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The effect of hunting regimes on tree regeneration in lowland beech (*Fagus sylvatica* L.) forests

Der Einfluss des Jagdregimes auf die Naturverjüngung in Tiefland-Buchenwäldern

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Abstract

Browsing ungulates are one of the most important determinants in regeneration dynamics. Although research on the impact of ungulates on forest ecosystems has become well established over the past few decades, direct links between different hunting regimes and sapling growth have been rarely reported. To address this need, we assessed the impact of a controlled and a lease hunting system on the sapling performance in lowland beech forests of Northwest Germany, investigating 111 randomly placed plots of 40 m² (2 x 20 m) with a total of 18,425 saplings. For each species, abundance, browsing status and size class were recorded during March and April 2007 and 2008. We applied generalised linear mixed models (GLMMs) to account for the effects of distinct study plots. Overall and species-specific browsing intensity notably decreased under a controlled hunting regime, whereas sapling abundance and species composition of the current regeneration stages were not affected by hunting management. Our results demonstrate that the improved regeneration potential depends largely on hunting strategy. The effectiveness of hunting is thus a relevant factor in realising the objective of near-natural mixed forests in the future.

Key words: natural regeneration, browsing intensity, hunting strategy, *Fagus sylvatica*, mixed modelling

Kurzfassung

Die Entwicklung der Naturverjüngung wird maßgeblich durch das Wild beeinflusst. Über dessen Auswirkungen auf Waldökosysteme liegen seit mehreren Jahrzehnten fundierte Kenntnisse vor, dennoch konzentrierten sich nur wenige Arbeiten auf die Bedeutung des Jagdregimes. Die vorliegende Arbeit versucht, diese Kenntnislücke durch eine auf 18.425 Schösslingen basierende Studie zu schließen. Dazu wurde der Einfluss von Regie- und Pachtjagd auf die Ausbildung der Naturverjüngung in Tiefland-Buchenwäldern Nordwestdeutschlands untersucht. Während der Monate März und April 2007 und 2008 wurden auf 111, zufällig ausgewählten, 40 m² (2 x 20 m) großen Untersuchungsflächen für jede Art die Abundanz, der Verbissstatus und die Höhenklasse erhoben. Um potenzielle Unterschiede zwischen den Untersuchungsflächen zu berücksichtigen, wurden generalisierte lineare gemischte Modelle (GLMMs) zur Analyse verwendet. Unter Regiejagd ist die Verbissintensität deutlich geringer, was sich auch auf Artniveau bestätigt. Im Gegensatz dazu lassen sich bezüglich des Verjüngungsspektrums und der Verjüngungsdichte keine statistisch gesicherten Unterschiede zwischen Regie- und Pachtjagd nachweisen. Unsere Ergebnisse zeigen, dass das höhere Verjüngungspotenzial vorrangig von der Jagdstrategie abhängt. Die Effektivität der Jagd stellt somit einen Schlüsselfaktor beim Aufbau naturnaher Laubmischwälder da.

Schlüsselwörter: Naturverjüngung, Verbissintensität, Jagdstrategie, *Fagus sylvatica*, Gemischte Modelle

Introduction

Natural regeneration is a key aspect in sustainable forest management and understanding the determinants of regeneration success is relevant for both ecological and economical reasons (Knoke et al. 2005, Felton et al. 2010).

Seedling recruitment in forests depends on various factors, such as natural disturbances, vegetation type, distribution of seed sources, soil properties or climatic conditions (Topoliantz and Ponge 2000, Tripler et al. 2002, Westphal et al. 2004, Vandenberghe et al. 2006), whereas regeneration success is mainly determined by ungulate browsing (Gill 1992, Kuiters et al. 1996, Harmer et al. 1997). Browsing by ungulates has long been considered as a challenge for forestry (Leopold 1936) and is equally important nowadays (Ammer et al. 2010). In most temperate forests ungulate densities increased progressively to a level that impedes the natural forest development (Gill and Morgan 2010). As browsing can trigger significant changes to forest dynamics by altering plant community composition, structure and nutrient status (Ammer 1996, Coomes et al. 2003, Weisberg and Bugman 2003, Rooney and Waller 2003, Kuijper et al. 2010), the knowledge of browsing effects is crucial for close-to-nature management practices. Rare admixed broadleaved species and valuable hardwoods are particularly affected (Ellenberg 1988, Tixier et al. 1997, Boulanger et al. 2009), which impedes the establishment of mixed forests as well as the conversion from anthropogenous coniferous stands into mixed forests (Zerbe 2002). Hence, the likelihood of a sufficient forest regeneration of deciduous trees based on natural regeneration processes depends, among other factors, on wildlife management.

