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Effects of natural and artificial beech regeneration methods on food diversity and browsing intensity in the Inner Western Carpathians

Auswirkungen von natürlicher und künstlicher Buchenwaldverjüngung auf Nahrungsangebot und Wildverbiss in den Innerwestkarpaten

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Schlüsselbegriffe: Huftiere; Forstwirtschaft; Wildschäden; alternatives Nahrungsangebot

Abstract

The European beech (*Fagus sylvatica*) is one of the most important broad-leaved species in Europe. Beech forests are vulnerable to both climate change and herbivory pressure. Their sensitivity to game browsing depends on forest regeneration methods and stand age influencing vegetation diversity. We investigated the available food supply to and the browsing effect of ungulates on natural and artificial beech regeneration sites of different ages in the even-aged forests of Mátra Mountains, Hungary. Density of beech saplings and number of available and browsed shoots of all woody species were estimated seasonally. We found significantly more beech

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saplings only in summer, but always significantly more shoots, concurrent lower food diversity and higher browsing impact on beech in the natural than in artifical sites. The highest browsing values for beech were detected when the proportion of the alternative woody food supply was less than 10 %. The proportion of browsed beech shoots in all browsed shoots was lower at the points of a site where other alternative woody species were also accessible to ungulates. We propose to maintain natural species diversity in beech regeneration sites from the very first period after felling to give ungulate species the chance not to browse the target tree species of forest management, but other preferred food species occurring in relatively high abundance. Based on our results diverse woody vegetation and relatively high abundance of alternative plant food sources could decrease negative ungulate impact not only in artificial monospecies beech regeneration sites, but even in the case of natural beech regeneration.

Zusammenfassung

Die Europäische Buche (*Fagus sylvatica*) ist eine der wichtigsten Arten der Laubbäume in Europa. Buchenwälder sind in zweierlei Hinsicht gefährdet; durch den Klimawandel und den zunehmenden Druck durch Pflanzenfresser. Ihre Empfindlichkeit gegenüber Wildverbiss hängt zum einen von den Waldregenerationsmethoden und zum anderen von der altersbedingten Vegetationsdiversifikation des Bestandes ab. In dieser Studie untersuchten wir die Intensität von Wildverbiss durch Huftiere an natürlich und künstlich gezogenen Buchenwäldern unterschiedlichen Alters, im gleichaltrigen Wald der Mátra Berge, Ungarn. Die Dichte von Buchenjungbäumen und die Anzahl vorhandener und verbissener Baumtriebe von allen Gehölzarten wurde saisonal geschätzt. Im Sommer konnten signifikant mehr Buchenjungbäume gefunden werden, aber immer signifikant mehr Buchentriebe, bei zwischenzeitlich geringerer Nahrungsdiversität und höherer Verbissintensität auf Standorten mit natürlicher Buchenverjüngung im Vergleich zur künstlich gezogenen Buche. Wenn der Anteil des alternativen Futterangebotes unter 10 % absinkt, waren die höchsten Wildverbisswerte zu verzeichnen. Der Anteil verbissener Buchentriebe an allen Trieben war an den Orten geringer, wo den Huftieren auch andere Baumarten zugänglich waren. Wir empfehlen daher an Buchenwald-Verjüngungsstandorten die natürliche Artenvielfalt von Beginn an nach Baumfällung zu erhalten, um Huftieren die Möglichkeit zu geben, nicht gerade die Zielbaumgruppe des Waldmanagements abfressen zu müssen, sondern andere Pflanzenarten. Basierend auf unseren Ergebnissen können wir schlussfolgern, dass eine hohe Vegetationsdiversifikation im Wald sowie ein relativ hoher Überfluss an alternativen Pflanzenresourcen nicht nur den negativen Einfluss von Huftieren bei künstlicher Reinbestands-Buchenverjüngung verringert, sondern dass dies auch in Gebieten mit natürlicher Buchenwaldregeneration gilt.

Introduction

Even-aged forestry destroys the various ecological functions of forests, and additionally erodes the beneficial public services provided by forest ecosystems (Agetsuma 2007). Several recent papers recommend the transformation of sylviculture systems from "even-aged" to "close to nature" or "Continuous Cover Forestry – CCF" systems, as a desirable alternative of industrial forestry (Gamborg and Bo Larsen 2003; Standovár and Gálhidy 2003; Davies and Kerr 2011). As one of the most important European tree species, the European beech (Fagus sylvatica) plays a key role in transition strategies (Gessler et al. 2007). European beech has wide European distribution and due to its drought-susceptibility it must get intensive attention in case of further global warming tendency (Fotelli et al. 2009).

