


Article

Assessing Browsing Impact in Beech Forests: The Importance of Tree Responses after Browsing

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Abstract: Browsing by ungulates can affect the development of a forest stand due to selective browsing and shifts in the growth ranking between tree species. Assessing browsing impact in an objective way is difficult in patchily distributed beech forests. In systematically arranged plots near Kirchberg, Switzerland, the height increment of the two saplings nearest to the plot center (k-tree method) was measured for each height class and tree species, and the within-tree browsing intensity and damage frequency were assessed. In total, 21 tree species were found. Browsing was particularly frequent in climate-adapted species. Winter browsing was more frequent than summer browsing, which was also true for deciduous species, and it significantly reduced height growth. Former damage along the main stem further reduced upgrowth. Browsing shifted the height increment ratio in favor of *Fagus sylvatica*. Many winter-browsed saplings of *Abies alba*, *Fagus sylvatica*, *Acer pseudoplatanus*, *Fraxinus excelsior* and *Prunus avium* had no new leader shoot by the end of the next growing season, i.e., browsing had a long-lasting impact. For estimating browsing impact, it is thus important to assess delays in the response after browsing. Foresters could easily apply the k-tree method in autumn for effective assessments of browsing impact.

Keywords: *Abies alba*; growth rate; herbivory; tree regeneration; ungulate browsing



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1. Introduction

Wild ungulates, such as roe deer (*Capreolus capreolus* L.), red deer (*Cervus elaphus* L.) and chamois (*Rupicapra rupicapra* L.), browse on plants [1,2]. In particular, by browsing on the leader shoot (also called the terminal shoot), these animals can influence tree regeneration. Ungulates selectively browse specific ‘palatable’ tree species [3,4]. In addition, not all tree species are able to respond quickly and effectively to browsing (see review by [5]). For example, *Abies alba* Mill. saplings from high-elevation provenances showed a delayed response to simulated browsing, whereas *Picea abies* (L.) H. Karst. and *Fagus sylvatica* L. saplings did not [6,7]. Both effects can lead to browsing-induced retarded growth of palatable saplings (e.g., oak) relative to competing less palatable tree saplings [8], sometimes changing the growth rate ranking between the species [9,10]. Observations, experiments and model simulations in many temperate and boreal forests have shown that selective browsing by wild ungulates can affect the development of a forest stand and lead to substantial changes in the composition and structure of plant communities [11,12], such as a decline of *A. alba* [13].

In forest stands with few tree species, like many mountain forests, biodiversity losses are more apparent than in forests with many tree species. Nonetheless, a loss of admix tree species in, e.g., vigorous beech forests (Milio-Fagetum or Carici-Fagetum) can have important consequences. In many sub- to lower montane beech forests in Switzerland, *F. sylvatica* is expected to grow less vigorously and thus become less dominant in the future due to climate change. Therefore, other tree species should be promoted, such as *Acer platanoides* L., *Acer pseudoplatanus* L., *Fraxinus excelsior* L., *Quercus petraea* (Matt.) Liebl. and *Quercus robur* L., as well as *Acer campestre* L., *Sorbus aria* (L.) Crantz and *Tilia cordata* Mill.

on drier sites (see recommendations in the Tree App [www.tree-app.ch]). Further, *A. alba*, *Prunus avium* L., *Taxus baccata* L., *Ulmus glabra* Huds., *Betula pendula* Roth and *Juglans regia* L. are conditionally recommended (Tree App). This means a wide range of tree species, some of which demand more light than *F. sylvatica* (e.g., *Q. robur* [14]) and/or are very attractive to wild ungulates (Table 1; [15]). Thus, ungulate browsing may also limit the silvicultural potential with respect to climate adaptation.

In many vigorous forests, foresters and wildlife managers evaluate the situation regarding the browsing influence of wild ungulates only through estimations, often with very different outcomes. In simplified terms, the latter consider the abundance of all saplings, while the former focus on the browsed saplings. Browsing percentage, i.e., the number of saplings with a browsed leader shoot, expressed as a percentage of all observed saplings, is often used as an objective and reproducible measure of the frequency of browsing on tree saplings [16]. However, frequent browsing does not imply a relevant browsing impact. Indeed, browsing percentage alone captures little of the effective long-term influence of browsing on tree regeneration, such as reduction in stem number or loss of tree species in the future stand [17]. Apart from the proportion of browsed saplings, at least the following factors have been stated to be important for estimating the long-term influence of browsing: (i) the spatial distribution and quantity (e.g., density) of tree saplings of all species; (ii) the within-tree browsing intensity (i.e., if only buds or large parts of the leader shoot are eaten) per season; (iii) the site-specific height growth of the tree saplings, and thus the time needed for trees to grow out of the reach of browsers, and the browsing-induced changes in growth rate ranking between the differently selected species; (iv) the possible delay in the tree response after browsing; and (v) the tree mortality induced by browsing (e.g., [18,19]). Mortality caused by ungulates can only be assessed by individually marking saplings and tracking them over time (e.g., [20]) or by comparing fenced and unfenced sites (e.g., [21]). Both methods are very costly and time-consuming. In addition, tree mortality due to browsing is often less important than the number of tree saplings that survive [19]. Determining browsing-induced mortality is, therefore, usually not necessary for an initial assessment of the browsing impact. In contrast, the first four of the factors listed above can be assessed easily in inventories by using the k-tree method, i.e., by measuring and assessing at least the two tree saplings nearest to the plot center per species and height class (i.e., $k > 1$; see k-tree sampling [22] or inventories by [23–25]).

Alternative methods in which all tree saplings are counted within a predefined area (i.e., fixed-area plots [26–28] or plot count methods [29]) have greater accuracy for tree density assessments. Theoretically, height increments and each individual tree's response after browsing could also be evaluated with these methods. However, in stands with a large number of saplings, this would mean that many trees would have to be measured, and many trees of the same species or height class would be sampled per plot. Generally, the large number of trees in densely regenerated areas is the main reason why the selected sample area size in large plot-count inventories is very small (e.g., 0.9 m in the Swiss National Forest Inventory [30]), at the expense of sampling of rarer tree species. The k-tree method is much faster and more efficient for collecting information on rarer species as well. On the one hand, only some saplings of common species, selected according to clear criteria, are measured (the k trees nearest to the plot center). On the other hand, large areas can be searched for rarer species (up to the maximum defined search distance [29]). The k-tree method also has disadvantages, as density calculations based on this method are prone to biases [27,31]. However, if the density calculation is omitted and the focus is instead laid on the calculation of the occupied area per species [29] or on the stocking percentage [27], the advantages outweigh the disadvantages in terms of the detailed evaluation of trees [25,32] selected according to their proximity to the plot center (and thus the method is not biased by choosing the largest trees per species and plot, cf. [33]).

As wild ungulates move in space and selectively choose their food, and as favorable areas for tree regeneration are irregularly distributed, the measured frequency of browsing depends on the spatial distribution of the sample plots. First, differences are expected

between plots sampled in a systematic grid over the entire forest (i.e., in all stages of development and across all forest types) and plots sampled only in open sites where tree regeneration is more likely [34]. Second, forest edge density has a large influence on deer [35] and, thus, on browsing [36]. Small ‘islands’ of forests within agricultural land may, therefore, have more browsing than larger forest complexes. Thus, an inventory adapted to local conditions and silvicultural practices is important.

The main objectives of this study were (i) to launch an objective but easily feasible survey to assess the impact of browsing in the species-rich, patchily distributed beech forests of the eastern Swiss Plateau; (ii) to estimate the browsing impact based on the first four factors listed above (i.e., excluding browsing-induced mortality); and (iii) to reduce the number of factors to be assessed in future inventories at this location or in comparable beech forests while still including the main factors needed to estimate not only the frequency but also the impact of browsing, e.g., the browsing-induced shifts in the growth rate ranking between the species.

The following hypotheses were tested:

- 1 Browsing is selective regarding preference for known palatable tree species and individual vigorously growing saplings. Species recommended for enhancing the adaptation of these beech forests to climate change are particularly selected by ungulates.
- 2 The vigorous growth of saplings leads to light browsing and thus few impacts.
- 3 Coniferous tree species are mainly lightly browsed in winter and respond in the following vegetation period by forming a new leader shoot. Thus, there are no delays in the tree response after browsing, which can be neglected in further surveys.
- 4 Deciduous tree species are mainly lightly browsed in summer and can respond within the same vegetation period. Therefore, a survey in autumn is optimal for capturing the impact of browsing on these tree species.
- 5 Browsing in forest islands is more frequent than in larger forest complexes, and this difference should be considered when systematic grids are established.

2. Materials and Methods

2.1. Study Site

The study was conducted in the Kirchberg forest district in the canton of St. Gallen, Switzerland. The landscape is hilly, with forests covering varying topographical features such as hilltops, slopes and ravines. The elevation ranges from 525 to 923 m a.s.l. There are some larger forest complexes, but many forests are like islands within the agricultural land, resulting in a small-scale mosaic of farmland and forests. Most of the forests are classified as sub- and lower montane beech forests (above all *Milio-Fagetum mercurialietosum*, *Milio-Fagetum luzuletosum* and *Milio-Fagetum stachyetosum*, but also *Mercuriali-Fagetum typicum* and *Carici-Fagetum caricetosum montanae*; classification following [37]).

Over the last 30 years, the mean monthly rainfall was between 61 and 91 mm in Kirchberg [38]. The driest months were April and October, and the wettest month was December. In July 2022, there was <40 mm of rainfall, and in the first half of August, only ca. 6 mm. The mean monthly temperature maximum over the last 30 years was between 3 °C in December, January and February and 21 °C in August. In 2022, however, it was >25 °C in June, July and August. Thus, the local foresters characterized summer 2022 as very dry and hot.

The Kirchberg forest district includes three hunting zones, Dietschwil, Gähwil and Müselbach. Roe deer are present in all forests, whereas chamois occur locally in steep areas, and red deer have been seen only sporadically in recent years.

