

Rozprawa doktorska



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The influence of browsing pressure on natural regeneration of disturbed forest communities; comparison between different forest ecosystems and various guilds of ungulate herbivores

Wpływ presji zgryzania na naturalne odnowienia w zaburzonych zbiorowiskach leśnych; porównanie różnych ekosystemów leśnych i różnych zespołów kopytnych roślinożerców

> Promotor rozprawy doktorskiej Prof. dr hab. Inż. Jerzy Szwagrzyk Uniwersytet Rolniczy im. Hugona Kołłątaja w Krakowie Wydział Leśny, Katedra Różnorodności Biologicznej Leśnej Kraków, Luty 2025



Acknowledgements

I would like to express my deepest gratitude to Prof. Jerzy Szwagrzyk, my esteemed academic advisor, whose invaluable guidance, insightful expertise, and unwavering support have been instrumental in shaping my research and scientific direction. His mentorship has been critical to my success.

I would also like to express my sincere appreciation to Mr. Bartłomiej Surmacz, Kacper Foremnik, and Amisalu Milkias Misebo for their exceptional support in the statistical analyses of my research. Their dedication, expertise, and meticulous contributions have played a significant role in my publications.

My sincere thanks go to the staff of the Faculty of Forestry, the Department of Forest Biodiversity, and the Doctoral School for their continuous support throughout my academic journey. Their assistance has been invaluable in fostering an environment conducive to research and personal growth.

Finally, I am deeply grateful to my family and friends, whose unwavering encouragement, patience, and belief in me have been a constant source of strength and motivation throughout this journey. Their support has been truly indispensable.

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Summary

In this research, we estimated the amount of forage available to ungulate herbivores in two research areas. We determined the role of environmental factors, like soil quality and light intensity upon the intensity of browsing on saplings of various species. First, we conducted the laboratory measurements of saplings collected in the study areas to develop allometric equations relating tree height, stem thickness, and other traits to twig dry mass available for ungulate browsing. These equations and data from field measurements in 44 sample plots were then used to calculate the amount of forage available for ungulates in the study areas.

Research plots were established in two national parks: the Tatra N. P. and the Roztoczański N. P. There were 22 research plots in each study area. Each plot was a belt transect 30 m long and 5 m wide. Within transects, we measured morphological parameters of tree saplings and diameters of browsed twigs; based on these measurements, we calculated the index of browsing intensity BI. In the Roztoczański N. P., we collected soil samples from each transect; in the lab, we measured soil parameters and calculated the soil quality index. The browsing intensity of various tree species was then related to the soil quality index and the amount of forage available for ungulate herbivores within each sample plot.

The results show that soil quality significantly influences browsing pressure and varies by species. Higher soil quality generally increases browse abundance and shifts browsing pressure from more palatable species such as *Acer pseudoplatanus* to less palatable species such as *Fagus sylvatica*. Increasing browse abundance effectively reduces browsing pressure on palatable species, facilitating a more balanced composition of regeneration and maintaining higher biodiversity in the natural forest ecosystems. This suggests that canopy disturbance by increasing browse availability may be critical for supporting the regeneration of ungulate browsing-vulnerable tree species.

Streszczenie

W toku naszych badań oszacowaliśmy ilość żeru pędowego dostępnego dla kopytnych roślinożerców w dwóch terenach badań i określiliśmy role czynników środowiskowych, takich jak cechy gleby i dostępność promieniowania słonecznego na intensywność zgryzania podrostów różnych gatunków drzew. Na początku przeprowadziliśmy w laboratorium pomiary podrostów zebranych w obu obszarach badawczych w celu stworzenia równań allometrycznych pozwalających oszacować suchą masę pędów dostępnych dla kopytnych roślinożerców na podstawie wysokości i grubości młodych drzewek oraz innych parametrów morfologicznych. Te równania zostały następnie wykorzystane wraz z danymi pochodzącymi z pomiarów terenowych na 44 powierzchniach badawczych do obliczenia ilości żeru pędowego dostępnego dla kopytnych roślinożerców w terenach naszych badan. Powierzchnie badawcze zostały założone w dwóch parkach narodowych: w Tatrzańskim P. N. i w Roztoczańskim P. N. W każdym z parków założono po 22 powierzchnie badawcze. Miały one formę transektów pasowych o długości 30 m i szerokości 5 m. W granicach transektów pomierzyliśmy parametry morfologiczne podrostów drzew oraz średnice zgryzionych pędów; na podstawie tych pomiarów dla każdego podrostu wyliczyliśmy wskaźnik intensywności zgryzania BI. W Roztoczańskim P. N. pobraliśmy próbki glebowe z każdego transektu; zostały one poddane analizom laboratoryjnym, a w oparciu o wyniki analiz laboratoryjnych został wyliczony wskaźnik jakości gleby. Intensywność zgryzania podrostów różnych gatunków drzew została następnie odniesiona do wskaźnika żyzności gleby oraz do ilości żeru pędowego dostępnego dla roślinożerców na każdej z powierzchni badawczych.

Wyniki wskazują na istotny wpływ jakości gleby na presję roślinożerców; związek ten jest zróżnicowany i zależy od gatunku drzewa. Wyższa żyzność gleby jest powiązana z większą dostępnością żeru pędowego i skutkuje przesunięciem presji zgryzania z gatunków bardziej podatnych na zgryzanie, takich jak *Acer pseudoplatanus* na gatunki mniej podatne, takie jak *Fagus sylvatica*. Większa dostępność żeru pędowego efektywnie redukuje presję roślinożerców na gatunki bardziej podatne na zgryzanie, co może sprzyjać bardziej zróżnicowanemu składowi gatunkowemu odnowień i utrzymaniem wyższej bioróżnorodności w naturalnych zbiorowiskach leśnych. To wskazuje, że naturalne zaburzenia w drzewostanie poprzez zwiększanie dostępności żeru pędowego mogą mieć krytyczne znaczenie dla podtrzymania odnowienia gatunków drzew wrażliwych na presję roślinożerców.

List of publications included in the thesis

The thesis is prepared based on three research articles published in peer-reviewed scientific journals under the following topics:

Publication 1:

Madalcho, A. B., Szwagrzyk, J., Maciejewski, Z., Gazda, A., & Bodziarczyk, J. (2023). Allometric scaling models for tree saplings: Assessing potential fodder for ungulate herbivores. *Trees, Forests and People, 13*. <u>https://doi.org/10.1016/j.tfp.2023.100424</u>

(MEiN list 20 points, IF 2.7); Authors' contributions (ABM - 70%, JS - 10%, ZM - 5%, AG-10%, JB-5%).

Publication 2:

Madalcho, A. B., Gazda, A., Wanic, T., & Szwagrzyk, J. (2024). Influence of Soil Quality on the Browsing Intensity of Ungulate Herbivores on Tree Species in European Forests. *Forests*, *15*(4). <u>https://doi.org/10.3390/f15040708</u>

(MEiN list 100 points, IF 2.4); Authors' contributions (MAB - 80%, GA-5%, WT-5%, SJ - 10%).

Publication 3:

Madalcho, A. B., Gazda, A., & Szwagrzyk, J. (2025). Ungulate browsing patterns and forage abundance determine the regeneration of palatable tree species: Using new perspectives in assessing ungulate browsing pressure in temperate forests. *Forest Ecosystems*, *12*(November 2024), 100288. <u>https://doi.org/10.1016/j.fecs.2024.100288</u>

(MEiN list 140 points, IF 3.8); Authors' contributions (MAB - 80%, GA-10%, SJ - 10%).

*corresponding author

Total MEiN score (according to year of publication): 260 Total IF (according to year of publication): 8.9

1. Introduction

1.1. Background

Wild ungulate browsing is one of the most important ecological factors impeding the survival and recruitment of young trees (Churski et al., 2017; Didion et al., 2009; Faison, 2015), and results in a considerable change in the forest ecosystem functioning (Heuze et al., 2005; Konôpka et al., 2020). Selectively browsing on some tree species, ungulate herbivory causes unpalatable, chemically defended plants to dominate the ecosystem (Augustine & McNaughton, 1998). However, several factors, including forest gaps, tree composition, elevation, former management, and soil properties, affect the ungulate browsing intensity of tree saplings (Bodziarczyk et al., 2017; Kuijper, 2011; Kuijper et al., 2009).

Soil factors are essential for tree growth and tree regeneration. (Augusto & Boča, 2022; Jiang et al., 2022), and may also lead to shifts in community composition (Kardol et al., 2014). Thus, soil quality operates as a filter for the pool of species that can flourish in a specific location. For instance, poor soils may lead to lower quality and quantities of browse, which can, in turn, increase browsing intensity on individual plants (Angst & Kupferschmid, 2023; Sardar et al., 2023). Indirectly, soil conditions influence the share of various tree species in the forest canopy, thus altering light availability on the forest floor. Shade-tolerant tree species dominate the forest canopy in nutrient-rich ecosystems, allowing less light to reach the forest floor (Canham et al., 1994). In contrast, shade-intolerant tree species usually form the canopy layer in poorer habitats, and the amount of light beneath their canopies is greater.

The ungulate browsing is influenced by forage resources, especially in spatial variations in biomass, structure/height, phenology, and species composition (Fynn et al., 2019). The susceptibility of tree saplings to ungulate browsing can be influenced by the co-existing vegetation, growth rates, and variations in their palatability (Boulanger et al., 2009; Heuze et al., 2005). The composition of young-generation trees with palatable species is more likely to be heavily browsed than less palatable species in the forest ecosystem (Borowski et al., 2021; D'Aprile et al., 2020). While some species are actively avoided by browsing animals, others are selectively targeted (Bodziarczyk et al., 2017).

Due to high spatial variability and fast changes over time in browse availability, (Barbosa et al., 2014; Szwagrzyk et al., 2020), there are different arguments regarding the relationship between browsing intensity and browse availability. According to Sample et al. (2023), browsing intensity is reduced by increased browse availability from a higher density of patches. In contrast, Borowski et al., (2021) hypothesized that patches with abundant forage and species diversity attract ungulates and increase the likelihood of browsing on saplings. Hence, it is challenging to draw general conclusions as the findings are also limited by the methodological approaches applied.

In addition, according to the results of earlier studies, there are huge differences in the intensity of browsing among tree species (Boulanger et al. 2009, Szwagrzyk et al. 2020), and winter browsing is a continuous process rather than a single event for each sapling (Kupferschmid et al., 2015). Consequently, a customized method is required to narrow the knowledge gap in determining the browsing pressure that ungulate herbivores exert on tree regeneration regardless of the unknown number of ungulates visiting the saplings in natural forest ecosystems.

1.2. Objectives of the thesis

This study aimed to:

- Develop allometric equations for estimating browse abundance, and browsing loss on tree species in different forest ecosystems.
- 2) Answer the question: does soil quality and the tree species identity affect the browsing intensity and reduce the risk of eliminating palatable species due to ungulate browsing?
- 3) Analyzing the relationship between forage abundance and the browsing pressure exerted by ungulates.

2. Methods and materials

2.1. Site Description

Tatra National Park (TNP) and Roztoczański National Park (RNP) are characterized by a high density of ungulates. The forests of the TNP are dominated by Norway spruce (*Picea abies* (L.) H. Karst.), European beech (*Fagus sylvatica* L.) and Silver fir (*Abies alba* Mill.). Among the other species, Sycamore maple (*Acer pseudoplatanus* L.) and Rowan (*Sorbus aucuparia* L.) have been increasing in numbers, especially among the youngest trees

(Bodziarczyk et al., 2019; Pielech et al., 2021). The guild of ungulate herbivores in the TNP consists of chamois (2 ind./km²), red deer (1 ind./km²), and roe deer (0.5 ind./km²) (Source: Tatra National Park archives). However, in the RNP forest stands mainly consist of Scots pine, Silver fir, and European beech, and the most common herbivores are red deer (5.6 ind./km²) and roe deer (4.8 ind./km²) (Borowski et al., 2021).

In this work, a "twig dry mass (g)" represents a browse abundance. We classified our focal tree species into three functional groups based on palatability (Angst & Kupferschmid, 2023) to examine the relationship between browse abundance and ungulate browsing pressure. Accordingly, *Sorbus aucuparia, Acer pseudoplatanus, Carpinus betulus, and Abies alba* were classified as highly palatable, *Fagus sylvatica* as moderately palatable, and *Picea abies* as less palatable tree species.

2.2. Research design and field data collection

We analyzed the twig dry mass of 16 saplings from each species, collected in two study areas by selecting unbrowsed saplings in the following height ranges: 0.5–1.0, 1.0–1.5, 1.5–2.0, and 2.0–3.0 m. In the laboratory, we measured architectural parameters such as tree sapling height, basal diameter, shoot diameter, shoot length, crown width, and crown length. We cut off the twigs from the stem and grouped the twigs into five diameter classes (2–3, 3–4, 4–5, 5–6, and 6–7 mm), and oven-dried at 65 °C for 72 hours to develop allometric equations (Publication 1).

We recorded 15 tree species, with six—*Picea abies, Fagus sylvatica, Abies alba, Acer pseudoplatanus, Sorbus aucuparia, and Carpinus betulus*—present in sufficient numbers to allow for meaningful statistical analysis. In our sample plots, we recorded 2838 tree saplings and measured the height and diameter at the stem base, crown length, and maximum crown width, and the diameter, and height of shoots at the point where they were browsed considering a maximum of 50 browsed shoots per one sapling.

In Roztoczański N. P. we collected soil samples from the transects to investigate the relationship between the soil quality index and the ungulate browsing intensity on tree saplings from different species. We generated data based on the field measurements and the soil lab results for this relationship. Thus, we calculated the tree species density, relative

density, twig dry mass of the tree saplings, soil bulk density, and soil quality index (SQI) (Publication 2, Equations 1-4).

We estimated the twig dry mass removal due to ungulate browsing using allometric equations based on twig diameter classes. The browsed shoots of tree saplings with thicknesses between 2 and 7 mm were classified into five diameter classes: 2 mm, 3 mm, 4 mm, 5 mm, and 6 mm. The vertical distribution of twig dry mass consumed by ungulates was analyzed by grouping measurements into three height classes: ≤ 1 m, 1-2 m, and 2-3 m. These height classes corresponded to the positions where the browsed shoot diameters were measured.

We calculated the percent loss of twig dry mass for each species by dividing the actual twig dry mass loss (g) by the total twig dry mass (g) per transect, then multiplying the result by 100. This metric, which we call the index of browsing pressure, reflects the actual browsing pressure, whereas the BI measures theoretical browsing pressure on each tree species.

2.3. Statistical analysis

We applied the ordinary least squares method to develop the allometric equation of the twig dry mass of all tree species. Of the multiple explanatory variables included in the model, the best-fitted estimator combination was selected based on the Akaike information criterion (AIC) and used to develop the final model for each species. Whereas, the generalized additive model (GAM) was used to develop the equations for the twig dry mass distribution of saplings at different diameter classes of shoots (Publication 1).

We evaluated the indirect relationship between ungulate browsing intensity and soil quality index, by analyzing the relationship between soil quality index and relative density of tree species as well as the twig dry mass (g) as important indicators. We applied the linear model with the Ordinary Least Squares method based on the assumptions of a normal distribution, and Bonferroni correction to adjust the significance level (α) to control the family-wise error rate (FWER) when performing multiple comparisons (Publication 2).

We applied various methods, including a zero-intercept linear regression model, multiple linear regression, ANOVA, and Mann-Whitney tests, to analyze the relationship between browse abundance and ungulate browsing (Publication 3).

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3. Main findings

3.1. Allometric scaling models for tree saplings: Assessing potential fodder for ungulate herbivores.

3.1.1. Modeling twig dry mass distribution along twig diameter classes

The twig dry mass of the saplings showed a significant positive relationship with the shoot diameter classes (SDCs) for all tree species (Publication 1, Table 1). However, the twig dry mass amount and the increase rate across shoot diameter classes differed among tree species. As a result, *Picea abies, Abies alba, Carpinus betulus, Fagus sylvatica, Sorbus aucuparia,* and *Acer pseudoplatanus* were in order of higher to lower twig dry mass distribution rate along the shoot diameter classes (Publication 1, Fig. 1). And, the formulas developed to calculate the twig dry mass along the twig diameter class was a crucial step to estimate the amount of twig dry mass lost to ungulate browsing as an alternative metrics of browsing pressure on tree saplings.

3.1.2. Modeling twig dry mass distribution along sapling height classes

The twig dry mass of *Picea abies* and *Abies alba* was significantly related to the sapling height class, and a rapid increase was observed for *Picea abies*. Across all height classes, the twig dry mass of these species was much higher than that of the other species (Publication 1, Fig. 2). The twig dry mass of *Picea abies* saplings increased at 99.9% confidence level and, that of *Abies alba* at 95% confidence level across all tree height classes while, it was not significant for the rest of tree species (Publication 1, Table 2).

3.1.3. Modeling twig dry mass with multiple variables

As the basal diameter of a tree increases, so does the twig dry mass (Publication 1, Fig. 3). This is because the basal diameter is often correlated with the overall size and biomass of the tree, including the number and size of branches and twigs. As the tree grows, it typically produces more and larger branches and twigs, contributing to the overall twig dry mass. However, the relationship between twig dry mass and basal diameter was different across tree species. For instance, the twig dry mass model of *Acer pseudoplatanus* (Adj R²=56.7%), *Carpinus betulus* (Adj R²=51.8%), and *Picea abies* (Adj R²=60.4%) saplings is well

explained by basal diameter. However, the utilization of combined explanatory variables such as mean largest crown length (MLCL) and mean basal diameters improved the model quality of the twig dry mass for *Picea abies* (Publication 1, Table 3).

Similarly, the allometric relationship between twig dry mass and sapling height was positive (Publication 1, Fig. 4), but varies among tree species. Fagus sylvatica (Adj R²=56.9%), Abies alba (Adj R²=62.6%), and Picea abies (Adj R²=65.0%) displayed a strong correlation (Publication 1, Table 4). In our finding, the sapling height-twig dry mass relationship was not strong for Carpinus betulus, Sorbus aucuparia, and Acer pseudoplatanus. However, the best twig dry mass allometric models were developed for species such as Fagus sylvatica and Sorbus aucuparia by using log(H) and log(MLCW), which were selected as the best-fit explanatory variables according to the AIC. Log(H) is also a strong estimator of the twig dry mass of Abies alba saplings. This finding is supported by Miyata et al. (2011), who found that the allometry of leader shoots was convergent, and the changes were also heightdependent. Similarly, height-dependent changes in the total biomass of current-year shoots varied across species (Osada, 2011). In general, depending on the tree species, the basal diameter and height of the tree saplings are the key variables in estimating the twig dry mass while, the MLCW and CL in certain species were utilized to enhance the overall quality of the models. The best twig dry mass allometric models developed to estimate the browse abundance of the tree saplings in natural forest ecosystems were presented in publication 1.