According to Rooney (2001) and Tremblay et al. (2007), a reduction in deer densities can lead to improved sapling growth and establishment success; other studies however, could not support these findings (Kuijper et al. 2009, Tanentzap et al. 2009). Moreover, different authors report varying impacts with regard to tree species (Kuiters and Slim 2002, Månsson 2009, Kamler et al. 2010), but only few studies address the link between hunting regime and tree regeneration (Martin and Baltzinger 2002, Hothorn and Müller 2010). Therefore, we investigated how hunting management effects sapling performance, comparing species composition, density and browsing status of characteristic beech forest species of differently managed hunting areas.

Materials and methods

Study sites

Study sites were located within European beech (*Fagus sylvatica*) forests of the forest district Stadtwald Lübeck, which is situated in a moraine landscape of Schleswig-Holstein, Northwest Germany (Fig.1). The forest area is dominated by deciduous trees (72%) and comprises 4,297 ha. Elevation ranges from 0 to 90 m a.s.l. The climate regime in this area is sub-oceanic with a mean annual precipitation between 580 and 871 mm and a mean annual temperature of 8.3 °C (Gauer and Aldinger 2005).

Most of the investigated stands occur on well-drained (pseudogleyic) Luvisols, developed on deposits of the Weichselian glacial period. Soil texture predominantly consists of boulder clay (clay/sandy loam) with varying carbonate content. The prevailing phytocoenoses are affiliated to the *Galio odorati-Fagetum* association. The study site 'Albsfelder Tannen' is located within the same growth area, but differs with regard to the geological substrate. At this site, soils are mostly covered by glacial sands of varying thickness. The dominant soil types are podsolic Cambisols and the predominant forest communities can be assigned to the *Deschampsio-Fagetum* association. Study site characteristics are summarised in Table 1.

Hunting management and ungulate occurrence

Our study aimed to assess the relationship between hunting regime and natural regeneration. For this reason, study sites were grouped by their hunting management: lease hunting (LH) and controlled hunting (CH). CH was defined as hunting under the supervision of the forestry department, whereas in the case of lease hunting, private hunters control the hunting measures and strategies themselves. Three of the study sites (Albsfelder Tannen, Hevenbruch, Ritzerauer Hauptrevier) are under forestry departmental supervision; the remaining six forest compartments are leased for hunting. Hunting strategies and measures distinctly differ between the two hunting regimes. Controlled hunting is characterised by approximately 5 individual hunts on male ungulates and 2 pressing hunts on female animals per season. In contrast, lease hunting strategies consist of a large number of individual hunts (app. 40 per season) with a focus on male ungulates. Moreover, controlled hunting provides an improved hunting regulation, since an adjustment of hunting pressure (e. g. hunting type and frequency) by the local forester or forestry department is feasible.

The local browsing ungulate communities are dominated by roe deer (*Capreolus capreolus*) and low abundance of red (*Cervus elaphus*) and fallow deer (*Dama dama*). Ungulate densities in 2008 varied between 7.7 and 16.9 individuals per 100 ha (mean ± SD: CH = 14.9 ± 2.1; LH = 13.1 ± 3.1; Tab. 1). However, the specific population size is not always predictable on the basis of living or harvested ungulate counts (Hemami et al. 2005). The diverse structure of the investigated forests offer favourable habitat conditions for browsing ungulates and the high proportion of forest edge compared to total forest area has an additional supportive effect. Due to increased light availability, the margins provide both larger grazing quantities and a broader spectrum of species. Furthermore, the forests are surrounded by agricultural land, providing additional food resources for ungulate communities.

