

Quantification of Deer Browsing in Summer and Its Importance for Game Management in Latvia

ARVIDS PRIEDĪTIS, SAMANTHA JANE HOWLETT*, JĀNIS BAUMANIS, GUNA BAGRADE, GUNDEGA DONE, ĀRIS JANSONS, UNA NEIMANE, AIVARS ORNICĀNS, ALDA STEPANOVA, AGNIS ŠMITS, AGRITA ŽUNNA AND JĀNIS OZOLIŅŠ

Latvian State Forest Research Institute "Silava", Riga str. 111, Salaspils, LV-2169, Latvia

*Corresponding author: Samantha Howlett (e-mail: samantha.howlett@silava.lv)

Priedītis, A., Howlett, S. J., Baumanis, J., Bagrađe, G., Done, G., Jansons, Ā., Neimane, U., Ornicāns, A., Stepanova, A., Šmits, A., Žunna, A. and Ozoliņš, J. 2017. Quantification of Deer Browsing in Summer and Its Importance for Game Management in Latvia. *Baltic Forestry* 23(2): 423-431.

Abstract

Browsing by large herbivores can have significant impacts on various ecosystems, and the industries associated with them. However, little is done to explain animal–plant interactions on the basis of browsing frequency. Our study indicates that assessment of summer browsing at the end of the growing season can give a clearer understanding of these interactions and therefore better guide management decisions. In order to quantify the impact of browsers on forest biomass production, a four year long browsing simulation experiment was performed by clipping fresh unripe shoot tops within a freshly clear felled aspen stand. Tree tops were clipped 1, 3-5 and 8 times per growing season with intervals of 2 – 8 weeks. A number of factors were measured; removed fresh apical biomass (A), which represented biomass consumed by animals, the green biomass remaining in autumn (B) and the sum of both A and B (A+B), which composes the total yield of green biomass after each growing season. The frequency of total apical removal during the vegetation period had a significant impact on all three indices. A significant negative relationship between A and B up to a level of fivefold clipping indicates that this is the threshold of compensatory growth, as all indices diminished at eightfold clipping. An 8-fold treating over the period of four years results in the development of grass cover instead of young small deciduous trees and shrubs. Comparison of our results with studies in nature allowed us to standardize the assessment of browsing intensity. Summer browsing intensity is the first index of plant response to browsing and gives an indication of deer fitness before winter. Any compensatory growth caused by deer switches to decompensatory growth, when browsing intensity exceeds 50%, whereby the biomass produced cannot effectively replace the biomass consumed.

Key words: deer, deciduous woods, summer browsing, browsing simulation, apical removal.

Introduction

The foraging of large herbivores has a significant influence on the structure and function of many ecosystems (Vera 1997, Olofsson et al. 2004, De Knecht et al. 2008, Gornal et al. 2009, Stewart et al. 2009, Davidson et al. 2010). Large herbivores may cause different responses regarding growth parameters of plants; both under and overcompensation of removed biomass has been recorded (McNaughton 1983, Danell and Huss-Danell 1985, Paige 1992, Oba et al. 2000).

Typically, the impact of herbivorous mammals on woody vegetation has been described considering winter damage caused by animals (Kuiters et al. 1996, Takada et al. 2002, Liberg et al. 2010, Belova 2012); however, summer browsing has also been shown to cause major effects on plant responses (Bergström and Danell 1995) and it can be more important for animals than winter browsing (Bobek 1977, Priedītis and Bambi 1983, Schwartz et al. 1987). Moderate use by brows-

ing or grazing stimulates compensatory abilities in plants while overuse causes a delay of that process (McNaughton 1983, Danell and Huss-Danell 1985, Paige 1992, Oba et al. 2000). These opposite reactions to browsing are characteristic for fast growing species such as aspen (*Populus* spp.), willows (*Salix* spp.) and birches (*Betula* spp.). These species are preferred by browsers in summer and they also compensate removed parts better under good growing conditions (Guillet and Bergström 2006). These compensatory reactions can supply deer with winter food when the browsing frequency allows the new saplings to reach a sufficient height by autumn, whereby these are accessible to animals while dwarf shrubs, forbs and grasses might be covered by deep snow.

Some studies have found that browsing by deer reduces survival and decreases the biomass of seedlings in some broadleaved tree species (Harmer 2001). The abundance of resources, which are preferred during spring and autumn, shapes winter fawn body mass

of roe deer (Pettorelli et al. 2003). A study by Priedītis and Bambe (1983) observed remarkable associations between browsing percentage and the development of vegetation by keeping 16-20 roe deer individuals in a 16-ha large enclosure during the summer period. Similar clear felling areas were also surveyed for browsing intensity outside the enclosure. The live weight of the captive roe deer (especially fawns) in autumn was 1-3 kg less compared to those hunted in free nature. This deficit, however, was regained soon (mostly in December) by artificial feeding in the winter garden. It enabled us to conclude that summer browsing has a significant influence on the development of plants and the body condition of animals. In a study by Priedītis and Ozoliņš (2005), summer browsing caused by three deer species at a level of 60% or more in the zone up to a height of 2.5 m was associated with degradation of vegetation and cachexia of free ranging animals also.