A close to nature sylviculture system obtains higher forest biodiversity giving wider ability to forest ecosystems to buffer recent ecological changes (including climate change) which reduces both ecological and economic risks in forestry (Standovár and Gálhidy 2003). Climate change will have profound impact on the biodiversity, conservation and management of Central European forest ecosystems (Milad et al. 2011). In Hungary the probability and severity (warmer and dryer) of droughts is projected to be higher than it was during the end of the 20th century (Gálos et al. 2008). Due to relative higher sensitivity of European beech toward these climate factors, beech forests may be particulary affected (Peuke et al. 2002; Olesen and Madsen 2008).

Herbivory may both strengthen and counteract the effects of changing climate on tree species distribution and survival (Cairns and Moen 2004). The combination of extreme rainy events with reduced herbivory can be key in woody cover expansion in many semiarid ecosystems (Holmgren et al. 2006). Since the drought-sensitive European beech is generally avoided by ungulates (Boulanger et al. 2009; Katona et al. 2013b), the joint impact of ungulate browsing and increasing aridity on the success of beech regenerations strongly depends on the food supply diversity of the forest regeneration sites.

Deer browsing may have a telling effect on tree seedlings, saplings and matured individuals too; however the most endangered age classes are the youngests (Merganic et al. 2009). Ungulates can take both, damage and beneficial influence on reforestation at the same time (Reimoser 2003). Usually their suppressive impact on seedlings occurs locally on reforestation sites (Putman and Moore 1998; Rooney 2001). The browsing pressure can decrease the growth and increase the mortality of seedlings (Gill and Beardall 2001). The game damage problem should be approached by suitable forestry interventions (Moser et al. 2006) as a general habitat management. For example the grazing damage by livestock to tree regeneration may be reduced via presence of shrubs or other physical shields (Bakker et al. 2004; Pellerin et al. 2010; Jensen et al. 2011). The presence of abundant alternative forage sources as shrubs and herbs has great importance in decreasing browsing intensity on seedlings and saplings (Gill 1992). In our study we analysed and compared the ungulate-vegetation relationships in different beech regeneration sites. We described the forest regeneration capability, the food supply for game species and ungulate impact on forest regeneration in all areas.

We assumed that there are more beech saplings and shoots as deer forage in the natural regeneration sites than in artificial ones and more shoots in older than in younger ones. This is because the artificial regeneration usually starts with much lower sapling density than natural one (Katona et al. 2013a) and there should be much taller saplings with more shoots in older sites than in younger ones.

We expected lower browsing impact on beech in areas with more diverse food supply, which was predicted to be in natural regeneration sites. It is based on earlier results, that alternative woody browse supply available in an area can deprive browsing impact from main target species (e.g. beech) not preferred by ungulates (Katona et al. 2013b). Similarly, we predicted lower browsing impact on beech within a given site in patches where other woody species are also present.

In this research, therefore, we investigated the density of beech saplings (as regeneration unit) and availability of shoots (as ungulate forage) and the ungulate browsing impact on them. We compared those data between the two regeneration technologies (natural and artificial) and three age classes (1, 5 and 10 years old) of beech regeneration sites. We also analysed the influence of woody species diversity on the browsing intensity on beech.

Materials and Methods

Study area

Our study was carried out in Mátra Mountains in the northern part of Hungary. These are layered volcanic mountains with geohistorical and ecological connection to the Carpathians. The soil of the Mátra is mainly chernozem brown forest soil with argillaceous brown forest soil on andesite stone base. The annual mean temperature is 5.7 °C. Annual rain amount is around 635 mm/year; rainy days occur more often in May and June. The flora belongs to the temperate woodland zone.

The study area was located in the operating area of Mátrafüred Forestry of Egererdő joint-stock company. The designated study sites were within a 3.5 km radius from a centroid with coordinates: 47°89’N, 19°93’E.

