) was also similar (Table 1). Hence, we could make relevant interspecific analyses in terms of red deer browsing.

In both species an increase in browsing frequency with distance from the ground level was recorded at first and the most frequent branch browsing (20% and 26% in ash and maple, respectively) was found at the distance of 76–100 cm (Fig. 2a). Very frequent browsing was also recorded between 101 cm and 150 cm, then browsing sharply decreases as the distance from the ground increases. In fact, browsing preferences of red deer are probably related to their body size. Red deer browse shoots at

Table 1. Descriptive statistics for basic properties of measured ash and maple trees

Tree species	Characteristics (unit)	Mean	Min.	Max.	Percentile		Skewness
					25th	75th	
European ash	tree height (cm)	167.3	20.0	500.0	85.0	191.0	1.362
	diameter at stem base (mm)	19.9	3.9	67.1	12.7	25.0	1.165
	number of browsed branches (per tree)	3.2	0	13	1	5	0.933
	diameter of browsed branches (mm)	4.2	1.1	16.5	2.6	4.9	1.938
	distance of browsed branches from the ground level (cm)	104.7	4.0	290.0	69.0	140.0	0.587
Sycamore maple	tree height (cm)	169.7	15.0	500.0	85.0	230.0	1.044
	diameter at stem base (mm)	19.0	2.6	62.5	11.3	24.9	1.068
	number of browsed branches (per tree)	5.3	0	55	1	7	2.710
	diameter of browsed branches (mm)	3.1	0.5	17.0	2.3	3.7	1.948
	distance of browsed branches from the ground level (cm)	109.3	10.0	210.0	85.0	130.0	-0.034

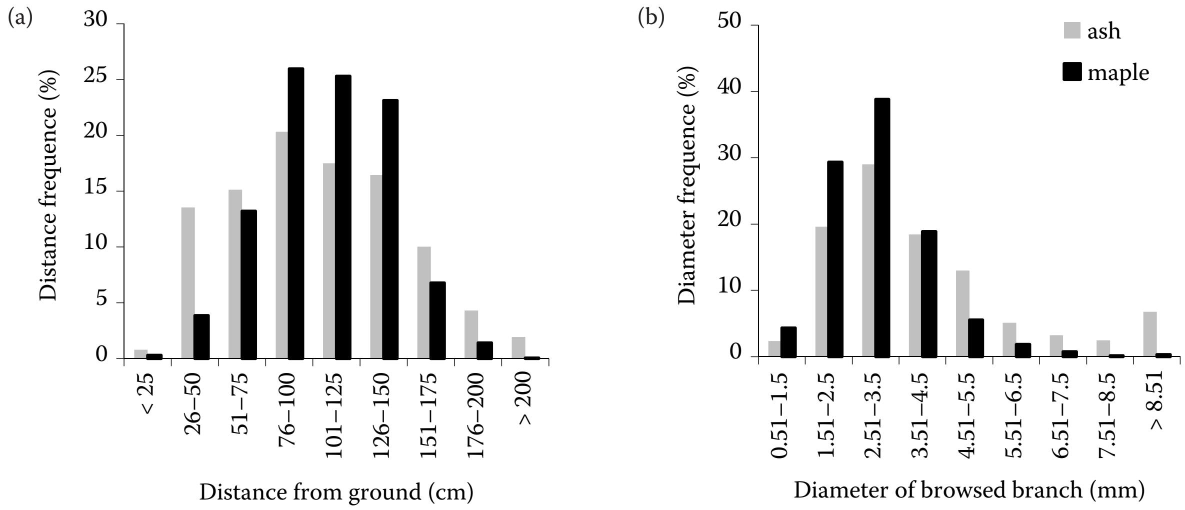

Fig. 2. Browsing frequency in relation to a distance from the ground level (a) and diameter of browsed branches (b)

the height of their shoulders (Renaud et al. 2001). Our previous work (Konôpka et al. 2012) showed that browsing frequently occurred on ash trees at heights between 40 and 160 cm with an extreme upper limit of 260 cm. For example, Hodge and Pepper (1998) observed that the most frequent browsing by red deer is up to a height of 180 cm. Finďo and Petráš (2011) suggested that while terminal browsing by red deer occurred in most tree species up to 200–210 cm, in ash the distance can be exceeded, sometimes up to as much as 280 to 290 cm (since the ash is more flexible than other tree species so it can bend if the deer pulls on the branches).