Population densities of herbivores have been used as an indicator of herbivory and the impact of animal populations on vegetation (Takada et al. 2002, Stewart et al. 2009). Indices for animal-plant interactions related to summer browsing intensity were of particular concern in our study. Our aim was for a consolidated assessment of both the individual response of young deciduous trees to browsing and the total supply of forage composed by trees browsed at different inten-

sities. A few studies are known on the responses of deciduous woody plants during the vegetative period in relation to defoliation (Bergström and Danell 1995) and apical removal (Hjilten et al. 1993, Harmer 2001). Little is done, however, to explain animal-plant interactions on the basis of browsing frequency, though it is known that browsing of terminal shoots in the vegetative period leads to increased branching in the same season (Blasko et al. 2014). One way to quantify browsing intensity regarding plant above-ground biomass is as a ratio (percentage) of saplings showing browsing signs in comparison to the total supply of all saplings present by the end of the vegetation period (Priedītis and Bambe 1983, Priedītis 1996). Since large herbivores prefer to pick just the tops of the trees (Danell and Huss-Danell 1985) this can result in both visible and invisible browsing signs available in autumn. One can observe either very recently browsed shoots, which have had no time to regenerate or those browsed a few times repeatedly. The more visible browsing signs present by the end of vegetation period, the less trees have been left intact or had time to completely form new buds and tops. If the above-mentioned processes are considered, observations suggest that the percentage of woody plants with visible browsing signs in autumn can be used as an index of animal-plant interaction, e.g. for monitoring of population status and their habitats (Figure 1).

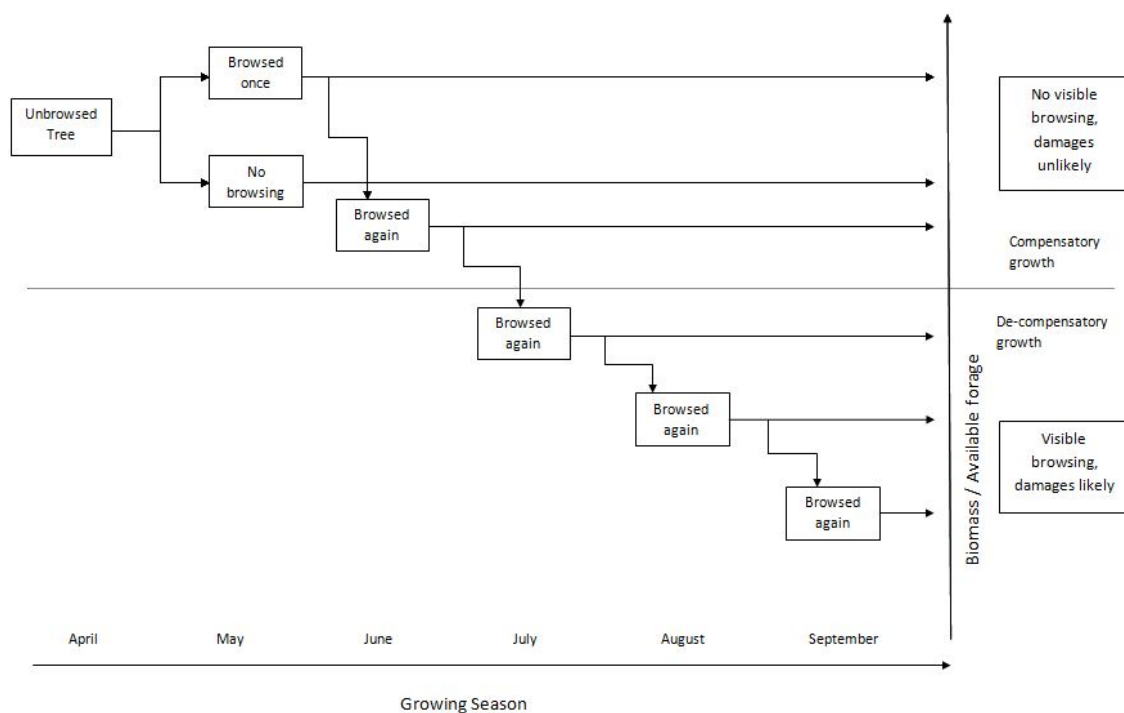


Figure 1. Flow chart summarising predicted effects of browsing during the growing season on amount of forage available in autumn. Browsing frequency in each month from May to July and even in August can be performed twice; therefore, in reality browsing times can be more than shown

Therefore, four hypotheses result from our previous experience on browsing processes:

1) Biomass of deciduous tree shoots can recover completely if tops are removed at low intensity during the growing season.

2) After a single clipping of tree tops, the lost biomass can be overcompensated within the same growing season, i.e. the total biomass produced within a growing season in the saplings treated only once is greater in comparison to those without removal.

3) Multiple top removals in young deciduous tree saplings will cross a threshold, which leads to decompensatory growth; when the amount of biomass produced within a growing season diminishes in comparison with untouched trees.

4) The percentage of visible browsing signs present in autumn can be used as an index of animal – plant interaction.