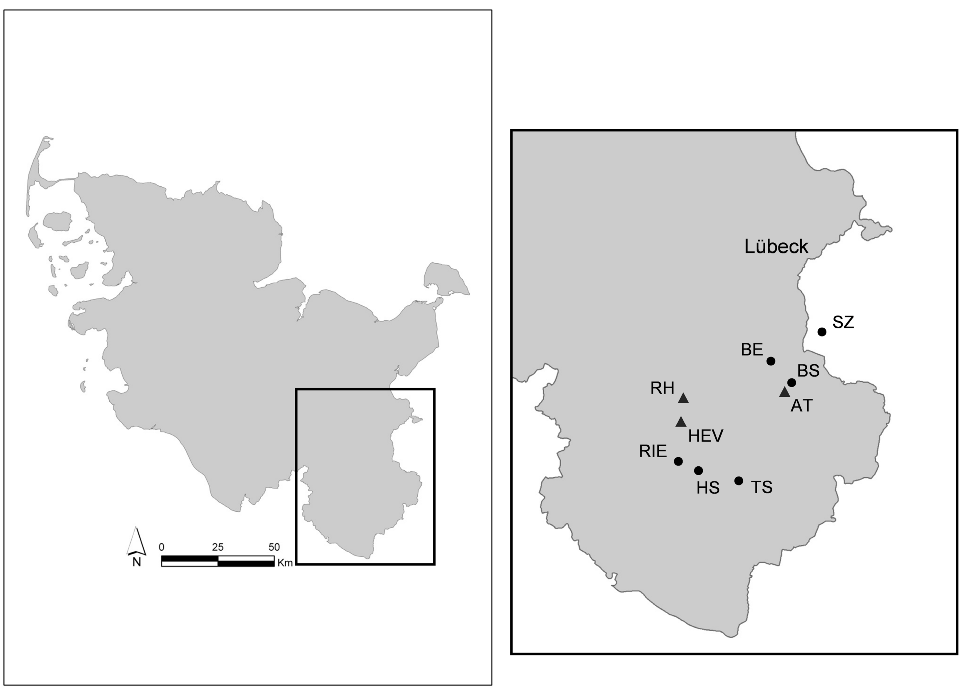

Figure 1. Location of the study sites and their corresponding hunting regime (• lease hunting; ▲ controlled hunting). AT: Albsfelder Tannen, BE: Behlendorf, BS: Berkenstrücken, HS: Hägesahl/Ohlenwegen, HEV: Hevenbruch, RIE: Riepenholz, RH: Ritzerauer Hauptrevier, SZ: Schattinber Zuschlag, TS: Trammer Stubben.

Lage der untersuchten Waldstandorte und ihr entsprechendes Jagdregime (• Pachtjagd; ▲ Regiejagd).

Table 1. Study site characteristics. Harvest numbers include roe deer (*Capreolus capreolus*), red deer (*Cervus elaphus*) and fallow deer (*Dama dama*). Differences in harvest number between the two hunting regimes were not significant (ANOVA: F = 0.79, P = 0.40). CH: controlled hunting; LH: lease hunting.
Kennwerte der untersuchten Waldstandorte. Die Jagdstrecke umfasst Reh-, Rot- und Damwild. Unterschiede in der Jagdstrecke zwischen den untersuchten Jagdregimen waren statistisch nicht signifikant (ANOVA: F = 0.79, P = 0.40). CH: Regiejagd; LH: Pachtjagd.

Study site	Forest area (ha)	n (plots)	Hunting regime	Harvest number per 100 ha	n (hunters) per 100 ha	Stand age main stand (mean ± SD)	Stand density index (mean ± SD)
Albsfelder Tannen	167.5	10	CH	14.9	2.4	100.9 ± 44.4	0.76 ± 0.23
Ritzerauer Hauptrevier	420.0	10	CH	12.8	1.0	98.5 ± 40.6	0.84 ± 0.13
Hevenbruch	179.0	20	CH	16.9	0.6	103.6 ± 34.0	0.93 ± 0.16
Behlendorf	175.0	11	LH	16.0	0.6	62.8 ± 38.5	0.85 ± 0.37
Berkenstrücken	107.5	10	LH	14.9	1.9	101.7 ± 51.6	0.94 ± 0.18
Hägesahl/Ohlenwegen	113.5	11	LH	11.5	1.8	76.4 ± 26.9	1.00 ± 0.18
Riepenholz	154.0	10	LH	14.9	1.3	94.5 ± 30.5	0.78 ± 0.10
Schattinber Zuschlag	45.0	20	LH	7.7	0.4	96.2 ± 28.6	0.98 ± 0.11
Trammer Stubben	183.5	9	LH	13.6	1.1	100.5 ± 33.6	0.87 ± 0.17

Browsing assessment

Natural regeneration was mapped using 2 x 20 m randomly placed plots within regeneration areas in March and April 2007 and 2008. This resulted in a total of 111 sampling plots, of which 40 where under forestry departmental supervision and 71 managed by private hunters (Tab. 1). The plot location followed three criteria, defined by Hermann Ellenberg: two random directions and one random distance. For details see Buhmann (1999). Within each plot, the abundance of all tree and shrub species was quantified and their corresponding heights were measured. Sapling height was grouped into 5 size classes and regeneration stages, respectively: (1) 0-20 cm, (2) 21-40 cm, (3) 41-80 cm, (4) 81-160 cm, (5) 161-320 cm. Browsing status (leading shoot browsed vs. non-browsed) was assessed for each individual. Taxonomy and nomenclature followed Wisskirchen and Haeupler (1998).