This company manages approx. 72000 ha state owned forest in Mátra and Bükk Mountains. Those woodlands are medium quality from an economic point of view, but ecologically these are highly valuable habitats; 68% of their total range is under environmental protection. The three main forest types of the Mátrafüred Forestry area are sessile oak (*Quercus petraea*) forests (3443 ha, 33.7%), hornbeam (*Carpinus betulus*) - oak forests (2805 ha, 27.4%) and beech forests (2633 ha, 25.8 %). The most common shrub species are common dogwood (*Cornus sanguinea*), European cornel (*Cornus mas*), blackberry (*Rubus fruticosus*) and European privet (*Ligustrum vulgare*). In the hedges the most frequent species are blackthorn (*Prunus spinosa*), dog rose (*Rosa canina*) and hawthorn (*Crataegus monogyna*).

Most forests of Egererdő joint-stock company are under even-aged forestry system dominated by clear-cut and uniform shelterwood regeneration methods. The extension of sites under natural regeneration was 853 ha, meanwhile the sites under artificial reforestation occupied 65 ha in 2009. The proportion of forest stands under CCF silviculture is around 10% of the total area. The proportion of fenced areas is also around 10%, which, however, means a relatively low value in Hungary. The reduction of fenced areas was 46% in the last 15 years from 59% to 13%.

The estimated ungulate density in the hunting area covering our sites was 7 ind./ 100 ha in 2009 based on National Game Management Database. Abundance of red deer (*Cervus elaphus*), wild boar (*Sus scrofa*) and mouflon (*Ovis aries*) was 2 ind./100ha; that of roe deer (*Capreolus capreolus*) was 1 ind./100ha.

In our research we designated six different beech regeneration sites for comparison. We aimed to find investigation areas with similar environmental conditions and representative to the general view of beech regeneration sites in their vegetation and management. We categorized those areas by their age since the year, when the area lastly became entirely harvested (1-2; 5-6; 8-10 years) and by the type of reforestation (natural or artificial). These sites were situated from each other within a distance of between 0.5 and 7 kilometers. The average size of the sites was 13.69 ha (from 4.67 ha to 20.62 ha). None of the investigated sites were fenced.

Field data collection

We collected seasonal field data four times (March, May, July, November) in 2009. For field sampling we followed the methods elaborated in previous studies (Katona et al. 2011, 2013a,b). We designated transects consisting of 25 to 50 sampling points at 5 to 10 meters intervals in each sampling area in each season.

In each area we estimated the woody species composition of available food supply and the relative utilisation of those species available. At the sampling points we counted the number of shoots of all woody species available and accessible to large herbivores and the number of browsed ones in the understory layer. We had four height categories: between 0 and 50, 50 and 100, 100 and 150, 150 and 200 cm from the ground surface. We counted the number of shoots available and browsed in a three-dimensional sample unit of 50 cm high, 50 cm wide and 30 cm deep within all vertical levels. Four sampling units placed on top of each other at every sampling point made it possible for us to count shoots easily and reliably. Generally woody plants were identified as species, but in some cases only the genus was registered. Based on our earlier observations on herbivore browsing, one shoot item was defined as the final ramification of the plant individual, which is longer than 3 cm and obtains leaves in the vegetation period. The only exception was blackberry, where the compound leaves were also identified as the subject unit of browsing because the number of browsing events on the elongated stems was not possible to estimate reliably. We registered the relatively fresh injuries caused by ungulates and old ones separately. Freshness was determined by the shape, pattern and colour of the damaged surface of the plant. We were not able to distinguish which ungulate species foraged on the given plant individual. However, the dominance of red deer in these areas suggests that this species was the main consumer.

We also counted the number of beech saplings at the sampling points in a quadrant of 2 m^2. This measure was carried out two times, in July and November for determining the sapling density in the peak and at the end of yearly vegetation period.

Data analysis

Normality of data was tested by Kolmogorov-Smirnov normality tests. Two-way ANOVA tests were run separately for each season to make comparisons between natural and artificial regeneration sites of different age. Variables compared were as follows: beech sapling and beech shoot density, browsing intensity on beech, the proportion of alternative woody species beside beech in the food supply and in the browsed food material. To reveal differences between regeneration types within age classes in the same season Mann-Whitney U-tests were used. Age classes were compared within the type of regeneration by Kruskal-Wallis tests followed by post-hoc Dunn's multiple comparisons tests in all seasons.

Shoot density of alternative species was compared between the two regeneration types by paired t-test using seasonal values of each site.

Influence of the availability of other woody forage species on the browsing intensity on beech was analysed by Spearman-correlation test.

We compared the proportion of browsed beech shoots in sampling points where beech saplings were only available to the points where besides beech saplings other woody species were also accessible by paired t-tests.