3.2. Influence of Soil Quality on the Browsing Intensity of Ungulate Herbivores on Tree Species.

The range of adaptation to different soil quality levels varies among tree species. The variation among the tree species regarding the relationship between the soil quality index and browsing intensity on the tree species (Publication 2, Fig. 6) shows that, out of the five tree species analyzed in our study, three (*Fagus sylvatica*, *Carpinus betulus*, and *Acer pseudoplatanus*) cover a broad range of soil quality levels. However, *Acer pseudoplatanus* does not occur in the poorest-quality soils. The other species (*Abies alba* and *Sorbus aucuparia*) are confined to poorer- to medium-quality soils, corresponding to these species' ecological characteristics (Hawkes et al., 1997).

The browsing intensity in *Acer pseudoplatanus* significantly decreased along the gradient from moderate to richer soil quality, whereas it increased significantly in the case of *Fagus sylvatica*. As rapid canopy cover is partly explained by soil quality status, browsing intensity was higher under the more open canopies for *Acer pseudoplatanus* (Ohse et al., 2017). The lower density of *Acer pseudoplatanus* in transects with high soil quality is probably due to reduced light availability on the forest floor. In rich habitats, the canopy is often very dense and dominated by shade-tolerant species such as *Fagus sylvatica* and *Carpinus betulus*, potentially leading to a lower density of *Acer pseudoplatanus* in such areas. As a result, following changes in browse availability and species composition mediated by soil quality, browsing intensity on tree species gradually shifts from palatable species such as *Acer pseudoplatanus* to less palatable species such as *Fagus sylvatica*. *Fagus sylvatica* and *Carpinus betulus* saplings, two shade-tolerant broadleaved species, are abundant in all transects and increase in number with increasing soil quality. They are therefore at the forefront of high intensity of browsing, as their dominance in richer soils makes them the primary food source for ungulates.

Soil quality is a crucial environmental factor influencing the adaptation of *Abies alba* in forest ecosystems and its vulnerability to browsing pressure by ungulates (Kobal et al., 2015). In our case, the reduction in browsing intensity for this species in the richer soils is justified by the declining tendency of browse availability from this species. Most *Abies alba* saplings are found in poor habitats, although mature trees of the same species are also observed as a small admixture in rich habitats. In the case of *Abies alba*, a very shade-tolerant species, the lack of saplings in the richer habitats is probably unrelated to lower light intensities. Instead, it may be related to soil factors, possibly indirectly through interactions with fungi (Baranowska et al., 2023; Kowalski, 1982).

3.3. The effect of ungulate browsing patterns and forage abundance on the regeneration of palatable tree species

3.3.1. The relationship between the browsing intensity index (BI) and the index of browsing pressure (% loss of twig dry mass)

The browsing intensity index (BI) is a theoretical measure of ungulate browsing pressure on tree saplings. However, the index of browsing pressure directly quantifies the actual loss in twig dry mass from what is available for browsing. In terms of practical application, BI is

easier to measure in the field, whereas calculating the index of browsing pressure involves much more work (Publication 3). Therefore, we found that the model relationship between these variables is also relevant for large-scale studies of browsing pressure on the tree species in an easier way.

3.3.2. Patterns of vertical distribution of ungulate browsing damage

Similarly, the vertical distribution of twig dry mass loss due to ungulate browsing (g) is high on the saplings of all species at shorter heights. However, there is variation in the vertical distribution of browsing loss of twig dry mass among the tree species and between the study sites. As a result, Acer pseudoplatanus, Sorbus aucuparia, and Abies alba showed significantly higher twig dry mass loss (g) at heights ≤ 1 m in the Tatra N. P. In addition, Acer pseudoplatanus and Sorbus aucuparia experienced browsing damage at taller heights of up to 3 m at this site, suggesting that, the species' palatability exacerbated the browsing impact. On the other hand, for Fagus sylvatica and Picea abies, there was no significant difference in browsing loss between the shorter height classes, and twig dry mass loss did not extend to 3 m sapling height (Publication 3, Fig. 3c). In the RNP, Acer pseudoplatanus, Sorbus *aucuparia*, and *Abies alba* showed browsing loss up to heights of ≤ 2 m with no significant difference between these shorter height classes. In contrast, Fagus sylvatica and Carpinus *betulus* had significantly higher browsing loss to twig dry mass at ≤ 1 m sapling browsing height. The results indicate that the differences in browsing patterns across forest communities for each species may be due to variations in natural disturbances (Publication 3).

3.3.3. The relationship between browse abundance and ungulate browsing pressure

i. The effect of browse abundance on the ungulate browsing pressure on palatable species

The availability of browse resources influences the browsing behavior of ungulates on each tree species. Consequently, as browse abundance for a particular species increases, ungulates tend to exert greater browsing pressure on that species, consistent with the findings of Gaudry et al., (2022).

However, an increase in browse abundance at the community level leads to a decrease in browsing pressure on more palatable species. Highly palatable species experience the greatest baseline browsing loss, but as browse abundance increases, their browsing pressure decreases more rapidly than less palatable species, showing a strong negative relationship between browse abundance and browsing pressure; and it confirms our third hypothesis (Publication 3). This observation supports the argument that browsing pressure decreases as the overall abundance of browse resources increases (Sample et al., 2023).

ii. Comparison of browse abundance across study sites and among tree species

The browse abundance showed differences between the two national parks for each tree species. In particular, the higher browse abundance of *Picea abies, Sorbus aucuparia, Abies alba*, and *Acer pseudoplatanus* in the Tatra N. P. compared to the Roztoczański N. P. can be attributed to differences in canopy closure. In Tatra N.P. there are many large and medium-sized gaps, resulting from natural disturbances, especially winds and bark beetle outbreaks. On the other hand, the saplings of *Fagus sylvatica* are distributed in all transects in the Roztoczański N. P., where canopy gaps are small (Publication 3, Fig. 1). When comparing tree species in the Tatra N. P., *Picea abies*, followed by *Sorbus aucuparia* and Abies alba, provides a substantial amount of browse, while *Acer pseudoplatanus* contributes the least.

iii. Comparison of the index of ungulate browsing pressure across study sites and between tree species

The ungulate browsing pressure significantly varies across the study sites in the case of *Fagus sylvatica* and *Sorbus aucuparia*. The increased browsing pressure on *Fagus sylvatica* in the RNP could be attributed to differences in browse availability and species composition between the study sites, influenced by differences in canopy gaps. The shade-tolerant *Fagus sylvatica* saplings dominate most of the transects in the study area in the Roztoczański N. P. and remain the main browse source for ungulate herbivores. On the other hand, the highly palatable *Sorbus aucuparia* experienced more browsing pressure in the Tatra N. P. than in the Roztoczański N. P. This is due to the fact, that saplings of *Sorbus aucuparia* are very abundant in Tatra N. P., while in Roztoczański N. P. there are few and scattered.

When the ungulate browsing pressure index was compared between the tree species, the higher impact was observed on *Acer pseudoplatanus* and *Sorbus aucuparia* in the Tatra N. P. and *Carpinus betulus* in the Roztoczański N. P. This intense browsing pressure is, related to

the palatability of the saplings and the total browse contribution of each species. Palatable broadleaf species were selectively targeted by ungulates while contributing relatively less twig dry mas than coniferous species.

3.3.4. Post-browsing remnants: Consequences for the regeneration of palatable tree species

Despite the substantial browsing pressure on the tree saplings, the results indicate that some twig dry mass remains even in places that are heavily browsed by ungulates. Among tree species, *Picea abies* retains the greatest amount of twig dry mass after ungulate browsing in the Tatra N. P. Similarly, *Fagus sylvatica* retains the greatest twig dry mass in the Roztoczański N. P. On the other hand, *Carpinus betulus* and *Acer pseudoplatanus* were the less abundant, resulting in the smallest residual browse among the species. This is likely due to the overall abundance of these species in their respective habitats (Publication 3, Fig. 5). The higher abundance of potential fodder provided by less palatable focal tree species mitigates the impact of browsing pressure on palatable trees. Furthermore, the ungulate browsing pressure may affect the species composition of the regeneration following natural disturbance and slow the transition from a historically conifer-dominated forest to one with diverse stands with deciduous species dominance.

4. Conclusion

This study examines the relationships between soil quality, ungulate browsing patterns, browse abundance, and species identity, providing insights into how palatable species regenerate in temperate forests under browsing pressure. Twig dry mass increases linearly with sapling height, with conifer species exhibiting higher dry mass and stronger allometric relationships than deciduous species. Soil quality significantly influences browsing intensity and varies by species, as higher soil quality generally increases browse abundance and shifts browsing pressure from more palatable species such as *Acer pseudoplatanus* to less palatable species such as *Fagus sylvatica*. The browse abundance and twig dry mass loss due to ungulate browsing are most pronounced in the saplings of shorter heights, with palatable species in the young generation of trees is aided by the presence of palatable species. Increasing browse abundance in the forest ecosystem effectively reduces browsing pressure on palatable species, facilitating balanced regeneration and biodiversity. Furthermore, our results are

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essential for informing conservation strategies to protect vulnerable tree species from ungulate browsing. We recommend further research on the combined influence of canopy gaps and species susceptibility over time to improve our understanding of forest dynamics and the role of browsing pressure in shaping ecosystem composition.

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6. List of achievements in scientific research work

6.1. List of other published papers (not being the subject of the doctoral dissertation) and *indicators of scientific achievement*

- I. Cacciatori, C., Gazda, A., Bodziarczyk, J., Foremnik, K., Madalcho, A. B., Maciejewski, Z., Pielech, R., Tomski, A., Zięba, A., Zwijacz-Kozica, T., & Szwagrzyk, J. (2025). Deer Browsing Increases Stem Slenderness and Crown Irregularity and Modifies the Effects of Light Gradients on Architecture of Forest Tree Saplings. *Ecology and Evolution*, 15(1), 1–13. https://doi.org/10.1002/ece3.70837
- II. Gota, H. G., Madalcho, A. B., Kerse, B. L., Szwagrzyk, J., & Solomon, T. (2024). The impact of native trees, Cordia africana, and Ficus sur, and the economically valuable Manihot esculenta on soil chemical properties in an agroforestry system. *Trees, Forests and People*, 15(November 2023), 100471. https://doi.org/10.1016/j.tfp.2023.100471
- III. Madalcho, A. B., Szwagrzyk, J., & Solomon, T. (2022). Woody species diversity and regeneration challenges in Ethiopia: Review article to identify research gaps. *Trees, Forests* and People, 8. https://doi.org/10.1016/j.tfp.2022.100224

6.2. List of ongoing unpublished papers (not being the subject of the doctoral dissertation) and

indicators of scientific achievement

- ✓ Jerzy Szwagrzyk; Anna Gazda; Cecilia Caciatori; Andrzej Tomski; Zbigniew Maciejewski; Tomasz Zwijacz-Kozica; Antoni Zięba; Kacper Foremnik; Aklilu Bajigo Madalcho; Jan Bodziarczyk. "Differences in vertical patterns of ungulate browsing among functional groups of trees". *Forestry* (under review).
- Canopy disturbance offsets the effect of deer browsing on tree regeneration across the forest communities Ongoing preparation.

6.3. List of international and national scientific conferences and seminars attended

Aklilu Bajigo Madalcho, Jerzy Szwagrzyk, Zbigniew Maciejewski, Anna Gazda, Jan Bodziarczyk, 2023. How much of potential fodder is available for ungulate herbivores in tree saplings of various sizes and species identity? Oral presentation in the 3rd International Multidisciplinary Doctoral conference at the University of Szczecin, 21-23.06.2023.

- Aklilu Bajigo Madalcho, Jerzy Szwagrzyk, Zbigniew Maciejewski, Anna Gazda, Jan Bodziarczyk, 2023. *How much potential fodder is available for ungulate herbivores in tree saplings of various sizes and species identities? Oral presentation in the* International Conference on Sustainable Development, Information Technology Systems, Engineering, Forestry & Applied Science (ICSDITSEFAS-23), 14th September 2023, Bahir Dar, Ethiopia.
- Aklilu Bajigo Madalcho, Anna Gazda, Tomasz Wanic, & Jerzy Szwagrzyk (2024). Influence of Soil Quality on the Browsing Intensity of Ungulate Herbivores on Tree Species in European Forests. *Forests*, 15(4). Oral presentation on a 10th International Conference for young researchers-ICYR at the University of Agriculture in Krakow organized on 13-14/05/2024 Krakow, Poland.
- Joint and individual effects of climate change and natural disturbances on forest vegetation in temperate mountain forests: a century-long perspective", held at: 01.12.2022, Department of Forest Biodiversity, Krakow, Poland.
- ✤ Leaf functional traits of *Rhododendron ponticum* invasive populations along an environmental gradient", 08.12.2022, Department of Forest Biodiversity, Krakow, Poland.
- ✤ WEBINARS Rising From The Ashes: Post-Fire Regeneration Management Strategies From Recent Front Range Fires. Zoom webinars on December 7, 2022, 1:00 – 2:30 PM MST.
- Earth and Environmental Science international webinar conference 2021 (EESIWC-2021) on the Zoom platform jointly hosted by the University of Zululand and Chang'an University. Organized on 1 & 2 February 2021.
- Virtual conference on Heir's property sustainable forest management. February 08, 2021. Organized by Warnell School of Forestry and Natural Resources, University of Georgia.

6.4. Internship experience

I completed a two-month internship at the Department of Natural Resources Management at Wachemo University, Ethiopia, from September to November 20, 2023. During this time, I contributed to the project "Implementation of Agroforestry Practices for Restoration of Nutrient-Depleted Ecosystems in Hadiya Zone, Central Ethiopia". My role included participating in soil sampling in the field, preparing soil samples in the laboratory, and collaborating with post-graduate students to share knowledge and insights.

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Allometric scaling models for tree saplings: Assessing potential fodder for ungulate herbivores

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ARTICLE INFO

Keywords: Broad leaved species Browse resources Coniferous species Tree sapling allometry Twig dry mass

ABSTRACT

Knowledge of the quantity of twig dry mass (available fodder) of saplings is crucial for understanding tree recruitment under wild ungulate browsing pressure in forest ecosystems. Therefore, this study aimed to develop allometric equations for estimating twig dry mass using sapling structural data and to model the twig dry mass of saplings of various species in various size classes while quantitatively describing the variations among tree species. Sapling biomass samples were taken for six widely spread tree species in two national parks in Poland. After drying the biomass samples in the oven for 72 h at 65 °C, the data were analyzed, and models were generated using the ordinary least squares and generalized additive methods. The results confirmed our hypothesis that different tree species differ in their allometric properties. The twig dry masses of Acer pseudoplatanus and Carpinus betulus were best estimated by basal diameter, whereas those of Picea abies, Abies alba, and Fagus sylvatica were best estimated by sapling height. In contrast, the model quality for Fagus sylvatica and Sorbus aucuparia was enhanced by combining the sapling height with the mean largest crown length (MLCL). For all species, the twig dry mass distribution was linear along sapling height classes and exponentially increased with shoot diameter classes, with coniferous species exhibiting the highest correlation. On the other hand, the proportion of twig dry mass to total sapling dry mass followed the order S. aucuparia > A. alba > P. abies > F. sylvatica > C. betulus > A. pseudoplatanus. The developed allometric equations contribute significantly to the already available collection of published biomass equations. Moreover, they extremely useful in estimating the browsing potential of tree saplings falling within size ranges conducive to herbivore browsing.

1. Introduction

The effect of browsing by wild ungulate "ruminating" herbivores is one of the most important ecological factors impeding the survival and recruitment of young trees (Bodziarczyk et al., 2017). Browsing impacts can cause considerable changes in the forest regeneration process and forest ecosystem functioning (Churski et al., 2017; Didion et al., 2009; Faison, 2015; Heuze et al., 2005; Konôpka et al., 2020). Walters et al. (2020) showed that 54% of saplings were killed by deer browsing, and when deer browsing interacted with shrub competition, the mortality increased to 64%. Under a closed canopy, where there is insufficient light to compensate for browsing losses, and herbivores eliminate seedlings (Mårell et al., 2018). However, the browsing impact level is highly dependent on factors such as ungulate density (Brandner et al., 2011; Hidding et al., 2012), selective browsing pressure (Kupferschmid, 2018), and availability of fodder edible by herbivores (Brandner et al., 2011).

Because tree species differ in their palatability (Bodziarczyk et al., 2017), some species, such as sycamore maple (*Acer pseudoplatanus*) and silver fir (*Abies alba*) are heavily browsed (Götmark et al., 2005; Heuze et al., 2005), while other species are less intensively or even sporadically browsed under the same conditions (Szwagrzyk et al., 2020). Regardless of whether they are strongly preferred by herbivores, some tree species, such as European hornbeam (*Carpinus betulus*) compensate for browsing loss by developing numerous secondary shoots (Churski et al., 2017; Samojlik and Kuijper, 2013). Therefore, in forest communities under high browsing pressure, the share of *C. betulus* among the young generation of trees actually increases, as other species grow slowly and survive poorly (Kuijper et al., 2009).

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https://doi.org/10.1016/j.tfp.2023.100424

Available online 10 August 2023

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Likewise, the number of herbivores and the availability of browse (twigs up to a specific diameter threshold that are within the reach of herbivores) are important factors influencing the impact of browsing on young trees. The availability of browse is extremely variable in time and space, as it is influenced by species identity (Szwagrzyk et al., 2012), young tree architecture, young tree density and light availability (Aszalós et al., 2022; Häsler and Senn, 2012; Shen et al., 2021). Additionally, because different tree species react differently to these environmental factors, the availability of browse will vary from place to place as well (Barbosa et al., 2014). This complex and dynamic relationship between browsing and tree species growth habits determine tree recruitment to the forest canopy (Häsler and Senn, 2012). Understanding this interaction is therefore crucial in the management of natural regeneration in forest ecosystems where herbivory causes serious damage to young individuals.