Statistical analysis

Generalised linear mixed models (GLMMs) with study plot as random factor were used to evaluate the effects of hunting regime and size class on browsing intensity. Models were scaled to correct for over-dispersion using a quasi-binomial distribution and a logit link function (*glmmPQL* function). To test for species-specific effects, all autochthonous trees were stratified into 4 tree species groups and the GLMMs were performed for each size class separately: (1) *Fagus sylvatica,* (2) *Quercus robur,* (3) further valuable hardwoods (*Acer platanoides*, *Acer pseudoplatanus*, *Fraxinus excelsior*, *Prunus avium*, *Ulmus glabra*), (4) further hard- and softwoods (*Acer campestre, Alnus glutinosa, Carpinus betulus, Ilex aquifolium*, *Populus tremula, Prunus padus, Sorbus aucuparia*). Post hoc comparisons were conducted with a Tukey HSD test.

Following the same variance-covariance structure, a negative binomial GLMM was used to analyse differences in the sapling abundance between hunting regime and regeneration stage. To accommodate the large spread in the sapling counts, models were fitted to the data with the *glmmADMB* function using the log link function and a negative binomial distribution (Zuur et al. 2009). Different competing models were evaluated by sequential comparison (forward and backward selection) using the likelihood ratio test (LRT) followed by a Bonferroni adjustment (α = 0.05). Further we used analysis of dissimilarity (ADONIS) to assess changes in sapling assemblages related to hunting management (Anderson 2001). The analysis was based on a matrix of Bray-Curtis dissimilarities, which was calculated from the sapling counts. To reduce the effect of dominant species, abundance data were square-root transformed prior to analysis. All analyses were performed using R (version 2.10.1).

Results

We analysed 18,425 saplings of 14 characteristic tree species of beech communities. Moreover, 9 shrubs (*Corylus avellana*, *Crataegus* spec., *Euonymus europaea*, *Frangula alnus*, *Prunus spinosa*, *Ribes nigrum*, *Rosa arvensis*, *Rosa canina*, *Sambucus nigra*) and 6 allochthonous species (*Aesculus hippocastanum*, *Larix* spec., *Picea abies*, *Prunus serotina*, *Pseudotsuga menziesii*, *Quercus rubra*) were observed in the browsing survey, but their proportions on the total species composition were negligible (means: *shrubs* = 1.9%; *allochthonous trees* = 0.6%). To meet the study objective, the characterisation of the autochthonous tree species regeneration status, the latter two species groups were omitted in the analysis.

Species composition

We found all 14 autochthonous tree species in LH plots, whereas only 8 species were recorded in CH plots. Many species occurred at low frequencies and abundances. 50% of the species (*Acer campestre*, *Acer platanoides*, *Alnus glutinosa*, *Ilex aquifolium*, *Populus tremula*, *Prunus padus*, *Ulmus glabra*) were found in less than 7% of the plots. *Alnus glutinosa*, *Ilex aquifolium*, *Populus tremula* and *Prunus padus* were identified with less than 11 individuals each.

Changes in species composition with regeneration stage did not significantly differ between the investigated hunting regimes (ADONIS: F = 1.26, P = 0.27). A trend towards an increasing percentage of beech and a decreasing proportion of further valuable hardwoods with sapling height could be observed (Fig. 2). On average, *Fraxinus excelsior* (40%) was the most abundant species among seedlings (0-20 cm), followed by *Acer pseudoplatanus/platanoides* (17%), *Fagus sylvatica* (16%), *Carpinus betulus* (6%) and *Quercus robur* (5%). Other species accounted for less than 5%. However, high-value trees, such as *Acer platanoides*, *Quercus robur* and *Ulmus glabra* did not reach heights of more than 80 cm. As a result, the regeneration composition of tall saplings (161-320 cm) was dominated by *Acer pseudoplatanus* (37%) and *Fagus sylvatica* (33%). *Carpinus betulus* accounted for 13%, but other species were rare in these dimensions (< 10%: *Fraxinus excelsior*, *Ilex aquifolium*, *Prunus avium*, *Sorbus aucuparia*).

