Number and height of unbrowsed saplings are more appropriate than the proportion of browsed saplings for predicting silvicultural regeneration success

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Abstract
• **Key message** The browsing level of oak (Quercus petraea and Quercus robur) and fir (Abies alba) provided only a rough estimate of the expected regeneration success. Thus, it cannot be recommended as a standard measurement to predict forest development, unless the number of saplings and the height of those saplings are considered.
• **Context** Browsing by large herbivores may affect regeneration success and forest development, with an impact that lasts for decades.
• **Aims** Whether the browsing level of a tree species can be used in forestry as a standard measure to assess whether the target values (for instance regeneration success) of highly selected tree species, such as oak (Quercus petraea (Mattuschka) Liebl., Quercus robur (L.)) and fir (Abies alba (Mill.)), will be reached is unclear and need specification.
• **Methods** In this study, 985 sampling plots (10 m²) in Southern Germany (Baden-Württemberg) containing browsed and unbrowsed oak and fir-saplings were analysed. Both the browsing level and a measure of the expected regeneration success that considered not only the sapling density but also different height classes (≤ 20 cm; 21–50 cm; 51–130 cm) were calculated.
• **Results** The use of the browsing level as a proxy for the expected regeneration success was statistically only partly justified. For fir the relationship between browsing level and expected regeneration success became even weaker for a new indicator variable which considers two height classes rather than one class for saplings exceeding 50 cm (51–80 cm and 81–130 cm).
• **Conclusion** According to these results, the browsing level cannot be recommended as a standard measurement and/or predictor of damage, unless the number of saplings and the height of those saplings are considered. Thus, in efforts to mitigate conflicts between foresters and hunters, a measurement is needed that addresses the successful establishment of a sufficient number of trees despite browsing, rather than the browsing of trees alone.

Keywords Oak · Fir · Roe deer · Damage

1 Introduction

That the browsing of large herbivores affects tree growth and the survival probability of single young trees is well-established (Kupferschmid and Bugmann 2008; Kupferschmid 2018). Foresters frequently suspect that browsing

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by large herbivores such as roe deer (*Capreolus capreolus* (*L.*) ) of trees undergoing natural regeneration causes damage that reduces their regeneration success and thus affects forest management objectives (Gill 1992; Reimoser and Gossow 1996). However, damage should be defined with respect to both a predefined management objective and comparisons of variables of interest with defined target values (Reimoser et al. 1997, 1999; Reimoser 2003). A target value for regeneration success might be (i) the minimum number of unbrowsed regeneration trees per area and tree height class that is needed for the establishment of a predefined stand (i.e. regeneration success, Beguin et al. 2016), (ii) a defined proportion of trees of one or more species (Reimoser et al. 1999) or (iii) the number of years needed until a germinated tree of a particular species reaches a height of 130 cm (Reimoser et al. 1999).

The presence of saplings of a certain height is a necessary precondition to reach a minimum number of unbrowsed regeneration trees per area and tree height. Whether seedlings and saplings of a certain tree species can be found at a certain forest site depends on a large number of factors, such as light availability (Weisberg et al. 2005; Kupferschmid et al. 2014), herbaceous vegetation cover, tree composition in the mature forest stand, soil fertility (Kuijper et al. 2010a) and the browsing level (Hidding et al. 2013; Kupferschmid et al. 2014). An impact of the browsing of large herbivores on tree regeneration is mostly confined to trees smaller than 130 cm (Zai 1964; Welch et al. 1992; Roth 1995).

However, based on the results of long-term experiments, Pretzsch and co-authors (Pretzsch et al. 2019) were able to identify a relationship between the number of trees per ha that can be expected to emerge even in the absence of browsing and the diameters of those trees. Specifically, the logarithm of the number of trees per ha decreased with the logarithm of tree diameter (Pretzsch et al. 2019). Thus, major forest stands typically have a stem density of ~ 1000 per ha (1 stem per 10 m²) (McCarthy and Weetman 2007; Pretzsch et al. 2019), while the tree density in regeneration stands (diameter at 130 cm of < 1 cm) frequently exceed 100,000 trees per ha (Pretzsch et al. 2019). Precisely, using the browsing level as a reliable indicator of regeneration success has several drawbacks. Suchant and co-authors linked both the abundance of regeneration trees per height class and the browsing of trees to an expected regeneration success (FVA-approach—Appendix 1—cf. Suchant et al. 2012). In this context the FVA-approach may be applied to estimate the regeneration success of any indigenous tree species in the northern hemisphere. In this study, we calculated the expected regeneration success of oak (*Quercus petraea*, *(Mattuschka)* Liebl. and *Quercus robur* (*L.*)) and fir (*Abies alba* (*Mill.*)) and then compared the results with the browsing level. Ours is the first study to quantify the relationship of these two variables.