Interspecific comparisons of diameters on browsed branches suggest that red deer bites thicker branches in maple than in ash (Fig. 2b). While in ash trees as much as 30.6% of all bites were recorded on branches with a diameter over 4.5 mm, this was the case only for 8.6% of maples. As for the number of browsed branches, 1–2 bites per tree were recorded in both species for trees of 0.5 m in height as well as for trees between 3.5 m and 5.0 m in height (Fig. 3a). On the other hand, more browsed branches were found in maple than in ash trees with heights between 0.5 m and 3.5 m. At the same time, large interspecific differences in diameters of browsed branches were found in the height class of 2.51–3.50 m and negligible differences were found between small trees up to 0.50 m (Fig. 3b).

To estimate the mass of branches and foliage consumed by red deer, branch-level regression models were constructed (Fig. 4). The models show for both tree species that the tree dry mass available for red deer browsing in summer (i.e. branches with foliage) is more than double than is available in winter (branches without foliage). For instance, while maple branches of 10 mm in diameter represented 20 g

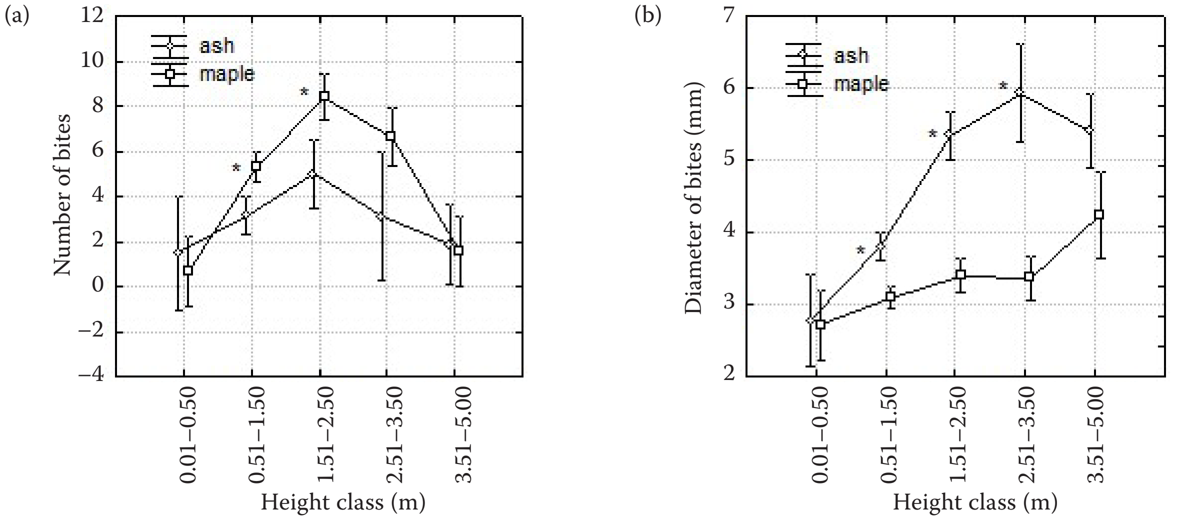

Fig. 3. The mean number (a) and diameter (b) of browsed branches per tree against height classes (asterisks indicates interspecific differences by the particular height class – Tukey's test; $P < 0.05$)