Results

Sapling and shoot density

Sapling density was significantly higher in natural (10112±3655 ind./ha) than in artificial regeneration sites (7171±855 ind./ha) irregularly (Two-way ANOVA: $F(1,214)=24.86$, $p<0.001$ in summer; $F(1,294)=1.56$, $p=0.21$ in autumn). In turn age of the regeneration sites had a more clear effect on sapling density (Two-way ANOVA: $F(2,214)=4.49$, $p=0.012$ in summer; $F(2,294)=15.51$, $p<0.001$ in autumn). There were more beech saplings in the 1- and 10-year old natural sites than in artifical ones in summer (Mann-Whitney U-tests: $p<0.05$); but only the 5-year-old natural site showed higher sapling density in autumn ($p<0.05$) (Fig. 1). Sapling density, therefore, showed a high decrease in 1- and 10-year-old natural sites until the end of the vegetation period. The density of saplings remained on similar level with the changing age of the artificial regeneration sites (Kruskal-Wallis-tests: $p>0.05$ for both seasons). But we found significant differences in case of natural sites. In summer the 10-year-old site has higher sapling density than the 5-year-old one (Dunn's test: $p<0.01$).; meanwhile in autumn the 5-year-old site had higher values than the two others (Dunn's tests: $p<0.001$).

There were significantly more beech shoots as food supply in the natural sites (3956000±3205000 shoots/ha) than in artifical ones (1803000±1149000 shoots/ha) (Two-way ANOVA: $p<0.001$ in all seasons) (Fig. 2). This difference was discovered in most cases (Mann-Whitney U-tests: $p<0.05$; except 5-year-old ones in summer and in winter). Shoot density significantly increased with the age of the sites considering any season or regeneration type (Kruskal-Wallis-tests: $p<0.001$).

Forage supply diversity

Our data did not support our hypothesis about the higher forage diversity of natural regeneration sites. The proportion of other woody species as alternative food sources beside beech was larger on artificial (21.2±14.94%) than on natural sites (8.5±8.33%) in each season (Fig. 3). Although, the difference was statistically significant only in autumn and winter (Two-way ANOVA: $p<0.001$). When pair-wise comparisons proved real or nearly statistical differences (Mann-Whitney U-tests: $p<0.05$), always the values of artificial sites were higher than that of natural ones. In turn, the average seasonal abundance of alternative woody species in the natural (219827±250641 shoots/ha) and artificial regeneration sites (216361±142178 shoots/ha) was similar (Paired t-test: $t=0.08$, $df=11$, $p=0.94$). It, therefore, shows that the higher proportion of alternative woody species in the artificial regeneration sites was due to the lower abundance of beech shoots in those areas.

The proportion of alternative food was similar in different age categories in artificial sites (Kruskal-Wallis tests: $p>0.05$, except spring), but it was statistically different in natural ones ($p<0.01$, except autumn). The difference was always revealed between 5- and 10-year-old categories, the earlier having higher values.

The most frequent alternative species beside beech on the natural sites were hornbeam (3.72±3.71%), blackberry (2.43±2.84%) and sessile oak (1.52±3.79%), meanwile on the artificial sites these were poplar (Populus spp.) species (7.31±8.46%), blackberry (4.78±4.16%) and pine (Pinus spp.) species (4.42±6.02%) (Fig. 3).

Browsing impact on beech

We found that the browsing intensity (proportion of freshly browsed beech shoots to the total number of available beech shoots) was significantly higher in the natural (18.43±14.29%) than in artificial sites (5.09±4.41%) (Two-way ANOVA: $p<0.001$ in all seasons) (Fig. 4). Values of the 10-year-old sites were always significantly higher than that of one-year-old ones (Kruskal-Wallis tests: $p<0.01$; except artifical site in winter).

The proportion of beech in the browsed food material in the natural sites (86.84±14.06%) exceeded the values of artificial sites (73.36±16.63%); but it was statistically significant only in autumn and winter (Two-way ANOVA: $p<0.0001$) (Fig. 5). We did not reveal differences in case of this variable among age classes of artificial sites (Kruskal-Wallis tests: $p>0.05$), but among natural sites the 10-year-old site had higher values than the 5-year-old one (Kruskal-Wallis tests: $p<0.05$; except in autumn). The most frequently browsed alternative species beside beech were hornbeam (suffering the 9.89±12.32% of total browsing impact), sessile oak (4.44±11.39%) and blackberry (2.27±2.65%) on the natural sites; meanwile on the artificial sites these were sessile oak (11.13±13.55%), poplar species (9.98±14.43%) and blackberry (5.89±4.43%) (Fig. 5).