In this article, we summarize episodic studies examining these four hypotheses and compare our simulation data with field data. We suggest assessment of summer browsing as an indicator for deer population control.

Material and Methods

Browsing simulation experiment

A 10 × 10 m large area within an aspen (*Populus tremula*) clear cut in Ceraukste parish in southern Latvia (Figure 2) was fenced on the 13th June 1985 when the height of the trees was 5-10 cm above the ground. Within the fenced area eight 1 × 10 m large permanent experimental plots were selected and two 1 × 10 m large plots were left untouched for comparison. The experiment was performed by clipping fresh unripe shoots with leaves up to 5 cm from the top in all deciduous woody plants and forbs present in the plot. Clipping frequency during the four-year experiment period in different plots was 1, 3 to 5 and 8 times per growing season with a minimum interval of two weeks. All biomass removed during the growing seasons was delivered to the laboratory and weighed without drying within 24 hours of cutting to the nearest full grams.

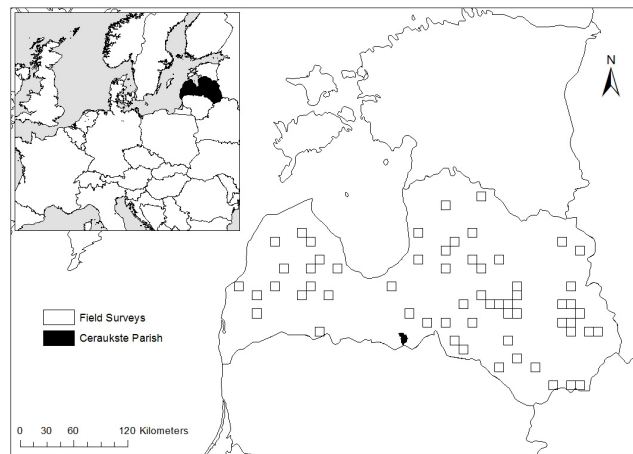


Figure 2. Map showing regional locality of Latvia, and locations of both the simulation experiment and field surveys

Due to a large amount of wood-pulp in winter and autumn, weighing was performed right in the field using spring scales and results were approximated to the nearest 100 g. The number of saplings was recorded per plot and all values mentioned below were calculated in accordance to the average number of saplings per plot.

In winter, all plots including the control plots were completely cleared to return the plot to a fresh clear-cut, so that the following year clipping was applied to fresh saplings. While clearing was done for all four years, the amount of woody material was only measured for the first two years. In some plots clipping regime was changed for different years while in others it remained constant throughout the study period (Table 1). Changes to clipping regimes were done to allow us to test how both date and frequency of apical removal affected the re-growing shoots. In the first year of the experiment, most plots were clipped only once but on different dates. Since all plots were cleared in winter, and treatments the following year were to new saplings, it allowed us to change regimes between plots, and pool information from all years. It should be also noted that in the second year, the aspen leaf eating beetles (*Melasoma* sp.) infected trees

Plots	First year		Second year		*Invasion	Third year
	Frequency	Date 1st treatment	Frequency	Date 1st treatment		Frequency
1.	1 x	13.June	1 x	4.June	0	1 x
2.	8 x	13.June	8 x	4.June	0	8 x
3.	4 x	13.June	4 x	4.June	0	5 x
4.	1 x	4.July	3 x	4.June	0	4 x
5.	1 x	1.August	8 x	4.June	1	8 x
6.	1 x	3.September	4 x	4.June	1	5 x
7.	1 x	1.October	3 x	4.June	1	4 x
8.	0 x	1.October	0 x	23.September	1	0 x

Table 1. Regime of apical removal in all plots throughout whole period of treatment.NB: Treatments in the 3rd and 4th summer started on the 26th May and finished on the 23rd and 25th September

* Presence of aspen beetles (*Melasoma* sp.) 0= absent, 1=present

in four plots, and consequently we only used results from the remaining unaffected plots (Table 1).

To assess the response of woody plants to our experimental apical removal, three indices of biomass were taken into consideration. The first index (A) was the removed fresh non-lignified biomass from clipping that presumably represented the biomass actively consumed by the animals during the growing period. The second category (B) was all the above-ground, unripe green biomass that remained in autumn. Thus, the sum of both A and B (A+B) composed the total yield of green biomass after the respective growing season. For all calculations, the weight of wood biomass was related to the average number of saplings per 10 square meters ($\text{g}/10 \text{ m}^2$). Sapling height was measured from the ground to the top of the apical stem.

Field surveys for summer browsing

In order to compare browsing intensity with the respective abundance of deer, broad scale field surveys for summer browsing were carried out in sample plots from 2010 to 2013 across the whole country (Ozoliņš et al. 2010). Individual $10 \text{ km} \times 10 \text{ km}$ squares were randomly selected (Figure 2), and within these 30 sites areas consisting of both forest regeneration and open summer habitat were crossed by a linear transect. All trees and shrubs at a height accessible to deer were surveyed for the presence of browsing signs. Tree species and degrees of browsing were not recorded in order to survey large areas in a short space of time. All deciduous trees were surveyed except for alder *Alnus* spp. In areas, where woody vegetation was very dense, a 1 m^2 large spot was assessed. Separate trees or shrubs were checked if they were located far from one another. The presence of one or more lost tops or stripped leaves in either the 1 m^2 checking spot or of separate trees were counted as browsed. Pellet groups for that winter were also counted in the following spring after the snow had melted in the same sample plots.