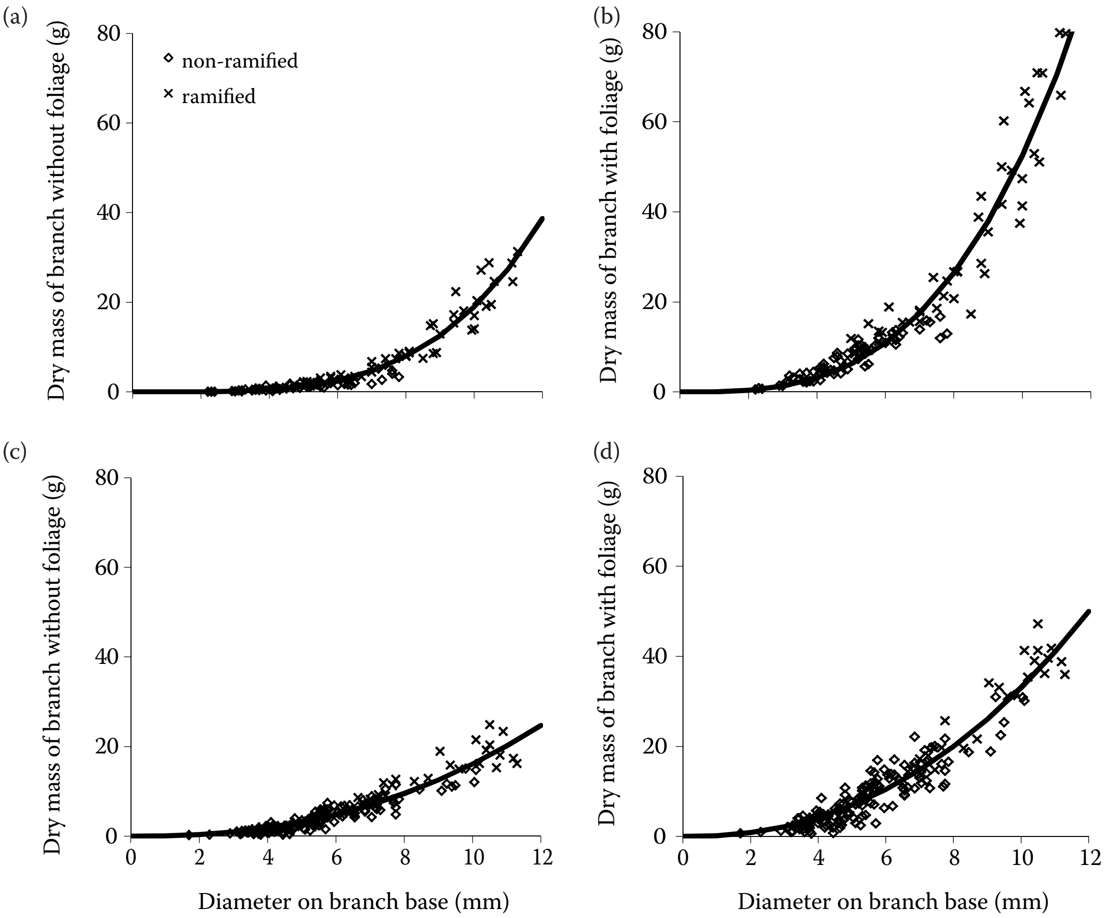

Fig. 4. Dry mass of branches without (a, c) and with foliage (b, d) for maple (a, b) and ash (c, d) trees

of wood, the combined mass of wood and foliage was 55 g. As for ash, branches of 10 mm in diameter made up 16 g of wood and at the same time, 35 g of wood and foliage together. Interestingly, while thin branches (up to ca 6 mm) were typical with more mass of wood and foliage in ash than in maple trees, the opposite situation was recorded for thicker branches. Data on the number (Fig. 3a) as well as diameter (Fig. 3b) of browsed branches together with branch models (Fig. 4) gave estimates of winter (branch mass) and summer (branch and foliage mass) browsing by red deer (Table 2). These estimates also indicate significant interspecific differences between ash and maple trees (Fig. 5). In both summer and winter browsing, differences were found for all tree height classes, except trees up to 0.5 m in height. The largest differences in summer browsing were observed for the height class of 1.51–2.50 m with estimated mass of 24 g in ash and 4 g in maple. Similarly in summer browsing, the largest interspecific contrasts were found out for the height class between 1.51 and 2.50 m with total mass values of 51 and 20 g in ash and maple, respectively. However, these estimates are theoretical and do not