Based on a recent report by Hagen and Suchant (2020) showing that browsing level and sapling density are characterised by a spatial auto-correlation for a neighbourhood of 100 m, in the present study, we calculated Moran’s *I* (Moran 1950) for neighbourhood distances of 50 m and 100 m (Appendix 2).

### 2 Data and methods

The study sites (*N* = 98) were located in the German federal state of Baden-Württemberg and consisted of forest patches with an expected natural regeneration of fir or oak (Hagen et al. 2019). In Baden-Württemberg, the browsing of young oaks and firs is mainly attributable to roe deer (*Capreolus capreolus*) (Hagen et al. 2019). Field surveys of the sites were conducted between 31.07.2017 and 29.09.2017 (deciduous forest) and between 26.03.2018 and 14.06.2018 (coniferous forest). The field surveys were timed taking into account the chance that the saplings would be browsed (oak in summer; fir in winter—cf. Odermatt 2014). A browsed tree was defined as a tree (height ≤ 130 cm) whose terminal bud was browsed (cf. Odermatt 2014). A browsed tree was defined as a tree (height ≤ 130 cm) whose terminal bud was browsed (cf. Odermatt 2014).
resulting in a total of 985 plots. The minimum distance between study sites was 1.4 km. The sampling plots in the study sites were circular. Analogous to Zai (1964) the area of each sampling plots was 10 m² ($r = 1.79$ m). The distance between two sampling plots was 25 m (+ 5 m). In each plot, the number of browsed and unbrowsed trees (height ≤ 130 cm) was documented (Hagen et al. 2021). Specifically, three different tree height classes were designated (1: ≤ 20 cm, 2: 21–50 cm, 3: 51–130 cm), which allowed the plot-specific browsing level to be linked to an expected regeneration success (FVA-approach—cf. Suchant et al. 2012). As the FVA approach has been described only in German, we briefly present the basic aspects of its methodology in Appendix 1. The number of plots that fulfilled the criteria of the FVA approach (minimum number of regeneration trees per tree species) was 631 for fir and 197 for oak (see Fig. 1 for the spatial distribution of the study sites).

We then tested whether the browsing level differed according to the class value describing the regeneration success. This was done by applying a non-parametric correlation (Spearman), given that the distribution of the browsing level partly violates the assumption of a Gaussian distribution.

![Fig. 1 Study sites containing saplings of oak (circles) and fir (triangles) where the number of saplings exceeded a defined minimum (4 trees \[≤ 20 \text{ cm}\], 2 trees \[21–50 \text{ cm}\] or 1 tree \[51–130 \text{ cm}\]). The background shows the distribution of forest in Baden-Württemberg (Southern Germany). We used a geographic transformation to translate coordinates of the field survey from EPSG: 4326 to EPSG: 31467.](image)
Statistical calculations were carried out using R version 3.4.4 (R Core Team 2018) and the R package spdep (Bivand et al. 2006).

### 3 Results

The overall browsing level for all 985 sampling plots was 0.35 (fir, \(N = 10,731\)) and 0.48 (oak, \(N = 7802\)), but browsing was not evenly distributed over the different height classes (Fig. 2) as fir and oak saplings smaller than 20 cm were less frequently browsed than saplings exceeding 20 cm.

A comparison between the browsing level and the expected regeneration success revealed a positive and significant correlation between the browsing level and limitations of the regeneration success. The Spearman correlation coefficient \(\rho\) was 0.79 (\(S = 8,652,700\), \(p < 0.0001\)) for fir and 0.71 (\(S = 365,820\), \(p < 0.0001\)) for oak (\(\rho^2_{\text{Fir}} = 0.63; \rho^2_{\text{Oak}} = 0.5\)). Class values II, III, and IV were linked to a mean browsing level of 0.43, 0.64, and 0.8 for both tree species (see Table 1). Moreover, these three classes can be well distinguished according to the browsing level (Fig. 3).

For a plot with an oak browsing level of 0.8, the likelihood that it would be assigned class 4 (expected regeneration failure) was very high (Fig. 3). This assignment could be made without any specific knowledge about the height classes of the saplings. While the browsing level differed between sampling plots of class values II, III, and IV, the difference in the browsing level between class 0 and class I was small, which demonstrated the difficulty of linking a browsing level below 0.3 to any expected limitation of the regeneration success (Table 1 and Fig. 3).