The term "browse availability" in this context refers to the amount of twigs that are within a certain range in terms of their diameter and height above the ground for the major ruminating herbivores. The two deer species; red deer Cervus elaphus and roe deer Capreolus capreolus are the major browsers of the tree saplings in Poland. Roe deer (Capreolus capreolus) can browse only up to 1.3 m height of tree saplings (Chianucci et al., 2015) while the tallest of local wild herbivores, moose (Alces alces) can browse up to a height of 3.05 m (Andreozzi et al., 2014). From our field studies conducted in the study area (Szwagrzyk et al., manuscript in preparation), we learned that the largest diameter of shoots browsed by herbivores was 7 mm and the height was 0.5-3 m. As a result, to accurately assess browse availability in natural forests, it is essential to concentrate on evaluating twigs, defined as shoots with diameters up to 7 mm and heights ranging from 0.5 to 3 m. The allometric models presented in this paper for estimating twig dry mass in tree saplings are specifically built on the basis of twigs with diameters below 7 mm.

There is much information concerning tree biomass in forest ecosystems encompassing a single location up to multiple regions (Konôpka et al., 2020; Sylvester and Avalos, 2013; Visscher et al., 2006; Weiskittel et al., 2015) as well as advancements in measuring techniques. For instance, tree-ring methods (Xu et al., 2023), airborne technologies (Li et al., 2020; Roy et al., 2021), and land surface temperature and evaporation data-based estimation (Rosas-Chavoya et al., 2023) have been employed to estimate tree biomass in forests. In addition, the single tree-based biomass estimation model (Makungwa et al., 2013) has been occasionally used in forest ecology.

However, there is little information about the amount of browse available for herbivpores in forest ecosystems. Published studies include a regression model developed to estimate the browsed mass of European ash (Fraxinus excelsior) and sycamore maple (A. pseudoplatanus) by red deer (Konôpka and Pajtík, 2015) and the model developed to estimate the dry mass potential of browsed items of rowan tree components in the Tatra Mountains (Pajtik et al., 2015). However, most findings cannot be generalized because of high spatial variability and fast changes over time. Methods used for estimating the amount of browse are time-consuming (Weiskittel et al., 2015) and cannot be applied at a broader scale. There are no methods to estimate the amount of browse on the basis of more frequently available data concerning the size structure of the young generation of trees. Furthermore, physio-morphological variations in tree species affect the environmental resource assimilation efficiency and biomass production of tree saplings in natural forest ecosystems (Frerker et al., 2013; Häsler and Senn, 2012; Kupferschmid et al., 2015). Approaches that can combine several biomass estimating variables for sapling twigs are therefore not well developed.

Thus, the purpose of this study was to 1) model the relationship between the twig dry mass of saplings of different species and i) the sapling shoot diameter classes and ii) the sapling height classes; 2) develop allometric equations for estimating the twig dry mass of saplings of various species; and 3) describe the distribution of proportion of twig dry mass in saplings of different species. We tested three hypotheses: H1: The variation in twig dry mass of saplings of different species increases across all shoot diameter classes; H2: Evergreen coniferous species display a stronger response of twig dry mass to sapling height along the height classes than do deciduous species; and H3: Given that tree species differ in their morphology, the explanatory variables in the twig dry mass models of saplings are species-specific.

2. Material and methods

2.1. Description of the study sites

The study was conducted based on the laboratory biomass results of tree saplings from two national parks in southern Poland: Roztocze National Park (RNP) and Tatra National Park (TNP). The RNP is located in the Roztocze region, and over 95% of the park area is covered with forests. It has an average annual air temperature ranging from 7.4–7.5 $^{\circ}$ C and an annual precipitation of 600–650 mm (Grabowski et al., 2022). The TNP covers one of the two Alpine mountain ranges in Poland, and it is a part of the Western Carpathian Mountains, with 17 peaks over 2500 m a.s.l (Pajtík et al., 2015). The annual temperature in the elevation zone where the study was conducted is up to 5 $^{\circ}$ C, and the annual rainfall is 1100 mm.

Among the popular tree species in the stands of RNP, European beech (*F. sylvatica*), and Silver fir (*A. alba*) are commonly abundant. *F. sylvatica*, *A. alba*, and *A. pseudoplatanus* are regenerated together in some plots in the forest ecosystem (Maciejewski, 2010). Whereas, Norway spruce (*P. abies*) is the most popular tree species among others in TNP. The national parks are also a home range to herbivores such as red deer, roe deer, wild boar, and all of the large carnivores typical of Central Europe (Szwagrzyk et al., 2020).

In our study, we focused on six tree species, which, according to our earlier studies (Szwagrzyk et al., 2020), played a major role in natural regeneration in our study areas. The saplings of two evergreen coniferous species (*A. alba* and *P. abies*) and four deciduous broad-leaved species (*F. sylvatica*, Hornbean (*C betulus*), Mountain-ash (*S. aucuparia*), and *A. pseudoplatanus*) represented a disturbed natural forest in the study sites. *F. sylvatica* and *A. alba* are the most shade-tolerant, yet herbivores also browse them under the forest canopy, while *C. betulus* needs little disturbance to the forest canopy to regenerate in the forest floor. *S. aucuparia* is a shade-intolerant plant that requires disturbance in the forest canopy to regenerate. In turn, *P. abies* and *A. pseudoplatanus* are moderately shade-tolerant.

2.2. Study design and measurements

We selected unbrowsed saplings of the study tree species based on some strict criteria to avoid the variability between among that might occur due to the inherent heterogeneity in the natural environment. For each species, we gathered saplings in the four following size ranges: 0.5-1.0, 1.0-1.5, 1.5-2.0, and 2.0-3.0 m. We analyzed the twig dry mass of 16 tree saplings from each species in each forest community. Architectural parameters, such as tree sapling height, basal diameter, shoot diameter, shoot length, crown width and crown length, were measured in the laboratory. Basal and shoot diameters measured in two perpendicular directions and mean values were taken. Similarly, the mean crown width at the largest point of the sapling crown from the vertical aspect was measured from two perpendicular directions of the canopy.

The saplings were partitioned into three main parts: 1) coarse biomass (diameter \geq 7 mm), 2) clipped and oven-dried twigs (diameter up to 7 mm), with 5 replications in each diameter class, and 3) extra twigs (diameter up to 7 mm) were also counted and dried together with the coarse biomass sample. The twigs were grouped into five diameter classes (2–3, 3–4, 4–5, 5–6, and 6–7 mm), with 5 replications per class. The twigs were cut off the stem beginning at the top with the smallest (2–3 mm) twig diameter class.

As a general rule, the twig samples for each diameter class were typically cut from the first-order branch. The branches of successive diameter classes of the monopodial branching coniferous species (*A. alba* and *P. abies*) were cut from the stem, starting at the top branch in each diameter class for individual saplings. Consecutive first-order branches were used for species with sympodial branching habit, particularly *F. sylvatica* and *C. betulus*. However, in most instances where the saplings lacked adequate replications in the corresponding diameter classes from the first-order branches, samples were taken from the second- and third-order branches, and the twig of the leading shoot represented at least one diameter class.

In contrast, the *S. aucuparia* and *A. pseudoplatanus* saplings lacked a dense branch structure. As a result, the leading shoots were divided into a number of diameter classes and counted as twigs in addition to the first-order branches. When the sapling basal diameter was less than 7 mm, the entire sapling was considered a fine shoot. The specimens for this research were gathered during the winter season when deciduous species had shed their leaves, leaving only the woody shoots available for winter browsing. In contrast, the coniferous species were collected during the same winter season, but their leaves remained intact, serving as a source of forage for herbivores.

The clipped shoots in each diameter class were kept in separate envelopes labeled with the following information: species identity, specimen number, diameter class, and envelope number. The extra twigs in different diameter classes were counted and separately labeled for each sapling and placed in a metal plate together with the coarse biomass samples. The drying process for all the samples took place in an oven. As there is currently no established standard for drying temperatures and durations of biomass samples, previous studies have reported a wide range of drying temperatures (ranging from 18 to 110 °C) and drying durations (spanning from 5 to 360 h) (Doraisami et al., 2022). To maintain consistency in this study, the samples were dried at 65 °C for 72 h. After drying, the samples were weighed using an Adventure™ digital balance (with a maximum capacity of 2200 g and a minimum capacity of 0.5 g) in a controlled, wind-free environment, following the methods described in the works of (Albert et al., 2014; Golisz et al., 2020).

Based on the twig dry mass in each diameter class and the corresponding total twig count in each diameter class, the extra twig dry mass was calculated for each sapling and subtracted from the gross coarse dry mass to obtain the net coarse dry mass. With the help of the net coarse dry mass of each sapling and the sum of the twig dry mass in all diameter classes, the percent of twig dry mass was calculated for all species:

$$TDM\% = \left(\frac{TDM}{NetTDM + CDM}\right) * 100$$

where TDM is the total sum of the twig dry mass of the sapling in all diameter classes and CDM is the coarse dry mass of the sapling.

2.3. Data analysis

The assumptions of data distribution normality and redundancy between explanatory variables were checked. Since the normality and lack of redundancy assumptions were rejected, two commonly used regression analyses were applied. First, the ordinary least squares method was used to develop the allometric equation of the twig dry mass of all tree species. This method is a more commonly used approach for fitting allometric models to data by bilogarithmic transformation (a linearized version of logarithmic data transformations). Of the multiple explanatory variables included in the model, the best-fitted estimator combination was selected based on the Akaike information criterion (AIC) and used to develop the final model for each species. As the sapling mean basal diameter and sapling height were the most important estimators, the data were assessed using these estimators alone and in conjunction with additional estimators specific to the tree species in question. The coefficient of determination (Adj R²), and the probability of each estimator variable at different confidence intervals were used according to Visscher et al. (2006).

$$\mathbf{Log}(y) = \log(a) + b * \log(x)$$

where y is the twig dry mass, a and x are estimator variables and b is the slope. In addition, the twig dry mass of the tree species was plotted using linear regression against the sapling mean basal diameter and sapling height.

Second, the twig dry mass distribution of saplings at different diameter classes was analyzed using the generalized additive model (GAM). The GAM is the best modeling method to overcome the lack of data distribution normality and the collinearity between explanatory variables. Consequently, the model was decided based on the smooth fitting criteria and Adj R^2 . The scatter plots were developed using geom_smooth (formula = $y \sim poly (x, 2)$). Linear regression was employed to fit the twig dry mass distribution of the saplings to the height classes using the ordinary least squares method.

Furthermore, to identify the predictor parameters for the twig dry mass of different tree species, explanatory variables, such as sapling height, basal diameter, crown length, and crown width, were used. The proportion of twig dry mass of saplings of different species were computed with the use of descriptive statistics in box plots. All data were analyzed in R software version 4.2.2.

3. Results

3.1. Modeling twig dry mass distribution along twig diameter classes

The twig dry mass of the saplings showed a significant positive relationship with the shoot diameter classes (SDCs) for all tree species (Table 1). However, the amount of twig dry mass and rate of increase across shoot diameter classes were different according to the tree species. As a result, *P. abies, A. alba, C. betulus, F. sylvatica, S. aucuparia*, and *A. pseudoplatanus* were in order of biggest to smallest twig dry mass distribution throughout shoot diameter classes (Fig. 1). After evaluating the data with log(SDC) or SDC and comparing the Adj R² values, the strongest model correlation between twig dry mass and SDC was identified. The Adj R² was higher for *A. pseudoplatanus, A. alba* and *P. abies* using log(SDC) and for *C. betulus* using SDC. However, the relationship was not strong for the rest of the tree species regardless of the significant values at p = 0.05 (Table 1).

3.2. Modeling twig dry mass distribution along sapling height classes

The twig dry mass of *P. abies* and *A. alba* was significantly related to the sapling height class, and a rapid increase was observed for *P. abies*. Across the height classes, the twig dry mass of these species was far higher than that of the other species (Fig. 2). The twig dry mass of *P. abies* saplings at the 99.9% confidence level and that of *A. alba* at the 95% confidence level increased across the tree height classes. However, the value for the rest of the tree species was not significantly changed except for a slight positive change for *F. sylvatica* and *S. aucuparia* at the 90% confidence interval (Table 2).

3.3. Modeling twig dry mass with multiple variables

3.3.1. Linear regression of twig dry mass vs. basal diameter

The plot of the linear regression model for the twig dry mass of the saplings of different tree species against their basal diameter is presented in Fig. 3. It shows that the models are significant for all tree species except *A. alba*. Moreover, highly significant models based upon the basal diameter of the tree saplings were developed for *A. pseudoplatanus* and *P. abies*.

Fagus sylvatica: The model of twig dry mass of F. sylvatica was

Fitting of the twig dry mass to its respective shoot diameter classes in the generalized additive model (GAM). The six shoot diameter classes (SDCs) are in mm: 2 (2–3 mm), 3 (3–4 mm), 4 (4–5 mm), 5 (5–6 mm), and 6 (6–7 mm). N represents the number of samples per tree species.

Species	Estimator	Coefficient	Std. Error	t value	Pr(> t)	Adj R ²	Ν
Fagus sylvatica	Intercept	-1.731	0.345	-5.020	0.000***	0.318	387
	SDC	1.314	0.098	13.460	0.000***		
Acer pseudoplatanus	Intercept	-3.029	0.103	-29.360	0.000***	0.676	319
	log(SDC)	2.134	0.083	25.790	0.000***		
Carpinus betulus	Intercept	-1.638	0.395	-4.150	0.000***	0.641	83
	SDC	1.602	0.132	12.130	0.000***		
Sorbus aucuparia	Intercept	-0.637	0.238	-2.677	0.008**	0.268	326
	SDC	0.689	0.063	10.965	0.000***		
Abies alba	Intercept	-1.608	0.114	-14.150	0.000***	0.652	367
	log(SDC)	2.144	0.082	26.190	0.000***		
Picea abies	Intercept	-0.800	0.106	-7.551	0.000***	0.577	353
	log(SDC)	1.760	0.080	21.947	0.000***		

Significance codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1



Fig. 1. Distribution of the twig dry mass of different sapling species across shoot diameter classes. The numbers on the x-axis, 2, 3, 4, 5, and 6, represent the twig diameter classes, 2–3, 3–4, 4–5, 5–6 and 6–7 mm, respectively.

significantly explained by the log(basal diameter) of the saplings with Adj R^2 =0.333 and p == 0.001 (Fig. 3). At the 99.9% confidence level, log(basal diameter (BD)) best explains the model, while the intercept was nonsignificant. The overall allometric equation of *F. sylvatica* sapling twig dry mass (g) was (Table 3):

TDMFagussylvatica = Exp(1.551 * log(BD[mm]))

Acer pseudoplatanus: The model of the twig dry mass of *A. pseudoplatanus* saplings was highly significant, with Adj R^2 =0.567 and p == 0.000 (Fig. 3). At the 99.9% and 95% confidence levels, the mean basal diameter of the saplings and the intercept explained the twig dry mass model, respectively. Accordingly, the allometric equation of *A. pseudoplatanus* sapling twig dry mass (g) was (Table 3):

TDMAcerpseudoplatanus = 1.149 * (BD[mm]) - 7.696

Carpinus betulus: The model of twig dry mass of *C. betulus* saplings was significant with log(mean basal diameter) as the best fitting variable with Adj R^2 =0.518 and p == 0.001 (Fig. 3). At the 99.9% confidence level, log(mean basal diameter) was confirmed to be a highly significant model estimator, while the intercept was slightly significant at the 90% confidence level with a negative coefficient. The allometric equation of twig dry mass (g) of *C. betulus* saplings was (Table 3):

TDMCarpinusbetulus = Exp(2.039 * log(BD[mm]) - 2.186)

Sorbus aucuparia: The *S. aucuparia* sapling twig dry mass model was significant, with mean basal diameter serving as the best estimator, with Adj R^2 =0.303 and *p*=0.001 (Fig. 3). The estimator was significant at the 99.9% confidence level; however, the intercept had no significant impact on the model. As a result, the allometric equation for the twig dry mass (g) of *S. aucuparia* saplings was (Table 3):

TDM Sorbusaucuparia = 2.188 * BD[mm]

Abies alba: The model of twig dry mass of *A. alba* saplings was not significantly explained by any form of the basal diameter model. Nevertheless, a better fit was found with log(mean basal diameter) with Adj R²=0.000 and p == 0.335 (Fig. 4, Table 3).

Picea abies: The twig dry mass of *P. abies* saplings was best fitted to basal diameter and crown length (CL) from among many of the explanatory variables used in the model, with Adj R^2 =0.823 and *p* == 0.000. The model was strongly significantly explained by mean basal diameter at the 95% confidence level and sapling crown length at the 99.9% confidence level. However, the intercept was not significant (Table 3). As a result, the allometric equation of the sapling twig dry



Fig. 2. Distribution of the twig dry mass of different tree species across sapling height classes. The numbers on the x-axis, 1, 2, 3 and 4, represent the height classes, 0.5–1.0, 1.0–1.5, 1.5–2.0, and 2.0–3.0 m, respectively.

Model of the relationship between sapling height classes (0.5-1, 1.0-1.5, 1.5-2.0, 2.0-3.0 m) and the twig dry mass of saplings for various tree species.

