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Original article

Effects of browsing on shoots and roots of naturally regenerated sessile oak seedlings

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Abstract – Comparison of 145 6- to 7-year-old seedlings of sessile oak (*Quercus petraea* (Matt.) Liebl.) sampled from adjacent fenced and non-fenced plots in an area of a natural regeneration showed only small but significant differences in plant form allometry between plants damaged by browsing and unbrowsed plants. Browsing reduced plant size and changed biomass distribution. Browsed plants had more branches and greater leaf biomass than unbrowsed plants and allocated a higher proportion of biomass to the root system, particularly to coarse and tap roots, while the stem biomass was not affected. The results suggest that the young tree may survive moderate animal browsing (10 roe-deer per 100 ha, 68% of browsed plants with a mean of 4 shoots damaged), although it reduces height growth and thus development towards a tree canopy height.

browsing / natural regeneration / *Quercus petraea* / root / shoot / seedling

Résumé – Effets de l'abroutissement sur les parties aérienne et racinaire de semis naturels de chêne sessile. Dans une régénération naturelle de chêne sessile (*Quercus petraea* (Matt.) Liebl.) nous avons comparé la croissance de 145 semis âgés de 6 à 7 ans prélevés à l'intérieur et à l'extérieur d'enclos. Des différences significatives de forme et d'allométrie ont été trouvées entre les plants abroutis et non abroutis. L'abroutissement a réduit la taille du plant et modifié la répartition de la biomasse. Par rapport aux plants non abroutis, les plants abroutis présentaient un nombre de branches et une biomasse foliaire plus grande et un rapport de la biomasse des racines plus élevé à celle de la tige. Par contre, la biomasse de la tige ne différait pas. Il apparaît que le jeune arbre peut survivre à un abroutissement modéré (10 chevreuils/100 ha et 68 % des plants abroutis avec une moyenne de 4 pousses endommagées), même si sa croissance en hauteur est réduite en retardant ainsi son accès à la strate arborescente.

abroutissement / régénération naturelle / *Quercus petraea* / racine / tige / semis

1. INTRODUCTION

One important objective in forestry is to establish and to maintain natural regeneration of young trees with good height growth and a future timber quality. Besides other factors such as winter frosts, water stress, insect and fungal attacks, young trees are frequently at risk from animal damage. Browsing has been reported as a severe problem in artificial and natural regeneration of forests in many countries [16, 17, 20, 23, 24, 31, 32, 36, 37], and in the North-eastern part of France it has caused damages to oak regeneration [5, 6]. Plants may undergo major morphological changes after browsing such as reduced height, and less side shoots combined with reduced foliage density, which can affect growth rate and may result in severe growth loss [11, 20]. The physical damage is influenced by the intensity, frequency, and seedling flushing stage at the time of the herbivore attack [19]. Repeated browsing damages the plant more than a single attack, has negative effects on height growth and stem form and can create an imbalance in the shoot-root ratio [12, 19, 20]. Severe attacks can even kill seedlings [13, 17, 19]. Nevertheless, oak is known to survive repeated partial or complete removal of the above-stump parts by resprouting and/or by remaining in a suppressed state for several years [1, 4, 17, 21]. Hibbs and Yoder [24], for example, found for saplings of white oak that tap roots were much older than the above-stump part. One reason for this might be that plants under severe browsing stress allocated a major part of their resources into the root system, as was reported for grazed shrubs of *Quercus cocciferea* (L.) [28]. Repeated shoot removal might have the effect that more food reserves will be allocated to the roots. A large and well-developed root system is important as a source of carbohydrates for regrowth or resprouting [10]. A higher biomass partitioning to the roots may lead to a bigger tap root

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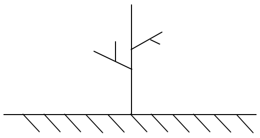
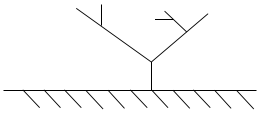
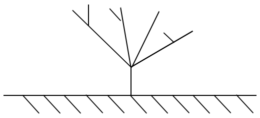
Table I. Seedlings are classified into three types: type I, one main stem; type II, two main stems; type III, several competitive stems.