### 4 Discussion

The correlation between the browsing level of oak and fir and the expected limitation of the regeneration success was significant and positive (cf. Fig. 3 and Table 2). This result partly reflects the process of assigning a class value according to the FVA-approach (Appendix 1, Figs. 5 and 6) and thus may support the conclusions of Hothorn and Müller (Hothorn and Müller 2010), who proposed the use of browsing level as a standard measure describing the effects on the development of tree saplings. However, the calculated \(\rho^2\) values of 0.5 (oak) and 0.63

![Fig. 2](image-url)
(fir) indicate that application of the browsing level as a proxy for the expected regeneration success is statistically only partly justified (by rule of thumb a value of $\rho^2 \geq 0.64$ is necessary). This restriction derives from the fact that plots characterised by a browsing level of $< 20\%$ were assigned to class IV (regeneration failure caused by browsing) and plots characterised by a high browsing level ($> 70\%$) were assigned to class 0 (browsing is very unlikely to affect regeneration success) (Fig. 3). These differences between browsing level and regeneration success support our initial suspicion that the browsing level would not serve as a reliable indicator of forest development. Whether a specific browsing level will affect the target values depends on various factors, such as light conditions, soil conditions or local climate conditions (cf. Gerhardt et al. 2013). Moreover, application of the browsing level in the absence of knowledge about the sapling density considered (for instance 5, 10, 100 or any other number of saplings per 10 m²) or the height-class distribution of the saplings (Fig. 2) may lead to false conclusions about the possibility to reach silvicultural target values. For instance, it might reasonably be assumed that a documented browsing level of 60–80% will necessarily cause regeneration failure for any tree species, as the intense browsing will prohibit the regeneration of trees to a height of at least 130 cm (Weisberg et al. 2005). This assumption held either for an even-aged saplings $\leq 50$ cm in height or for a constant browsing level for saplings in each height class. However, regeneration may occur patchily (Yokozawa et al. 1999) or in waves (Wiegand et al. 1998) such that the number of saplings per height class may be approximated by a negative exponential distribution (Zai 1964; Coomes and Allen 2007; McCarthy and Weetman 2007). Thus, while browsing clearly affects forest development (Kuijper et al. 2010b; Pellerin et al. 2010; Hidding et al. 2012; Bernard et al. 2017; Bernes et al. 2018), a link between a certain browsing level and any future damage remains speculative. Long-term monitoring of the browsing level with respect to tree height may provide important insights into the spatio-temporal dynamics of both tree regeneration and herbivore activities (cf. Gill et al. 1996).

Our results showed that browsing was lowest on firs and oaks in height class 1 (smaller than 20 cm), the class with the largest number of saplings (Fig. 2). These results are in line with former results about tree height and browsing level (Zai 1964; Welch et al. 1992; Roth 1995; Chianucci et al. 2015). Welch and co-authors showed a higher browsing level (roe deer, red deer [Cervus Elaphus (L.)]) of trees (Sitka spruce) between 20 and 50 cm then of trees $< 20$ cm or $> 50$ cm in height (Welch et al. 1992). Their results are in line with the findings of both Zai (1964) and Roth (1995). Zai showed that saplings of fir with a height of 40–60 cm were those with the highest browsing level (roe deer), while in the study of Roth, browsing level was highest for trees with a height of 60–80 cm (Roth 1995). In a study about the browsing of oaks (Quercus laevis (Walt.)), Chianucci showed that the browsing level correlated negatively with the height of the saplings (Chianucci et al. 2015). All of these studies showed that for trees $< 130$ cm, a browsing level exceeding 60% may not endanger regeneration success when (i) browsing is concentrated on trees 20–80 cm in height and (ii) at least one unbrowsed tree per 10 m² exceeds a height of 80 cm. This conclusion is supported by the findings from some of our sampling plots. One

### Table 2

Upper limit (UL) of the number of saplings within an area of 10 m² that were considered in an estimation of regeneration success

| Height Class | < 20 cm | 20–50 cm | 50–80 cm | 80–130 cm |
|-------------|--------|---------|---------|---------|
| UL coniferous trees | 12 | 6 | 2 | 1 |
| UL deciduous trees | 20 | 10 | 3 | 2 |
plot, for example, contained 13 firs smaller than 130 cm. Although 11 of the 13 trees had been browsed, the only tree taller than 50 cm (in fact, it was taller than 80 cm) was not affected by browsing.