Parameter	Estimate	Std. Error	t value	Pr(> t)	Adj R ²	P value
Intercept	10.060	6.399	1.572	0.126	0.064	0.084
Height class	4.224	2.368	1.784	0.084.		
Intercept	1.104	0.408	2.710	0.011*	0.023	0.197
Log(Height class)	0.566	0.429	1.320	0.197		
Intercept	3.022	0.281	10.754	0.000***	-0.053	0.664
log(Height class)	0.133	0.300	0.443	0.664		
Intercept	65.753	19.925	3.300	0.002**	0.062	0.083
Height class	-12.878	7.205	-1.787	0.083.		
Intercept	4.252	0.186	22.817	0.000***	0.422	0.004
log(Height class)	0.678	0.196	3.457	0.004**		
Intercept	4.222	0.154	27.394	0.000***	0.635	0.000
log(Height class)	0.866	0.167	5.202	0.000***		
	Parameter ntercept leight class ntercept .og(Height class) ntercept og(Height class) ntercept leight class) ntercept og(Height class) intercept og(Height class)	Parameter Estimate ntercept 10.060 leight class 4.224 ntercept 1.104 .og(Height class) 0.566 ntercept 3.022 og(Height class) 0.133 ntercept 65.753 Height class -12.878 ntercept 4.252 og(Height class) 0.678 intercept 4.222 og(Height class) 0.866	Parameter Estimate Std. Error Intercept 10.060 6.399 leight class 4.224 2.368 intercept 1.104 0.408 .og(Height class) 0.566 0.429 intercept 3.022 0.281 og(Height class) 0.133 0.300 intercept 65.753 19.925 leight class -12.878 7.205 intercept 4.252 0.186 og(Height class) 0.678 0.196 intercept 4.222 0.154 og(Height class) 0.866 0.167	branche Estimate Std. Error t value ntercept 10.060 6.399 1.572 leight class 4.224 2.368 1.784 ntercept 1.104 0.408 2.710 .og(Height class) 0.566 0.429 1.320 ntercept 3.022 0.281 10.754 og(Height class) 0.133 0.300 0.443 ntercept 65.753 19.925 3.300 leight class -12.878 7.205 -1.787 ntercept 4.252 0.186 22.817 og(Height class) 0.678 0.196 3.457 ntercept 4.222 0.154 27.394 og(Height class) 0.866 0.167 5.202	'arameterEstimateStd. Errort value $Pr(> t)$ ntercept10.0606.3991.5720.126leight class4.2242.3681.7840.084.ntercept1.1040.4082.7100.011*.og(Height class)0.5660.4291.3200.197ntercept3.0220.28110.7540.000***og(Height class)0.1330.3000.4430.664ntercept65.75319.9253.3000.002**leight class-12.8787.205-1.7870.083.ntercept4.2520.18622.8170.000***og(Height class)0.6780.1963.4570.004**og(Height class)0.8660.1675.2020.000***	'arameterEstimateStd. Errort value $Pr(> t)$ Adj R2ntercept10.0606.3991.5720.1260.064leight class4.2242.3681.7840.084.ntercept1.1040.4082.7100.011*0.023.og(Height class)0.5660.4291.3200.197ntercept3.0220.28110.7540.000***-0.053og(Height class)0.1330.3000.4430.664ntercept65.75319.9253.3000.002**0.062leight class-12.8787.205-1.7870.083ntercept4.2520.18622.8170.000***0.422og(Height class)0.6780.1963.4570.004**-ntercept4.2220.15427.3940.000***0.635og(Height class)0.8660.1675.2020.00***-

Significance codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

mass (g) of P. abies was (Table 3):

TDMPiceaabies = 3.335 * (BD[mm]) + 0.906 * (CL[cm])

3.3.2. Linear regression of twig dry mass vs. sapling height

Fagus sylvatica: The model of twig dry mass of *F. sylvatica* with a single estimator, log(sapling height (H)), is depicted on the plot in Fig. 4. However, log(mean largest crown width (MLCW)) was added to the model using the AIC to select the best model estimators from among several measured variables. Thus, the combination of both parameters in the model resulted in the optimum sapling twig dry mass of *F. sylvatica* with Adj R²=0.569 and p == 0.000. Accordingly, at the 95% confidence level, the log(MLCW) significantly explained the sapling twig dry mass. Despite the nonsignificant values of log(height (H)), it brought a considerable improvement to the model quality. The Adj R² was 49.87 with log(H), 54.17 with log(MLCW), and 56.93 with the combination of

both (log(MLCW)+ log(H)) in the model. The model intercept, in contrast, significantly impacted the model at the 95% confidence level with a negative magnitude. Therefore, the allometric equation of *F. sylvatica* sapling twig dry mass (g) was (Table 4):

$$TDMFagussylvatica = \mathbf{Exp}(0.857 * \log(\mathrm{H[cm]}) + 0.873 * \log(\mathrm{MLCW[cm]}) - 4.407)$$

Acer pseudoplanus: The twig dry mass of *A. pseudoplatanus* was significantly explained by the sapling height. At the 99.9% confidence level, the sapling height explained the twig dry mass with Adj R^2 =0.381 and *p*=0.000 (Fig. 4). However, intercept was not significantly important in the model. Hence, the allometric equation was formulated as (Table 4):

TDMAcerpseudoplatanus = Exp(0.080 * log(H[cm]))



Fig. 3. Linear regression of the twig dry mass of the tree saplings versus the mean basal diameter. A, B, C, D, E, and F: F. sylvatica, A. pseudoplatanus, C. betulus, S. aucuparia, A. alba, and P. abies, respectively.

Model of sapling twig dry mass explained by the mean basal diameter (mm) of the tree species. The twig dry mass of F. sylvatica, C. betulus, and A. alba was log-transformed, while that of A. pseudoplatanus, S. aucuparia, and P. abies was not transformed to obtain the optimum model value fitted in the linear model.

Tree species	Parameter	Estimate coefficient	Std. Error	t value	Pr(> t)	\mathbb{R}^2	Adj R ²	p value
Fagus sylvatica	Intercept	-0.742	1.066	-0.696	0.493	0.358	0.333	0.001
	log(Basal diameter)	1.551	0.407	3.807	0.001***			
Acer pseudoplatanus	Intercept	-7.696	2.822	-2.727	0.011*	0.581	0.567	0.000
	Basal diameter	1.149	0.178	6.443	0.000***			
Carpinus betulus	Intercept	-2.186	1.117	-1.958	0.069.	0.548	0.518	0.001
	log(Basal diameter)	2.039	0.478	4.264	0.001***			
Sorbus aucuparia	Intercept	-9.174	7.592	-1.208	0.236	0.326	0.303	0.001
	Basal diameter	2.188	0.575	3.805	0.001***			
Abies alba	Intercept	3.369	1.431	2.355	0.034*	0.066	0.000	0.335
	log(Basal diameter)	0.441	0.442	0.998	0.335			
Picea abies	Intercept	-32.773	24.641	-1.330	0.206	0.846	0.823	0.000
	Basal diameter	3.335	1.301	2.563	0.024*			
	Crown length	0.906	0.212	4.277	0.001***			

Significance codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Carpinus betulus: The twig dry mass of *C. betulus* was weakly explained by the sapling height. The linear model with log-transformed data shows that only a small amount of variability in the twig dry mass of *C. betulus* is explained by the sapling height, with Adj R^2 =0.150 and *p* == 0.069 at the 90% confidence level (Fig. 4). The allometric equation of the twig dry mass (g) of *C. betulus* was (Table 4):

TDMCarpinusbetulus = Exp(1.305 * log(H[cm]))

Sorbus aucuparia: The height of *S. aucuparia* saplings did not show a strong significance in explaining the twig dry mass, as indicated by both the log-transformed and non-transformed data, with an adjusted R2 = 0.077 and *p*-value = 0.068 (Fig. 4). Nevertheless, it explained the variability at the 90% confidence level, while the intercept was not significantly important. The twig dry mass model of *S. aucuparia* saplings, however, was significant with Adj R²=0.470 and p == 0.000 when additional variables were used and the best fit was chosen. Accordingly, the allometric equation of the *S. aucuparia* sapling twig dry mass (g) was (Table 4):

$$TDMSorbusaucuparia = Exp(6.492 + 0.691 * log(MLCW[cm]) - 1.129 * log(H[cm]))$$

Abies alba: The linear regression with log-transformed values of the variables in the model shows that the twig dry mass of *A. alba* saplings was well explained by log(H), while the intercept was not significant in the model. The twig dry mass of *A. alba* was significant with Adj R^2 =0.626 and *p*=0.000 at the 99.9% confidence level (Fig. 4). Consequently, the allometric equation for the sapling twig dry mass (g) of *A. alba* was (Table 4):

TDMAbiesalba = Exp(0.932 * log(H[cm]))

Picea abies: The linear model of the twig dry mass of *P. abies*, developed with log-transformed data, was significantly explained by the sapling height with Adj R^2 =0.650 and *p*=0.000 at the 99.9% confidence level (Fig. 4). As a result, the allometric equation for the sapling twig dry mass (g) of *P. abies* was (Table 4):

$$TDMPiceaabies = Exp(1.229 * log(H[cm]))$$



Fig. 4. Linear regression of the twig dry mass of the saplings versus sapling height. A, B, C, D, E, and F: F. sylvatica, A. pseudoplatanus, C. betulus, S. aucuparia, A. alba, and P. abies, respectively.

Model of sapling twig dry mass explained by the height (cm) of the tree species. Except for A. pseudoplatanus, the twig dry mass of all the tree species was log-transformed and fitted in the linear model.

Tree species	Parameter	Estimate coefficients	Std. Error	t value	Pr(> t)	R ²	Adj R ²	p value
Fagus sylvatica	Intercept	-4.407	1.723	-2.558	0.017*	0.601	0.569	0.000
	log(Height)	0.857	0.525	1.633	0.115			
	Log(MLCW)	0.873	0.386	2.26	0.033*			
Acer pseudoplatanus	Intercept	-3.853	3.167	-1.217	0.233	0.401	0.381	0.010
	Height	0.080	0.018	4.477	0.000***			
Carpinus betulus	Intercept	-4.096	3.387	-1.209	0.245	0.203	0.150	0.069
	log(Height)	1.305	0.667	1.957	0.069.			
Sorbus aucuparia	Intercept	6.492	1.936	3.353	0.002**	0.508	0.470	0.000
	Log(Height)	-1.129	0.420	-2.686	0.012*			
	Log(MLCW)	0.691	0.135	5.123	0.000***			
Abies alba	Intercept	0.169	0.908	0.186	0.855	0.651	0.626	0.000
	log(Height)	0.932	0.182	5.114	0.000***			
Picea abies	Intercept	-1.189	1.135	-1.047	0.313	0.673	0.650	0.000
	Log(Height)	1.229	0.229	5.367	0.000***			

Significance codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

3.4. Proportion of twig dry mass in the total dry mass of saplings of different species

The figure (Fig. 5) illustrates the percentage of twig dry mass relative to the total dry mass of saplings for different tree species, along with their mean, standard deviation, 95% confidence range, and quartiles. Additionally, the data compares the contribution of winter browse by each tree species in terms of their total dry weight. Among the species studied, *S. aucuparia* exhibited the highest proportion of twig dry mass compared to the overall dry mass of its saplings. In terms of the median value, the percent twig dry mass of the tree species showed following order: *S. aucuparia* > *P. abies* > *A. alba* > *F. sylvatica* > *C. betulus* > *A. pseudoplatanus.*

4. Discussion

4.1. Relationship between twig dry mass and twig diameter

The twig dry mass of all tree species showed an exponential increase with the diameter increment of saplings. The distribution of the twig dry mass of tree saplings can vary along the shoot diameter classes due to a number of factors, including resource allocation and mechanical stability. Resource allocation plays a major role in determining the distribution of twig dry mass along shoot diameter classes (Mensah et al., 2016). As a tree grows, it allocates more resources to the larger-diameter shoots, which can support more foliage and photosynthetic capacity. This in turn suggests that the larger diameter classes of tree saplings contain a greater concentration of forage for herbivores, although this varies with the tree species. As a result, compared to broad-leaved deciduous species, coniferous species contribute more to the forage of herbivores when the twig diameter is larger.

Our findings also demonstrate that the dry mass of twigs in all tree species is a function of their diameter. As the twig dry mass is strongly determined by this allometric relationship, it is possible to estimate the amount of twig dry mass that is lost by browsing herbivores using the sapling diameter.

4.2. Relationship between twig dry mass and sapling height

The relationship between sapling height classes and twig dry mass is



Fig. 5. The proportions of twig dry-mass in the total dry-mass of saplings of different tree species.

an important aspect of forest ecology research. Some studies have demonstrated that the mass growth rate of most young tree species increases continuously with tree size (Galia Selaya et al., 2008; Stephenson et al., 2014) due to increased carbon assimilation. Accordingly, the relationship between sapling height and twig dry mass is often used as an indicator of tree growth and productivity.

These findings are supported by the physiological theory that taller trees require greater structural support and transport of water and nutrients, which in turn leads to greater twig dry mass (Poorter et al., 2012). In fact, there is increased photosynthetic capacity and greater allocation of resources to shoot growth as saplings grow taller. Similarly, Osada et al. (2014) found that twig dry mass was positively correlated with sapling height in five deciduous tree species.

Nevertheless, the link between twig dry mass and sapling height class varies with tree species. According to the present study, there is a significant difference between coniferous and broad-leaved species with regard to the twig dry mass along with sapling height classes. The strongest relationship between twig dry mass and sapling height class was found in the coniferous group (P. abies and A. alba), and the difference was most noticeable in tall saplings. This may be due to the multiple shoots that these tree species have in each lateral branch. As a result, the amount of forage from a single plant at a time lowers the likelihood that the terminal shoot will be browsed. Except for F. sylvatica, which exhibited a somewhat higher twig dry mass at taller height classes, twig dry mass did not change considerably along with the height class in the broad-leaved group. The findings imply that the broad-leaved species F. sylvatica, S. aucuparia, C. betulus, and A. pseudoplatanus, particularly the latter two, have similar forage availability to herbivores across several height classes.

4.3. Allometric modeling of sapling twig dry mass

As the basal diameter of a tree increases, so does the twig dry mass. This is because the basal diameter is often correlated with the overall size and biomass of the tree, including the number and size of branches and twigs. As the tree grows larger, it typically produces more and larger branches and twigs, which contribute to the overall twig dry mass.

However, it is important to note that the relationship between twig dry mass and basal diameter is not always linear or consistent across all species. Some tree species may have a stronger relationship between these variables than others, while some may exhibit more variation in twig dry mass for a given basal diameter. For instance, the twig dry mass model of *A. pseudoplatanus* (Adj R²=56.7%), *C. betulus* (Adj R²=51.8%), and *P. abies* (Adj R²=60.4%) saplings is well explained by basal diameter. However, the twig dry mass models of *F. sylvatica*, *S. aucuparia*, and *A. alba* are not well explained by basal diameter.

The physio-morphological variety of plants affects the relationship between the twig dry mass and structural characteristics of saplings. Because of this, each estimator's power of determination varies with the species, and in some circumstances, a model may benefit from having numerous explanatory variables. For instance, the model quality of *P. abies* is improved with Adj R^2 =82.3% thanks to the combination of the estimators MLCL and mean basal diameter.

Similarly, the general allometric relationship between twig dry mass and sapling height of tree species is positive, meaning that as sapling height increases, twig dry mass also tends to increase. This relationship is because as trees grow taller, they need to support more foliage to maintain their structure and carry out physiological functions (Osada, 2011). This increased biomass includes not only leaves but also twigs and branches.

The allometric relationship between twig dry mass and sapling height, quantified using regression analysis, varies among tree species. F. sylvatica (Adj R^2 =56.9%), A. alba (Adj R^2 =62.6%), and P. abies (Adj R^2 =65.0%) displayed a strong correlation between twig dry mass and sapling height. Nonetheless, our findings contrast with the study conducted by Annighöfer et al. (2016). They illustrated that relying solely on height could accurately estimate the biomass of young trees from various species. Conversely, we found that this correlation is not strong in certain species like C. betulus, S. aucuparia, and A. pseudoplatanus. However, the best twig dry mass models for F. sylvatica and S. aucuparia were developed when using log(H) and log(MLCW) in the model. The two best-fit explanatory variables, log(H) and log(MLCW), were selected from among the multiple variables used in the model based on the AIC. Since there was no multicollinearity between explanatory variables, the model determination role of the explanatory variables is acceptable. Log(H) is also a strong estimator of the twig dry mass of A. alba saplings. Despite the strong relationship between the twig dry mass and the log(H) of *P. abies*, the highest Adj R^2 was obtained with the mean basal diameter of the tree saplings. This finding is supported by Miyata et al. (2011), who found that the allometry of leader shoots was convergent, and the changes were also height-dependent. Similarly, height-dependent changes in the total biomass of current-year shoots varied across species according to Osada (2011). This variation therefore suggests that the use of species-specific predictors could result in a more accurate model.

Nevertheless, the allometric equations developed for calculating the twig dry mass of saplings of some tree species require a minimum threshold level of the estimator variables. For instance, the allometric equation of twig dry mass (g) of *A. pseudoplatanus* saplings was = 1.149^{*} (mean basal diameter [mm])-7.696. Thus, the minimum threshold level of the mean basal diameter of the saplings should be >6.698 mm to obtain >0 g twig dry mass. The allometric equation for the twig dry mass (g) of *C. betulus* was = Exp(2.039*log(mean basal diameter [mm])-2.186); thus, the minimum mean basal diameter was 0.03 mm. Similarly, the allometric equation of twig dry mass (g) for *F. sylvatica* saplings was = Exp(0.857*log(H [cm])+0.873*log(MLCW [cm])-4.407). Since the minimum height of the sample tree is 0.5 m, the log(MLCW) is 5.331 cm.

The twig dry mass allometric models of tree saplings can have various applications, especially in understanding the interaction between wild ungulate browsing pressure and recruitment of tree saplings in natural forest ecosystems. The potential application of these models is to estimate the browse potential of tree saplings in the large-scale, comparable with the home ranges of ungulate herbivores. The allometric models can also be used to predict the impact of wild ungulate browsing pressure on tree saplings in natural ecosystems, and developing management strategies to mitigate the negative effects of browsing on tree regeneration (Frank et al., 2019; Konôpka et al., 2018; Weisberg et al., 2005; Woolnough and Du Toit, 2001).

4.4. The proportion of twig dry mass to the total dry mass of saplings

The findings regarding the proportion of twig dry mass to the total dry mass of the saplings of various species are very interesting. *S. aucuparia* had the highest proportion of twig dry mass. We argue that because the *S. aucuparia* saplings had thin stems that lie within the range of twig diameter classes, they had a less coarse dry mass. *P. abies* and *A. alba*, in contrast, produces numerous shoots, including lateral branches, and showed the second highest proportion of contribution to the winter browse. The twig dry mass percentages for the different tree species followed the order: *S. aucuparia* > *P. abies* > *A. alba* > *F. sylvatica* > *C. betulus* > *A. pseudoplatanus*.

5. Conclusion

The variation in twig dry mass increases across all shoot diameter classes. Coniferous species yield much higher twig dry mass than deciduous species at all twig diameter classes. The amount of twig dry mass of the different tree saplings increases linearly with the sapling height class. However, the relationship between the amount of twig dry mass and height class is stronger for saplings of coniferous species than for those of deciduous species. Conversely, the broad-leaved species *F. sylvatica, A. pseudoplatanus, S. aucuparia,* and *C. betulus* have a more complex branching pattern with multiple leader shoots, a shorter crown length, and a lower shoot dry mass than coniferous species across the height classes.

The allometric relationships between the morphology of tree saplings and twig dry mass are species-specific. The twig dry mass of coniferous species and broad-leaved species differs due to the differences in their growth patterns and structures. Depending on the tree species, basal diameter and height of the tree saplings are the key variables in estimating the dry mass of twigs in the current finding. However, in certain species, the MLCW and MLCL measurements are utilized to enhance the overall quality of the model of twig dry mass of the tree saplings.

In general, the generic equations are likely to produce more uncertainty than well-implemented, locally designed models, which may be a preferable solution (Chave et al. 2014). The species specific allometric models for estimating twig dry mass of tree saplings in the current study can have important applications in forest management, particularly in understanding the influence of herbivore browsing pressure on sapling growth by comparing the predicted dry mass of browsed and unbrowsed saplings in the large scale. This information can help forest managers to understand the extent of browsing pressure and develop strategies to mitigate its effects (Seagle and Liang, 2001). The allometric models can also be used to identify tree species that are particularly vulnerable to browsing pressure and prioritize their protection (Frank et al., 2019).