2.2. Study Design and Plot-Level Data

Across the canton of St. Gallen, seven systematic grids of sample plots were placed (A-grid to G-grid). The largest grid was 500 m × 500 m (A-grid), while the smallest grid was 125 m × 125 m (G-grid). The B-grid was also 500 m × 500 m but was shifted diagonally from the A-grid so that A and B together resulted in a 353 m × 353 m grid. For this study, all

A and B plots were sampled throughout the Kirchberg forest district, resulting in 101 plots (Appendix A Figure A1).

In order to additionally sample the forest islands within this district, plots from grids C to G were also sampled. Forest islands with no plots in the regular 125 m × 125 m grid were neglected. Up to three plots were sampled for all the other forest islands, starting with plots belonging to the largest of these grids (C), then D, E and F, and if necessary, G (Appendix A Figure A1). This resulted in 52 additional plots. Thus, a total of 153 plots were sampled between 22 August and 10 October 2022.

Each sample plot was first assessed regarding accessibility and forest cover. If >20% of a 5-m radius around the center of the plot lay outside the forest, in a body of water, on a cliff or on a forest road, the plot was moved exactly 15 m away perpendicular to this obstacle. A total of 20 plots (12 in grids A and B, 8 in grids C to G) were still not accessible or did not cover forests, and thus no sampling took place there. The center of each of the 133 recordable plots was marked by a wooden pole painted blue. For three trees in or close to the plot with a diameter at breast height (DBH) > 12 cm, the distance to the plot center and azimuth were measured, and their bark was marked with paint just above the soil.

The slope of each plot was measured and used to calculate the slope-corrected radius. At the plot center, a photo of the canopy cover was taken with a tablet camera (Samsung Galaxy S4 Tablet or Nautiz X6 Handheld) aligned to the north and held horizontally with the help of a spirit level. The canopy cover was also estimated in 10% intervals by one person standing at the plot center, according to the recording method of the Swiss National Forest Inventory (NFI) 3 [39]. Whether each plot was in a deciduous forest, coniferous forest or mixed forest was also assessed. The cover of neophytes and competing vegetation was estimated within circles with a slope-corrected radius of 5 m around each plot center. The structure of the forest around each plot was characterized as single-layered, multi-layered (2–3 layers), stratified or clustered. Seven developmental stages were distinguished, i.e., young growth (<1.5 m tree height), thicket (DBH < 12 cm), pole timber (DBH 12–30 cm), young timber (DBH 31–40 cm), medium timber (DBH 41–50 cm), old timber (DBH > 50 cm) and mixed uneven-aged stands. Whether sapling recruitment was possible and desirable ('regeneration possibility') was additionally evaluated, along with whether there had been recent, old or no logging to promote regeneration. In addition, elevation data (in meters above sea level) and forest-type data were available from the geoportal of St. Gallen [<https://www.geoportal.ch/ktsg>, accessed on 18 August 2022].

2.3. Tree Regeneration Data

In each plot, the two saplings nearest to the plot center were assessed for each tree species and height class. Shrubs (e.g., *Corylus avellana* and *Sambucus racemosa*) were not included. The height classes were HC1 (10–39.5 cm), HC2 (40–69.5 cm), HC3 (70–99.5 cm), HC4 (100–129.5 cm) and HC5 (130–200 cm), except for *A. alba* and *T. baccata*, for which HC0 (last year's seedlings up to 9.5 cm height) was also recorded. The maximum distance to the plot center at which saplings were assessed was 5 m slope-corrected.

For each individual sapling, the distance to the plot center and the tree height (measured as the length of the main axis) were measured. This tree height determined the height class assignment. The state of the leader shoot formed in 2022 was determined as (i) leader shoot of the current year present (i.e., shoots with leaves for deciduous species or with light green needles for coniferous species like *A. alba* and *P. abies*), (ii) formation of a proleptic shoot (second to xth flushes formed in the current year), (iii) response to browsing in the current vegetation period, or (iv) no leader shoot present (often clearly visible due to the formation of new twigs). The length of the leader shoot (i), of the first flush (ii) or of the remaining shoot piece after browsing in the 2022 vegetation period (iii) was measured to an accuracy of 5 mm. Separately, the length of the further flushes (ii) or the length of the shoot formed in response to browsing (iii) was measured. As proleptic shoots are only easily distinguishable when they have leaves or fresh needles, for the previous year's leader shoot, only the last flush was measured (i.e., until the next bud scar). The within-tree browsing

intensity, defined as the severity of browsing of the annual height increment of the leading shoot [18,40], was noted separately for summer 2022 (i.e., during the vegetation season on the current-year height increment of the leader shoot) and for winter 2021/2022 (during the dormant period on the lignified height increment of the shoot formed in the previous year). The categories included ‘not’ (not browsed or damaged), ‘light’ (light browsing of the leader shoot, such as bud removal), ‘heavy’ (more than ca. half of the annual height increment of the leader shoot browsed), ‘dry’ (i.e., dead leader shoot), ‘other’ (some other type of damage, such as frost or insect damage) and ‘no shoot’ (no leader shoot was formed in that year). Further, the browsing or other damage along the main stem axis was counted as damage frequency. Leaf and twig browsing in summer were recorded, as well as light (single twigs to max. half of the twigs browsed in the lignified stage) or heavy (more than half of the twigs browsed in the lignified stage) twig browsing in winter.

2.4. Statistical Analyses

2.4.1. Descriptive Analysis

The height increment from the year 2022 was calculated as the length of the first flush and of all further flushes in the case of proleptic shoots. To compare saplings of different height classes, we calculated the relative height growth by dividing the height increment by the tree height (hereafter called relative growth rate, RGR).

For each plot and height class, the RGR of the nearest sapling to the plot center of a given species was divided by the RGR of the nearest *F. sylvatica* sapling. The same was performed for the second nearest sapling. If the resulting measure was 1, both saplings were growing equally well; if it was >1 , the other species was growing better than *F. sylvatica* and if it was <1 , *F. sylvatica* was growing better. This was performed to analyze browsing-induced shifts in the growth rate ranking between the species [40].

The proportion of stocked area was estimated by dividing the number of plots in which the nearest tree of species *x* could be found by the total number of plots that could be assessed (133), then multiplying by 100 to express the proportion as a percentage. In addition, the k-tree method was considered optimal for assessing the overall stocking goal [27,29]. If exactly one sapling was found within the 5 m circular area searched, this would correspond to 127 trees per ha. Here, it was checked whether these forests had at least 3000 trees per hectare, as suggested for beech forests [41,42]. One tree would occupy 3.33 m², assuming a uniform spatial distribution of the trees. This would lead to a maximum search distance of 1.03 m. A sample plot was considered ‘stocked’ if at least one sapling was found (in our case, within the radius of 1.03 m) and ‘unstocked’ if no tree sapling was found [27]. The reduced search distance of 1.03 m was used only to calculate the overall stocked area, not to calculate the stocked area of each individual species.

As a measure of browsing frequency, the following calculations were completed for the nearest saplings of each species to the plot center (irrespective of height class HC1 to HC4): (i) the proportion of browsed area (also called the proportion of occupied stand area for the group of browsed saplings, calculated as the number of plots with a browsed nearest sapling out of all assessed plots, expressed as a percentage; and (ii) the proportion of browsed area out of the total stocked area, calculated as the number of plots with a browsed nearest sapling of species *x* out of all plots with the nearest sapling of this species, again expressed as a percentage.

Further, the percentage of saplings with browsing damage was calculated for each species. For this evaluation, all saplings assessed in height classes HC1 to HC4, i.e., the nearest and second nearest sapling per height class (max 1064 saplings per species (133 plots * 4 HC * 2 saplings)), were considered. In the literature, browsing percentages typically consider a whole year. Therefore, a figure was generated displaying the percentage of saplings browsed only in summer, only in winter, and in both seasons, as well as the percentage of saplings with no signs of browsing but with another type of damage. A tree was classified as browsed regardless of the presence of other damage.

The time needed to grow out of the reach of roe deer was calculated for each tree species using the third quartile of the height increment in 2021 or in 2022 per height class. This corresponded to 10 cm plus the increment corresponding to the third quartile of HC1, plus the next increment, plus the next, until the tree exceeded 40 cm (height class limit). Then, the third quartile of HC2 was used, and so on, until a height of 130 cm was reached. The required years were summed. This calculation was based on the third quartile of only unbrowsed and undamaged saplings or of unbrowsed/undamaged saplings and lightly browsed ones.

2.4.2. Regression Analysis

Linear mixed effects models (lmer function in package lme4 [43]) were applied with R software (R version 4.0.3 (10 October 2020) [44]) to analyze differences in growth between the species of height classes HC1 to HC4. The full model for the height increment in 2021 or for RGR2021 included species, tree height, winter within-tree browsing intensity (omitting all trees with ‘no shoot’), twig winter browsing, damage frequency, developmental stage, canopy cover or gap fraction, deciduous vs. coniferous forest, forest structure, hunting zone, forest island, regeneration possibility, logging, cover of competing vegetation, elevation and hill slope as fixed effects and plot as a random effect. The cover of neophytes was not included, as no neophytes were found. Forest type was also excluded, as only three plots were classified as ash forest. The gap fraction was calculated with the hemispher package [45] in R as one minus the mean of the fractions. As canopy cover and gap fraction were highly correlated ($\text{cor} = 0.694$, stats R package), only one of these light measures was integrated into the model. Both the height increment in 2021 and RGR2021 were log-transformed. The random effects were tested using the ranova function of the lmerTest R package [46]. The fixed effects were tested by manually eliminating one variable after another and comparing the Akaike information criterion (AIC) with an analysis of variance (ANOVA). In the case of significant fixed effect factors with $p \leq 0.01$, a multiple comparison of means was performed with the Holm method using the glht function of the multcomp R package [47]. For this post-hoc test, the significance level was set to $p \leq 0.05$.