	Type I		Type II		Type III	
	N	%	N	%	N	%
Unbrowsed	92	63	53	37	-	-
Browsed	30	21	71	49	44	30
						

and higher amount of lateral roots which maintains better anchorage, supports soil exploitation and confers a high degree of drought tolerance [15, 16].

The shoot/root ratio is reported to be reduced by browsing for several species [19]. It is well known that there is a functional balance between shoot and root in plants, which might be severely disturbed by defoliation as, for example, has been simulated by a shoot/root allocation model [35]. Nevertheless, the effect of browsing on above- and below-stump distribution of dry matter is still rarely quantified especially in sessile or pedunculate oak seedlings [2]. The latter authors investigated 12 weeks old pedunculate oak in greenhouse experiments and suggested that well-developed root system is an important source of carbohydrates for regrowth after grazing.

The objective of the present study is to compare above- and below-stump characteristics between seedlings of sessile oak undamaged and damaged by browsing for two purposes: to investigate browsing effects on (a) seedlings growing under natural field conditions and (b) the distribution of dry matter in plants.

2. MATERIALS AND METHODS

2.1. Site description

The site is located in North-eastern of France (237 m altitude 48° 44’ N, longitude 6° 14’ E), approximately 15 km east of Nancy. The site was relatively flat, with a soil which was a weakly leached brown earth with a silty clay texture developed over a pseudogley horizon. Soil depths ranged from 0.7 to 1.0 m and were characterised by low base saturations, and pH_{H2O} of 4.8–5.0 at the forest floor and 6.0–6.5 at 1 m depth. The soils of both plots were similarly stratified into an A-horizon with a depth of 4–23 cm, a Ag-horizon with a depth of 23–41 cm, a compact Btg-Horizon with a depth of 41–74 cm, a B-Cg-horizon with a depth of 74–98 cm, and a C-horizon with a depth of 98–153 cm. The soil was intensively exploited by fine roots down to a depth of 41 cm and less down to 98 cm. Rainfall was well distributed with an average of 769 mm over the last 20 yr and late spring frosts may occur once every two years [7].

2.2. Sampling and measurements

The investigation was undertaken on a large sample of sessile seedlings selected from a natural regeneration birthed from the abundant acorn crop of 1989 [6]. The seedlings were growing in open areas where mature oaks had been harvested at the beginning of the 1993 growing season. Seedling density was approximately 80 seedlings m^{-2} in 1995 [7]. In this forest, roe deer (*Capreolus capreolus*) cause damage by browsing (consuming young shoots). The local forest service provided an estimation of approximately 10 animals per 100 ha. The area of experiment consisted of a plot of 35*15 m surrounded by a fence of 2 m high with a mesh size of 5 cm erected in the winter of 1992/93 to exclude browsing animals (fenced = unbrowsed, non-fenced = browsed) [6]. In- and outside the fence, the area from where plants were taken was free from other ground flora than oak seedlings. In the springtime of 1997 following the first flushing period, 145 seedlings from each area fenced and non-fenced were extracted by a caterpillar tractor with a mechanical shovel fit with a special tooth [8] from in- and outside the fence in closest proximity. The root systems were then completely dug out by hand from the extracted soil bulk to avoid root damages and fine root losses. Seedlings were determined to be six or seven years old from annual ring counts just above the root collar at seedling base. They were classified into three categories (*table I*): type I, intact seedlings with one main stem; type II, seedlings with two main stems; type III, seedling with several main stems. The number of shoots damaged by browsing occurred in any year was recorded. The following variables were measured for each seedling (*table II*): (i) total height, (ii) number of branches, (iii) diameter at the height of the root collar (transition point between stem and root to be identified by a scar [34], (iv) rooting depth, (v) number of coarse lateral roots with a diameter ≥ 2 mm (only first-order roots) and fine lateral roots with a diameter < 2 mm (first and higher order roots), and (vi) total root biomass. A subsample of 35 plants from each group were taken and separated into leaves, stems and roots before 48 h of oven drying at 70 °C to determine biomass (*table II*, *figures 1–3*). The roots were separated into tap roots, coarse and fine – lateral roots and weighed (*figure 4*). Projected leaf areas of the fresh leaf samples (5–7 leaves per seedling randomly selected from a sub-sample of 25 plants from each group) were determined using the Delta-T Image analysis system (Cambridge, UK) (*table II*).