Availability of data and materials

Not applicable.

Code availability

Not applicable.

Author contributions

The study conceptualization, and investigation, validation and writing review and editing involved contributions from all authors. However, Aklilu Bajigo Madalcho was primarily responsible for the formal analysis, visualization and writing original draft of the manuscript. Aklilu Bajigo Madalcho, Jerzy Szwagrzyk, and Anna Gazda collaborated on the methodology and data curation.

Declaration of Competing Interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Jerzy Szwagrzyk reports financial support was provided by Polish National Science Foundation (NCN). Jerzy Szwagrzyk reports a relationship with Polish National Science Foundation (NCN) that includes: funding grants. Not yet has patent pending to -. There is no conflict of interest to be disclosed

Data availability

Data will be made available on request.

Acknowledgement

The research leading to these results received funding from the Polish National Science Foundation (NCN) grant No. 2018/31/B/NZ8/02786 (project title: "How do large-scale disturbances influence the relationship between herbivory and natural regeneration in temperate forests?"), Ministry of Science and Higher Education of the Republic of Poland in frame of statutory activities SUB/040011-D019/2020 of Department of Forest Biodiversity, University of Agriculture in Krakow.

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Article Influence of Soil Quality on the Browsing Intensity of Ungulate Herbivores on Tree Species in European Forests

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Abstract: The impact of ungulate browsing on tree saplings has been found to have a negative effect on the regeneration of temperate forests. However, it remains ambiguous whether a relationship exists between browsing intensity and soil quality in natural forests. Therefore, we conducted a study in Roztoczańskie National Park to investigate the relationship between soil quality and browsing intensity for tree saplings. The aim was to gain a better understanding of how soil quality affects the browsing of ungulates on tree species. Baseline data (sapling height, basal diameter, crown length and width, browsed-shoot diameter, and soil samples) were collected from the 22 belt transects established in the permanent research plots. The soil quality index was calculated using physical and chemical soil properties. Twig dry mass was determined using allometric equations. Species relative density and browsing intensity were assessed through field measurements. Relationships between the variables were established using a linear regression model. The results suggest that browsing intensity is influenced by the gradient of the soil quality index and that it varies between tree species. Along the increasing soil quality gradient, tree species' relative density (p = 0.012) and twig dry mass m^{-2} (p = 0.005) significantly decreased for A. pseudoplatanus. In contrast, browsing intensity increased significantly with an increasing species relative density for A. pseudoplatanus (p = 0.00) and *C. betulus* (p = 0.001) and with an increasing twig dry mass for *F. sylvatica* (p = 0.034)and C. betulus (p = 0.004). Browsing intensity increased significantly with an increasing soil quality index for F. sylvatica (p = 0.027) and decreased significantly for A. pseudoplatanus (p = 0.036). Notably, there was a significant positive relationship between browsing intensity and species relative density and twig dry mass, indicating that ungulate browsing is concentrated where browsing is abundant. These results provide insights that can be used to improve management and conservation strategies to protect tree species vulnerable to ungulate herbivory.

Keywords: browsing; soil quality; species density; tree species; twig dry mass

1. Introduction

The impact of ungulate herbivory on ecosystems has been an important ecological concern in Europe [1,2]. This is due to the fact that browsing by wild ungulates plays an important role in the regeneration of forests and the dynamics of tree stands [3–5]. In forests that have experienced natural disturbances, a high ungulate density significantly affects the frequency of browsing on young trees [6] and is often considered to be a threat to tree regeneration [7,8]. Ungulate browsers directly affect the survivorship and recruitment of tree saplings, which in turn can affect ecosystem function [9,10]. Furthermore, selective ungulate herbivory causes unpalatable, chemically defended plants to dominate the ecosystem [11].



Citation: Madalcho, A.B.; Gazda, A.; Wanic, T.; Szwagrzyk, J. Influence of Soil Quality on the Browsing Intensity of Ungulate Herbivores on Tree Species in European Forests. *Forests* 2024, *15*, 708. https://doi.org/ 10.3390/f15040708

Academic Editor: Giovanna Battipaglia

Received: 13 February 2024 Revised: 26 March 2024 Accepted: 15 April 2024 Published: 17 April 2024



Copyright: © 2024 by the authors. Licensee MDPI, Basel, Switzerland. This article is an open access article distributed under the terms and conditions of the Creative Commons Attribution (CC BY) license (https:// creativecommons.org/licenses/by/ 4.0/). Browsing intensity on tree saplings is determined by several factors, including the presence of forest gaps, tree composition, elevation, former management, and soil properties [12–14]. In particular, studies have shown that browsing intensity on specific tree species is indirectly impacted by the prevailing soil conditions [12]. Other reports suggest that soil quality may influence the response of plant communities to browsing by wild ungulates [15–17].

The logic in this regard is that soil is a center for the process of material and energy exchange and circulation in terrestrial ecosystems. It provides the water and nutrients necessary for plants to grow and develop, thus influencing tree regeneration [18,19].

Soil nutrient status is highly related to vegetation growth and plant diversity [20,21] and may also lead to a shift in community composition [22]. Thus, soil quality operates as a filter for the pool of species that can flourish in a specific location. For instance, poor soils may lead to lower quality and quantities of browse, which can, in turn, increase browsing intensity on individual plants [4,23]. Indirectly, soil conditions influence the share of various tree species in the forest canopy, thus altering light availability on the forest floor. Shade-tolerant tree species dominate the forest canopy in nutrient-rich ecosystems, allowing less light to reach the forest floor [24]. In contrast, shade-intolerant tree species usually form the canopy layer in poorer habitats, and the amount of light beneath their canopies is greater. As a result, forest floor vegetation in poorer habitats may be more productive and have higher biomass than that in richer environments [25,26], which, in turn, can affect ungulate browsing relations. Niche theory predicts that plant species are adapted for survival and growth in a particular environment and have different habitat preferences [27,28], and their variation is expected elsewhere.

Many studies have examined the effects of forest cover and specific tree species on soil properties [23,29–32]. Others have investigated the effects of ungulate browsing on soil properties in general [33] and on soil organic matter and nutrient cycling [34].

However, the effect of soil quality on the intensity of ungulate browsing on saplings in temperate forests has not been well studied and, where it has been studied, the reports have been inconsistent. There are conflicting results in the existing literature. While some studies have suggested that soil properties indirectly affect the amount of browsing on certain tree species, others have found no significant effects [6,18,35,36]. This discrepancy indicates that there is a gap in our knowledge of the precise mechanistic relationship between soil quality and browsing intensity by wild ungulates in natural forest ecosystems, and generalizations have remained elusive.

Thus, the novelty of this study lies in answering the following questions: (1) Does the impact of ungulate browsing on different tree species vary across a gradient of soil quality? (2) Does soil quality along with the species identity of a tree affect the intensity of browsing and reduce the risk of the elimination of palatable species due to ungulate browsing pressure? We used a novel approach to investigate the relationship between browsing intensity on tree seedlings and soil quality. Because this relationship was investigated in depth by assessing the measurable values of browse abundance, this study can be replicated on a large scale and used for generalizations. Answering these questions is also important to improve our understanding of the complex interactions between ungulate browsing and soil quality and inform practical efforts to manage and conserve natural ecosystems. To answer these questions, we formulated two hypotheses:

Hypothesis 1 (H1). Ungulate browsing on tree saplings is less intense on fertile soils because of higher vegetation productivity and higher availability of fodder.

Hypothesis 2 (H2). In temperate forests, where light availability plays a major role in the development of ground vegetation, browsing on woody plants is more intense on fertile soils, because ground vegetation is sparse.

2. Materials and Methods

2.1. Study Site Description

This research was carried out in Roztoczańskie National Park, situated in the Roztocze region of Poland, where more than 95% of the park's expanse is covered by forests. This park covers 8483 hectares and is divided into five strict protection zones. The park experiences an average yearly air temperature within the range of 7.4–7.5 °C, coupled with an annual precipitation of 600–650 mm [37]. The highest elevation in the region is 360 m above sea level.

Within the natural forest stands of Roztoczańskie National Park, the European beech (*Fagus sylvatica*) and Silver fir (*Abies alba*) are notably abundant tree species, regenerating naturally. European hornbeam (*Carpinus betulus*), Sycamore maple (*Acer pseudoplatanus*) and Rowan (*Sorbus aucuparia*) occur mostly as admixtures but are also present among the younger generations of trees [38]. Furthermore, this national park serves as a habitat for various herbivores, such as red deer, roe deer, and wild boar, as well as all the major carnivores characteristic of Central Europe. According to unpublished official data for the study area, in 2019, there were 380 red deer and 360 roe deer. In 2021, the number of red deer increased to 400, while the number of roe deer decreased to 277.

2.2. Study Design and Plot-Level-Data

A total of 22 belt transects were established in the years 2020–2022 to study the relationship between ungulate herbivores' browsing intensity on tree saplings and soil properties (Figure 1). Each transect had a width of 5 m and a length of 30 m. Within these designated areas, tree saplings ranging in height from 0.5 m to 3 m were measured. For each tree species, a maximum of 30 individual saplings (located closest to the long axis of the transect) were examined. Accordingly, a total of 1060 tree saplings of all species showing signs of recent (within a year) browsing were found in all transects. The measurements conducted on saplings included sapling height (cm), basal diameter (mm), diameter of the browsed shoot (mm), crown length (cm), and maximum crown width (cm). Furthermore, any visible signs of browsing, such as bite marks on the top and side branches of the saplings with a diameter greater than 1 mm, were recorded, with a maximum of 50 browsing signs being tallied for each sapling within a transect.

Concurrently, soil samples were collected from the same transects to investigate the correlation between soil properties and the browsing potential of various tree saplings from different species. For each transect, the parent material is similar. The general characteristics of the tested soils are mineral soils with light grain size (from loose sand to sandy loam). In each transect, two soil samples (one soil sample at each of the 15 m intervals along the 30 m belt transect) were taken. The soil on the forest floor contains a considerable amount of undecomposed and partially decomposed litter. Therefore, soil samples were taken after the litter cover had been removed. Due to the varying thickness of the soil horizons at different locations of a transect, samples were taken from the top 30 cm of soil depth, which included the A horizon. These individual samples were then combined to form a single representative aliquot.

2.3. Data Generation and Soil Lab Analysis

The species density was calculated by using the number of saplings and the transect area (30 m \times 5 m). Then, the relative density was calculated by dividing each species' density by the sum of all species' densities per transect and multiplying the result by 100 (Equations (1) and (2)).

Tree species density	$\dots\dots\dots SD = \frac{n_i}{A}$	(1)
Tree species relative density	$\dots \dots RD = \frac{SD_i}{\sum SD_i} * 100$	(2)



Figure 1. The map of the transects located in the forest area in Roztoczańskie National Park. The red dots stands for the transects used for data collection in each of the permanent research plots.

SD stands for the species density, ni is the number of individuals of the i-th species per transect, A is the transect area (150 m²), and RD is the relative density of the i-th species per transect.

According to the results of our earlier studies, there are huge differences in the intensity of browsing among tree saplings. In some instances, we recorded up to fifty browsed shoots per sapling, while there were only single shoots that had been browsed in other cases. Therefore, we needed a quantitative measure of browsing intensity; we took into account both the number of browsed shoots and their thickness (as a proxy for their mass) and related these values to the sapling size (with the squared basal diameter of sapling serving as a proxy for the total dry mass of a plant). Browsing intensity index (BI) was calculated using the following formula (Equation (3)).

Browsing intensity index BI =
$$\sum_{i=1}^{N} \frac{d_i^2}{D^2}$$
 (3)

where d is the diameter of the browsed shoot (mm), N is the number of browsed shoots per plant, and D (mm) is the basal diameter of the tree sapling (mm). As a result, the sum of the BIs and mean BI for each species per transect were calculated.

The measurements taken for tree saplings, such as height (cm), basal diameter (mm), crown length (cm), and crown width (cm), were employed to compute the total dry mass of twigs for each species per transect and then per m². This computation was carried out using newly established allometric equations specific to the particular tree species and study location [39].

The soil samples were subjected to laboratory analyses to determine factors such as soil textures, soil reaction, organic matter content (OC), and various soil chemical attributes like nitrogen (N), phosphorus (P), calcium (Ca), magnesium (Mg), and potassium (K) content. These analyses were conducted according to established soil laboratory procedures in the Geochemistry of Forest Environment and Reclaimed Areas (Department of Ecology and Silviculture) laboratory at the University of Agriculture in Krakow, Poland.

The soil samples were air-dried and sieved through a 2.0 mm sieve. The pH of the samples was measured in H₂O (pHH₂O) and a 1 M KCl solution (pHKCl) (soil/liquid ratio 1:5, v/v) using a digital pH meter (CPC-411, ELMETRON) at 20 °C. Exchangeable acidity (EA) was determined in 1 M of Ca(OAc)2; the basic exchangeable cations (Ca²⁺, Mg²⁺, K⁺, and Na⁺) were determined in 1 M of NH4Ac using ICP-OES (iCAPTM 6000 Series). The cation exchange capacity (CEC) was determined by calculating the sum of exchangeable cations and exchangeable acidity (EA). Organic carbon (OC) and total nitrogen (N) content were measured using a LECO TruMac[®] CNS analyzer. The percentage of base saturation (BS%) was computed by multiplying the sum of basic exchangeable cations by 100 and then dividing the resulting value by the cation exchange capacity (BS% = BEC * 100/CEC). C:N ratio, and N²/C were calculated based on existing values. Soil texture was analyzed with a Fritsch GmbH Laser Particle Sizer ANALYSETTE 22. Bulk density was calculated based on the soil depth and organic carbon content, employing the formula developed by [40]:

Bulk density of the soil
$$D = 1.3773 * Exp(1)^{-0.054/*x}$$
, (4)

where D stands for the soil bulk density (g m⁻³), and x stands for the content of organic carbon (%).

Soil properties were then used to calculate the soil quality index (SQI). The method of calculating the SQI was developed for soil profiles that are 1.5 m deep. As our samples were taken from the upper 30 cm of the soil profile, the content of fine fractions (grains <0.02 mm), base cations (Ca, Mg, K, and Na), and soil acidity obtained from our analyses were then multiplied by 5 to make them comparable with the SQI values obtained based on regular soil profiles according to the approach described in [41].

The soil quality index was considered to be the main factor influencing the relative density of tree species and browse availability per m². These relationships were thus, used to test the relationship between the soil quality index and the browsing intensity of tree saplings by ungulates. The SQI values were interpreted based on the descriptions (Table 1).

Table 1. The table describes soil quality index ranges, and the corresponding forest habitat types.

Soil Quality Range	Forest Habitat Type	Trophic Variety of Soil Subtype
SQI of 4 to 13	Coniferous forests	Dystrophic
SQI of 14 to 23	Mixed coniferous forests	Oligotrophic
SQI of 24 to 33	Mixed deciduous forests	Mesotrophic
SQI of 34 to 40	Deciduous forests	Eutrophic

2.4. Statistical Analysis

In order to draw conclusions on the relationship between browsing intensity and soil quality index, we used the relationship of relative density of tree species and twig dry mass (g) with soil quality index as important indicators. Therefore, tree species' relative density and twig dry mass (g) were fitted to the soil quality index across soil quality gradients one by one. These variables, which indicate the level of browse abundance, were then fitted to ungulate browsing intensity on the saplings. The relationship between the soil quality index and browsing intensity was analyzed by fitting the data with the linear model.

The linear regression model was used in this study because it makes it easier to interpret complex relationships and multiple comparisons. It is used to estimate the relationship between an independent variable and a dependent variable. This model has been applied in similar data analyses [32,34,42]. The linear model with the Ordinary Least Squares method was used based on the assumptions of a normal distribution, independence between variables, and equal variance across the regression line. Hence, the normality of the data was checked using the Shapiro–Wilk test, and for those variables that were not normally distributed, log transformation was conducted.

The goodness of fit of the regression was determined using beta coefficients as well as the adjusted R^2 . To control for the family-wise error rate (FWER) when performing multiple comparisons, the Bonferroni correction was used, which adjusts the significance level (α). All of the statistical computations were executed using the R programming language (version R4.3.1).

3. Results

3.1. The Relative Proportion of Tree Species and Descriptive Summary of the Soil Properties

During the field measurements, several tree species were noted within the transects. However, we focused on five specific tree species that were abundant enough to permit statistical analyses: *A. alba, A. pseudoplatanus, C. betulus, F. sylvatica,* and *S. aucuparia.* Nevertheless, these species were not evenly distributed throughout the forest community; *F. sylvatica* (53%), *C. betulus* (25%), and *A. pseudoplatanus* (14%) were the predominant tree species in most of the transects (Figure 2).



Figure 2. Relative proportions of tree species among the surveyed saplings.

The ascertained soil properties (Table 2) were used to derive the soil quality index for our study plots. The table below also describes the chemical and physical properties of the soil in our study transects.

Variable	Mean	SE	Med.	SD.	Var.	Kurtosis	Skewness	Range	Minimum	Maximum
pH_H ₂ O	4.350	0.097	4.353	0.454	0.206	-0.691	0.183	1.640	3.545	5.185
pH_KCl	3.953	0.102	4.005	0.479	0.230	0.102	-0.168	2.005	2.860	4.865
Ca	3.424	0.657	2.409	3.080	9.485	1.386	1.476	10.406	0.383	10.789
Κ	0.300	0.045	0.243	0.212	0.045	-0.562	0.673	0.677	0.061	0.738
Mg	0.250	0.037	0.223	0.172	0.030	-0.070	0.998	0.555	0.058	0.613
Na	0.037	0.004	0.035	0.020	0.000	-0.451	0.785	0.064	0.017	0.081
BEC	4.012	0.725	3.035	3.399	11.556	1.097	1.374	11.387	0.525	11.912
EA	12.367	2.598	9.632	12.184	148.440	13.581	3.527	56.656	4.814	61.470
CEC	16.378	2.734	12.959	12.822	164.395	9.126	2.748	57.853	6.283	64.136
BS	22.767	2.955	22.042	13.858	192.056	-0.414	0.477	49.332	2.813	52.145
Ν	0.182	0.029	0.137	0.134	0.018	5.805	2.379	0.549	0.080	0.629
OC	3.201	0.770	2.010	3.613	13.056	7.982	2.879	14.561	1.181	15.742
C:N	13.852	0.745	12.987	3.493	12.202	3.221	1.822	13.312	10.206	23.518
N ² :C	0.011	0.001	0.010	0.006	0.000	0.941	1.260	0.020	0.005	0.025
Sand	76.364	3.368	83.250	15.799	249.600	-1.592	-0.380	44.500	49.000	93.500
Silt	19.932	2.867	13.750	13.447	180.817	-1.495	0.428	39.000	5.500	44.500
Clay	3.705	0.517	3.000	2.423	5.873	-1.783	0.249	6.500	1.000	7.500

Table 2. A descriptive statistical summary regarding the soil. SE stands for standard error, SD stands for standard deviation, and var stands for sample variance.