Given the relationship between the number of trees per ha (saplings—> major trees), tree height and browsing level, any measure aimed at providing an estimate of the regeneration success (such as the FVA-approach) should take into account both the total sapling number and the number of unbrowsed saplings, even though spatial independence cannot be expected. However, for fir and oak, we suggest an indicator that further determines sapling height for saplings exceeding 50 cm, including two separate height classes for sapling heights between 51 and 130 cm, such as 51–80 cm and 81–130 cm (Table 2). Regeneration success may then be estimated by applying the FVA-approach (Appendix 1) although the linear relationship between browsing level and expected regeneration success will likely become even weaker (Fig. 4).

However, variables trying to quantify the regeneration success are only partly suitable for predicting forest development (i.e. they cannot predict droughts, storm events, beetle attacks). Rather, variables that take into account sapling abundance and sapling height will be more appropriate than those based on the proportion of browsed trees in estimating the likelihood of reaching silvicultural target values.

### 5 Conclusion

The browsing level cannot be recommended as a predictor of both regeneration success and forest development unless the number of saplings and the height of those saplings are considered. Thus, in efforts to mitigate conflicts between foresters and hunters, a measurement is needed that addresses the successful establishment of a sufficient number of trees despite browsing, rather than the browsing of trees alone. The indicator variable introduced in this manuscript may serve as such a measurement. It is based on the FVA-approach (Appendix 1) but considers two height classes rather than one class for saplings exceeding 50 cm (51–80 cm and 81–130 cm) and thus accounts for the circumstance that browsing of large herbivores on tree regeneration is mostly confined to trees smaller than 80 cm.

### Appendix 1

The FVA approach has been applied in the Federal State of Baden-Württemberg since 2010. It links the seasonal browsing (last 6 months) to an expected regeneration success. The occurrence of a minimum number of saplings
per height class and per tree species is a necessary pre-
condition for its application. The minimum number was
defined according to Suchant et al. (2012) as:

- 4 trees (height class 1; ≤ 20 cm),
- 2 trees (height class 2; 21–50 cm) or
- 1 tree (height class 3; 51–130 cm).

Thus, only plots containing either 4 trees in the
height ≤ 20 cm, 2 trees in the height 21 to ≤ 50 cm or 1 tree
in the height 51 to ≤ 130 cm were used for further analyses.

On the basis of the number of browsed and unbrowsed
trees, each sampling plot is assigned a class value (class
0–IV) representing the expected regeneration success.
Class 0 means that browsing is very unlikely to affect
regeneration success, and class IV that regeneration

### Table 3

Upper limit (UL) of the number of saplings within an area of
10 m² that were considered in an estimation of regeneration success
according to the FVA approach

| Height class 1 | Height class 2 | Height class 3 |
|----------------|----------------|----------------|
| UL coniferous trees | 12             | 6              | 3              |
| UL deciduous trees  | 20             | 10             | 5              |
has failed due to browsing. The number of unbrowsed trees is counted for height classes 3, 2, and 1, starting at height class 3. If the number of tree saplings exceeds the required minimum, only this height class has to be evaluated. If the number of unbrowsed trees per 10 m² exceeds the upper limit for this height class (Table 3), then the plot is assigned class 0. Otherwise, the class value for deciduous and coniferous trees is assigned according to Fig. 5, assuming a linear relationship between browsing level, the estimated Moran’s I, and limitations in regeneration success. The class values for different combinations of browsed and unbrowsed trees are provided in Fig. 6.

The definition of an upper limit per height class accounts for different sapling densities of deciduous and coniferous trees and further reflects that the number of trees per height class (reflected by the diameter) can be modelled by a negative exponential distribution. Thus, the meaning of browsing in the context of regeneration success differs according to tree height and tree species.

### Appendix 2

In this study, data on sapling density and browsing level were analysed for three different height classes (H1: < 20 cm; H2: 20–50 cm; H3: 50–130 cm) using sampling plots separated by a distance of 25 m (+ 5 m). The study design allowed investigations of the spatial patterns of these variables even for a neighbourhood distance of less than 200 m or 100 m, the typical distance between sampling units in scientific investigations (cf. Hagen and Suchant 2020). In that study, a pattern of spatial-auto-correlation in sapling density and browsing level was determined for a neighbourhood distance of 100 m and 200 m for fir and 100 m for oak (positive association). Taking into account the differences in seed dispersal between fir and oak (fir seeds are wind dispersed while oak seeds either germinate in the direct neighbourhood of the parent tree or are transported by birds or mammals), we expected (i) a spatial auto-correlation for the density of oak saplings at neighbourhood distances of 50 m and (ii) that the effect size of this auto-correlation will be larger for oak.