There was no significantly strong relationship between the availability of alternative food supply (proportion of "non-beech" shoots) and browsing intensity on beech (browsed/all beech shoots) in the entire area (Spearman-correlation: for all browsed shoots: $N=24$, $R=-0.32$ $p=0.13$; for freshly browsed ones: $N=24$, $R=0.15$ $p=0.49$). However, in case of the highest browsing values found (more than 20%), the proportion of the alternative food supply was less than 10%. (Fig. 6). Considering at a smaller scale no browsing on beech was found when the presence of other species was more than half of the available shoots within the three-dimensional sample unit. Nevertheless, the relationship for the whole dataset was similarly weak at this resolution (Spearman-correlation: for all browsed shoots: $N=807$, $R=-0.128$ $p=0.0003$).

The proportion of browsed beech shoots in all browsed shoots was lower at the points where other alternative woody species were accessible to ungulates near to beech (100±0% vs. 58.79±25.97%, sampling points without and with other species, respectively) (Paired t-test: $t=5.722$, $df=12$, $p<0.0001$). In turn the browsing intensity on beech did not decrease by the presence of other species (11.79±12.27% vs. 7.82±8.38%, without and with other species, respectively) (Paired t-test: $t=0.11$, $df=14$, $p=0.91$).

Discussion

The European beech is considered in Europe as the most common economically important broadleaved tree species (Paule 1997). However, this tree species is highly susceptible to increasing droughts due to global climate change (Fotelli et al. 2009). Additionally, beech seedlings are sensitive to frost and animal predation and may suffer from herbaceous competition (Wagner et al. 2010). In the increasing parts of the Carpathian Basin beech forests have become threatened by the counteracting impact of climate change, ungulate herbivory and other above-mentioned factors (Katona et al. 2013b). There are several management tools and practices supporting the maintenance of these vulnerable forest ecosystems and avoid their irreversible destruction (Völk, 1998). Probably the most effective way to increase natural immunity of forests would be the transition from clear cutting to close to nature forestry (Diaci 2006). Reimoser and Gossow (1996) recommended to avoid clear cutting systems to decrease predisposition of forests against wildlife damage. Although single-tree selection would be an effectively adaptable tool in beech forests, even-aged forestry still dominates in Hungary (Katona et al. 2013b). Population control of large herbivores alone often could not be able to solve the failures of forest regeneration (Csányi 1994), mainly if it is conducted without a careful consideration of the sociobiological relationships of ungulate populations maintaining their stability (Miller and Ozoga 1997).

In most parts of the natural range of the European beech, such as the middle European temperate forests, beech stands are regenerated naturally (Paule 1997). It ensures a reliable basis for natural silvicultivation (Gessler et al. 2007). Based on this ability for natural renewing of European beech forests we expected higher sapling density and shoot availability of beech in natural than in artificial regeneration sites. Our results confirmed this hypothesis in case of shoots, but not entirely for saplings. The artificial regeneration generally starts with much lower sapling density than the usual natural sapling density due to the high costs of regeneration material and works. However, in this study beech sapling density in the natural regeneration sites was not very high compared to another Hungarian beech forest in Pilis Mountains managed under selection system. There the density of beech saplings ranged within an interval of 30000 and 60000 saplings/ha (Katona et al. 2013a), which values are 3 or 6 times higher than in this area. Moreover in the related literatures there are also published data about even much higher beech sapling density; between 200000 and 300000 individuals/ha (Peña et al. 2010). However, the higher initial density of saplings does not necessarily guarantee for higher number of trees. Survival rate of saplings could be very variable and presumably it might depend on a number of biotic factors, such as seeds, microorganisms, insects, herbivores, humans and abiotic environmental conditions, such as light, climate, soil, moisture, etc. (Jarcuška 2008). Our partly contradictory results about the differences in sapling density between seasons and different age categories also support this statement. The high variability in the cumulative impact of different factors could result in hardly predictable levels of surviving saplings. However, beech shoot density, as the measure of the available dietary units for ungulates, showed the expected relationships; i.e. shoot density increased with the age of sites and was higher in natural than in artificial sites. Much higher shoot density in natural sites in spite of irregular differences in sapling density could reveal a difference in the health condition of saplings. Shoot growth could be a good indicator of the condition and development potential of saplings (Kullberg and Welander 2003). Higher shoot density in natural sites could, therefore, reflect a better condition of abiotic environment and beech saplings.