3.2. Relationship between Soil Quality Index, Tree Species Relative Density, and Browsing Intensity

The relationship between the soil quality index and the relative species density showed variation among tree species (Figure 3a). The relative densities of *F. sylvatica* and *C. betulus*, which were distributed across the whole range of habitats, tended to increase from poorer to richer soil quality. In contrast, the relative densities of *A. alba* and *S. aucuparia* tended to decrease and their distribution was restricted to locations with poor soil quality. However, neither of the aforementioned relationships were statistically significant. On the other hand, the relationship for *A. pseudoplatanus*, which was distributed from moderate to rich soils, was significantly decreased along the soil quality gradient with 95% confidence (Table 3(a)).



Figure 3. The relationship between soil quality and tree species relative density (**a**) and relative density and browsing intensity per species per transect (**b**).

(a) Species Relative Density Predicted Using the Soil Quality Index									
Species	Explanatory Variable	Estimate	Std. Error	t Value	Pr (> t)	Adj. <i>p</i> Value	Adj. R ²		
A. pseudoplatanus	(Intercept)	144.13	29.434	4.897	0.001 ***		0.6247		
	Soil quality index	-4.328	1.03	-4.201	0.002 **	0.012 *			
F. sylvatica	(Intercept)	25.694	24.46	1.05	0.306		0.02297		
	Soil quality index	1.178	0.964	1.222	0.236	1.000			
S. aucuparia	(Intercept)	35.756	43.235	0.827	0.56		-0.4333		
	Soil quality index	-1.442	2.293	-0.629	0.643	1.000			
C. betulus	(Intercept)	12.849	25.602	0.502	0.626		-0.03806		
	Soil quality index	0.679	0.908	0.748	0.47	1.000			
A. alba	(Intercept)	164.358	91.109	1.804	0.169		0.2315		
	Soil quality index	-7.379	4.969	-1.485	0.234	1.000			
(b) Bro	owsing Intensity per Specie	es per Transe	ct Predicted U	sing Species	Relative Den	sity			
A. pseudoplatanus	(Intercept)	-0.239	0.538	-0.444	0.667				
	Species relative density	0.188	0.016	11.622	0.000 ***	0.000 ***	0.931		
F. sylvatica	(Intercept)	2.179	1.227	1.776	0.091.				
-	Species relative density	0.028	0.02	1.4	0.177	0.884	0.044		
S. aucuparia	(Intercept)	0.065	0.021	3.093	0.199				
	Species relative density	0.077	0.002	45.09	0.014 *	0.071	0.999		
C. betulus	(Intercept)	-1.576	1.472	-1.071	0.307				
	Species relative density	0.222	0.041	5.424	0.000 ***	0.001 ***	0.703		
A. alba	(Intercept)	0.521	0.652	0.799	0.482				
	Species relative density	0.036	0.015	2.306	0.104	0.522	0.519		

Table 3. The relationship between soil quality and tree species relative density (**a**) and relative density and browsing intensity (**b**).

Significance codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1.

The relationship between the relative density of tree species and total browsing intensity per transect (Figure 3b) was strongly positive for *A. pseudoplatanus* and *C. betulus*, corresponding to a 99.9% confidence level, while that for *S. aucuparia* was significant at a 90% confidence level. For *F. sylvatica* and *A. alba*, on the other hand, browsing intensity did not change significantly with an increasing species relative density, although a high value of the adjusted R-squared (51.9%) indicates the better fit of the regression model in the case of *A. alba* (Table 3(b)).

The relationship between mean browsing intensity and the relative density of the species varied between tree species (Figure 4). Table 4 shows that there was a strong positive relationship between relative density and mean browsing intensity in the case of *A. pseudoplatanus*, whereas for *S. aucuparia* and *A. alba*, the relationship was negative and weakly significant, corresponding to a 90% confidence. However, according to the Bonferroni correction test for multiple comparisons, the relationship between relative density and mean browsing intensity of tree species was not significant for all species except *A. pseudoplatanus*.

Table 4. Relationship between a relative density of tree species and mean BI for a given species in a transect.

Species	Explanatory Variable	Estimate	Std. Error	t Value	Pr (> t)	Adj. <i>p</i> Value	Adj R ²
A. pseudoplatanus	(Intercept)	0.148	0.034	4.392	0.002 **		
	Species relative density	0.004	0.001	3.782	0.004 **	0.021 *	0.571
F. sylvatica	(Intercept)	0.12	0.036	3.293	0.004 **		
·	Species relative density	0	0.001	0.611	0.548	1.000	-0.031
S. aucuparia	(Intercept)	0.203	0.002	115.76	0.006 **		
	Species relative density	-0.002	0	-12.34	0.052	0.257	0.987
C. betulus	(Intercept)	0.209	0.06	3.497	0.005 **		
	Species relative density	0.002	0.002	1.05	0.316	1.000	0.008
A. alba	(Intercept)	0.406	0.079	5.113	0.015 *		
	Species relative density	-0.005	0.002	-2.406	0.095	0.476	0.545

Significance codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1.



Figure 4. The relationship between the relative density of species and the mean browsing intensity of species per transect.

3.3. The Relationship between Soil Quality Index, Twig Dry Mass and Browsing Intensity

The species-specific relationship between soil quality and the dry mass of twigs m^{-2} for *A. pseudoplatanus* was significantly negative at the 95% confidence level, while it was weakly positive at the 90% confidence level for *F. sylvatica* (Table 5(a)). For the rest of the species, the relationship was not statistically significant despite a rapid decrease along the soil quality gradient in the case of *A. alba* (Figure 5a).



Figure 5. The relationship between soil quality index and total twig dry mass of tree species m^{-2} (**a**) and between the total twig dry mass of tree species m^{-2} and browsing intensity on tree species (**b**).

(a) Total Twig Dry Mass of Tree Species (g) m^{-2} Explained by the Soil Quality Index									
Species	Explanatory Variable	Estimate	Std. Error	t Value	Pr (> t)	Adj. <i>p</i> Value	Adj. R ²		
A. pseudoplatanus	(Intercept)	2.480	0.449	5.529	0.000 ***		0.6923		
	Soil quality index	-0.076	0.016	-4.847	0.001 ***	0.005 **			
F. sylvatica	(Intercept)	0.289	0.271	1.065	0.300		0.2105		
·	Soil quality index	0.027	0.011	2.569	0.018 *	0.091			
S. aucuparia	(Intercept)	0.570	0.816	0.698	0.612		-0.5718		
	Soil quality index	-0.023	0.043	-0.522	0.694	1.000			
C. betulus	(Intercept)	0.072	0.098	0.729	0.481		-0.0819		
	Soil quality index	0.001	0.003	0.303	0.768	1.000			
A. alba	(Intercept)	3.197	1.867	1.712	0.185		0.2006		
	Soil quality index	-0.144	0.102	-1.416	0.252	1.000			
(b) Browsin	ng Intensity of Tree Specie	s Explained l	y the Total T	wig Dry Mas	s of Tree Spec	ies m $^{-2}$			
A. pseudoplatanus	(Intercept)	1.221	1.476	0.827	0.430		0.430		
	Twig dry mass (g) m ^{-2}	8.035	2.748	2.924	0.017 *	0.084			
F. sylvatica	(Intercept)	-0.362	1.434	-0.252	0.803		0.279		
•	Twig dry mass (g) m^{-2}	4.220	1.398	3.020	0.007 **	0.034 *			
S. aucuparia	(Intercept)	0.114	0.053	2.149	0.277		0.993		
	Twig dry mass (g) m^{-2}	4.272	0.249	17.185	0.037 *	0.185			
C. betulus	(Intercept)	-0.646	1.215	-0.532	0.605		0.741		
	Twig dry mass (g) m^{-2}	60.334	10.141	5.949	0.000 ***	0.004 ***			
A. alba	(Intercept)	0.631	0.692	0.912	0.429		0.429		
	Twig dry mass (g) m ^{-2}	1.682	0.840	2.002	0.139	0.695			

Table 5. Statistical summary of the relationship between soil quality index and mean twig dry mass of tree species m^{-2} (**a**) and between mean twig dry mass of tree species m^{-2} and browsing intensity on tree species (**b**).

Significance codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1.

According to the adjusted *p*-values (Figure 5b), the browsing intensity of ungulates on the tree species increased significantly with an increasing twig dry mass m^{-2} for *F. sylvatica* and *C. betulus* at the 95% confidence level and at the 90% confidence level for *A. pseudoplatanus*. However, the relationship was not significant for *S. aucuparia* and *A. alba* (Table 5(b)).

3.4. The Relationship between Soil Quality Index and Browsing Intensity

The results showed variation among the tree species regarding the relationship between the soil quality index and browsing intensity of the tree species (Figure 6). The browsing intensity for *A. pseudoplatanus* per transect significantly decreased along the gradient from moderate to richer soil quality, whereas in the case of *F. sylvatica*, it significantly increased. However, the relationship for the other species was weak and insignificant: positive in the case of *C. betulus* and negative in the case of *S. aucuparia* and *A. Alba* (Table 6).

Table 6. The relationship between soil quality index and browsing intensity of species per transect.

Species	Explanatory Variable	Estimate	Std. Error	t Value	Pr (> t)	Adj. <i>p</i> Values	Adj. R ²
A. pseudoplatanus	(Intercept)	25.845	6.429	4.02	0.003 **		
	Soil quality index	-0.778	0.225	-3.458	0.007 **	0.036 *	0.523
F. sylvatica	(Intercept)	-0.707	2.125	-0.332	0.743		
•	Soil quality index	0.179	0.084	2.143	0.045 *	0.027 *	0.146
S. aucuparia	(Intercept)	2.75	3.381	0.813	0.565		
	Soil quality index	-0.107	0.179	-0.598	0.657	1.000	-0.473
C. betulus	(Intercept)	-0.024	6.611	-0.004	0.997		
	Soil quality index	0.198	0.234	0.843	0.417	1.000	-0.025
A. alba	(Intercept)	7.138	4.284	1.666	0.194		
	Soil quality index	-0.305	0.234	-1.304	0.283	1.000	0.149

Significance codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1.



Figure 6. Relationship between soil quality index and browsing intensity of tree species per transect.

4. Discussion

4.1. Relationship between Soil Quality Index, Tree Species Relative Density, and Browsing Intensity

Our results on the relationship between soil quality index and tree species' relative density showed different responses for different tree species along the soil quality gradients. The increasing tendency of species relative density for *F. sylvatica* and *C. betulus* and the decreasing tendency for *A. alba* and *S. aucuparia*, whose distributions were restricted to poor-quality soil, as well as to medium-to-richer-quality soil for *A. pseudoplatanus*, indicate that soil quality is one of the important factors determining the distribution and abundance of saplings for various tree species. This finding is consistent with a report stating that soil is positively correlated with vegetation richness in coniferous, mixed coniferous, and deciduous forests [42], indicating that soil directly determines the survival and growth of plant species. Similarly, there is some evidence of niche partitioning between silver fir and beech, suggesting that corresponding forests are likely to reach an alternative stable state dominated by beech within a few decades, although many processes may be masked by the avoidance strategy of *A. alba* [43].

The relationship between the relative density of tree species and browsing intensity of tree species per transect provides insight into browse abundance and ungulate attraction to available resources. Our results contrast with the findings in [44], in which it was reported that browsing intensity decreased with increasing winter food availability for deer, calculated as the number of available saplings. In our study, browsing intensity on *A. pseudoplatanus*, *C. betulus*, and *S. aucuparia* saplings increased significantly with an increasing relative density. Browsing intensity on *F. sylvatica* and *A. alba* showed a trend similar to the other species' trends, although the relationship was not statistically significant. This suggests that ungulate herbivores are likely to concentrate their foraging activities in areas with abundant resources, which may vary for different tree species as a function of soil quality. These findings are consistent with the report by [45], which stated that an abundance of browse allows ungulates to spend more time opportunistically foraging in places with ample food supply, thereby increasing the level of damage.

The current findings highlight that soil quality plays a fundamental role in determining the distribution and abundance of tree saplings, which, in turn, influence the browsing intensity for different tree species within their respective soil-quality niches. For example, the higher relative density of *A. pseudoplatanus* in the low–medium soil-quality ranges

is associated with increased browsing pressure, whereas it is lowest in the high soilquality range.

4.2. The Relationship between Soil Quality Index, Twig Dry Mass, and Browsing Intensity

Our findings show a general decrease in browse availability (m^{-2}) along the soil quality gradient, although this relationship is not statistically significant. However, the relationship between soil quality index and browse availability varies between species. This is due to the tree species' habitat preferences in the forest ecosystem [25,42,46]. Accordingly, the browse availability for the two broadleaved species significantly increases for *F. sylvatica*, while for *C. betulus*, the increase along the soil quality gradient was not strongly significant. These two species are distributed over a broad range of soil quality levels and provide higher browse resources in places with higher soil quality. This finding is in agreement with reports by some authors [47,48].

In the case of *A. pseudoplatanus*, which was found in moderate-to-rich soils, a higher availability of browse was found in lower-quality soil, and it declined more rapidly in richer soils. This phenomenon may be due to an increase in competition between tree species and the lower light availability under canopies dominated by shade-tolerant trees in richer soils [49]. In full light, *A. pseudoplatanus* can out-compete beech, but under a dense canopy where light is limited, it can remain a small seedling with high survival and slow growth [50], resulting in low browse availability of this species.

The availability of browse from *A. alba* is limited to poor-to-medium soils. This browse exhibits a higher availability in the lower soil quality ranges, which then decreases with an increasing soil quality index. *S. aucuparia* also follows a similar trend, but the contribution of this species to browse is minimal within the same range of soil quality. This finding suggests that soil quality plays a crucial role in determining the distribution and abundance of browse in forest habitats through the shaping of species' ecological niches in temperate forests [47]. On the other hand, the lower impact of browsing on *A. alba* in nutrient-rich soils is a strong indication that this species is less abundant in fertile habitats, partly due to competition from shade-tolerant species, and this finding agrees with a report that light availability on the forest floor is associated with soil quality [25].

4.3. The Relationship between Soil Quality Index and Browsing Intensity

The range of adaptation to different levels of soil quality varies among tree species. Out of the five tree species analyzed in our study, three (*F. sylvatica*, *C. betulus*, and *A. pseudoplatanus*) cover a broad range of soil quality levels, although *A. pseudoplatanus* does not occur in the poorest-quality soils. The other two species (*A. alba* and *S. aucuparia*) are confined to poorer- to medium-quality soils. This result corresponds to the ecological characteristics of these species [51] but also reflects their abundance within the study area.

The total browsing intensity per species per transect shows a significant negative correlation between the soil quality index and browsing intensity for *A. pseudoplatanus*. This finding indicates that *A. pseudoplatanus* saplings are not only more heavily browsed but also more abundant in habitats with moderate soil quality. As rapid canopy cover is partly explained by soil quality status, browsing intensity was higher under the more open canopies for *A. pseudoplatanus* [52]. The lower density of *A. pseudoplatanus* in transects with high soil quality is probably due to reduced light availability on the forest floor. In rich habitats, the canopy is often very dense and dominated by shade-tolerant species such as *F. sylvatica* and *C. betulus*, potentially leading to a lower density of *A. pseudoplatanus* in such areas. This explanation is supported by the relationship between soil quality, browse availability, and relative species densities revealed in our current study. As a result, following changes in browse access and species composition mediated by soil quality, browsing intensity on tree species gradually shifts from palatable species such as *A. pseudoplatanus* to less palatable species such as *F. sylvatica*.

The positive and statistically significant relationship between the soil quality index and the browsing intensity found for *F. sylvatica* may be due to the increased relative density and twig dry mass (browse availability) of this species in the higher soil quality range. The relationship between the soil quality index and browsing intensity per species per transect is consistent with the results regarding species relative density and browse availability shown in Figures 3a and 5a. On the other hand, *F. sylvatica* and *C. betulus* saplings, two shade-tolerant broadleaved species, are abundant in all transects and increase in number with increasing soil quality. This reflects their preference for moderately rich and rich habitats. They are therefore at the forefront of heavy browsing, as their dominance in richer soils makes them the primary food source for ungulates.

Soil quality is a crucial environmental factor influencing the adaptation of *A. alba* in forest ecosystems and its subsequent browsing pressure with respect to ungulates [53]. In our case, the reduction in browsing intensity for this species in the richer soils is justified by the availability of browse from this species. The majority of *A. alba* saplings are found in poor habitats, although mature trees of the same species are also present as a small admixture in rich habitats. In the case of *A. alba*, which is a very shade-tolerant species, the lack of saplings in the richer habitats is probably unrelated to lower light intensities but is instead related to soil factors, possibly indirectly through interactions with fungi [54,55]. Research on the effect of microsites on *A. alba* survival, density, and ectomycorrhizal status has shown that habitat quality reinforces this interaction. Consequently, sites with an abundance of older regeneration had higher local stand density, lower canopy openness, and lower soil quality [56]. On the other hand, the narrow range of occupied habitats in the case of *S. aucuparia* can be partly explained by the low number of saplings in our sample (with only 12 individuals).

On the other hand, mean browsing pressure on *A. pseudoplatanus* increased significantly with an increasing relative density of the species, which was negatively correlated with the soil quality index. In medium-to-rich habitats, where the relative density of this species decreases, the mean browsing intensity significantly decreases. This may be related to the morphology of the species. *A. pseudoplatanus*, which has few lateral shoots and is even modified by competition in the richer habitats, does not provide much browse for ungulates in comparison to *F. sylvatica* and *C. betulus*, but it can survive under dense canopies [57].