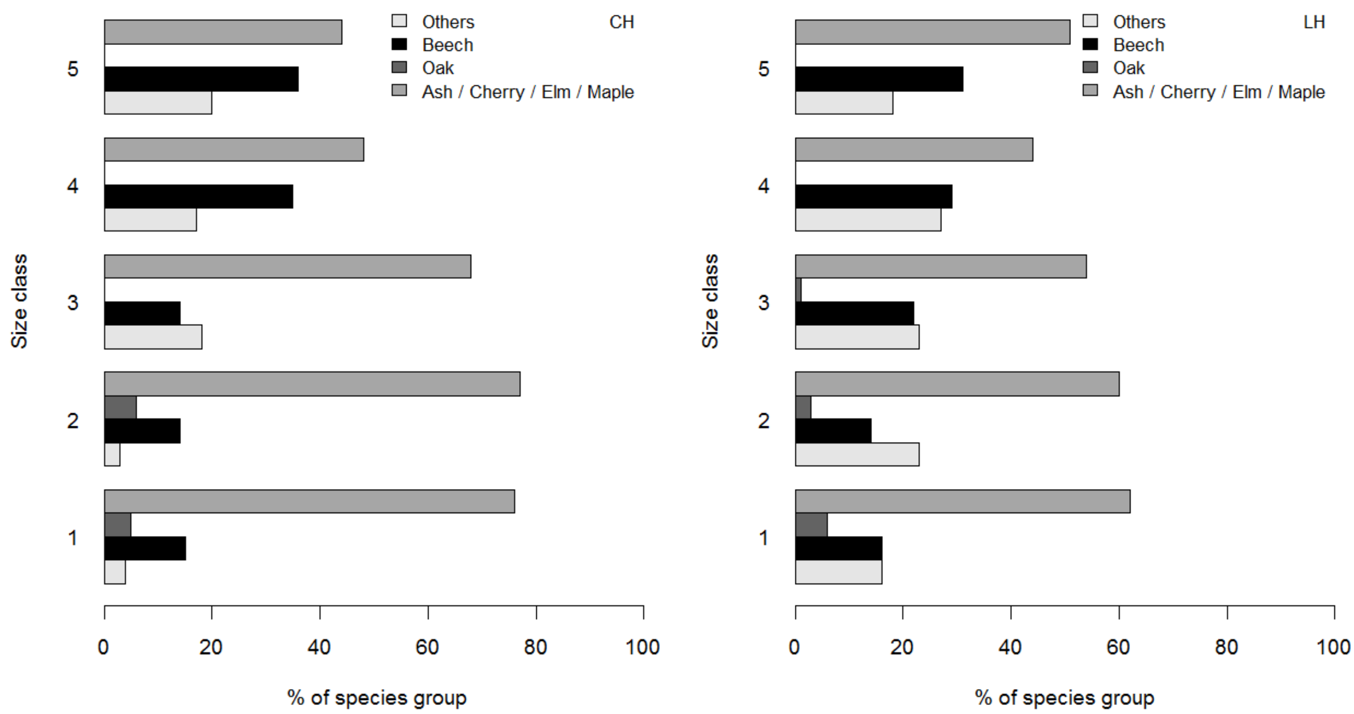

Figure 2. Changes in species composition of autochthonous tree species with height development (size class 1: 0-20 cm, 2: 21-40 cm, 3: 41-80 cm, 4: 81-160 cm, 5: 161-320 cm) and hunting regime (CH: controlled hunting; LH: lease hunting).
Beech = *Fagus sylvatica*, Oak = *Quercus robur*, Ash/Cherry/Elm/Maple = *Acer platanoides*, *Acer pseudoplatanus*, *Fraxinus excelsior*, *Prunus avium*, *Ulmus glabra*; Others = *Acer campestre*, *Alnus glutinosa*, *Carpinus betulus*, *Ilex aquifolium*, *Populus tremula*, *Prunus padus*, *Sorbus aucuparia*.
Prozentuale Veränderung im Verjüngungsspektrum standortsheimischer Baumarten im Verlauf der Höhenentwicklung in Abhängigkeit des Jagdregimes (CH: Regiejagd; LH: Pachtjagd).