Data analysis

A mixed model analysis was run on the three biomass indices A, B and A+B to test whether frequency had an effect. As we found evidence that biomass values could be higher in different years due to different growing conditions, we included year as a factor. Furthermore, as it appeared that previous clipping regimes could have had an effect on subsequent years, we included plot as a random factor.

Linear regression was used to test for relationships between indices A and B. All analysis was done using R version 2.15.1, R Core Team (2012).

Results

The biomass of unripe soft tops (A) that was removed only once during the first summer of the experiment varied depending on the removal date. A increased when performed before the 1st August (Figure 3) and decreased after that date while indices B and A + B increased after the 4th July. At repeated removal of green mass, A, B and A+B varied depending on the frequency of removal (Figure 4). For all years excluding the third year, A and A+B were the largest at a picking frequency of 4 times. An eightfold apical removal with intervals of two weeks led to a decrease in all values, particularly for B. Observations were similar for the third year, however a higher value for A at an eightfold removal was observed. Frequency of removal also had an effect on sapling height. As frequency of removal increases, the sapling height at the end of the growing season decreases (Figure 5).

In the summer of 1986, aspen leaf eating beetles infected trees to various extents. Interestingly, the only plots free of beetles were those where apical removal in the first summer was performed during the active growing time of June to July, while the intact trees were

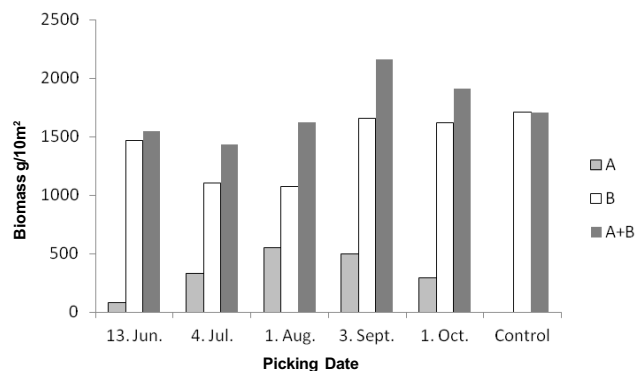


Figure 3. Impact of cutting date (performed only once) and total apical removal on biomass ($\text{g}/10\text{m}^2$) in the first summer of the experiment

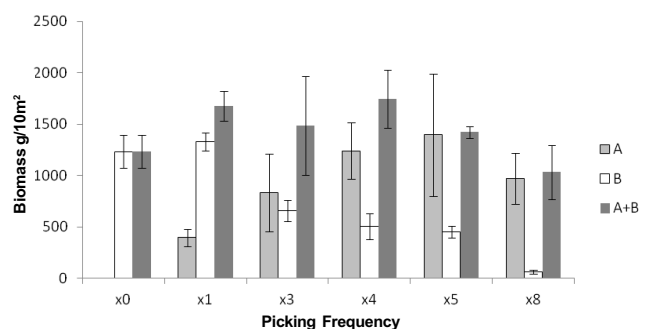


Figure 4. Impact of picking frequency on all three indices with all years combined

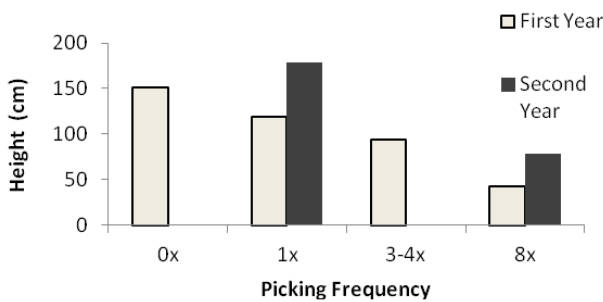


Figure 5. Impact of apical removal on lignified annual sapling height after the first and second year. The second year only includes the plots not invaded by beetles

heavily invaded. Some indices were considerably larger in the second year than in the first year at all regimes of apical removal. The higher values of biomass in the second year in comparison with the first one were related to the height of the new healthy saplings at the time of first apical removal. On the 4th June, when the summer browsing experiment was repeated, the saplings had already reached 50 – 60cm in height. This can be explained by the fact that root shoots in the first spring after the felling of the aspen stand appeared about one month later than the shoots from buds in the second spring. Thus, on 13th June 1985 the saplings were only about 5-10 cm high.

Summarizing the entire period of the four-year study, A, and (A+B) appeared maximal at three to five-fold experimental browsing while B reached its maximum at a single apical removal (Figure 4). Nevertheless, assuming that the untouched saplings in our experiment complied with 100% green mass yield, even a single apical removal performed mainly on the first dates of June caused an increase both of B (106.8%) and (A+B) (134.8%) (Figure 6). Performing three to fivefold apical removal, (A+B) was 139.1% although B was only 42.3% meaning that a high yield of green mass may be gained primarily due to A. At an eight-fold treatment, A+B remained relatively large (90.3%) while B decreased to only 6.0%.