Biodiversity is crucial for successful adaptation to changing environmental conditions and surviving (Scherer-Lorenzen et al. 2005). As such an elementary point it could be an indicator of natural silviculture (Kuuluvainen 2002). Species diversity of stands is also important in regard of timber production. The impact of neighborhood diversity was visible in beech trees showing higher mean radial stem growth rates when they were surrounded by a number of other tree species (Mölder 2009; Mölder et al. 2011). Increased plant diversity also provides an opportunity for ungulates to select among potential food sources (Boulanger 2009), resulting in lower impact on the main tree species (Katona et al. 2013b).

Based on this concept and on earlier results (Katona et al. 2011, 2013b) we expected less browsing impact on beech in areas with greater and more diverse food supply (with more alternative food besides beech). We hypothesised a more diverse woody species composition and less browsing effect in natural sites than in artifical ones, but we found the opposite. Artificial regeneration becomes necessary in areas of suboptimal environmental quality where natural beech regeneration is mitigated by abiotic factors. Hence, availability of more various food supply in artifical sites could be, at least partly, a consequence of this failure in spontaneous regrowth of beech saplings resulting in the expansion of other woody species. In natural regeneration sites, however, beech could possibly benefit from the more advantageous habitat characteristics and in dense abundance it could suppress the growing of other woody species. Limited light conditions in the matured predisturbance beech forests can inhibit the settlement of the more shade sensitive woody species like sessile oak. Lack of matured individuals of those species may lead to the absence of fertile seeds promoting their regeneration (Kuulavainen 2002; Wagner et al. 2010). This fundamental dependence on the actual level of abiotic factors and the stand structure of predisturbance beech forest is also reflected in the differing species composition of growing woody vegetation in our natural and artificial sites (beside beech and blackberry dominated by hornbeam and sessile oak vs. poplar and pine, respectively).

We found lower browsing intensity on beech in artificial regeneration sites. We suggest that this fact is due to higher diversity of food supply in those areas. Economically non-valuable woody species could be a useful tool to reduce browsing damage on saplings of target tree species of forest management. Jensen et al. (2011) clearly supported that protection of oak seedlings associated with natural presence of shrubs manifested in both decreased browsing frequency and browsing intensity on oak. In accordance to this relationship we found the highest browsing impact on beech in case of the highest beech proportion in the food supply. Hence if the local vegetation is poor in species ungulates can not optimally select and they browse just what is available to cover their nutrient requirements. However, it is a crucial task for managers and researchers to reveal the browsing preferences of different ungulate species. Based on this knowledge one could predict which woody species could take the herbivore pressure off the beech. Earlier analyses (Katona et al. 2013b) in Hungarian even-aged forests revealed that beech is usually an avoided species by ungulate browsing. Among the woody species occurring in these study sites especially blackberry, hornbeam, maple (Acer spp.) and ash (Fraxinus spp.) species would be preferred and selected more than beech. Nevertheless, our result demonstrates that although those species are consumed in large proportion (besides other non-preferred species), their food availability relative to the total ungulate pressure is too low to significantly diminish the browsing intensity on beech. In this field survey the seasonal browsing ratio in the sites did not exceed 20 or 30% of available beech shoots with some exceptional cases. In a Czech study Suchomel et al. (2010) found a total of 28.2% of beech young trees to be damaged to some degree in the plantations. But those values are certainly not high especially if we know that not every twig browsed mean damage from tree point of view and not every tree damaged mean damage from stand point of view (Reimoser et al. 1999).

Accordingly to literature and our results we propose to maintain a high level of natural species diversity in regeneration sites from the very first steps as primary protection of individuals of economically important species. Other woody species as diversionary elements offer the chance for ungulate species not to choose the target tree species (e.g. beech) for consumption. Based on our results diverse woody vegetation can have a great importance not only in artificial monospecies beech regeneration sites, but even in the case of natural beech regeneration. Among the key factors of this context are the choice of tree species and the ratio of other woody species in the area (Reimoser 2003). Although the benefits of mixed-species plantings are well-described in the literature (Nichols et al. 2006), there are few examples in the practice demonstrating the commercial success of maintaining forest biodiversity (Csépányi 2013). We promote moving towards forestry practices simulating the natural spatial and temporal pattern of vegetation changes in beech forest regeneration, which could steer those woodland ecosystems to higher tolerance of game damage and other threatening factors.