For the height increment in 2022 and for RGR2022, the same full models were used, but summer within-tree browsing intensity and summer leaf or twig browsing were additionally included as fixed effects.

Only tree species for which >100 saplings had been measured were included in all these models (i.e., *A. alba*, *P. abies*, *F. sylvatica*, *A. pseudoplatanus*, *F. excelsior* and *P. avium*; Table 1). As there were significant differences between these six species, separate linear mixed-effects models were performed for each species. An overall model with species as a fixed effect, including all tree species observed in the plots, was not possible because of the many rare species.

To consider more species in the analysis, we assigned an ungulate preference (opposite of avoidance [48]) to each tree species (Table 1), according to [49]. Tree species with a value of 1 were considered ‘unpalatable’, and those with a value of 5 were considered ‘highly palatable and preferentially browsed’. *Malus sylvestris* was not classified within these publications and was thus omitted from this analysis.

In addition, a separate model was applied for species classified as ‘susceptible’ based on the above preference, the growth potential and the ability to respond to browsing according to [49,50]. Susceptible species (i.e., ‘S’ in Table 1), for which no single species model for height increment 2022 or RGR2022 was applied, were included. If all susceptible species had been included, the results would have been dominated by the four main susceptible species for which we had already implemented individual models. Here, the aim was to study the rarer susceptible species. The same analysis could not be performed for ‘resistant’ species (i.e., ‘R’ in Table 1), as there were too few of them.

Table 1. Number of saplings observed per tree species and height class (HC). For species with >100 sapling in the HC1 to HC4, total numbers (HC0 to HC5) are printed in bold, these species are also referred to as ‘main species’. Information is given about the browsing preference by ungulate (BPU) class, with 1 = unpalatable and 5 = highly palatable and preferentially browsed, and the species-specific sensitivity to browsing (S) following [50], with S = susceptible and R = resistant. The species are sorted into evergreen and deciduous species in descending order of total occurrence.

	BPU	S	HC0	HC1	HC2	HC3	HC4	HC5	Total
<i>Abies alba</i>	5	S	178	197	87	50	27	28	567
<i>Picea abies</i>	1	R		112	63	35	28	22	260
<i>Taxus baccata</i>	5	S	34	26	0	0	0	0	60
<i>Pinus sylvestris</i>	2	R		3	0	0	0	0	3
<i>Fagus sylvatica</i>	3	R		150	145	128	107	115	645
<i>Acer pseudoplatanus</i>	5	S		195	99	62	39	37	432
<i>Fraxinus excelsior</i>	5	S		200	108	40	19	13	380
<i>Prunus avium</i>	4	S		60	27	18	5	6	116
<i>Ulmus</i> spp.	5	S		28	22	9	8	9	76
<i>Sorbus aucuparia</i>	5	S		34	20	6	3	4	67
<i>Quercus</i> spp.	4	S		25	5	1	0	0	31
<i>Sorbus aria</i>	5	S		9	7	3	0	2	21
<i>Juglans regia</i>	1	R		6	6	2	2	0	16
<i>Acer campestre</i>	5	S		7	4	4	0	0	15
<i>Acer platanoides</i>	5	S		7	5	0	1	0	13
<i>Betula</i> spp.	2	R		1	3	2	1	0	7
<i>Tilia</i> spp.	3	R		2	3	2	0	0	7
<i>Carpinus betulus</i>	4	R		3	0	0	0	1	4
<i>Salix</i> spp. *	5	R		1	2	0	0	0	3
<i>Malus sylvestris</i>				2	1	0	0	0	3
<i>Populus</i> spp.	4	R		1	0	0	0	0	1
Total all species			212	1069	607	362	240	237	2727

* Only *Salix* growing as trees were included, e.g., *S. caprea* and *S. alba*.

An additional linear mixed effects model was calculated for the damage frequency of the six main species. In the full model, species, tree height, developmental stage, canopy cover or gap fraction, deciduous vs. coniferous forest, forest structure, hunting zone, forest island, regeneration possibility, logging, cover of competing vegetation, elevation and hill slope were included as fixed effects, and the plot was included as a random effect. Thus, summer and winter within-tree browsing intensity were omitted, as these events were already counted in the damage frequency.

Further, to examine which tree saplings responded to winter browsing with a new shoot, mixed effects logistic regression models were used for light and heavily browsed saplings, i.e., generalized linear mixed models with a Bernoulli conditional distribution and a logit link (glmmTMB function in glmmTMB R package [51]). The full model included tree height, winter within-tree browsing intensity (i.e., light or heavy), twig winter browsing, damage frequency and canopy cover as fixed effects and plot as a random effect.

3. Results

Twenty-one different tree species were found (Table 1). The most common species were *F. sylvatica*, *A. alba*, *A. pseudoplatanus*, *F. excelsior*, *P. abies* and *P. avium*. These species, however, were not equally distributed within the height classes. HC5 included 17.6% of all *F. sylvatica* saplings but only 3.4% of *F. excelsior*, 5.2% of *P. avium*, 7.2% of *A. alba*, 8.5% of *Picea* and 8.6% of *A. pseudoplatanus* saplings. Other relatively frequent but palatable and susceptible species, such as *T. baccata*, *Sorbus aucuparia* L. and *Quercus* spp., were not found in larger height classes (Table 1). In contrast, 11.8% of *Ulmus* spp. were found in HC5.

3.1. Stocked Stand Area and Spatial Distribution

No tree regeneration was found within the maximum search distance of 5 m in only 2 of the 133 surveyed plots. In all other plots, at least one tree sapling was found. The proportion of stocked area, with a stocking goal of 3000 saplings per hectare (artificial reduction to 1.03 m search distance), was $98.5 \pm 0.8\%$ for saplings in HC1 to HC5.

Though more *F. sylvatica* saplings were measured (Table 1), the proportion of stocked area was largest for *A. alba*, *F. excelsior* and *A. pseudoplatanus*; (black symbols in Figure 1). *Prunus avium* was found in only ca. one-third of the plots. Nevertheless, *P. avium* was quite evenly distributed throughout the Kirchberg forest district (Figure 2). All species that were found in several plots were spread over the entire territory and not only in a small local area (Figure 2). Just *S. aria* was missing from the northern part, and *J. regia* was missing from the southeastern part of the territory (Figure 2).

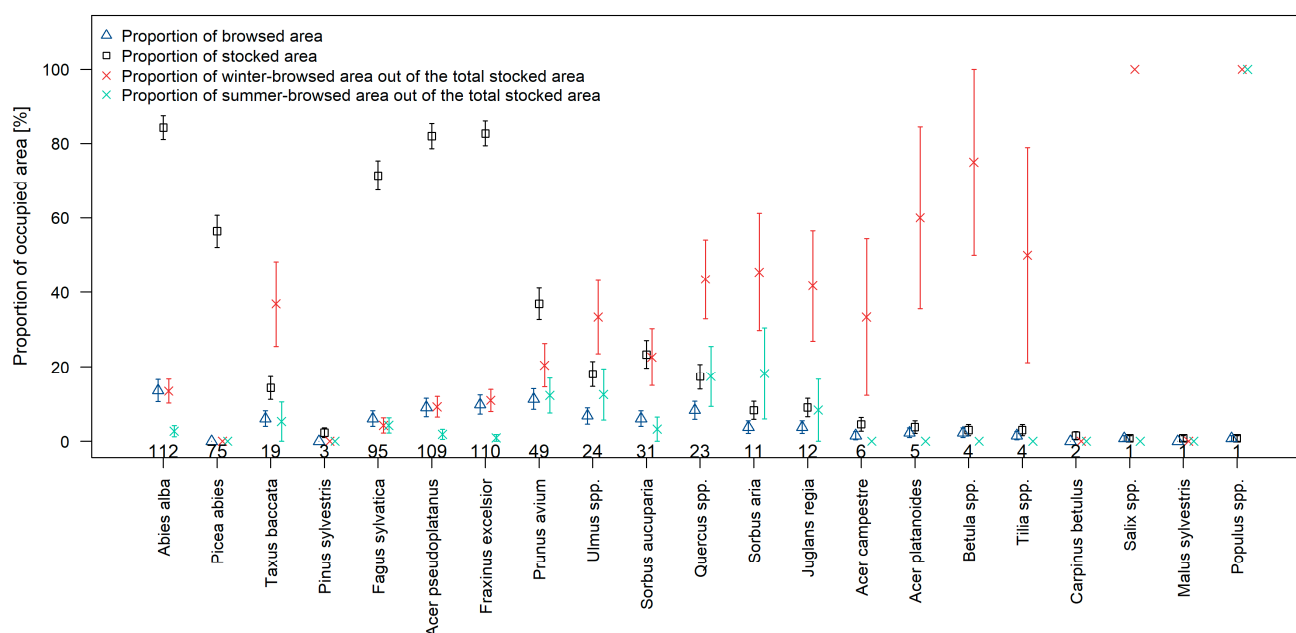


Figure 1. Proportion of occupied area per species. The species are sorted into evergreen and deciduous species and in descending order of total occurrence. The number of plots with saplings of each species is displayed (maximum = 133 assessed plots).

The proportion of stocked area per developmental stage was also calculated. Young growth (3 plots), thicket (2 plots) and pole timber (12 plots) were too seldom within the 133 plots for this analysis. *Picea* was more widespread in mixed uneven-aged stands ($79.2 \pm 8.5\%$) than in young to old timber ($40 \pm 10\%$ to $57.6 \pm 8.7\%$). *Fagus sylvatica* was less widespread in young timber ($60 \pm 10\%$) than in medium to old timber and mixed uneven-aged stands ($81.8 \pm 6.8\%$ to $83.3 \pm 7.8\%$). *Prunus avium* was less frequent in medium timber ($27.3 \pm 7.9\%$) than in old timber ($50.0 \pm 8.7\%$). All other species showed no significant differences in the proportion of stocked area between the developmental stages.