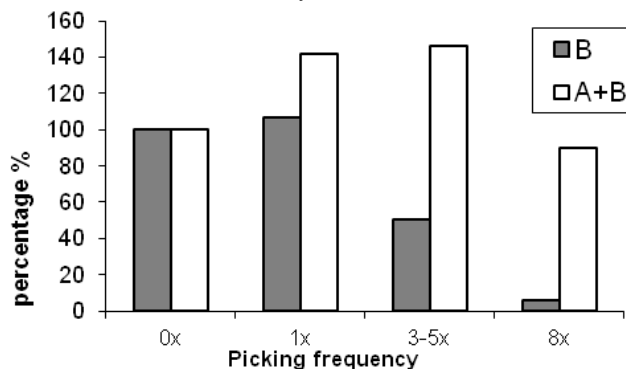


Figure 6. Impact of apical removal transformed into percentages

Combining all years together, we can see that by increasing the amount of A it has a negative effect on B (Figure 7). Running a regression using all picking frequencies excluding eightfold picking results in the significant negative relationship ($P = 0.02$), however, when eightfold picking is included, this relationship becomes insignificant. This is not surprising as at eightfold picking all indices begin to decrease, meaning that the trend begins to deviate away from a linear relationship. The mixed model analysis comparing picking rates and biomass values gave a significant output for all three indices (A, B, A+B) ($P = <0.01$ for all models).

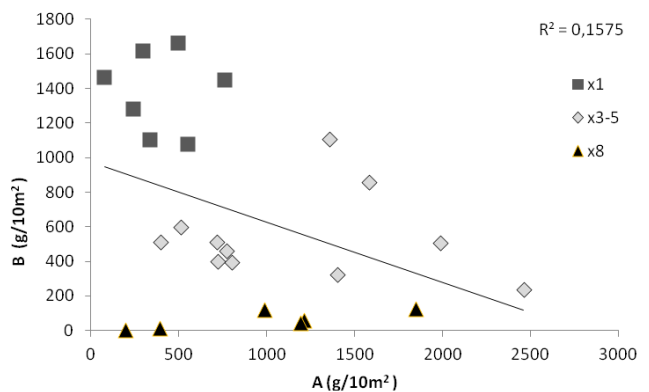


Figure 7. Negative relationship between indices A and B at different picking intensities. The trend line calculated using all three picking frequencies

We found an evidence that picking frequencies impacted subsequent years. In the fifth summer following the completion of the experiment (i.e. after the first winter without re-clearing) the plots were visually different from one another. Most plots were covered in 1 - 1.5 m trees, with only intact trees in the control plots considerably exceeding 2.5 m in height. The plot which had been clipped eightfold for every year of the experiment was covered in grass (Figure 8).

The recently obtained (2010-2013) field data confirmed that the percentage of summer browsing is associated with the abundance of deer as a positive significant correlation between browsing percentage and the numbers of winter pellet groups (Figure 9).

Discussion

Our results agreed with previous findings that herbivores have an influential role on the structure and productivity of vegetation (Vera 1997, Olofsson et al. 2004, De Knegt et al 2008, Gornall et al. 2009), especially when restocking of woodlands with deciduous trees after harvesting takes place (Harmer 2001).



Figure 8. Picture taken at the end of June from the summer following completion of the experiment. The centre of the photograph shows a plot, where shoot tops were removed eightfold every summer during the four years of the experiment and is now overgrown with grass

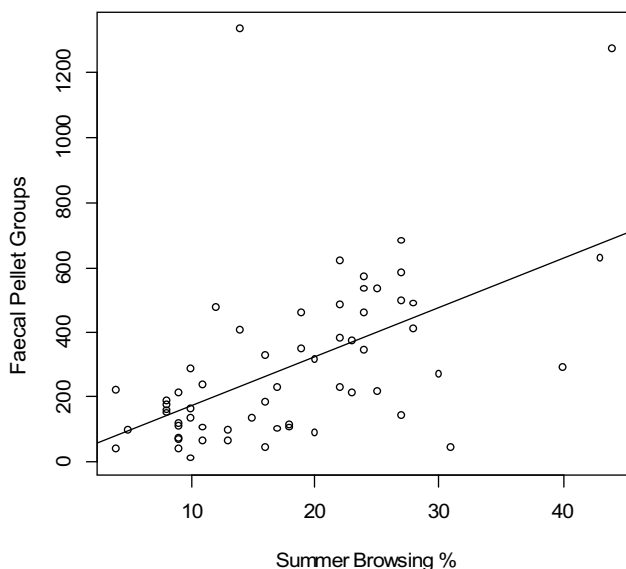


Figure 9. Relationship between summer browsing and faecal pellet groups from field surveys from 2010 to 2013 ($r^2 = 0.2867$, $N=60$)