5. Conclusions

In this study, we examined the relationship between soil quality and browsing intensity by analyzing the relationship between soil quality and tree species density, as well as soil quality and twig dry mass, which are indicators of browse availability. The findings confirm that ungulate browsing intensity on the tree species in temperate forests varies depending on the soil quality index. The relationship between the soil quality index and browsing intensity was not significant for A. alba, C. betulus, and S. aucuparia. Nevertheless, in the case of A. pseudoplatanus, this finding supports the original hypothesis that browsing intensity decreases with increasing soil quality. However, this phenomenon is not due to an increased productivity or abundance of food resources for this species. Rather, it was due to the soil quality limitations that hindered growth due to increased canopy closure. Similarly, for *F. sylvatica*, the results provided evidence for the second hypothesis, i.e., that browsing intensity significantly increases with increasing soil quality. The intensity of ungulate browsing on tree species is impacted by soil quality in a species-specific manner as different responses were found among tree species, while the pressure generally increases with increasing browse availability. Furthermore, the soil-quality-mediated changes in browse availability and species composition result in a gradual shift in browsing pressure from palatable tree species such as A. pseudoplatanus to those less palatable like F. sylvatica, thus allowing A. pseudoplatanus to survive and eventually recruit to the forest canopy.

Our method, in which quantitative values of browse are used to correlate browsing intensity with soil quality, is an objective and reliable approach that can be applied in large-scale studies. Additionally, the information in this research is vital for managing tree regeneration in natural forest ecosystems where ungulate herbivores interact with tree recruitment. The relationship between soil quality, browse availability, and browsing intensity is an important consideration in guiding conservation efforts aimed at protecting against and mitigating the impact of ungulate herbivory on tree species. In addition, the results of this research may be useful in developing a conservation strategy, particularly in situations where the regeneration of certain tree species is limited by increasing pressure from wild ungulates in temperate forests.

Author Contributions: All authors (A.B.M., A.G., T.W. and J.S.) contributed to the study in terms of conceptualization, investigation, methodology, data curation, and validation. A.B.M. carried out the formal analysis and visualization and wrote the original draft of the manuscript. J.S. supervised the project activities. All authors have read and agreed to the published version of the manuscript.

Funding: This research was funded by Polish National Science Foundation (NCN) grant No. 2018/31/B/NZ8/02786 (project title: "How do large-scale disturbances influence the relationship between ungulate herbivory and natural regeneration in temperate forests?") from the Ministry of Science and Higher Education of the Republic of Poland within the framework of statutory activities SUB/040011-D019/2020 of the Department of Forest Biodiversity, University of Agriculture in Krakow.

Data Availability Statement: The data in this study are available from the corresponding author upon request.

Acknowledgments: We acknowledge the Polish National Science Foundation (NCN), the Roztocze National Park, and the Department of Ecology and Silviculture for providing the research facilities and resources for this study.

Conflicts of Interest: The authors declare no conflicts of interest.

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Ungulate browsing patterns and forage abundance determine the regeneration of palatable tree species: Using new perspectives in assessing ungulate browsing pressure in temperate forests



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ARTICLE INFO

KeAi

Keywords: Browse abundance Browsing pressure Palatable species Tree regeneration Twig dry-mass Ungulate browsing

ABSTRACT

Herbivorous ungulates are vital elements of forest ecosystems, yet their impact on tree regeneration and forest dynamics is challenging to assess. Despite their significant influence, few studies measure browsing pressure independently of precise ungulate population data. This study aimed to determine the regeneration mechanisms of palatable tree species in natural forest ecosystems by measuring the forage abundance from young trees of focal species and estimating the browsing pressure exerted by ungulates. We analyzed an extensive dataset of 2,838 tree saplings in two national parks in Poland to examine relationships between variables using a zero-intercept linear regression, and multiple linear regression models, and performed parametric and nonparametric tests. We found that the browsing intensity index (BI) is a good predictor of browsing pressure. Both total abundance and twig dry mass loss due to ungulate browsing were more pronounced in shorter saplings, with these effects decreasing as sapling height increased. Picea abies was the most abundant browse source in the Tatra National Park (TNP), whereas Fagus sylvatica dominated in the Roztocze National Park (RNP). Acer pseudoplatanus and Sorbus aucuparia experienced significantly higher browsing pressure in the TNP, whereas Carpinus betulus was more heavily browsed than other species in the RNP. The increase in browse abundance rapidly reduced ungulate browsing pressure on highly palatable tree species. We conclude that despite the high browsing pressure on the palatable species, the contribution of browse from focal species helps to mitigate this pressure and supports their regeneration in the forest canopy. Therefore, this finding provides valuable insights for managing and conserving tree species vulnerable to ungulate browsing in natural forest ecosystems. In addition, the method we used in this study is novel to estimate browsing pressure and assess the recruitment potential of vulnerable tree species; hence, it can be applied in large-scale studies with similar scenarios.

1. Introduction

Browsing of young trees by ungulate herbivores has been recently one of the major issues in forest ecology and management of tree stands (Ammer, 1996; Beguin et al., 2016; Bödeker et al., 2021a, 2021b; Clasen et al., 2015). With the increasing numbers of ungulate herbivores throughout temperate regions of many countries, the problem with the regeneration of palatable tree species increases rapidly (Boulanger et al., 2009; Čermák et al., 2009). In certain conditions, browsing activity can even outweigh the consequences of climate change by altering the dynamics of forest regeneration (Champagne et al., 2021) and inducing profound compositional and structural changes in forests (Didion et al., 2009; Holm et al., 2013). The problem has been usually addressed by looking at the densities of ungulate herbivores and trying to determine the maximum density that allows for the successful regeneration of trees (Horsley et al., 2003; Tremblay et al., 2007).

However, the browsing pressure exerted by herbivores also depends on the number of young trees available for browsing (Brandner et al., 1990; Mclaren and Peterson, 1994). Browsing interactions on trees can be influenced by the functional nature of forage resources, which can be explained by spatial variations in biomass, structure/height, phenology, and species composition (Fynn et al., 2019). The susceptibility of tree saplings to ungulate browsing can be influenced by the co-existing vegetation, growth rates, and variations in their palatability (Boulanger et al., 2009; Heuze et al., 2005). The composition of young-generation

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https://doi.org/10.1016/j.fecs.2024.100288

Received 10 November 2024; Received in revised form 2 December 2024; Accepted 3 December 2024

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trees with palatable species is more likely to be heavily browsed than less palatable species in the forest ecosystem (Borowski et al., 2021; D'Aprile et al., 2020). While some species are actively avoided by browsing animals, others are selectively targeted (Bodziarczyk et al., 2017). Species like the European hornbeam Carpinus betulus, favored by ungulate browsers, possess the ability to offset losses by generating numerous secondary branches (Samojlik and Kuijper, 2013). Consequently, in forest ecosystems facing notable browsing pressure, the prevalence of Carpinus betulus in the new generation of trees tends to rise and other species exhibit slower development and reduced survival rates (Kuijper et al., 2009). Thus, the effects of ungulate browsing vary significantly based on the availability of young trees and the palatability level (Borkowski, 2004; Brandner et al., 1990; Hidding et al., 2012). Several reports describe the palatability level of different tree species: highly palatable tree species include Sorbus aucuparia, Acer pseudoplatanus, Carpinus betulus, and Abies Alba (Borowski et al., 2021; D'Aprile et al., 2020). Less palatable species include Picea abies (D'Aprile et al., 2020) and Fagus sylvatica (Borowski et al., 2021). According to Angst and Kupferschmid (2023), tree species are classified into five palatability levels, with Level 1 representing less palatable species and Level 5 representing highly palatable species.

Besides, research shows that light conditions influence the relationship between herbivore pressure and the growth or survival of young trees. Trees growing in deep shade struggle to compensate for browsing losses, limiting their potential to develop to higher sizes (Kupferschmid et al., 2015; Mårell et al., 2018; Petritan et al., 2009). However, the high pressure from ungulate herbivores can slow down the height growth of young trees and make them available for repeated browsing even in well-illuminated patches for a long time (Churski et al., 2017).

There are different arguments regarding the relationship between browsing intensity and food availability depending on the type of food and observational scale. According to some research, browsing intensity is reduced by increased browse availability from a higher density of patches (Sample et al., 2023). In contrast, Borowski et al. (2021) hypothesized that patches with abundant forage and species diversity attract ungulates and increase the likelihood of browsing on saplings. However, it is challenging to draw general conclusions as the findings are limited by the methodological approaches used.

Thus far, several methods have been used for studying how ungulate browsing affects the regeneration of trees in forest ecosystems. For example, some studies describe the effects of ungulate browsing on trees by considering ungulate species, density, and foraging behavior (Bohdan et al., 2020; Rhodes and St. Clair, 2018; Sample et al., 2023; Shipley and Spalinger, 1995). Others, however, compute confidence intervals rather than browsing intensity (Bödeker et al., 2021a, 2021b), as well as estimate the percentage of edible branches and foliage based on stem base diameter (Bohdan et al., 2020). Furthermore, Akashi et al. (2022) estimated the browsing pressure while accounting for the number of ungulates per area by dividing the number of browsed seedlings per year by the total number of available seedlings.

However, existing methods for assessing the impact of ungulate herbivores on young trees do not provide a complete understanding of the level of damage in natural forest ecosystems. In addition, relying solely on the ungulate population to establish a predator-prey relationship is costly and prone to error due to the open nature of natural forests and the possibility of individual browsers repeatedly visiting the same plant. According to the results of our earlier studies, there are huge differences in the intensity of browsing among tree species (Madalcho et al., 2024), and winter browsing is a continuous process rather than a single event for each sapling (Kupferschmid et al., 2015). Consequently, a customized method is required to close the knowledge gap in determining the browsing pressure that ungulate herbivores exert. Even in situations where the number of ungulates visiting the saplings is unknown, this method aids in understanding how palatable tree species recover under the functional influence of ungulate browsing in natural forest ecosystems.

This study aimed to determine the regeneration mechanisms of palatable tree species in natural forest ecosystems by measuring the forage abundance from young trees of focal species with different palatability levels and estimating the browsing pressure exerted by ungulates.

Our methods involved measuring the total abundance of forage, and the percentage of twig dry mass removed by ungulates for each focal species. Hence, we tested three hypotheses: 1) The relationship between the browsing intensity index (BI) and the percentage loss of twig dry mass to ungulate browsing is significant for focal species. 2) A greater amount of browse availability and higher browsing loss of twig dry mass is at shorter height classes for all focal species. 3) The browsing pressure on the focal palatable tree species decreases with the increase in browse abundance.

2. Methods

2.1. Site description

Tatra National Park (TNP) and Roztocze National Park (RNP) are characterized by a high density of ungulates. The TNP is located in the Carpathian Mountains and covers an area of approximately 21,000 ha. The bedrock consists of limestone and dolomite in the northern part, and gneiss and granite in the southern. The climate in the lower mountain zone is moderately cool, with an annual temperature of up to 5 °C and an annual rainfall of 1,100 mm. The forests of the TNP are dominated by Norway spruce (Picea abies (L.) H.Karst.), European beech (Fagus sylvatica L.) and silver fir (Abies alba Mill.). Among the other species, sycamore maple (Acer pseudoplatanus L.) and rowan (Sorbus aucuparia L.) have been increasing in numbers, especially among the youngest trees. The main forest types are rich beech forests, hygrophilous forests of silver fir and Norway spruce, and forests of silver fir and Norway spruce on acidic substrate (Bodziarczyk et al., 2019; Pielech et al., 2021). The mean density of live trees is 670 individuals per hectare, and the basal area amounts to 27.4 $m^2 ha^{-1}$. The dominant tree species is Norway spruce (88% of the total tree basal area), followed by silver fir (6%) and European beech (3%). Due to the high mortality resulting from windstorms and bark beetle outbreaks, the total amount of coarse woody debris is about 180 $\text{m}^3 \cdot \text{ha}^{-1}$, and 97% of that is Norway spruce. The mortality of canopy trees estimated based on tree volumes amounted to 41% over the last two decades (Bodziarczyk et al., 2019). The guild of ungulate herbivores in the Tatra Mountains consists of chamois (2 ind. km⁻²), red deer (1 ind.·km⁻²), and roe deer (0.5 ind.·km⁻²) (Tatra National Park archives).

The RNP is located in the central part of the meta-Carpathian upland and covers an area of 8,482 ha, 12% of which is under strict protection. The landscape of the Roztocze Highlands is characterized by long chains of Upper Cretaceous limestone hills reaching 390 m a.s.l. and surrounded by thick layers of postglacial deposits, sand, or loess. The mean yearly temperature is about 8.7 °C. The yearly amplitude of the mean temperatures often exceeds 22 °C. The mean annual precipitation is about 700 mm. Out of 40 species native to Poland, 32 naturally occur in the tree stands of the RNP. However, 94% of forest stands consist of three species: scots pine (53% of the total tree volume), silver fir (24%), and European beech (17%). The mean basal area amounted to 37.78 m²·ha⁻¹ (Łukaszewicz et al., 2020). In the RNP the most common herbivores are red deer (5.6 ind.·km⁻²) and roe deer (4.8 ind.·km⁻²) (Borowski et al., 2021).

To assess the amount of browse available from young trees for ungulate herbivores, and the browsing pressure, first we measured young trees in the lab to develop equations that describe the allometric relationships between tree height, stem thickness, and other morphological traits with the dry mass of twigs available for browsing (Madalcho et al., 2024). Second, we set up research plots in the forest as belt transects to measure sapling parameters. Then, we calculated the dry mass of available twigs, the amount of twig dry mass loss to ungulate browsing, and the percentage of twig dry mass loss to ungulate browsing for each tree species by using these measurements and allometric relationships. In this work, a "twig dry mass (g)" stands for a browse abundance, and the "percentage of twig dry mass loss to ungulate browsing (%)" stands for browsing pressure. We classified our focal tree species into three functional groups based on palatability (Angst and Kupferschmid, 2023) to examine the relationship between browse abundance and ungulate browsing pressure. Sorbus aucuparia, Acer pseudoplatanus, Carpinus betulus, and Abies Alba were classified as highly palatable, Fagus sylvatica as moderately palatable, and Picea abies as less palatable tree species.

2.2. Field data collection

At each study site, we set up 22 belt transects. The transects were 30 m long and 5 m wide. They were established using a stratified random approach in areas characterized by extensive tree regeneration, at least 100 m distant from roads and hiking trails, in strictly protected areas or the zone of active management, but not affected by human activities in recent years. Most of them run from the gap to the dense forest (with the forest/gap edge in the middle of the transect).

The forests contain diverse winter food sources like raspberry, blackberry, and blueberry. However, our research focuses on saplings of economically important species in our study areas. We recorded 15 tree species, with six - *Picea abies, Fagus sylvatica, Abies alba, Acer pseudoplatanus, Sorbus aucuparia,* and *Carpinus betulus* - present in sufficient numbers for meaningful statistical analysis. A maximum of 30 saplings (individuals from 0.5 to 3.0 m in height) of each tree species present at the study sites were sampled in each transect. To do that, we put a measuring tape along the long axis in the middle of the transect and then searched for saplings that were closest to the line, measuring distances from the transect axis to the stem base of individual saplings. For less abundant species we measured saplings over the entire transect area and in many cases the number of measured saplings was still less than 30 individuals although all individuals occurring within the transect were measured.

In each sapling, we measured its height, diameter at the stem base, the diameters of all shoots at the point where they were browsed, and the height of this point. We measured only shoots that were fully lignified to avoid the tiny shoots that could have been eaten either by rodents or by birds. In each case, we started recording the browsed shoots from the top of the tree saplings and measured at most 50 browsed shoots per transect for each species. We measured only the new browsing, as the signs of old browsing in some species are hard to identify. Fieldwork was carried out in late spring-early summer of 2020.

2.3. Data processing

We estimated twig dry mass for the saplings using species-specific allometric equations that relate dry mass to height class categories (Madalcho et al., 2023). This approach allowed us to calculate the potential twig dry mass for each tree species at the study sites. The calculation included all saplings of the target tree species, both browsed and unbrowsed, that fell within the height class range defined in our study to determine the total potential twig dry mass per unit area.

The twig dry mass removal due to ungulate browsing was determined using allometric equations based on twig diameter classes (Madalcho et al., 2023). The branches of tree saplings with thicknesses between 2 and 7 mm were classified into five diameter classes: 2, 3, 4, 5, and 6 mm. The vertical distribution of twig dry mass consumed by ungulates was analyzed by grouping measurements into three height classes: ≤ 1 , 1–2, and 2–3 m. These height classes corresponded to the positions where the browsed shoot diameters were measured. The vertical distribution pattern of ungulate browsing was assessed by considering both the diameter of the browsed twigs and the height at which these diameters were measured.

We calculated the percent twig dry mass loss of each species by dividing the actual twig dry mass loss (g) by the total amount of twig dry mass (g) per transect, then multiplying the result by 100. This metric reflects the actual browsing pressure, whereas the BI measures theoretical browsing pressure on each species.

Browsing pressure =
$$\left(\frac{\text{Twig dry mass lost to ungulate browsing }(g)}{\text{Browse abundance }(g)}\right) \times 100$$
(1)

$$\mathsf{BI} = \sum_{i=1}^{N} \frac{d_i^2}{D^2} \tag{2}$$

where d is the diameter of the browsed shoot (mm), N is the number of browsed shoots per plant, and D (mm) is the basal diameter of the tree sapling. As a result, the mean BI values of individual saplings per transect were considered to represent the species-level BI, which was then utilized to assess its relationship with the proportion of twig dry mass removed by ungulates for each species.

The twig dry mass that remained after ungulate browsing was calculated as the difference between the potential total twig dry mass and the twig dry mass consumed by ungulates for each species.

2.4. Data analysis

The relationship between browse availability and ungulate browsing was analyzed using a linear regression model with a zero intercept, reflecting the logical assumption that no browsing can occur without available browse material. The formula y = ax is expressed as $y \sim 0 + ax$. The vertical distribution of twig dry mass (g), the amount of twig dry mass removed by ungulate browsing (g), and the percentage of twig dry mass loss to ungulate browsing (hereafter, browsing pressure) were analyzed using one-way ANOVA, and Bonferroni tests of post-hoc were computed.

We considered a functional group-level analysis to observe the interactive effect of total browse abundance and palatability on the ungulate browsing pressure on the focal tree species. Hence, a multiple linear regression model with an interaction term was used to analyze the effect of browse abundance, species palatability, and their interaction term on ungulate browsing pressure on tree species. This model is often referred to as a two-way interaction model or moderated multiple regression.

Multiple linear regression

$$Y = \beta_0 + \beta_1 X_1 + \beta_2 X_2 + \beta_3 (X_1 X_2) + \varepsilon$$
(3)

where *Y* is the dependent variable (ungulate browsing pressure), *X*₁ is the first independent variable (browse abundance), *X*₂ is the second independent variable (species palatability), *X*₁*X*₂ is the interaction term, β_0 is the intercept, β_1 , β_2 , and β_3 are the regression coefficients, and ε is the error term.