2.3. Statistical Analyses

The cross-sectional area A_{rc} (cm^2) was estimated from the geometric mean of the diameter d_{max} and d_{min} (mm) determined just above the root collar (rc) at seedling base using the following equation [3]:

$$A_{rc} = \frac{d_{max} d_{min} \pi}{400}. \tag{1}$$

Several regressions for the two populations were compared using multiple regression analysis [27, 30]. Relationships between different tree variables were developed for shoot (M_s) and root (M_r) biomass and cross-sectional area (A_{rc}). Relationships among these variables were tested to see if they differed between unbrowsed and browsed trees. As the variances did not differ and the values of above- and

Table II. Mean values and standard error (*SE*) of various above- and below-stump characteristics in unbrowsed and browsed 6- to 7-year-old sessile oak.

	Unbrowsed	*SE*	Browsed	*SE*	*P*
Specific leaf area (cm^2 g^{-1})	157.73	3.77	147.22	3.50	< 0.05
Leaf area (cm^2)	19.80	0.88	18.89	0.85	n.s.
Leaf weight (g)	9.02	0.76	13.09	0.92	< 0.001
Leaf weight/stem weight	0.57	0.02	0.99	0.06	< 0.001
Stem biomass (g)	15.86	0.97	13.12	1.20	n.s.
Height (cm)	92.66	2.14	44.43	2.12	< 0.001
Number of branches	6.72	0.37	7.88	0.40	< 0.05
Number of branches/height (cm^{-1})	0.072	0.003	0.178	0.011	< 0.001
Root collar diameter (mm)	8.07	0.20	9.52	0.28	< 0.001
Rooting depth (cm)	33.91	0.69	33.36	0.74	n.s.
Total root biomass (g)	12.73	0.64	16.60	1.04	< 0.001
Number of coarse roots (≥ 2 mm)	1.30	0.14	2.38	0.19	< 0.001
Number of fine roots (< 2 mm)	3.74	0.24	4.96	0.29	< 0.01
Root/stem biomass	0.92	0.02	1.98	0.09	< 0.001

Note: n = 145 seedlings in all cases for both, except for the mean leaf weight where n = 35 and leaf area where n = 25 for each browsed and unbrowsed; n.s. is non significant.

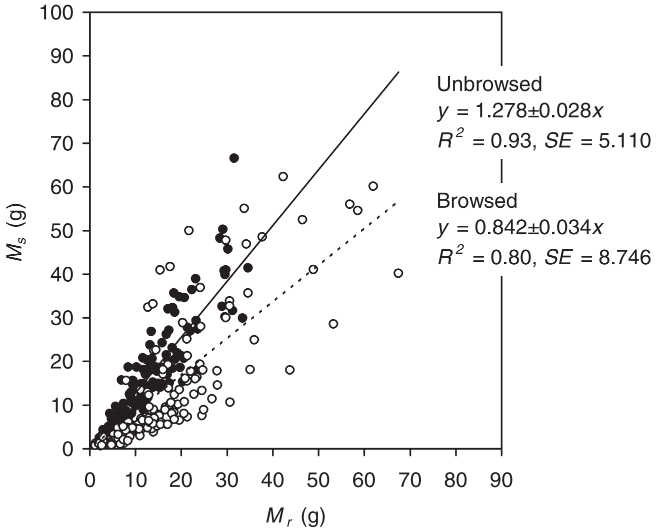


Figure 1. Relationship between root biomass M_r and shoot biomass M_s for unbrowsed (●) and browsed (○) 6- to 7-year old sessile oak. Equations are forced through the origin because the intercept was statistically non-significant ($P > 0.05$) and the response must be zero at the beginning. Relationships differed significantly at $^{***}P < 0.001$.

below-stump characteristics were normally distributed (Wilk-Shapiro-Test), Students *t* test was used for comparing the significance among means in *table II* and *figures 3* and *4*.