The frequency of total apical removal during the vegetation period had a significant impact on the amount of green biomass present in autumn. Green biomass in autumn tends to be overcompensated after a single apical removal performed at the beginning of June and rapidly decreases with an increase of removal frequency. The significant negative relationship between A and B up to a rate of fivefold clipping indicates that growth remains compensatory as an increase in A leads to a decrease in B, however, at eightfold clipping the compensatory threshold is crossed

and new growth cannot compensate for lost biomass (Figure 7). Furthermore, repeated biomass removal impacts the growth of new suckers and saplings not just in the current year but also in the next vegetation period. A study by Landhäuser and Lieffers (2002) found that cutting the above ground biomass of clonally regenerating aspen trees (*Populus tremuloides*) resulted in an imbalance between the ratio of root to leaf area, resulting in depleted carbohydrate reserves within the root system and extensive root mortality, meaning that growth in the following year was affected. While our study gives evidence that intense clipping of fresh green biomass could affect the root system, since the plot that received the highest clipping rate for all four years was eventually reduced to grassland, it does not answer whether incrementally increasing clipping has a direct linear relationship with root retention, or whether similar thresholds exist within the root system whereby compensatory growth can no longer be accounted for.

In a study by Priedītis et al. (2008), small 2 m × 2 m areas were fenced to prevent access of deer to deciduous trees during one growing season. The heights of the saplings were similar in autumn within the small fenced areas and in areas outside after they were cut in winter if browsing percentage was below 30%. Therefore, summer browsing at a level of < 30% corresponds to at least a single apical removal. If browsing percentage outside such enclosures were about 60% or more then sapling height was only about 5 cm which corresponds to eightfold apical removal. If browsing level by autumn reaches nearly 50%, we concluded that tree response to apical removal switches from compensatory growth to de-compensating growth i.e. only partial re-growth of removed biomass. This can be assumed as a threshold level for browsing that indicates a shift from favourable towards unfavourable impacts. Assessment of browsing percentage in the autumn not only characterises availability of food in the past summer but also for the coming winter and therefore can give some prognosis for deer overwintering success. At high levels of browsing, biomass required in winter can be consumed during the summer. At low browsing levels, productive forest areas overgrow with tree thickets after clear felling comparatively fast, whereas at high browsing pressure, young woodlands tend to turn to grasslands (Priedītis 1996). Furthermore, homogenization of vegetation can also take place (De Knecht et al. 2008). High damages to coniferous plantations have been observed in Latvia (Priedītis and Priedītis 1998) even at light overuse of summer habitats, at a browsing rate of deciduous saplings of 50%. The positive correlation between deer abundance and browsing percent-

age obtained by the 2010-2013 field data indicates that browsing percentages under 50% are not connected with a drop-in animal density, suggesting that these areas still have enough available forage to support such numbers.

It must be noted, however, that a number of factors likely play a role in determining browsing intensity and/or animal density in relation to biomass (Gill 1992(a), Reimoser and Putman 2011). Firstly, the locality of forests, the types of habitats surrounding forest areas and amount of available natural forage have been found to have an effect on browsing intensity (Gill 1992(b), Reimoser and Gossow 1996, Jarnemo et al. 2014). High browsing percentages have more often been recorded in openings of woodlands in forests far from agricultural fields (Takada et al. 2002). Takada et al. (2002) found that in sites with high deer population densities, plant coverage and species richness in the forest understory was significantly higher nearer to agricultural fields in comparison with the sites located far from the fields. Therefore, deer grazing in fields reduces browsing pressure in forest; therefore, field vicinity should be taken into account when using the browsing percentage as an indicator for deer management. The presence of carnivores and natural control mechanisms will also dictate how intensely different areas are utilised (Kuijper 2011). Finally, the species of ungulate also plays a role. Overuse (browsing percentage > 60%) of deciduous tree supply in Latvia was observed only in areas with high dominance of red deer in the ungulate community. Red deer are suggested to be adapted to consume a greater quantity of grass due to its large fore-stomach capacity and rumen pillar thickness (Clauss et al. 2003). Grasses and forbs formed the main component (81%) of red deer pre-winter diet in Estonia (Ligi and Randveer 2012). Roe deer and moose have a smaller fore-stomach and weaker reticulorumen muscles therefore they have higher demands to browse (Hofmann and Nygren 1992) and they are unable to consume large amounts of grass that tend to stratify fibrous raft in the reticulorumen (Clauss et al. 2003). Consequently, red deer are less dependent on the leaves of woody plants than roe deer and moose. Therefore, its population, unlike other deer species, is able to overuse deciduous woody plants without a prompt suffering from shortage of food and corresponding changes in population structure.