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Appendix

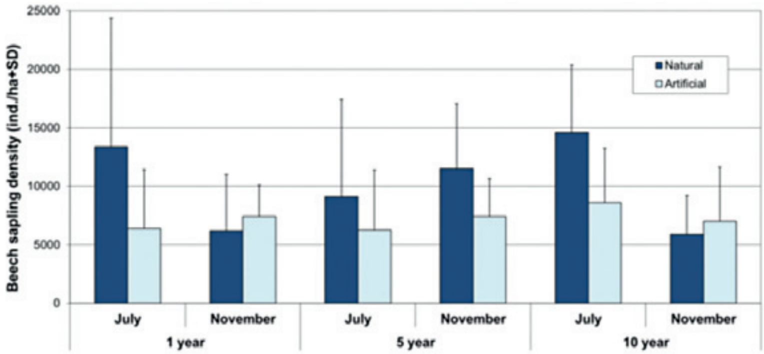

Fig. 1. Seasonal density of beech saplings in natural and artificial regeneration sites of different ages.

Fig. 1. Saisonale Verteilung von Buchenjungbäumen in natürlichen und künstlichen Regenerationsgebieten unterschiedlichen Alters.

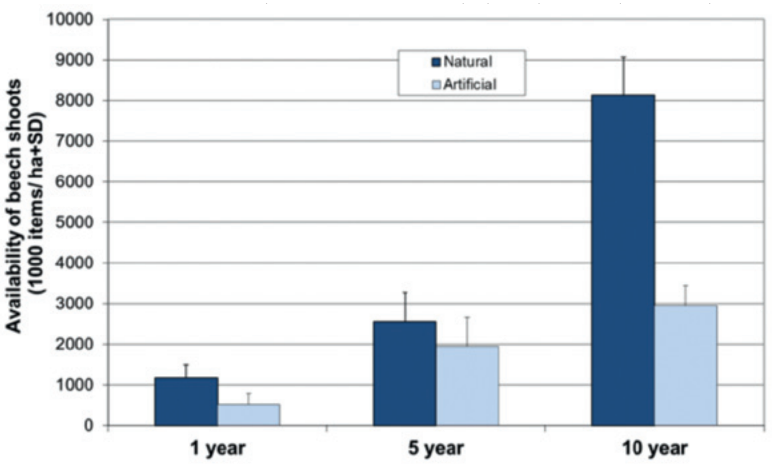

Fig. 2. Availability of beech shoots as food supply (average all seasons) in natural and artificial regeneration sites of different ages.

Fig. 2. Verfügbarkeit von Buchentrieben als Nahrungsquelle (Mittelwert aller Erhebungszeiten) in natürlichen und künstlichen Regenerationsgebieten unterschiedlichen Alters.

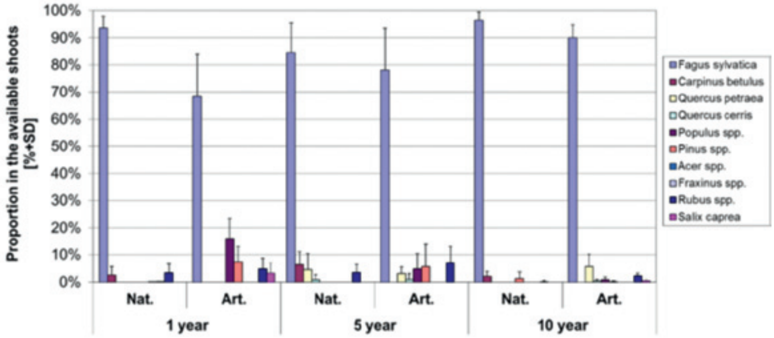

Fig. 3. Proportion of beech and other woody species in the food supply (average all seasons) in natural (Nat.) and artificial (Art.) regeneration sites of different ages.

Fig. 3. Anteil der Buche und anderer Baumarten als Nahrungsquelle (Mittelwert aller Erhebungszeiten) in natürlichen (Nat.) und künstlichen (Art.) Regenerationsgebieten unterschiedlichen Alters.