3. RESULTS

Mean values of several above- and below-stump parameters are shown for unbrowsed and browsed plants in *table II.* Outside the fence, a mean of 4 shoots per plant were damaged by repeated browsing of buds or flushes. Twenty-six percent of the browsed seedlings had 2, 21% had 3, 4 or 5, and 12% had 6 ord more damaged shoots. The maximum was 11 damaged shoots. Plants with dominant and codominant stems occurred in the population of unaffected seedlings, while 49% of the browsed plants showed forks (type II) and 30% showed the shrub form (type III) with competitive stems (*table I*). The browsed plants were half of the height but had only slightly lower stem biomass than the unbrowsed plants. The difference in stem biomass was not significant between browsed/unbrowsed areas. The lower seedling height was compensated for by a higher number of branches and a higher relative leaf weight (expressed as leaf weight per stem weight). Browsing did not affect leaf area but specific leaf area, so that the active photosynthetic area does seem to be negatively affected by browsing, even when the difference makes less then 10%.

All values of below-stump parameters were significantly higher in browsed than unbrowsed plants, except for the rooting depth where the soil is the main constraint factor and not browsing (*table II*).

Consequently, the relationships between root and shoot biomass differed significantly between unbrowsed and browsed plants (*figure 1*, *** $P < 0.001$). Furthermore, the root: shoot biomass range was wider for browsed plants as the damage intensity was not the same for all browsed plants. Thus, there were browsed plants with a high and very low shoot biomass in relation to unbrowsed plants. However, browsed seedlings seemed to allocate relatively more carbon to root biomass which is also confirmed by the fact that shoot mass relatively to A_{rc} is significantly lower in browsed than in unbrowsed (*figure 2A*, $^{***}P < 0.001$), while the relationships A_{rc} and root biomass did not differ between unbrowsed and browsed plants (*figure 2B*). The relative contribution of biomass in the different parts of plants showed that the leaf biomass contribution was the same for unbrowsed and browsed seedlings, while more biomass was allocated to the

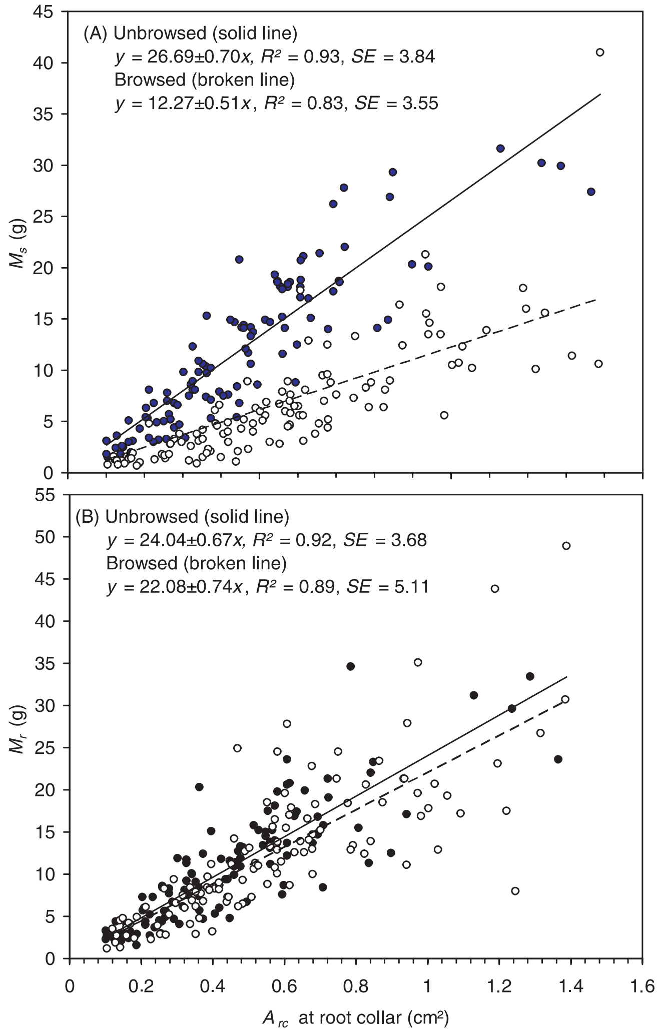


Figure 2. Relationships between cross-sectional area at the height of the root collar A_{rc} and (A) shoot biomass M_s and (B) root biomass M_r for unbrowsed (●) and browsed (○) 6- to 7-year old sessile oak seedlings. Equations are forced through the origin because the intercept was statistically non-significant ($P > 0.05$) and the response must be zero at the beginning. Relationships (A) differed significantly at ***$P < 0.001$, relationships (B) were not different.

stem in unbrowsed plants and to the roots in browsed plants (*figure 3*). This increased biomass allocation to the roots in browsed seedlings seemed to occur at the cost of investment in wood, but it can be also assumed that seedlings allocate to roots before they allocated to shoots, as can be seen from *figure 2B*.