Since animals are able to cause both a stimulating and delaying effect on productivity and availability of plants, their populations could be managed accordingly. Results of this study indicate that the maximum number of animals and highest productivity of plants (stimulation phase) is at a browsing percentage of 50% or lower. Perpetuation of this phase can

be possible by adapting harvest quotas to the reproductive rate of the animal population. So far in Latvia, forest districts with minimal and optimal browsing percentage dominate. In forest districts with over-browsed young woodlands, population densities of roe deer and moose are low even at very restricted hunting pressure, indicating areas characterised with poor forage availability. We suggest that the browsing percentage estimated in autumn gives the most accurate insight into plant – animal interaction while animal counts or assessment of winter browsing alone do not give complete information for adaptive management of deer populations. Areas with intense browsing can lead to a decrease in productivity and an increased risk to adjacent areas of agriculture or forestry. Damage can be mitigated by harvest, supplementary feeding sites situated away from the coniferous plantations and crop fields, or by protective means. However, any long-lasting over-browsing of winter food during summers will reduce both standing density in deer population and its recruitment ability as soon as mitigation activities fail, or harsh winters make deer survival more difficult. Therefore, we recommend to follow the summer browsing indices and to adjust harvest quotas accordingly thus keeping browsing pressure below 50%.

We believe the results of this study have achieved one of our primary aims: to increase our understanding of the effect of browsing on forest regeneration processes. Our study indicates important relationships between browsing and the period of growth for vegetation. Due to this, the authors must note that the recommended browsing threshold of this study is specific to Latvia and Latvia's seasonality. However, we believe that specific thresholds may be relatively constant in different environments due to the negative feedback between growth rate and growth condition. In good growing conditions browsed shoots recover faster, therefore to reach the threshold more frequent apical removal is necessary than in bad conditions. In one situation, the threshold may occur at a higher density of browsers than in another depending on the geographical region and productivity. However, the concept of utilising summer browsing as an indicator of deer fitness is an easy and applicable tool that can be implemented in most temperate/boreal forests.

Acknowledgments

We wish to acknowledge the support of our late colleague Mārtiņš Bičevskis at the early stages of this study. We thank the Ministry of Agriculture for financing field work on summer browsing and winter deer pellet counts within the project "Critically low and

maximally acceptable densities in ungulate populations" from 2009 to 2012. The final stage of the study was carried out and the article was written realising the project (No. L- KC-11-0004) of the National Forest Competence Centre.