We calculated Moran’s I for a predefined neighbourhood \( d_{nb} (d_{nb} = 50 \text{ m}, 100 \text{ m}) \) to test for spatial independence:

\[
I = \left( \frac{N/W}{\Sigma_i (\Sigma_j w_{ij} (x_i - \bar{x}_{\text{mean}}))} / \Sigma_i (x_i - \bar{x}_{\text{mean}})^2 \right)
\]

where \( N \) is the number of spatial units, \( x \) is the browsing level, \( \bar{x}_{\text{mean}} \) is the mean browsing level, \( w_{ij} \) is the weight according to the defined neighbourhood (\( w_{ij} = 0 \) for \( i = j \); \( w_{ij} = 0 \) for \( d(i, j) > d_{nb} \)) and \( W \) is the sum of all \( w_{ij} \).

A calculated value of \( I \) significantly less or greater than 0 negated the hypothesis that the browsing of young trees (height \( \leq 130 \text{ cm} \)) is a spatially independent process. The Bonferroni correction was used to correct for multiple testing effects (global \( p \) value of 0.05).

The calculation of Moran’s I showed that the browsing level of fir for one sampling plot correlated significantly with the browsing level of the surrounding sampling plots (\( d_{nb 50,100} \)), whereas the browsing level of oaks was not significant (\( d_{nb 50,100} \)). Although the index of the expected limitation of regeneration success showed spatial auto-correlation, the estimated Moran’s I was lower for both tree species. The sapling density of oak and fir showed a significant spatial auto-correlation (Table 4).

The fact that the density of oak saplings showed a significant auto-correlation only for a neighbourhood distance of 100 m is consistent with the findings of Günther and Kiffer, who showed that oak saplings may be clumped at a very local level (Götmark and Kiffer 2014). Thus, taking differences in the seed dispersal of fir and oak into consideration, spatial auto-correlation for oak at a neighbourhood distance of 50 m and a larger effect size for oak were expected. In our study, the sapling density of oak (neighbourhood distances of 50 m) was indeed characterised by spatial auto-correlation.

### Table 4

Moran’s I for a neighbourhood distance of 50 and 100 m (estimate \( I_{50} \) and estimate \( I_{100} \) based on sampling plots for fir (\( N = 631 \)) and oak (\( N = 197 \)). Italic values indicate statistical significance under a global \( p \) value of 0.05.

| Browsing level | Number of saplings | Expected limitation of regeneration success |
|----------------|--------------------|---------------------------------------------|
| Fir            |                    |                                             |
| Estimate \( I_{50} \) | 0.41               | 0.3                                         | 0.3 |
| \( p \) two sided | < 0.0001           | < 0.0001                                    | < 0.0001 |
| Estimate \( I_{100} \) | 0.34               | 0.24                                        | 0.25 |
| \( p \) two sided | < 0.0001           | < 0.0001                                    | < 0.0001 |
| Oak            |                    |                                             |
| Estimate \( I_{50} \) | 0.19               | 0.18                                        | 0.13 |
| \( p \) two sided | 0.03               | 0.003                                       | 0.11 |
| Estimate \( I_{100} \) | 0.18               | 0.19                                        | 0.09 |
| \( p \) two sided | 0.13               | 0.009                                       | 0.44 |
(positive association) (Table 4) but there was no support for a larger effect size, as the strength of the spatial auto-correlation was higher for fir (Table 4). Moreover, the browsing level of fir was characterised by a significant auto-correlation for neighbourhood distances of 50 m and 100 m, while the browsing level of oaks showed no significant spatial auto-correlation (neither for a neighbourhood distance of 50 m nor for a neighbourhood distance of 100 m). This result may reflect the assumption of Senn and Suter (2003), that at smaller scales the density of saplings varies more than that of large herbivores. The absence of a significant auto-correlation in the browsing level of oaks may also point to differences in the selection process of roe deer (Hagen et al. 2019). The home range size of roe deer is between 0.2 and 0.6 km² (Morellet et al. 2013; Richard et al. 2014; Lovari et al. 2017) and thus larger than the area defined by a neighbourhood distance of either 50 m or 100 m (area of 0.01 and 0.03 km² respectively), especially in the regions of Baden-Württemberg where oak regeneration naturally (cf. Hagen et al. 2019). However, an inability to detect a spatial auto-correlation for the browsing level of oak saplings may simply reflect the limited temporal and spatial dimensions of an annual field survey (cf. Hagen and Suchant 2020).

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Data availability The datasets generated and/or analysed during the current study are available in the Zenodo repository, http://doi.org/10.5281/zenodo.4435940

Declarations

Conflict of interest The authors declare that they have no conflict of interest.

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