The proportion of stocked area was higher in larger forested areas (total 108 plots) than in the forest islands (25 plots) for *A. alba*, *T. baccata*, *Ulmus spp.* and *S. aria*.

Notably, the very few plots with young growth and thicket had a mean canopy shading of $44 \pm 18.2\%$. All other plots were rather shaded, i.e., canopy shading in plots with pole timber was $80 \pm 9.5\%$, with young timber $82.4 \pm 9.7\%$, with median timber $80.9 \pm 11.8\%$, with old timber $82.9 \pm 10.3\%$, and with mixed uneven-aged stands $83.3 \pm 9.6\%$. Further, there was a negative correlation ($\text{cor} = -0.55$) between the percentage cover of competing vegetation and canopy shading. The competing plant species was mostly *Rubus fruticosus*.

There was no correlation between canopy shading and hill slope ($\text{cor} = 0.08$), canopy shading and elevation ($\text{cor} = -0.014$), or hill slope and elevation ($\text{cor} = 0.05$).

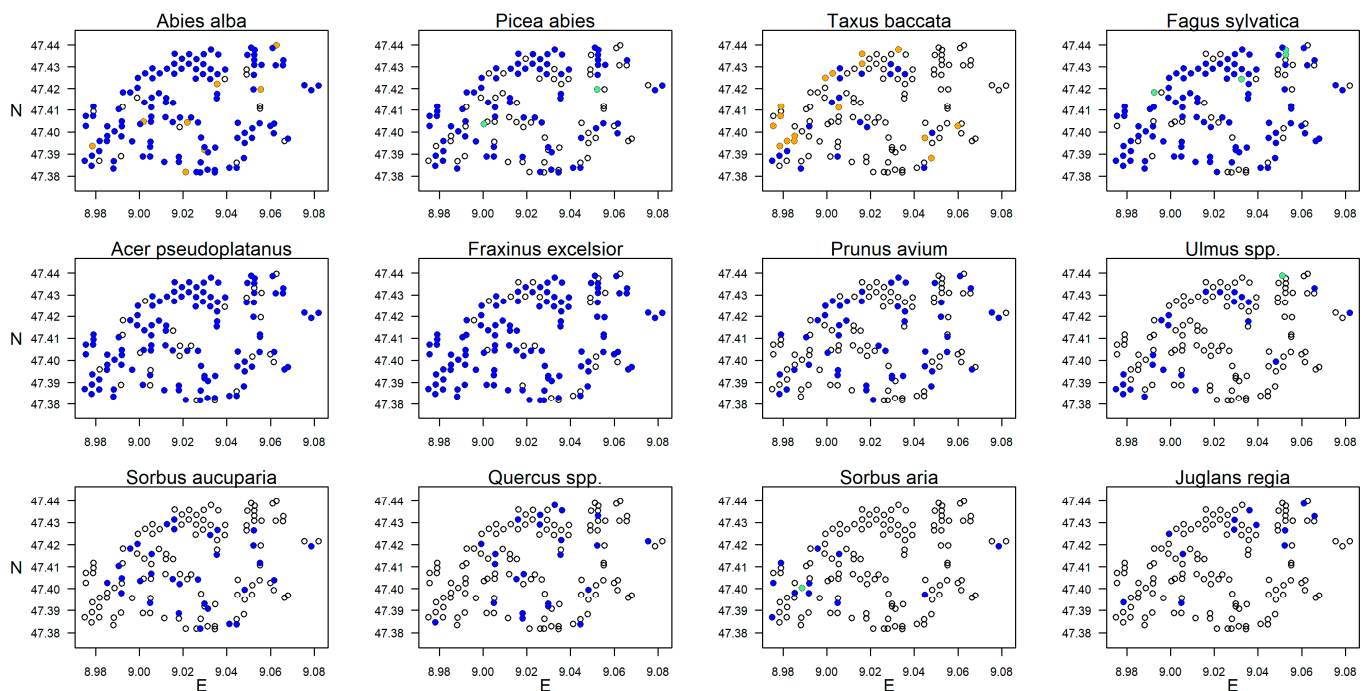


Figure 2. Spatial distribution (longitude and latitude) of the tree species found in >10 plots in the Kirchberg forest district. Open black circles represent plots without saplings, blue filled circles represent plots with saplings in HC1 to HC4 (for which the proportion of stocked area was calculated), green filled circles represent plots with no HC1 to HC4 saplings but with an HC5 sapling, and orange filled circles represent plots with no HC1 to HC4 saplings but with an HC0 sapling (only possible for *Abies alba* and *Taxus baccata*).

3.2. Frequency, Season and Within-Tree Browsing Intensity

The proportion of browsed area was largest for *A. alba* ($13.5 \pm 3.0\%$; blue triangles in Figure 1). The proportion of area occupied by saplings with other damage (drought, frost, insect) or with no leader shoot (e.g., after heavy browsing in the preceding year) was also highest for *A. alba* ($9.8 \pm 2.6\%$), while it was only $3.0 \pm 1.5\%$ for *F. excelsior*, $2.3 \pm 1.3\%$ for *A. pseudoplatanus* and *P. avium*, and $1.5 \pm 1.1\%$ for *P. abies* and *F. sylvatica*.

The proportion of browsed area out of the total stocked area was highest for *P. avium* ($30.6 \pm 6.7\%$), followed by *A. alba* ($16.1 \pm 3.6\%$), *F. excelsior* ($11.8 \pm 3.1\%$), *A. pseudoplatanus* ($11.0 \pm 3.0\%$), *F. sylvatica* ($8.4 \pm 2.9\%$) and, finally, *P. abies* (0%). Winter browsing was much more frequent than summer browsing for all species—both evergreen and deciduous, as the proportion of winter-browsed area out of the total stocked area was larger than the proportion of summer-browsed area out of the total stocked area (red and green x symbols in Figure 1). The only exception was *F. sylvatica*, with $4.2 \pm 2.1\%$ in both periods. The rarer the species, the higher the proportion of winter-browsed area out of the total stocked area (note that Figure 1 is sorted according to descending species occurrence). This was also the case for some species that were classified as unpalatable, i.e., ungulate preference class 1 (Table 1), such as *J. regia*. The only outliers were *Carpinus betulus* and *M. sylvestris*, with 0% browsing. However, area proportions of very rare species should be interpreted with caution.

The only important differences in the proportion of browsed area out of the total stocked area regarding developmental stage were observed for *F. excelsior*, with less winter browsing in young timber ($4.8 \pm 4.8\%$) than in mixed uneven-aged stands ($20.0 \pm 9.2\%$). *Taxus baccata*, *F. excelsior*, *P. avium* and *Ulmus* spp. had significantly higher proportions of browsed areas out of the total stocked area in larger forests compared to forest islands.

Considering the two nearest saplings per height class, winter browsing was more frequent than summer browsing for all tree species (including *F. sylvatica*), and light and heavy summer browsing were rare or even absent for some species (Figure 3).

For some species, light winter browsing was more frequent than heavy winter browsing, including *T. baccata*, *F. sylvatica*, *A. pseudoplatanus* and *P. avium*. In contrast, heavy winter browsing was more frequent for *A. alba*, *F. excelsior*, *Ulmus*, *S. aucuparia*, *Quercus*, *J. regia* and *A. campestre*, and all browsed *A. platanooides* were heavily browsed (Figure 3).

Few individuals of *F. sylvatica*, *A. pseudoplatanus* and *P. avium* were browsed in winter and in summer. For *Ulmus*, *S. aria* and *Quercus*, between 10% and 15% were browsed in both seasons. Notably, *J. regia* was among the most frequently and also most heavily browsed species here (Figure 3). Out of all assessed *A. alba* of HC0, 7.3% were browsed.

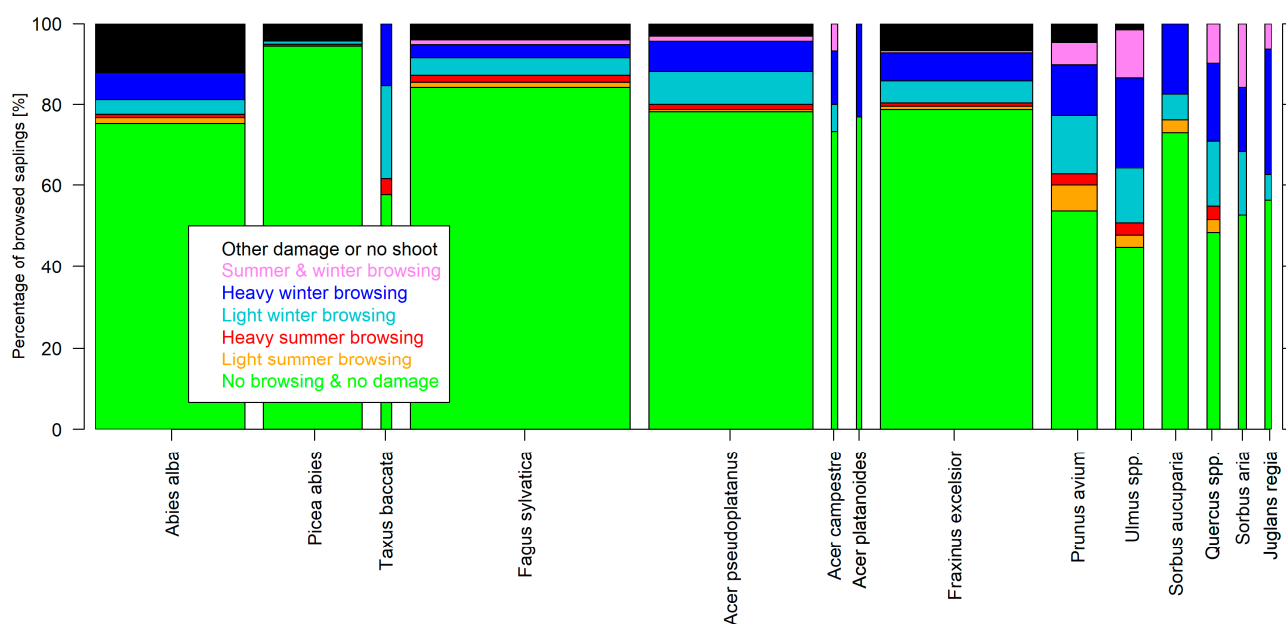


Figure 3. Percentage of browsed saplings of HC1 to HC4 per season and within-tree browsing intensity (including the nearest and second nearest saplings per height class). Only species with ≥ 13 observed trees in these height classes are displayed. The species are sorted into evergreen and deciduous species and according to descending occurrence, apart from *Acer campestre* and *Acer platanooides* for better comparison with *Acer pseudoplatanus*.