References

- Belova, O.** 2012. The impact of herbivorous mammals on woody vegetation at the different stages of forest succession. *Baltic Forestry* 18(1): 100-110.
- Bergström, R. and Danell, K.** 1995. Effects of simulated summer browsing by moose on leaf and shoot biomass of birch (*Betula pendula*). *Oikos* 72: 132-138.
- Blasko, L., Greiser, G. and Pechner, J.** 2014. Influence of hare (*Lepus europaeus*) on natural regeneration at the forest edge in the North-East German lowlands. In: M. Stubbe (Eds.): Beiträge zur Jagd- und Wildforschung Bd 39, GWJF, Halle/Saale, p. 381-401 (in German).
- Bobek, B.** 1977. Summer food as the factor limiting roe deer population size. *Nature* 268: 47-49.
- Clauss, M., Lechner-Doll, M. and Streich, W.J.** 2003. Ruminant diversification as an adaptation to the physico-mechanical characteristics of forage. *Oikos* 102(2): 253-262.
- Davidson, A.D., Ponce, E., Lightfoot, D.C., Fredrickson, E.L., Brown, J.H., Cruzado, J., Brantley, S.L., Sierra-Corona, R., List, R., Toledo, D. and Ceballos, G.** 2010. Rapid response of grassland ecosystem to an experimental manipulation of a keystone rodent and domestic livestock. *Ecology* 91: 3189 - 3200.
- De Knegt, H. J., Groen, A. T., Van De Vijver, C. A. D., Prins, H. H. T. and Van Langevelde, F.** 2008. Herbivores as architects of savannas: inducing and modifying spatial vegetation patterning. *Oikos* 117: 543-554.
- Danell, K. and Huss-Danell, K.** 1985. Feeding by insects and hares on birches earlier affected by moose browsing. *Oikos* 44: 75-81.
- Gill, R.M.A.** 1992(a). A review of damage by mammals in north temperate forests: 3. Impact on trees and forests. *Forestry* 65(4): 363-388.
- Gill, R.M.A.** 1992(b). A review of damage by mammals in north temperate forests: 1. Deer. *Forestry* 65(2): 145-169.
- Gornall, J.L., Woodin, S.J., Jónsdóttir, I.S. and Van der Wal, R.** 2009. Herbivore impacts to the moss layer determine tundra ecosystem response to grazing and warming. *Oecologia* 161: 747-758.
- Guillet, C. and Bergström, R.** 2006. Compensatory growth on fast growing willow (*Salix*) coppice in response to simulated large herbivore browsing. *Oikos* 113: 33-42.
- Harmer, R.** 2001. The effect of plant competition and simulated summer browsing by deer on tree regeneration. *Journal of Applied Ecology* 38(5): 1094 - 1103.
- Hjilten, J., Danell, K. and Ericson, L.** 1993. Effects of simulated herbivory and intraspecific competition on the compensatory ability of birches. *Ecology* 74 (4): 1136-1142.
- Hofmann, R.R. and Nygren, K.** 1992. Ruminal mucosa as indicator of nutritional status in wild and captive moose. *Alces* suppl. 1: 77 - 83.
- Jarnemo, A., Minderman, J., Bunnefeld, N., Zidar, J. and Månsson, J.** 2014. Managing landscapes for multiple objectives: alternative forage can reduce the conflict between deer and forestry. *Ecosphere* 5(8):1-14.
- Kuijper, D.P.J.** 2011. Lack of natural control mechanisms increases wildlife-forestry conflict in managed temperate European forest systems. *European Journal of Forest Research* 130(6): 895-909.
- Kuiters, A.T., Mohren, G.M.J. and Van Wieren, S.E.** 1996. Ungulates in temperate forest ecosystems. *Forest Ecology and Management* 88(1):1-5.
- Liberg, O., Bergström, R., Kindberg, J. and Von Essen, H.** 2010. Ungulates and their management in Sweden. In: Putman R. et al. (eds.): European ungulates and their management in the 21st century. Cambridge University Press, Cambridge, p. 37-70.
- Ligi, K. and Randveer, T.** 2012. Pre-winter diet composition of red deer (*Cervus elaphus* L.) in Estonia. *Baltic Forestry* 18(1): 150-155.
- McNaughton, S. J.** 1983. Compensatory plant growth as a response to herbivory. *Oikos* 40:329-336.
- Oba, G., Mengistu, Z. and Stenseth, N.C.** 2000. Compensatory growth of the African dwarf shrub *Indigofera Spinosa* following simulated herbivory. *Ecological Applications* 10(4): 1133-1146.
- Olofsson, J., Stark, S. and Oksanen, L.** 2004. Reindeer influence on ecosystem processes in the tundra. *Oikos* 105: 386-396.
- Ozoliņš, J., Baumanis, J., Žunna, A., Zariņš, J. and Ornicāns, A.** 2010. Methodological approach in conflict assessment and mitigation caused by game animals in Latvia. *Mežzinātne* 22(55): 3-18.
- Paige, K. N.** 1992. Overcompensation in response to mammalian herbivory: From mutualistic to antagonistic interactions. *Ecology* 73(6) 2076-2085.
- Pettorelli, N., Dray, S., Gaillard, J., Chessel, D., Duncan, P., Illius, A., Guillon, N., Klein, F. and Laere, G.V.** 2003. Spatial variations in spring time food resources induces the winter body mass of roe deer fawns. *Oecologia* 137(3): 363-369.
- Priedītis, A. and Bамbe, L.** 1983. Roe deer population in the Latvian SSR. LatZTIPI, Rīga ,70 pp. (in Latvian).
- Priedītis, A.** 1996. Browsing on woody plants and living conditions of cervid populations. In: Proceedings of the 22nd IUGB Congress, Pensoft Publishers, Sofia, Moscow, St. Petersburg: 239-244.
- Priedītis, A.** 1992. The average degree of browsing of deciduous woody plants and preference of definite plant species or genera by cervids in summer. In: Proceedings of the 1st Baltic Theological Conference, Tartu: 229 - 235.
- Priedītis, A. and Priedītis, Ā.** 1998. The use of woody plants by cervids during the vegetation period and winter. In: Proceedings of the Latvian Academy of Sciences, Section B 52 (1/2) (594/595): 58-62.
- Priedītis, A. and Ozoliņš, J.** 2005. Cervids and predators in relation to browsing percentage within some hunting grounds in Latvia. In: M. Stubbe (Eds.): Beiträge zur Jagd- und Wildforschung Bd. 30, GWJF, Halle/Saale, p. 237-245 (in German).
- Priedītis, A., Ozoliņš, J., Pupila, A., Ornicāns, A. and Uloth, W.** 2008. Results of simulated browsing on woody plants in fresh aspen clear cut. *Beiträge zur Jagd- und Wildforschung* Bd. 33, GWJF, Halle/Saal, p. 165-177 (in German).
- R Core Team.** 2012. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, Available online at: <http://www.R-project.org/>.
- Reimoser, F. and Gossow, H.,** 1996. Impact of ungulates on forest vegetation and its dependence on the silvicultural system. *Forest Ecology and Management* 88(1): 107-119.

- Reimoser, F. and Putman, R.** 2011. Impact of large ungulates on agriculture, forestry and conservation habitats in Europe. In: Putman et al. (Eds.): *Ungulate Management in Europe: problems and practices*. Cambridge University Press, Cambridge, UK, p.144-191.
- Schwartz, C.C., Regelin, W.L., Franzmann, A.W. and Hubbert, M.** 1987. Nutritional energetics of moose. *Swedish Wildlife Research* suppl. 1: 265-280.
- Stewart, K. M., Bowyer, R. T, Kie, J. G., Dick, B. L. and Ruess, R. W.** 2009. Population density of North American elk: effects on plant diversity. *Oecologia* 161(2): 303-312.
- Takada, M., Asada, M. and Miyashita, T.** 2002. Cross-habitat foraging by sika deer influences plant community structure in a forest-grassland landscape *Oecologia* 133(3): 389-394.
- Vera, S.** 1997. *Metaphors for the wilderness. Oak, hazel, cattle and horse*. Doctoral thesis. Agricultural University, Wagenengen. FWM, The Netherlands. 440 pp.

Received 17 November 2015

Accepted 24 February 2017