Table. 2. Descriptive statistics concerning red deer browsing in ash and maple trees

Tree species	Characteristics (g per tree)	Mean	Min.	Max.	Percentile		Skewness
					25th	75th	
European ash	consumed branch biomass, i.e. "winter browsing"	10.7	0.0	122.4	2.0	10.4	3.199
	consumed foliage biomass	12.0	0.0	126.8	2.6	12.2	3.072
	consumed branch and foliage biomass, i.e. "summer browsing"	22.7	0.0	249.2	4.6	22.6	3.134
Sycamore maple	consumed branch biomass, i.e. "winter browsing"	2.6	0.0	151.0	0.0	2.5	12.054
	consumed foliage biomass	9.6	0.0	118.0	0.4	12.5	2.835
	consumed branch and foliage biomass, i.e. "summer browsing"	12.2	0.0	269.0	0.4	15.2	4.496

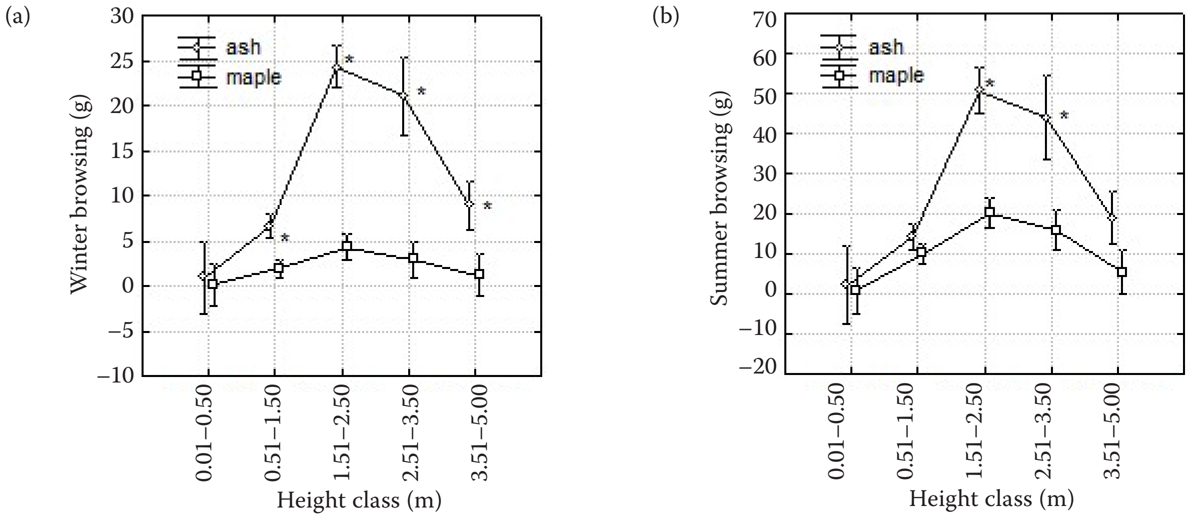

Fig. 5. Estimates of biomass of browsed branches without foliage (winter aspect) (a) and with foliage (summer aspect) (b) in ash and maple (asterisks indicates interspecific differences by the particular height class – Tukey's test; $P < 0.05$)

prove whether the branches were browsed in winter (without foliage) or during the summer season (carrying foliage). Homolka (1990) showed that the composition of red deer diet in forest environments fluctuates throughout the year. While woody plants contributed 40% to total forage during the growing season, this proportion was nearly 90% in winter. Thus, it is assumed that our estimates for winter browsing would be closer to reality than the estimates for summer browsing.