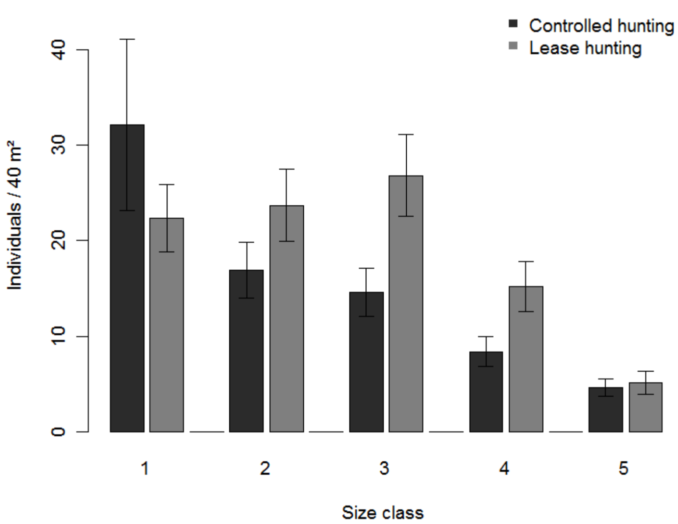

Figure 3. Changes in abundance (mean ± SE) of autochthonous tree species with height development (size class 1: 0-20 cm, 2: 21-40 cm, 3: 41-80 cm, 4: 81-160 cm, 5: 161-320 cm) conditional on hunting regime.
Veränderung der Verjüngungsdichte (Mittelw. ± Std.fehler) standortheimischer Baumarten im Verlauf der Höhenentwicklung in Abhängigkeit des Jagdregimes (Höhenklasse 1: 0-20 cm, 2: 21-40 cm, 3: 41-80 cm, 4: 81-160 cm, 5: 161-320 cm).

Regeneration density

The GLMM indicated that the density of saplings was affected by size class (L = 36.4, P < 0.001), but not by hunting regime (L = 0.12, P = 0.73) or the interaction between size class and hunting regime (L = 7.8, P = 0.09). Sapling growth was negatively related to density (Fig. 3). A distinct decline could be observed for saplings taller than 80 cm ($P_{adj.}$ < 0.01). Variations in sapling abundance of seedlings and small saplings were negligible ($P_{adj.}$ > 0.05).

Browsing pressure

The effect of hunting regime did not vary among size classes, as indicated by the non-significant interaction term (F = 1.50, P = 0.20). In all regeneration stages browsing intensity was considerably higher under LH regime (t = -4.34, P < 0.001). Relative differences were greatest in size class 1 (0-20 cm) and 5 (> 160 cm). Browsing intensities were more than twice as high for individuals recruited in the > 20 cm size classes than for saplings smaller than 20 cm (all Tukey tests: P < 0.001). Differences among these stages however, were statistically not significant (Fig. 4). The highest percentage of browsed individuals with values between 75 and 85% (size class 2 to 5) could be observed under LH.

At species level, a similar trend was revealed for all size classes with significant lower browsing intensities under CH management (Tab. 2). However, the interaction between hunting regime and tree species group was not significant in any model. On average, beech is the least browsed species and except for seedlings (0-20 cm), valuable hardwoods were associated with highest browsing values (all Tukey tests: P < 0.05).