There were statistical differences in fine, coarse and tap root biomass, due to browsing. Higher biomass values were pronounced in coarse and tap roots of browsed plants (*figure 4*). As can also be seen from *figure 4*, the ratios of biomass allocated to the different roots did not differ significantly.

4. DISCUSSION

Browsing by large herbivores influences regeneration dynamics and survival of broadleaved species [19]. One useful instrument to analyse differences in growth between browsed and unbrowsed plants is, besides simulation experiments, the comparison of seedlings from fenced and non-fenced subplots [12, 21, 25, 36].

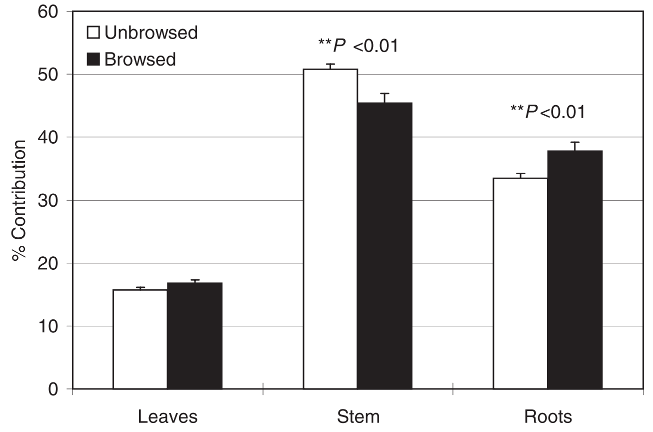


Figure 3. Percentage contribution of biomass in the different plant parts of unbrowsed and browsed 6- to 7-year old sessile oak seedlings.

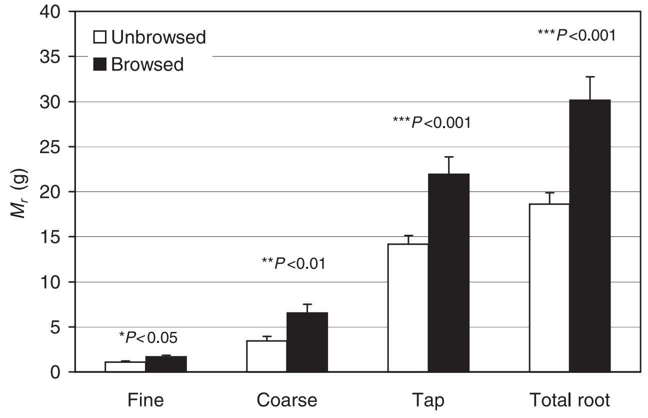


Figure 4. Mean root biomass calculated for a subsample each of 35 unbrowsed and browsed 6- to 7-year old sessile oak seedlings. The root biomass differed significantly between the two populations.

Browsing significantly affected above-stump plant parts of young naturally regenerated *Q. petraea* seedlings, although the browsing intensity was moderate, i.e. 10 roe-deer per 100 ha, 68% of browsed plants with a mean of 4 shoots damaged. Similar browsing effects were reported for 4- to 15-year-old *Q. robur* (L.) saplings from a Dutch forest area [36]. As in our study the browsing effects on biomass distribution were small but evident, except for leaf biomass. In our study, the browsed plants were smaller and 30% of them showed a shrubby form: all browsed seedlings had on average more branches and leaf biomass than unbrowsed plants while the stem biomass was not significantly different. Our results are somewhat in contrast to those of earlier studies [11, 36]. While Eiberle [11] reported less height growth, combined with less side shoots and less leaf density, Van Hees et al. [36] found that browsed pedunculate oak saplings had less leaf biomass and more branch biomass than unbrowsed plants with the same shoot biomass. The height growth is influenced by tree vigour and apical control of the height [9]. The reduction of the height increment and the changes in apical dominance detected in the browsed seedlings might be caused by regular browsing, i.e. repeated annual attacks over a period of several years. Thus, the biomass will be more evenly allocated to a higher number of competitive growth axes. Harmer and Baker [22] and Chaar et al. [5] showed for young *Q. petraea* seedlings that terminal bud decapitation stimulated lateral branch production due to the suppressed apical dominance. Furthermore, browsing in our study seemed to stimulate diameter growth measured at the root collar, which is known to be a zone of high meristem activity and of resprouting of shoots from dormant buds [9]. Collet et al. [9] reported that sprout shoots replacing the leader shoot and developing a multistemmed morphology frequently occurs following shoot dieback. This mechanism enhance the ability of the young tree to recover from damage.