3.3. Height Growth

Generally, RGR2021 values were rather small, as the median over all six frequent species was only 0.073 (blue line in Figure 4), e.g., 7 cm for a tree height of 1 m or 3.5 cm for a tree height of 50 cm. RGR was larger in 2021 (mean = 0.118) than in 2022 (mean = 0.099, median = 0.066). The actual difference was probably even more pronounced given that the first and all further flushes were measured for the height increment in 2022, while only the last flush was measured in 2021. However, only six *Ulmus* saplings and one single sapling of *P. abies*, *A. pseudoplatanus* and *F. excelsior* of HC1 to HC4 had a second flush in 2022. No *F. sylvatica* saplings in HC1 to HC4 had a second flush, and only three saplings in HC5 had one. The overall growth rate ranking calculated based on the height increment in 2021 was *P. avium* > *F. excelsior* > *A. alba* and *F. sylvatica* \geq *A. pseudoplatanus* \geq *P. abies*. For all species, similar variables were important in explaining RGR2021 and height increment in 2021 (Table 2). Canopy shading had a negative effect on all six main species and on all species together, except *P. avium* and the other susceptible species (Table 2). Tree height had a positive effect on the height increment of all species. For RGR, tree height had a negative influence on *F. sylvatica* and *A. pseudoplatanus*, and thus, also on all six main species or all species together. This indicates that the taller the tree, the larger the height increment, with a strictly linear relationship for *A. alba*, *P. abies*, *F. excelsior* and *P. avium* but with a flattening

for *F. sylvatica* and *A. pseudoplatanus*. Damage frequency negatively influenced tree growth for all species apart from *P. abies* (Table 2). Except for *P. abies*, within-tree browsing intensity was an important variable explaining RGR2021 (Figure 4) and height increment in 2021 (Table 2). For *A. alba* and *F. excelsior*, RGR2021 and height increment in 2021 were equal between saplings with no sign of browsing or damage on their leader shoot and for the lightly browsed saplings. For all the other species, lightly browsed saplings had a larger remaining terminal-shoot piece than unbrowsed trees (e.g., Figure 4). This suggests that the best-growing, most vital trees were browsed. Heavy browsing significantly reduced the height increment in 2021 and RGR2021 for all species (there were no *P. abies* with heavy browsing; Figure 3). There were too few saplings with a dried leader shoot or with other damage to interpret the results. Light twig browsing in winter had a negative effect on both height increment and RGR in the model with the six main species considered together, but in the separate models for single species, it only had a significant effect on RGR2021 of *F. excelsior*. All the other variables, such as developmental stage, forest structure, elevation, hill slope, hunting zone and cover of competing vegetation, had no effect on height increment in 2021 or on RGR2021.

Similar results were obtained for RGR2022 as for RGR2021. However, as there was much less summer than winter browsing (Figure 3), the summer within-tree browsing intensity dropped out of all single species models. However, ‘indirect’ browsing in earlier years had a negative effect, as damage frequency negatively affected RGR2022 of all species. Leaf browsing had no influence on leader shoot growth. Light twig browsing in winter reduced RGR2022 only in the single species model for *F. excelsior* and in the model with the six main species considered together.

Table 2. Regression model for the height increment in 2021 for saplings of height class (HC) 1 to HC4. The model with all 21 species included browsing preference by ungulate (BPU) class as a predictor, and models with the six main species included species (S) as a predictor. Susceptible species are defined in Table 1, but the ones included as main species were excluded. N = number of species in the respective analysis, * = significant at $p \leq 0.01$ and ns = not significant. All saplings with no terminal shoot in 2021 were omitted. The random factor ‘plot’ was significant in all models except that for *Prunus avium* (but was retained for comparison between models). Winter within-tree browsing intensity was highly significant in all models and thus is not shown.

Regression Model	N	Species	Tree Height	Damage Frequency	Twig Browsing	Canopy Shading
All 21 species	2226	BPU *	0.017	−0.144	*	−0.017
6 main species	1954	S *	0.017	−0.150	*	−0.020
<i>Abies alba</i>	334	-	0.020	−0.122	ns	−0.015
<i>Picea abies</i>	231	-	0.015	ns	ns	−0.019
<i>Fagus sylvatica</i>	527	-	0.012	−0.307	ns	−0.021
<i>Acer pseudoplatanus</i>	391	-	0.015	−0.123	ns	−0.022
<i>Fraxinus excelsior</i>	363	-	0.027	−0.193	*	−0.015
<i>Prunus avium</i>	108	-	0.022	−0.239	ns	ns
Susceptible species	232	-	0.019	−0.164	ns	ns

Depending on the year, *F. sylvatica*, *P. avium* and *F. excelsior* required the least amount of time to grow out of the reach of roe deer, with ca. 15 years. *P. abies* required around 28 years, *A. alba* 28–34 years, and *A. pseudoplatanus* 27–36 years. Additionally, taking into account the growth of lightly browsed saplings reduced the time by around 1–2 years.

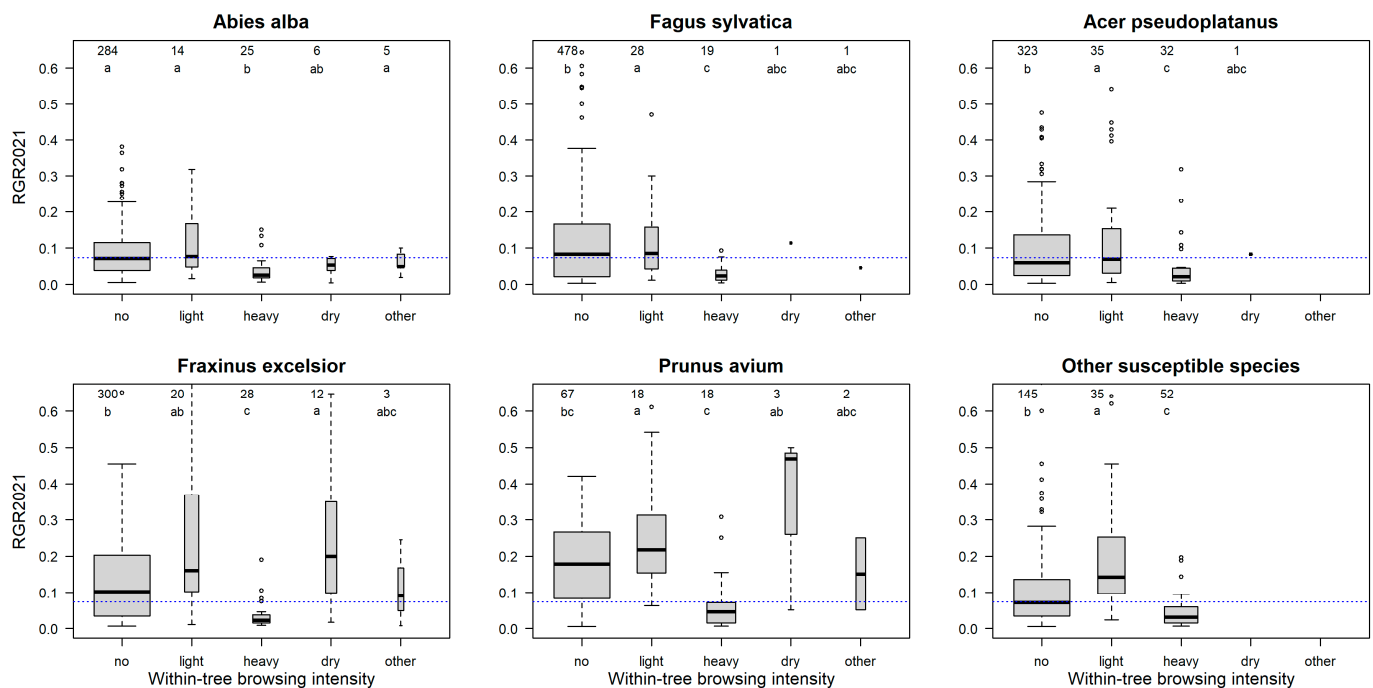


Figure 4. Relative growth rate in 2021 (RGR2021) per within-tree browsing intensity category in winter 2021/2022. Saplings from HC1 to HC4 are included. The blue dotted line represents the median growth rate over all tree species. The numbers given in all panels indicate the number of saplings sampled in the respective categories for that species. Different lower-case letters indicate significant differences at $p \leq 0.05$ between the within-tree browsing intensity in post-hoc tests (for cases where the variable was significant at $p < 0.01$ in the linear mixed effects models). Median (bold line), first and third quartile (bottom and top of box), quartile $\pm 1.5 \times$ interquartile range (whiskers) and individual points more extreme in value (circles) were drawn using the boxplot function in the base R package. The width of the boxes represents the number of trees within the various categories.