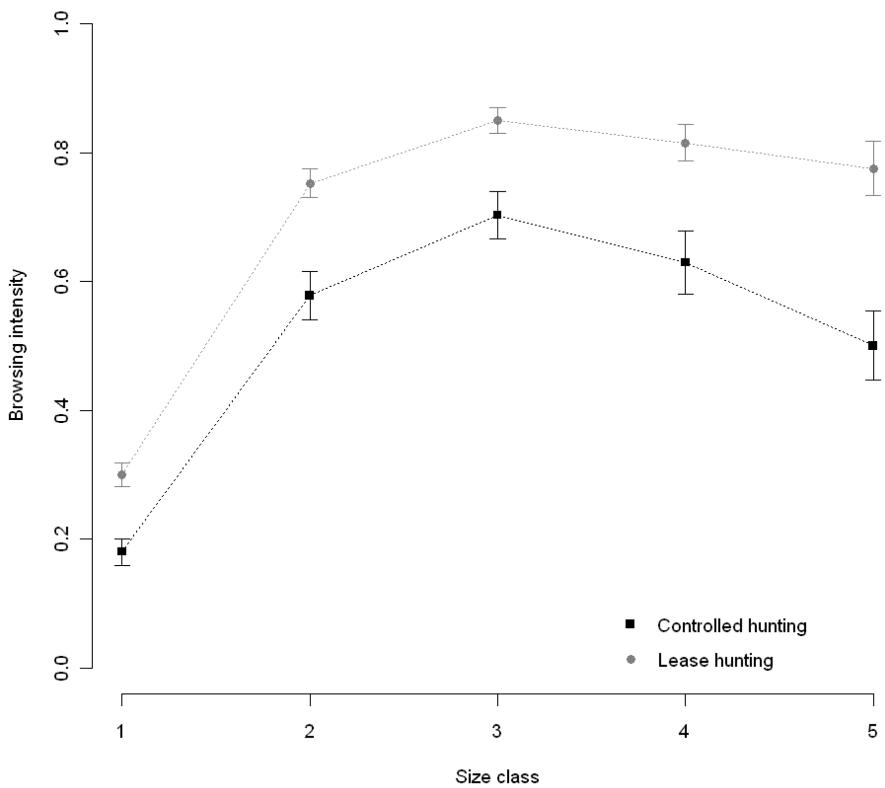

Figure 4. Variation in mean browsing intensity of autochthonous tree species with height development (size class 1: 0-20 cm, 2: 21-40 cm, 3: 41-80 cm, 4: 81-160 cm, 5: 161-320 cm) under controlled versus lease hunting regime. Error bars indicate 95% confidence intervals.

Unterschiede in den mittleren Verbissbelastung standortheimischer Baumarten zwischen Regiejagd und Pachtjagd im Verlauf der Höhenentwicklung (Höhenklasse 1: 0-20 cm, 2: 21-40 cm, 3: 41-80 cm, 4: 81-160 cm, 5: 161-320 cm). Die Fehlerbalken kennzeichnen das 95 %-Konfidenzintervall.

Table 2. Changes in browsing intensity (mean ± SE) with hunting regime and species group for different size classes. *t*- and *P*-values correspond to the hunting regime effect in a specific size class. Different letters indicate significant differences between tree species groups (Tukey HSD test, α = 0.05) within a size class; bold values indicate browsing intensities > 80%; n.a. = data not available.

Veränderungen der Verbissintensität (Mittelw. ± Std.fehler) in Abhängigkeit des Jagdregimes und der Baumartengruppe in den einzelnen Höhenklassen. *t*- und *P*-Werte beziehen sich auf den Effekt des Jagdregimes innerhalb der jeweiligen Höhenklasse. Unterschiedliche Buchstaben kennzeichnen signifikante Unterschiede zwischen den Baumartengruppen innerhalb der jeweiligen Höhenklasse (Tukey HSD test, α = 0.05); Verbissintensitäten > 80 % sind hervorgehoben; %; n.a. = Daten nicht vorhanden.

Size class	Controlled hunting	Lease hunting	*t*-value	*P*-value
0-20 cm			-2.62	0.0100
Fagus sylvatica [a]	0.15 ± 0.01	0.28 ± 0.10		
Quercus robur [a]	0.10 ± 0.02	0.23 ± 0.02		
Further valuable hardwoods [ab]	0.20 ± 0.01	0.33 ± 0.02		
Further hard- and softwoods [b]	0.29 ± 0.04	0.44 ± 0.03		
21-40 cm			-2.83	0.0056
Fagus sylvatica [a]	0.39 ± 0.02	0.54 ± 0.02		
Quercus robur [ac]	0.56 ± 0.02	0.70 ± 0.05		
Further valuable hardwoods [b]	**0.82 ± 0.01**	**0.90 ± 0.01**		
Further hard- and softwoods [c]	0.68 ± 0.04	**0.80 ± 0.02**		
41-80 cm			-3.70	0.0004
Fagus sylvatica [a]	0.40 ± 0.16	0.68 ± 0.02		
Quercus robur	n.a.	1.00 ± n.a.		
Further valuable hardwoods [b]	**0.94 ± 0.01**	**0.98 ± 0.01**		
Further hard- and softwoods [c]	0.76 ± 0.03	**0.90 ± 0.02**		
81-160 cm			-4.21	0.0001
Fagus sylvatica [ac]	0.28 ± 0.03	0.67 ± 0.02		
Quercus robur	n.a.	n.a.		
Further valuable hardwoods [b]	**0.95 ± 0.01**	**0.99 ± 0.01**		
Further hard- and softwoods [c]	0.50 ± 0.03	**0.81 ± 0.03**		
161-320 cm			-4.21	0.0016
Fagus sylvatica [ac]	0.29 ± 0.05	0.69 ± 0.05		
Quercus robur	n.a.	n.a.		
Further valuable hardwoods [b]	0.63 ± 0.04	**0.94 ± 0.02**		
Further hard- and softwoods [c]	0.23 ± 0.17	0.48 ± 0.16		

Discussion

Our study emphasizes the importance of hunting regime to the browsing of regenerating autochthonous trees in beech forests. Deciduous species were more likely browsed under the lease hunting than the controlled hunting management. This result was consistent for all individuals and for tree species groups. Thus, lease hunting lead to both reduced natural regeneration potential and lower timber quality (Côté et al. 2004, Didion et al. 2009).