It is already reported for white oak saplings that root systems might be older than stems [24]. The present study confirms the hypothesis that browsing influenced the distribution of biomass in the different plant parts, i.e. with greater amounts of biomass in below-stump parts, particularly into tap roots. However, the favoured allocation to the roots was less pronouned in *Q. petraea* than reported for *Q. coccifera* (L.) [28]. One explanation could be that the latter species grew under much more difficult conditions in an arid region with poor soils, and in that case a below-stump source of carbohydrates was discussed to be much more important for the regrowth and essential for resprouting. The relative contribution of the tap roots to the total root system of both unbrowsed and browsed plants was more than 70%. As shown for 9-year-old loblolly pine trees, sucrose is preferably allocated to the taproot and first-order lateral roots within the root system [33]. Although the construction costs for coarse and tap roots are high, the benefits are that they are long-lived, support the stem, anchor it to the soil, provide the conducting framework, and influence the distribution of fine roots [15, 29]. Furthermore, young oak are known to accumulate a certain amount of starch partitioning in their roots [39]. A large storage of reserve foods can cover the energy expenditure of the growing root system and have the advantage to be less susceptible to mammalian herbivory attack [28]. Nevertheless, root damages caused by below-ground herbivores such as voles and insects occur and can be heavy in peak years [18, 38].

Browsed seedlings may thus survive if they have sufficient reserves [10, 16]. Reserve carbohydrates stored in structural roots may play an important role for resprouting and early season growth, but the mechanisms of mobilisation and the pathway to above-stump compartments are poorly understood [26]. In our study, we are only able to state that browsed seedlings have more root system biomass in relation to the shoot. If and how sessile oak seedlings can use roots as source of carbohydrates cannot be answered here. Nevertheless, the favoured biomass accumulation in structural roots of browsed seedlings is an investment for a better root system architecture, anchorage, and acquisition of soil-based resources [14].

Although the growth conditions for controlled simulation experiments of browsing in nurseries differ from those for browsing in natural regereration, where several external factors such as climate, light and competition also influence plant growth, effects of browsing on shoots and roots may be the same for both. Braithwaite and Mayhead [4] simulated different levels of browsing on *Q. petraea* grown as 30–45 cm high 1+1 transplants at 1*1 m spacing in a nursery with fertile weed-free soil over a five year period. No tree mortality occur in all their treatments and this was explained by tree vigour and growth under optimum external conditions. In their study, the two severe treatments with two years of leading shoot removal twice a year with and without stumping back after three years significantly reduced not only height and stem diameter but also root and shoot biomass. If these extreme forms of browsing occur under natural conditions or correspond to our findings is difficult be answered here. The biomass values of naturally regenerated 6- to 7-year-old sessile oak were much lower than those of the transplants. Although we found significant differences in growth parameters between browsed and unbrowsed plants, they were much less pronounced than reported for the severe treatments in their study [4]. Our results can be perhaps more likely compared to those of the treatment which is defined by Braithwaite and Mayhead [4] as “mild browsing” and consisted in one year of leading shoot removal twice a year which may correspond more to “natural” browsing in our study with a mean of 4 shoots damaged for 68% of browsed plants after seven years. However, low levels of shoot removal in their treatment had no significant effect on growth of young sessile oak transplants [4].

5. CONCLUSION

Sessile oak was confirmed in our study as being resistant to moderate browsing, i.e. 68% of plants with a mean of 4 shoots damaged. There are relatively small but significant differences in growth between damaged plant by browsing and unbrowsed plants. Although the saplings survive damages, browsing will reduce longer term height growth, may influence tree architecture (risk of multistemmed forms) and certainly alter the partitioning of biomass for a long time during young plant’s growth. Browsed plants had a higher proportion of biomass in the root system, pronounced in coarse and tap roots. If and how the below-stump part of a plant serves as a storage of carbohydrates to enable faster recovery after browsing should be further investigated.

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