There were a considerable number of pairs of unbrowsed saplings of *A. alba*, *P. abies*, *A. pseudoplatanus*, *F. excelsior* and *P. avium* to unbrowsed *F. sylvatica* saplings of the same height class per plot (Figure 5). However, there were only a few pairs with browsed saplings to unbrowsed *F. sylvatica* saplings. At the sample plot level, none of these five species had a growth advantage over *F. sylvatica* in the unbrowsed/undamaged condition. However, the ‘remaining’ RGR2021 of lightly browsed saplings of these four species was still larger than that of unbrowsed *F. sylvatica* (winter within-tree browsing intensity $p < 0.01$; no–light $p = 0.047$). In contrast, the heavily browsed saplings had lower remaining RGR2021 than unbrowsed *F. sylvatica* (no–heavy $p < 0.01$, light–heavy $p < 0.01$).

3.4. Response to Browsing

After heavy browsing in winter 2021/2022, 40% of *A. alba* saplings, and a considerable number of *P. avium*, *F. sylvatica*, *A. pseudoplatanus* and *F. excelsior* saplings, had no leader shoot in 2022, i.e., did not respond after heavy browsing in the dormant season (Table 3). More *A. alba* saplings responded after light than after heavy winter browsing. All *F. excelsior* and *P. avium* saplings with light winter browsing formed a new shoot in 2022. Surprisingly, more *F. sylvatica* and *A. pseudoplatanus* saplings did not respond after light than after heavy winter browsing (Table 3). Only winter twig browsing significantly reduced the response ($p < 0.01$).

Of the *A. alba* saplings with no shoot in 2021, 73.7% had no new leader shoot by the end of the vegetation season in 2022, i.e., had a time lag in their response by at least two years. For all the other main species, there were only one to three saplings (none for *P. avium*) with no leader shoot in 2021, while none of them had formed a new leader shoot in 2022.

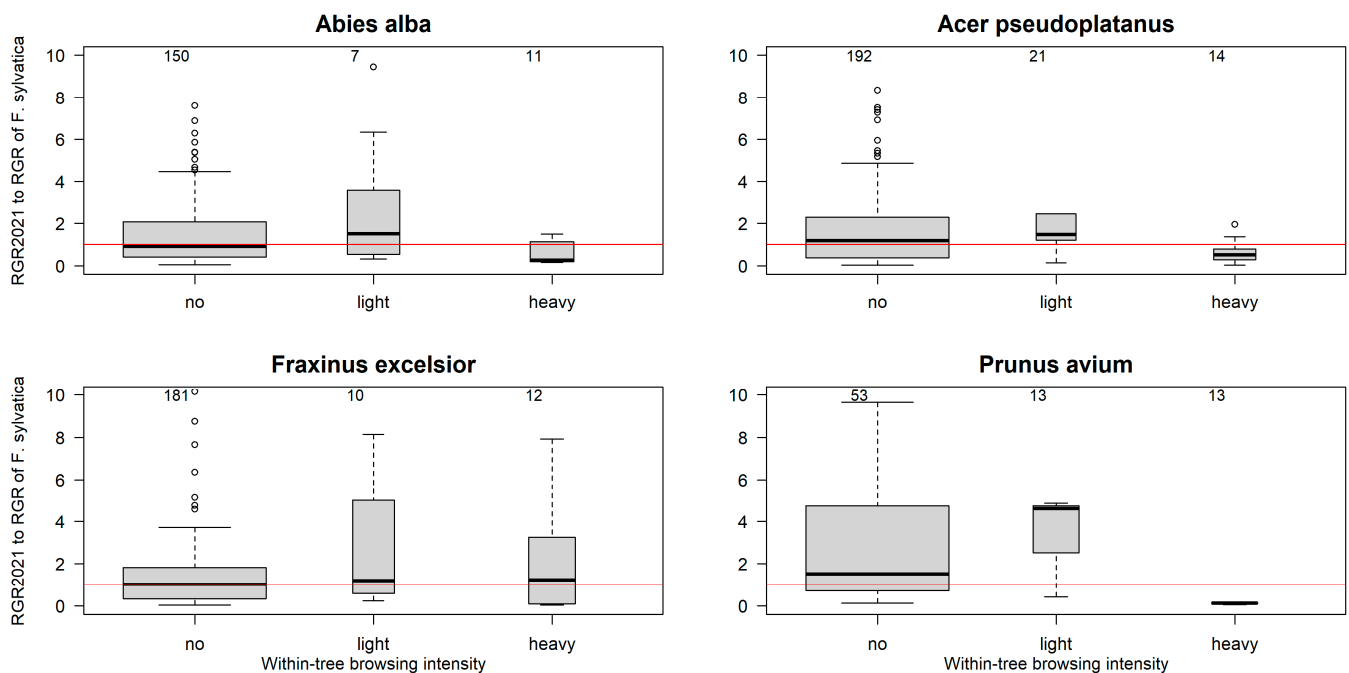


Figure 5. Relative growth rate in 2021 (RGR2021) of the corresponding species divided by the RGR2021 of *Fagus sylvatica* per height class and plot, i.e., only saplings of similar height were compared. The red line indicates equal growth of both species. For details about the box plot, see Figure 4. For better readability, some outliers have been omitted (e.g., *A. alba* 2 no, *A. pseudoplatanus* 4 no and 2 light, *F. excelsior* 3 no and 1 light, *P. avium* 3 no), but they are included in the numbers.

After browsing during the vegetation period, only 10% of *F. sylvatica*, but at least 40% of *A. pseudoplatanus*, 50% of *P. avium* and 67% of *F. excelsior* saplings responded to light browsing with the formation of a new shoot within the same vegetation period.

Table 3. Percentage of tree saplings with no leader shoot in 2022 after light or heavy winter browsing in 2021/2022 for the six main tree species of height class (HC) 1 to HC4 (*Picea abies* excluded, due to too few browsed saplings). Values in *italics* are based on only 14–24 saplings. Values in brackets include the HC0 saplings of *Abies alba*.

Species	Light Winter Browsing [%]	Heavy Winter Browsing [%]
<i>Abies alba</i>	28.6 (22.7)	40.0 (36.7)
<i>Fagus sylvatica</i>	35.7	21.1
<i>Acer pseudoplatanus</i>	22.9	15.6
<i>Fraxinus excelsior</i>	0.0	17.9
<i>Prunus avium</i>	0.0	27.8

3.5. Damage Frequency

The damage frequency ranking was *P. abies* < *F. sylvatica* < *A. alba* < *A. pseudoplatanus*. *F. excelsior* and *P. avium* had damage frequencies similar to those of *A. alba* and *A. pseudoplatanus*.

In the model for the damage frequency of the main six tree species, only tree species and tree height were significant. The greater the tree height, the higher the damage frequency (estimate \pm std. error 0.0079 ± 0.0005). Notably, there were already very small *A. pseudoplatanus* saplings with damage along the main stem axis, and there were only four *A. pseudoplatanus* taller than 50 cm that did not have at least one damage point (Figure 6). It should also be considered that it becomes more difficult to detect browsing damage from earlier years as a sapling becomes older and broader. Thus, it is likely that several of the

larger saplings were damaged when they were small (10–20 cm) but that this damage was not detected when the saplings were 1–2 m tall.

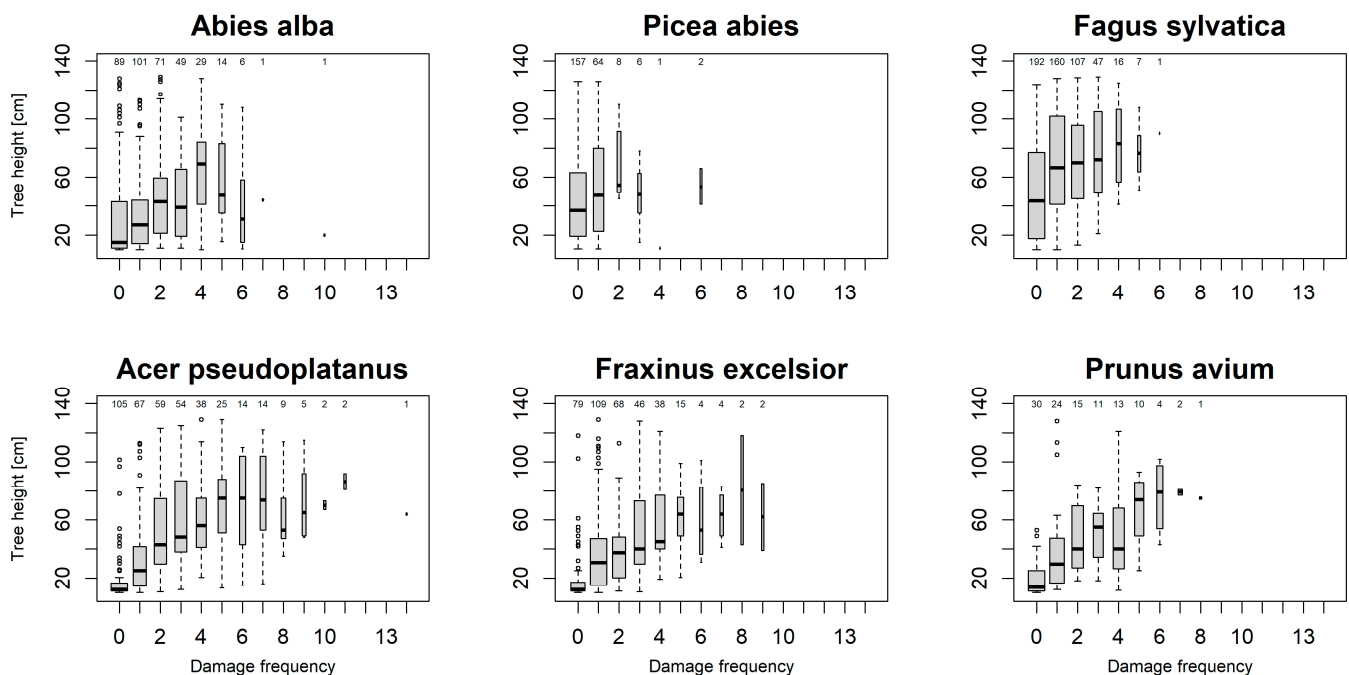


Figure 6. Frequency of damage along the main stem axis for the six main tree species. The numbers displayed in all panels indicate the number of saplings sampled with the respective damage frequency. For details about the box plot, see Figure 4.