Regardless of hunting management, the impact of ungulates on sapling abundance and browsing status varied with regeneration stage and tree species. The observed shift in species composition was, among other factors (e. g. light availability), strongly related to foraging preferences of ungulates. Browsing pressure was highest in the medium size class (41-80 cm), which is in accordance with the preferred foraging height of deer (Renaud et al. 2003, Boulanger et al. 2009). In this regeneration stage 70% (CH) to 85% (LH) of saplings suffered from damaged leading shoots, their ecological fitness being distinctly reduced. Differences in browsing pressure at species level however, could mainly be attributed to the feeding selectivity of deer (Ellenberg 1988, Boulanger et al. 2009, Kuijper et al. 2010). A relatively small impact was observed for beech, whereas the recruitment of ash, maple, sweet cherry and elm showed almost a twice as high risk of being browsed. These accompanying species typically respond with an accelerated growth to canopy gaps and increased light availability, respectively (Petrițan et al. 2009). High browsing pressure however, strongly impedes this strategy and saplings are trapped in preferred browsing zones (Kuijper et al. 2010). Accordingly, a further decline in the proportion of rare admixed species and thus of high silvicultural value might be expected in the future. On the other hand, such a loss in diversity of autochthonous tree species would negatively affect forest community integrity and biodiversity of other strata (Brunet et al. 2010).

Kamler et al. (2010) reported species-specific differences in the relationship between browsing and ungulate densities with positive effects for e. g. *Picea abies*, but not for broadleaved species. This is in accordance with our findings. Thus, the regeneration success of deciduous trees mainly depends on their palatability and not on ungulate density. We could not find consistent hunting regime effects with respect to species composition, regeneration density or study site-specific harvest number. This implies that the large variation in browsing intensity cannot be ascribed to the presence or absence of palatable species. Hence, browsing effects can be attributed primarily to differences in hunting strategies, although we could not directly relate our findings to population size at plot level. Similarly, we assume that small-scale variations in site conditions do not have a notable influence on sapling abundance. This assumption is supported by the estimated variance of the random plot effect, which indicates a relatively low variability (19%) in regeneration densities of the same plot (West et al. 2007).

Our results are based on the current regeneration status; thus predictions on the regeneration dynamics are hardly possible. Nevertheless, browsing intensity still can be used as an indicator for regeneration success, since intensive browsing results in reduced growth and fitness (Weisberg and Bugmann 2003). Despite small variations, hunting regime was not associated with sapling abundance throughout all regeneration stages. While the present situation is a result of past management, the current impact of browsing ungulates on sapling development indicates an improved situation at sites with controlled hunting, as shown by the overall lower browsing intensities and comparable densities, especially of "survivors" (individuals > 160 cm). This conclusion corroborates the new management concept implemented in the Stadtwald Lübeck in 1994, where hunting measures were altered (Fähser 1995).

In conclusion, an effective hunting management may be a main driver for a successful regeneration of autochthonous tree species in deciduous forests. This supports the work by Hothorn and Müller (2010), who reported positive effects of a managed sport hunting system. Certain differences between their and our findings may be explained by the scale-dependency of management success: On a large scale, Hothorn and Müller (2010) conclude, that a reduced browsing intensity is correlated to lower ungulate densities. Our study, however, suggests that on a small scale the reduction of ungulate browsing can be mainly attributed to a different hunting system, i. e. an improved hunting strategy (Martin and Baltzinger 2002).

The successful regeneration of species belonging to the natural forest communities is among the highest priorities in close-to-nature forestry. Accordingly, a sustainable forest development does not depend on a specific hunting regime or ungulate density, but on the effectiveness of the hunting management. Such effectiveness can be achieved by a spatial prioritisation of hunting measures, e. g. an increased hunting pressure near sensitive regeneration areas. Other main measures may include hunting regulation and adaptation by the forestry department and a combination of individual and pressing hunts. We suggest shifting the focus from ungulate densities to the effectiveness of hunting in order to realize the objective of near-natural mixed forests in the future.

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Obituary

Hermann Ellenberg died on 6 November 2009. This study was one of his last projects. We dedicate this article to his memory in recognition of his contribution to both the scientific and the non-scientific community.