Summarizing the results, we can ask the question why more bites were recorded on the maple trees than on the ash trees. Further, while more branch (and/or foliage) biomass was browsed in ash than in maple trees? The inconsistence relates to the size of browsed branches which was larger in ash than in maple. Different size of browsed branches would be subjected to some contrasting species-specific properties. Stephens and Krebs (1986) stated that red deer are selective herbivores for whom feed selection is determined not only by preference to quality and taste but also by the cost invested to obtain forage. Renaud et al. (2003) showed by a simulated experiment that deer preferred browsing saplings structured with a broad spread of branches located horizontally around the deer's optimum browsing height (around 100 cm from the ground level). The authors suggested that browsers probably select structures on the basis of their architectures, e.g. those with the lowest vertical distribution of biomass focused around their preferred consumption height. As for our case, we assume that the difference in the size of browsed branches between ash and maple might be related to species-specific morphological and structural features of branches. Our data on maple branches (Fig. 4a, b) suggest that nearly all branches of up to 5 mm in diameter were non-ramified (probably current year shoots). Some branches in the diameter interval between 5 and 8 mm were non-ramified and others ramified (current year and previous year shoots). Maple branches with diameter over 8 mm were extremely ramified. Different situations were found for ash branches (Fig. 4c, d). Nearly all ash branches with diameter up to 7 mm were non-ramified. Branches over 7 mm were both ramified and non-ramified. Thus it seems that ramification might limit the ability of red deer to browse branches behind the ramification point. This assumption also conforms to data related with browsing frequency by diameter (Fig. 2b). While in both tree species, frequent browsing was found for branch thickness up to 4.5 mm, browsing frequency in the diameter class of 4.5–5.5 mm was twofold in ash compared to maple and the interspecific differences increased with diameter. Another aspect which could also affect the browsing activity of red deer might be the angle between the axis of the main shoot and lateral branches. Our field observations indicated that the angle is more acute (perhaps a positive aspect for browsing activity) in ash than in maple. However, this assumption would be supported (objectively quantified) by further study.

Moreover, our field measurements indicate (see Table 1 – the line related to the number of browsed branches) that while some trees were browsed very intensively and perhaps repetitively, others were not damaged at all or just negligibly browsed by red deer. Some authors (Gordon, Prins 2003; Stolter et al. 2005) suggest that browsing can increase the quality (e.g. increased nitrogen content) and availability (regenerative growth of shoots at an optimum height for browser) of tree and shrub crowns in subsequent years for browsers. Repetitive browsing in consecutive years has been shown in several studies (Welch et al. 1991; Bowyer, Bowyer 1997; Faber, Lavsund 1999).

Finally, it should be noted that both ash and maple are known as tree species with fast growth in the first decade after establishment, which facilitates the fast restoration of cleared areas (Weber-Blaschke et al. 2008). Thus, especially in young growth stages they can play a considerable role in enhancing the carrying capacity of forest biotopes for red deer. Ash and maple (especially if they form dense clumps of trees from natural regeneration) might represent a suitable biological control for mitigating damage by red deer on commercially more important forest tree species (particularly planted individuals). This is also true of attractive forage tree species such as oaks, European beech, Norway spruce, silver fir, Scots pine or common larch (see also Čermák et al. 2009). A principal measure in harmonization of the relationship between forestry and the hunting sector, i.e. relevant decrease of damage caused by red deer browsing, is still focused on the reduction of game population density (see also Konôpka et al. 2015).

CONCLUSIONS

Interspecific differences in the frequency (higher in maple than in ash) and mass quantity (more in ash than maple) of red deer browsing can be explained in terms of contrasting the crown morphology rather than biochemical (palatability) properties of shoots. We have suggested that different patterns of ramification (shoot thickness when branches are ramifying, and possibly the angle between the main branch axis and lateral branches) could be a decisive factor. Another unclear question might be related to the availability or comfort of red deer browsing. To develop an understanding of these issues, further study on crown morphology and vertical distribution of biomass is needed. Thus, we will extend our experiment towards assessing and analyzing 3D architecture of crowns on a variety of tree species by means of magnetic digitizer (e.g. Danjon, Reubens 2008; Surový et al. 2012). Such studies provide the exact quantification of interspecific differences in edible tree mass as well as its vertical distribution along the crown. Moreover, this method can reveal intraspecific contrasts between individuals without serious damage by red deer and those exposed to intensive and/or repetitive browsing.

After summarizing available information we may conclude that our study should be understood as tentative and the findings should generalized with caution. As for future research activities, main attention must be paid to the relevance of the crown architecture in red deer browsing.

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