4. Discussion

In the beech forests of the Kirchberg forest district in the canton of St. Gallen, Switzerland, 21 different tree species were found to regenerate naturally in the browsing impact survey conducted in 133 systematically placed plots. All tree species recommended for such beech forests, in order to cope with the changing climate, were found. However, only *Acer pseudoplatanus* and *Fraxinus excelsior* from the highly recommended and *Abies alba* from the conditionally recommended species were very widespread. *Prunus avium* was found in at least ca. one-third of the plots, and *Taxus baccata*, *Quercus* spp., *Ulmus* spp. and *Sorbus aucuparia* in one of every five to seven plots. For these species, it can be assumed that there are enough seed trees to ensure natural regeneration. In addition, the stocking goal of 3000 tree saplings per hectare was fulfilled in all but two plots. Therefore, the natural potential to adapt to future conditions is present in these beech forests. However, browsing can jeopardize this adaptability to future climate conditions [52]. We will discuss some aspects based on our hypotheses.

1. Browsing is selective regarding preference for known palatable tree species and individual vigorously growing saplings. Species recommended for enhancing the adaptation of these beech forests to climate change are particularly selected by ungulates.

Browsing was indeed selective in terms of both species and individual trees. However, not only the species known to be palatable by wild ungulates were selected, and the differences were rather small. *Picea abies* saplings were hardly browsed at all, as expected [15]. However, the proportion of browsed area out of the total stocked area was not significantly different for *A. alba*, *F. excelsior*, *A. pseudoplatanus* and the generally much less palatable *F. sylvatica*. One possible reason for this is that these otherwise more palatable tree species were much more widespread than *F. sylvatica*. It is known that wild ungulates do not select species equally everywhere (e.g., [15,53]) and in any season [54] and often prefer rarer species [55,56], which makes these tree species even more rare [57]. For example, in the

Kirchberg forest district, the rarely admixed ‘unpalatable’ *Juglans regia* was also browsed frequently and heavily. This indicates that the animals in this region selected the common species (apart from *P. abies*) according to their frequency but also selectively browsed rare species. Rarer species currently include *Acer platanoides* and *A. campestre*, *Quercus* spp., *Sorbus aria*, *Tilia* spp., *T. baccata*, *Ulmus glabra*, *Betula pendula* and *J. regia*, which seem to be more suitable in terms of adaptation to future climates and are, therefore, recommended to foresters (TreeApp). Thus, ungulate browsing at least slows down the silvicultural potential concerning climate adaptation.

The most vigorously growing trees were browsed, so the length of the measured remnant after light browsing was equal to (*A. alba* and *F. excelsior*) or greater than the leader shoot length of the unbrowsed trees (all other species with browsing). This is in agreement with the plant vigor hypothesis [58] and other studies in beech forests (e.g., [40]).

2. The vigorous growth of saplings leads to light browsing and thus few impacts.

The tree saplings did not grow particularly well in these supposedly vigorous forests (cf. description of the forest communities [37]). Compared with other studies, RGR was rather low [25]. However, it has to be considered that, with a mean shading of $80.7 \pm 12.9\%$, the forests in the Kirchberg forest district were severely shaded. Even the shade-tolerant tree species *A. alba* [14] grows worse under >ca. 85–90% shade than under more open conditions [20,59]. In *A. alba* plantations in the Czech Republic, canopy openness of 30% was found to be optimal [60]. The best growth conditions for natural *A. alba* seedlings were found under the relatively light-permeable crowns of light-demanding tree species (*Larix decidua*, *Pinus sylvestris*), e.g., ca. 43–45% canopy openness in the Karkonosze Mountains [61]. In the case of *F. sylvatica*, increased growth with increased light (relative light intensity between 0% and 35%) has been reported [62]. The relatively shaded stands may also be one reason why *A. alba* grew as well as *F. sylvatica*, and *A. pseudoplatanus* grew as well as (2021) or less than (2022) *F. sylvatica*. *Quercus* spp. definitely need more light than these more shade-tolerant species, so low light availability, in addition to browsing, is probably one of the main reasons for the absence of larger oaks (but see the possible role of large grazing herbivores, e.g., [63]). The increment was smaller in 2022 than in 2021, probably due to the locally warm and dry summer of 2022. In addition to the shading, the warm and dry climate could be a reason why vegetation growth was completed early and practically no trees formed a second flush in 2022.

A hill slope of up to 30° was found to favor superior productivity classes for *A. alba* [64]. *Abies alba* saplings originating from steeper slopes had smaller height increments before and after browsing than those from flat areas [6]. In both studies, hill slope and elevation were positively correlated. The average slope of the forests in the Kirchberg forest district was $33 \pm 23\%$. Neither hill slope nor elevation had an influence on the height increment or damage frequency of any species. As hill slope, elevation and canopy shading were not correlated, we assume that canopy shading was indeed the main reason for the relatively poor growth.

When height increments are small, browsing is often heavier, as a single bite automatically removes a larger percentage of the terminal shoot. In fact, more heavy than light browsing was found for many species (Figure 3). Heavy browsing usually leads to greater damage to the individual tree as (i) tree height is reduced more, (ii) reserves and meristems are lost and (iii) the new terminal shoot is, therefore, often shorter and sometimes formed with a time delay (cf. review in [5]). For example, *F. sylvatica* saplings grew equally with or without light-simulated browsing (terminal bud removal) but were negatively affected by heavy clipping [7].

Despite the similar growth of *A. alba* and *F. sylvatica*, the time *A. alba* needed to grow out of the reach of roe deer was double that required by *F. sylvatica*. The same was true for *A. pseudoplatanus*. However, apart from *F. sylvatica*, there were rather few saplings in the larger height classes (Table 1), and many or all (e.g., *A. pseudoplatanus*) of them had been browsed several times on their main stem (Figure 6). Moreover, the linear mixed effects models revealed a negative relationship between damage frequency and height

increment (Table 2). The time needed to grow out of the reach of roe deer is, therefore, biased (prolonged) by ungulate browsing.

3. Coniferous tree species are mainly lightly browsed in winter and respond in the following vegetation period. Thus, there are no delays in the tree response after browsing, which can be neglected in further surveys.

Conifers, i.e., *A. alba*, were almost exclusively browsed in winter. However, browsing was more often heavy, and many *A. alba* saplings showed a delayed response even after light browsing. The increments of *A. alba* were rather small, and thus it can be assumed that practically no preformed buds remained on the remaining pieces from which the *A. alba* saplings could respond the following year. This is because trees that are taller prior to browsing have more buds remaining after browsing on the residual leader shoot sections [65], and a certain tree height has to be reached to have internodal buds out of which new leader shoots can grow [66]. In the Kirchberg forests, however, most *A. alba* saplings (still) belonged to HC1. The observed other damage in Figure 3 corresponds to *A. alba* trees without terminal shoots. If we look only at the proportion of browsed area out of the total stocked area (or percentage of browsed assessed saplings, cf. Figure 3), not many *A. alba* were affected by browsing (compared with a 15.4–19% threshold of tolerable browsing intensity in beech forests in Aargau [67] and Thurgau [68]). By summing the browsed saplings and the ones with no leader shoot after browsing, however, every fourth *A. alba* was affected. In addition, damage along the main stem axis reduced growth in the following years, i.e., the greater the damage frequency, the smaller the increment. This means that practically all *A. alba* had reduced growth as a result of current or former browsing. In an experiment with planted but naturally browsed *A. alba* saplings, the browsed saplings were not able to compensate partially. That is, even two years after browsing, they did not achieve the same height increment as unbrowsed saplings [65]. Thus, browsing-induced height differences increase over time. The stands in the cited experiment were also Milio-Fagetum stands, though at about 1000 m a.s.l. and with a northeastern aspect [65]. Therefore, it cannot simply be assumed that sites with a vigorous forest community have trees with a quick browsing response (no delay) and partial compensation.

Based on a clipping experiment in which *A. alba* originating from the Swiss Plateau (lowland provenances) responded with no time lag even when planted at 1090 m a.s.l. [6] and all *F. sylvatica* provenances fully compensated for light clipping [7], we had expected all tree species in the lowland Kirchberg forests to have a greater ability to recover from browsing. If only the browsing percentage had been measured, this lacking or at least delayed recovery would not have been detected. For this reason, it is important to carry out the browsing inventories in autumn so that the response to winter browsing can be considered in all forest stands, independent of vigor, tree species composition (coniferous and deciduous) and elevation.

4. Deciduous tree species are mainly lightly browsed in summer and can respond within the same vegetation period. Therefore, a survey in autumn is optimal for capturing the impact of browsing on these species.

In contrast to our expectations, many deciduous tree species were browsed more frequently in winter than in summer, and many saplings were unable to respond to browsing during the vegetation season. Both results are probably related to the low availability of light. Due to the darkness under the dense canopy of these beech forests, the shrub and herb layers are often only weakly developed [37]. This was also the case in the studied forests. This limits the food supply, especially in winter without herbs, and favors browsing in the dormant season [55].

More vigorously growing saplings have longer leader shoots, and more buds remain on the browsed remnant, meaning that resprouting is possible sooner. Nonetheless, growth in the Kirchberg forests was limited by the dark stand conditions (cf. section above). Second and further flushes, especially in beech, are clearly more frequent when more light is available [69] and are formed in fully open sites by all beech provenances [7]. In the

Kirchberg region, the stands were probably too dark for the formation of such further flushes. In addition, the growth of *F. sylvatica* was found to be inversely proportional to maximum summer temperatures [52], and 2022 was hotter than other years in the Kirchberg region. Therefore, it is not surprising that many trees were not able to form a second flush after browsing.