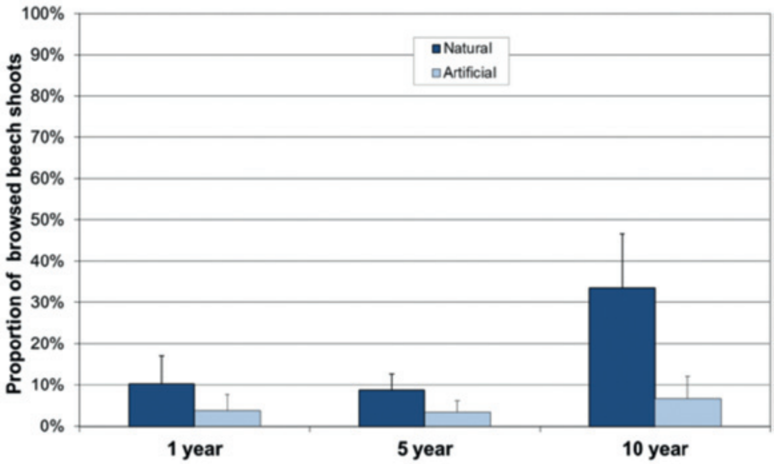

Fig. 4. Browsing intensity on beech (average all seasons) in natural and artifical regeneration sites of different ages. Ratio of browsed beech shoots to all beech shoots is shown.

Fig. 4. Mittelwert der saisonalen Wildverbissintensität bei der Buche (Mittelwert aller Erhebungszeiten) in natürlichen und künstlichen Regenerationsgebieten unterschiedlichen Alters. Der Anteil der abgefressenen Buchentriebe an der Gesamtanzahl der Buchentriebe ist dargestellt.

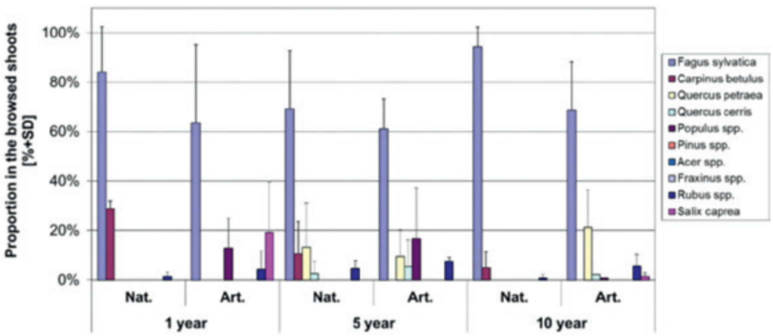

Fig. 5. Proportion of beech and other woody species in the browsed food material (average all seasons) in natural (Nat.) and artificial (Art.) regeneration sites of different ages.

Fig. 5. Anteil der abgefressenen Triebe von Buche und anderen Baumarten am verbissenen Nahrungsmaterial (Mittelwert aller Erhebungszeiten) in natürlichen (Nat.) und künstlichen (Art.) Regenerationsgebieten unterschiedlichen Alters.

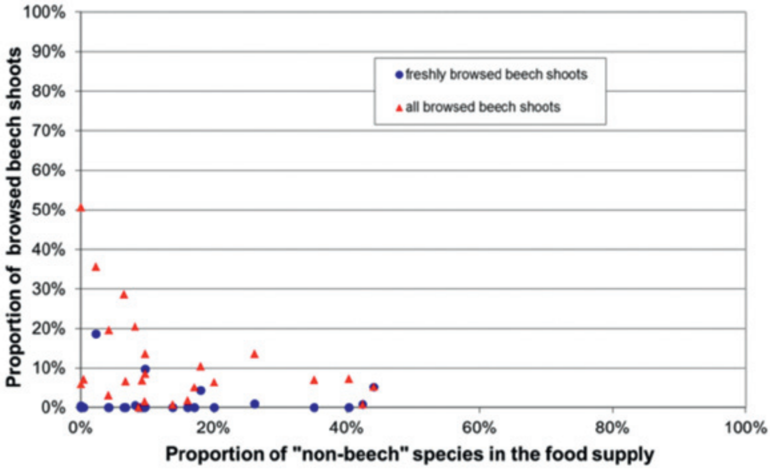

Fig. 6. Relationship between availability of alternative food supply in addition to beech (expressed by the proportion of their shoots) and browsing intensity on beech (browsed beech shoots / all beech shoots).

Fig. 6. Zusammenhang zwischen dem zusätzlich zur Buche verfügbarem Nahrungsangebot (dargestellt als Anteil der Triebe) und Verbissintensität an Buche (verbissene Buchentriebe / alle Buchentriebe).