Moreover, of the frequent deciduous trees, some saplings also responded with a delay of at least one year to light and heavy winter browsing (Table 3). As expected, all *F. excelsior* and *P. avium* saplings with light winter browsing formed a new shoot in 2022. In contrast, more *F. sylvatica* and *A. pseudoplatanus* saplings did not respond after light than after heavy winter browsing. We can only speculate that this result has to do with shading. However, in a different study, the sister species *Acer saccharum* was not sufficiently stimulated to compensate for the loss of the old leader meristems caused by the removal of the uppermost buds [70]. It could thus be a question of apical dominance in *A. pseudoplatanus*. In *F. sylvatica*, with sympodial branching according to the Troll architectural model [71] and all buds being ‘the same’, this seems unlikely.

The larger the trees, the higher the damage frequency. No larger *A. pseudoplatanus* saplings were without damage along the stem axis. The more damage there is, the smaller the height increment in the following year (in our study but also elsewhere [72]). Thus, the poor responsiveness of *A. pseudoplatanus* could also be due to a too large loss of reserves caused by former damage under already limited conditions (i.e., nonstructural carbohydrates decrease in darkness [73]).

Twig browsing reduces the height growth of the leader shoots in *F. excelsior*. It is known that when many twigs are browsed, reserve material in the twigs is lost [74], which can reduce height growth in subsequent years [75,76]. Apparently, this was a sufficiently widespread phenomenon in Kirchberg for *F. excelsior* but not for the other species.

Despite the less frequent summer browsing, we recommend keeping the autumn inventory in the Kirchberg forest district and carrying out inventories in autumn at other locations as well. First, an inventory should not be changed, if possible, so that long-term comparisons remain possible. Second, it is important to have information on how vigorous the ‘whole’ growth is to judge other beech forests (e.g., up to five flushes of *F. sylvatica* in open sites of beech forests in Birmensdorf, Switzerland [7], which would be recorded as separate years in inventories conducted in spring (or performed by assessing only the previous year, cf. Swiss National Forest Inventory [39]). Third, it cannot be assumed that deciduous trees respond to browsing in the current year or in the following growing season. The response must, therefore, be checked explicitly.

5. Browsing in forest islands is more frequent than in larger forest complexes, and this difference should be considered when systematic grids are established.

Unexpectedly, browsing in small forests isolated within agricultural land (forest islands) was not more frequent than browsing in larger forest complexes. The proportion of browsed area out of the total stocked area was not different or even smaller, and the variable ‘forest island’ dropped out of the models for height increment and damage frequency. This means that densification of the systematic grid in such small forests could be avoided. However, it is important to note the plot placement in this study. First, the sample plots were moved 15 m into the forest away from the forest edge area since the forest edge area in the canton of St. Gallen is upgraded and maintained specifically for wildlife and biodiversity and thus does not primarily serve for silvicultural production. However, this led to the omission of the smallest ‘forests’, less than approx. 50 m in diameter. Thus, to test whether browsing is more frequent or more intense at forest edges or in the smallest forest islands, no shift into the forest should be implemented. Second, the stocked area of four tree species was smaller in forest islands than in the larger forest complexes. Therefore, the mortality due to browsing could be higher in forest islands. Third, the form of the larger forest complexes probably plays a role. Many of these forests are intermeshed with the agricultural landscape (Appendix A Figure A1). The distance to forest edges would,

therefore, have to be explicitly considered (see, e.g., [36]). In a very small-scale landscape, however, most plots have small distances to the forest edge.

5. Conclusions

Browsing by wild ungulates was a selective process in these beech forests, i.e., the most vigorously growing saplings were affected. This slowed down the entire tree regeneration process. Many saplings did not respond in the vegetation season following browsing, even after light browsing, retarding the vertical growth process further. The height increment was reduced by the former leader shoot damage. Thus, browsing reduced upgrowth not only in the year of the browsing event but over multiple years. In addition, browsing shifted the height increment ratio of frequent species in favor of *Fagus sylvatica*. Browsing was particularly frequent on tree species expected to cope better with the warmer and drier conditions caused by climate change, negatively affecting the growth of all these species. Browsing, therefore, has a significant impact on the development of these beech forests towards more mixed forests.

Browsing had a significantly greater effect than would have been estimated based on the proportion of browsed area out of the total stocked area. Delays in the response after browsing and the frequency of damage should, therefore, be considered more in studies of the influence of browsing. The easiest way to do this would be to conduct a k-tree inventory in autumn and thus record the response to winter browsing.

Additional studies are needed to determine how much light is needed in such vigorous beech forests so that (i) more light-demanding species can regenerate [77], (ii) the palatable and currently still rare but desirable species can quickly grow out of reach of ungulates and quickly form a new leader shoot in response to any browsing and (iii) the competing vegetation, especially blackberry, does not absorb this light penetrating through the canopy and thus re-establish dark conditions unfavorable for tree regeneration.

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Appendix A

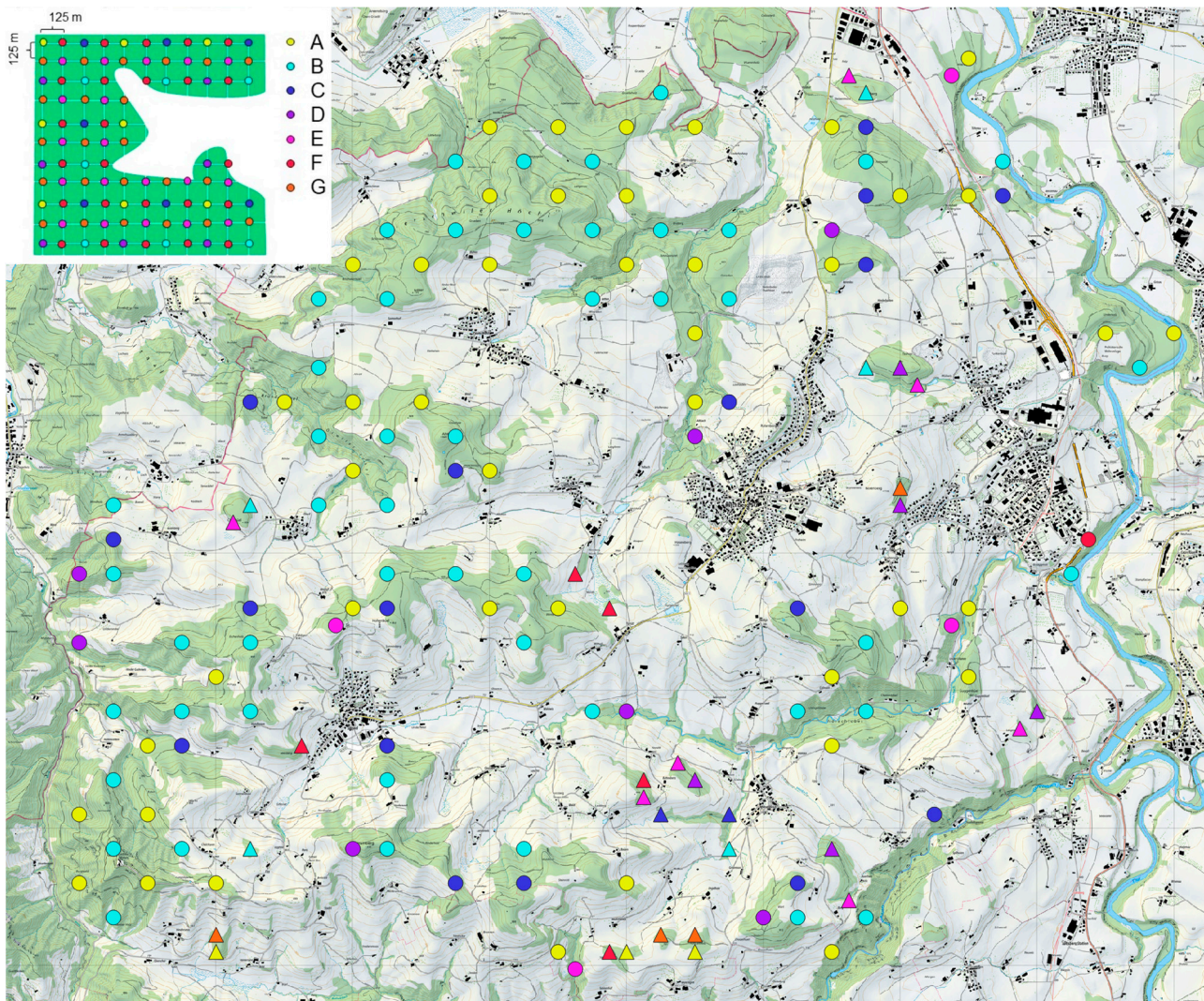


Figure A1. Seven systematic grids of sample plots were placed (A-grid to G-grid). A-grid: basic 500 m × 500 m; B-grid 500 m × 500 m but shifted diagonally from A-grid so that A and B together resulted in a 353 m × 353 m grid. C-grid and D-grid: 500 m × 500 m but shifted horizontally (C-grid) or vertically (D-grid) from A-grid, resulting in a 250 m × 250 m grid for A to D considered together. E-grid, F-grid and G-grid: 250 m × 250 m grid shifted diagonally (E-grid), horizontally (F-grid) or vertically (G-grid) from the combined A–D grid. Circles represent “larger” forest complexes, i.e., >10 ha cohesive forest, while triangles represent forest islands. Small forest areas that were attached to a larger forest complex via a narrow corridor were considered part of the forest complex. Large forest complexes (>20 ha) were represented by at least five plots and at least one in each connected part. In smaller forests (10 ha > x < 20 ha), a minimum of three plots were sampled, while in island forests a maximum of three plots were sampled.

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