We compared browsing pressure and remaining twig dry mass after ungulate browsing (g) between the study sites for the tree species using a nonparametric test (Mann-Whitney U). Hence, the group with a higher median rank was regarded as having a greater value. The difference between tree species for these variables in each study area was calculated using one-way ANOVA, and post-hoc mean separation was computed with the Scheffé test. The data was analyzed and visualized using Rversion 4.3.1, Statistica (TIBCO-version 14.0.0.15), and Microsoft Excel.

3. Results

3.1. Distribution of total browse abundance at each study site

Fig. 1a and b presents the distribution of browse abundance at each study site and within each transect. For each species, twig dry mass per transect represents the sum of the dry mass of up to 30 individual tree saplings. The distribution of twig dry mass exhibited notable differences



Fig. 1. The distribution of twig dry mass abundance per transect for each tree species in the Tatra National Park (a) and the Roztocze National Park (b). This general overview of transect-level distribution data helps to interpret the species-level analysis.

between the tree species and across the study sites (Fig. 1).

3.2. The relationship between the browsing intensity index (BI) and the browsing pressure

The relationship between BI and the ungulate browsing pressure was strongly significant for all species (Table 1). However, the strength of the relationships between these variables was significantly varied only for *Acer pseudoplatanus* and *Sorbus aucuparia* in the study areas. As a result, a stronger relationship was observed in the TNP than the RNP for these species, whereas there was no significant variation among the study sites for the rest of the focal species (Fig. 2).

3.3. Vertical distribution of twig dry mass abundance and ungulate browsing loss

The total abundance of twig dry mass decreased along the height classes for all species in both TNP and RNP, as short saplings were much more numerous than taller ones. In the TNP, the twig dry mass was distributed over all height classes for all tree species. For *Acer pseudoplatanus* and *Abies alba*, a significantly higher amount of browse was observed in the sapling height of ≤ 1 m, while there was no significant difference between the taller height classes. Also for *Sorbus aucuparia*, *Fagus sylvatica*, and *Picea abies*, the twig dry mass was significantly higher at the sapling height of ≤ 2 m. However, there were no significant differences between the height classes below 1 and 1–2 m (Fig. 3a). In the RNP, twig dry mass was distributed in all height classes for all species except *Acer pseudoplatanus* and *Sorbus aucuparia*, which were not found in heights >2 m. For *Acer pseudoplatanus*, *Sorbus aucuparia*, and *Abies alba*,

twig dry mass was significantly higher at heights ≤ 1 m and decreased with height. In the height classes below 2 m, the twig dry mass (g) was significantly higher for *Fagus sylvatica*, *Carpinus betulus*, and *P. abies*, while it did not differ significantly between the height classes ≤ 1 and 1–2 m (Fig. 3b).

The vertical distribution of twig dry mass loss (g) due to ungulate browsing varied by tree species and study area. In the TNP, *Acer pseudoplatanus, Sorbus aucuparia*, and *Abies alba* showed significantly higher twig dry mass loss (g) at heights ≤ 1 m. In addition, *Acer pseudoplatanus* and *Sorbus aucuparia* experienced browsing damage at taller heights of up to 3 m at this site. On the other hand, for *Fagus sylvatica* and *Picea abies*, there was no significant difference in browsing loss between the shorter height classes, and twig dry mass loss did not extend to 3 m twig height (Fig. 3c). In the RNP, *Acer pseudoplatanus, Sorbus aucuparia*, and *Abies alba* showed browsing loss up to heights of ≤ 2 m with no significant difference between these shorter height classes, while *Picea abies* had damage limited to ≤ 1 m. In contrast, *Fagus sylvatica* and *Carpinus betulus* had significantly higher browsing loss to twig dry mass at ≤ 1 m sapling browsing height, which decreased with height up to 3 m (Fig. 3d).

3.4. Browse abundance and browsing pressure on the focal tree species across forest communities

3.4.1. The effect of browse abundance on ungulate browsing pressure for palatable species

The browsing pressure on highly palatable species decreased rapidly with increasing browse abundance, while pressure on moderately and less palatable species increased gradually as browse abundance increased (Fig. 4).

Table 1

A zero-intercept linear model for the association between browsing intensity index (BI) and the percentage of twig dry mass of a sapling eliminated by ungulate browsing. BI as a predictor variable was used to estimate the ungulate browsing pressure at each of the study sites.

Species	Study sites	Predictor	Estimate	Std. Error	<i>t</i> value	Pr(> <i>t</i>)	Adj. <i>R</i> ² (%)
Acer pseudoplatanus	TNP	BI	77.459	3.061	25.300	0.000***	69.840
	RNP	BI	46.382	2.477	18.730	0.000***	71.710
Fagus sylvatica	TNP	BI	17.397	1.554	11.200	0.000***	69.730
	RNP	BI	18.055	0.435	41.490	0.000***	77.130
Sorbus aucuparia	TNP	BI	29.689	1.326	22.380	0.000***	49.120
	RNP	BI	8.348	0.888	9.398	0.000***	87.040
Carpinus betulus	RNP	BI	173.753	5.909	29.400	0.000***	81.890
Abies alba	TNP	BI	14.275	0.583	24.480	0.000***	65.430
	RNP	BI	14.088	1.279	11.020	0.000***	69.040
Picea abies	TNP	BI	17.084	1.529	11.170	0.000***	54.840
	RNP	BI	27.192	3.444	7.895	0.001***	91.090



Fig. 2. Zero-intercept linear model for the relationship between BI and ungulate browsing pressure: Comparison between the RNP and the TNP.



Fig. 3. The vertical distribution of total twig dry mass availability (**a** and **b**) and the twig dry mass loss by ungulate herbivores (**c** and **d**) is categorized into three height classes: ≤ 1 , 1–2, and 2–3 m. The height classes for twig dry mass loss by ungulate herbivores are based on the height at which the twig was browsed. The maximum height of the saplings is 3 m. According to the results of the post-hoc Scheffé test (p < 0.05), different letters indicate significant differences in values within height classes.

The model examined the relationship between browsing pressure and two predictors: browse abundance and palatability, with their interaction being significant. The intercept (18.63) represents the expected browsing pressure when browse abundance increases by zero units and palatability is at its reference level (presumably "high"). For each unit increase in browse abundance, browsing pressure decreased by 0.0022 units for highly palatable species. This effect is statistically significant (p < 0.001). On the other hand, low palatability reduced browsing pressure by 18.20 units compared to the reference level (p < 0.01) and moderate palatability reduced browsing loss by 17.70 units compared to the reference level (p < 0.001).

The interaction terms showed that the effect of browse abundance on browsing pressure varied across palatability levels. For species with low palatability (p < 0.01) and those with moderate palatability (p < 0.001), the effect of browse abundance on browsing pressure was significantly different from that of highly palatable species (Table 2).



Fig. 4. The effect of twig dry mass (the browse abundance) and the species palatability on the percentage of twig dry mass loss to ungulate browsing (browsing pressure) of focal tree saplings.

The effect of browse abundance and species palatability level on browsing pressure of tree species. The coefficients for "low-palatability" and "moderate-palatability" show how these levels differ from the high palatability level.

Variables	Estimate	Std. Error	t value	Pr(> <i>t</i>)
(Intercept) Twig dry mass Low-palatability Moderate-palatability Twig dry mass: Low- palatability Twig dry mass: Moderate- palatability	$18.6300 \\ -0.0022 \\ -18.2000 \\ -17.7000 \\ 0.0022 \\ 0.0023$	1.8450 0.0004 6.0760 4.7160 0.0007 0.0006	10.0970 -5.2850 -2.9950 -3.7520 2.9780 4.0500	0.0000*** 0.0000*** 0.0033** 0.0003*** 0.0034**

3.4.2. Differences in the total browse abundance between the study sites and among tree species

There was a large difference in total browse abundance, measured as twig dry mass (kg) per study site, between the two National Parks. In TNP, the abundance of *Picea abies, Abies alba, Sorbus aucuparia,* and *Acer pseudoplatanus* was much higher than in RNP, where *Fagus sylvatica* was much more abundant. Within the TNP, *Picea abies* had the highest total browse abundance, followed by *Sorbus aucuparia* and *Abies alba*. In contrast, *Acer pseudoplatanus* and *Fagus sylvatica* had very low browse abundance in this park. On the other hand, *Fagus sylvatica* had the highest total browse abundance and spatial distribution in the RNP, followed by *Abies alba* (Fig. 5).

3.4.3. Differences in the ungulate browsing pressure between the study sites and among the tree species

The actual loss of twig dry mass (Fig. 6a) and the percentage loss of twig dry mass due to ungulate browsing (Fig. 6b) were significantly different across the study sites for *Fagus sylvatica* and *Sorbus aucuparia*. *Fagus sylvatica* experienced considerably more browsing loss of twig dry mass in the RNP compared to the TNP. Conversely, *Sorbus aucuparia* experienced significantly more damage in the TNP. The pattern of browsing pressure mirrored the browsing damage observed in both

species. There was no significant difference between the study sites for the other tree species (Table 3).

The browsing pressure exhibited variation among tree species across study sites. In the TNP, *Acer pseudoplatanus* was found to experience the highest level of browsing pressure, followed by *Sorbus aucuparia*. The browsing pressure on *Fagus sylvatica*, *Abies alba*, and *Picea abies* was similar and relatively low, with no significant differences between the three species. At the RNP site, *Carpinus betulus* exhibited notably elevated levels of browsing pressure, while all other tree species demonstrated comparably lower browsing pressure (Fig. 7).

3.5. The remaining twig dry mass after ungulate browsing in different sites and species

Wilcoxon rank sum test results indicated a significant difference in the amount of twig dry mass remaining after ungulate browsing between TNP and RNP for *Fagus sylvatica* and *Sorbus aucuparia* (Table 4). Specifically, *Fagus sylvatica* had significantly more twig dry mass remaining in RNP, while *Sorbus aucuparia* had significantly more in TNP (Fig. 8). However, no significant differences between the study sites were observed for *Acer pseudoplatanus* and conifers.

The comparison among the species showed that *Picea abies* had a much higher dry mass of twigs left after ungulate browsing followed by *Sorbus aucuparia* and *Abies alba* in the TNP, while *Acer pseudoplatanus* had a significantly lowest twig dry mass. Whereas in the RNP, the dry mass of the remaining twigs of *Fagus sylvatica* was significantly higher than that of the other species (Fig. 9).

4. Discussion

4.1. The relationship between the browsing intensity index (BI) and the browsing pressure

The browsing intensity index (BI) is a theoretical measure of ungulate browsing pressure on tree saplings. However, the browsing pressure we calculated, reflects the percentage loss of twig dry mass, which directly





Fig. 5. Variations in the total browse abundance across the study sites and among tree species on each site (3,300 m²).



Fig. 6. (a) The actual loss of twig dry mass, and (b) the browsing pressure to ungulate herbivores: Comparison between the two study locations.

Wilcoxon rank sum test with continuity correction was used to compare twig dry mass loss due to ungulate browsing and the browsing pressure between RNP and TNP. A Non-parametric test (Mann Whitney U) (p < 0.05).

Species	Twig dry mass loss ungulate browsing	to (g)	Percentage of twig dry mass loss (%)		
	The sum of ranks (W)	<i>p</i> -value	The sum of ranks (W)	<i>p</i> -value	
Acer pseudoplatanus	69	0.7647	86	0.567	
Fagus sylvatica	158	0.001**	145	0.008**	
Carpinus betulus	-	-	-	-	
Sorbus aucuparia	2	0.004**	2	0.004**	
Abies alba	40	0.629	74	0.063.	
Picea abies	17	0.774	17	0.774	
Overall	2842.5	0.015*	3196	0.000***	

quantifies the actual loss in twig dry mass from what is available for browsing. In terms of practical application, BI is easier to measure in the field, whereas calculating browsing pressure involves a lengthy process. Therefore, the strong positive correlation between BI and ungulate browsing pressure on the tree species suggests that BI stands out as an alternative and simpler method for estimating the actual browsing pressure on tree saplings. The model relationship between these variables is also relevant for large-scale studies of browsing pressure on the tree species. Connecting these variables is necessary to propose a simpler method and to assess the actual browsing pressure, as the proportion of shoots consumed by ungulates offers reliable estimates of food availability and ungulate food consumption (Gaudry et al., 2022). Furthermore, the model is a better fit for *Acer pseudoplatanus* and *Sorbus aucuparia* in the TNP, however, for the rest of the focal species, the quality of capturing the error does not vary across the study sites.

4.2. Vertical distribution of browse abundance and ungulate browsing damage

Browse abundance was greater in shorter saplings (height classes ≤ 1 and 1–2 m) for all focal tree species. This may be due to the higher density of shorter height classes in both areas. The higher density of





Wilcoxon rank sum test with continuity correction for comparison between twig dry mass remaining after ungulate browsing in RNP and TNP. A nonparametric test (Mann Whitney U) with 95% confidence.

Species	Twig dry mass remaining (g)			
	The sum of ranks (W)	<i>p</i> -value		
Acer pseudoplatanus	40	0.055.		
Fagus sylvatica	152	0.002**		
Carpinus betulus	_	_		
Sorbus aucuparia	3	0.007**		
Abies alba	37	0.489		
Picea abies	17	0.779		
Overall	1993	0.2088		



Fig. 8. Comparing the remaining twig dry mass after ungulate browsing between RNP and TNP.

shorter saplings often results from their increased susceptibility to browsing. This density may lead to competition for light, water, and nutrients, and slow the height growth (Bödeker et al., 2023; Nopp-Mayr et al., 2020). The current results support our hypothesis that browsing slows sapling growth and maintains them at shorter heights for longer periods.

In the TNP, browse abundance was distributed across all height classes up to 3 m for each species, but it declined significantly as height increased. This pattern may be due to a historical natural disturbance that created a canopy gap, encouraging the growth of light-demanding broadleaf species. On the other hand, light-demanding species such as *Acer pseudoplatanus* and *Sorbus aucuparia* do not have browse availability above 2 m in the RNP, where natural disturbances are minimal (Fig. 3a

and b). Light availability is critical for sapling growth. Light-demanding species can thrive in canopy gaps created by disturbance, but if these gaps close and browsing pressure remains high, their growth may be restricted (Knapp et al., 2019).

Our results show that the vertical distribution of twig dry mass loss due to ungulate browsing is high on the saplings of all species at shorter heights. However, there is variation in the vertical distribution of browsing loss of twig dry mass among the tree species and between the study sites. This variation is likely influenced by multiple interacting biophysical factors such as elevation, competing sources of browse resources, and the wild ungulate population (Bernard et al., 2024; Hardalau et al., 2024; Pranzini et al., 2024).

We find a consistent pattern between the browse abundance of focal tree species and the vertical distribution of twig dry mass loss from ungulate browsing. Thus, the significantly higher twig dry mass loss from browsing at heights of 1 m or less is observed in *Acer pseudoplatanus, Sorbus aucuparia*, and *Abies alba* in the case of TNP. This finding supports the earlier research, including D'Aprile et al. (2020), which discovered that saplings under 150 cm tall are primarily impacted by ungulate browsing. Similarly, the most heavily browsed group of saplings are shorter ones, according to Szwagrzyk et al. (2020).

Ungulate herbivores, such as deer, play a significant role in shaping forest structure by affecting tree regeneration and growth. Browsing tends to be more intense on shorter saplings because they are within reach of herbivores. This results in slower growth rates and can keep saplings at shorter heights for longer periods, which could increase tree mortality (Bödeker et al., 2023).

However, the results also suggest that the palatability of the species may influence the vertical distribution of dry mass loss of twigs due to browsing by ungulates. For example, for palatable species such as *Acer pseudoplatanus* and *Sorbus aucuparia*, the vertical distribution of twig dry mass loss due to ungulate browsing on tree species reaches heights of up to 3 m. On the other hand, less palatable species such as *Picea abies*, *Abies alba*, and *Fagus sylvatica* do not show browsing incidence at heights above 2 m in the TNP.

In the RNP, browsing is restricted to heights of up to 2 m for *Acer pseudoplatanus* and *Sorbus aucuparia*, resulting in no browsing damage above this height. Nevertheless, the browsing loss of twig dry mass is comparable at height classes ≤ 1 and 1-2 m, suggesting that both species are subject to comparable browsing pressure at these heights. The lack of twig dry mass at a height taller than 2 m for these palatable species may be primarily associated with the influence of high browsing pressure in the past (Kupferschmid et al., 2019; Szwagrzyk et al., 2020), and low light intensity under the forest canopy (De Pauw et al., 2022). In contrast, *Abies alba* and *Picea abies*, which are shade-tolerant, have browse available in all height classes. Rather, ungulate browsers tend to avoid the taller saplings of these species. *Fagus sylvatica* and *Carpinus betulus*,



Fig. 9. Comparison of tree species according to the dry mass of twigs left over after ungulate browsing in each of the study sites (3,300 m²).

however, experience more vertically distributed browse loss due to ungulate herbivores in this forest ecosystem. They suffer significantly greater twig dry mass loss at heights up to 1 m, with a notable decline in loss as the height increases.

In general, the results of vertical distribution of twig dry mass loss to ungulate browsing on tree species indicate that, despite inter-species variation, saplings of palatable species show increased resilience to browsing intensity due to the burden shared by less palatable species. These species contribute by increasing the abundance of alternative browse, and reducing damage to the saplings of palatable species, as observed in the case of TNP (Fig. 3c). Tree species composition and browse availability significantly influence browsing intensity on individual species (Faison et al., 2016; Ohse et al., 2017).

4.3. The relationship between browse abundance and ungulate browsing pressure on the focal tree species across forest communities

4.3.1. The effect of browse abundance on the ungulate browsing pressure on palatable species

The availability of browse resources influences the browsing behavior of ungulates on each tree species. Consequently, as browse abundance for a particular species increases, ungulates tend to exert greater browsing pressure on that species, consistent with the findings of Gaudry et al. (2022).

However, an increase in browse abundance at the community level leads to a decrease in browsing pressure on more palatable species. Highly palatable species experience the greatest baseline browsing loss, but as browse abundance increases, their browsing pressure decreases more rapidly than less palatable species, showing a strong negative relationship between browse abundance and browsing pressure; and it confirms our third hypothesis. This observation supports the argument that browsing pressure decreases as the overall abundance of browse resources increases (Sample et al., 2023). Our result shows that as the total browse abundance of focal species increases, there is a marked decrease in browsing pressure on more palatable species. This effect is particularly pronounced for highly palatable species such as Acer pseudoplatanus, Sorbus aucuparia, Abies alba, and Carpinus betulus, which experience a rapid decline in browsing pressure as total browse abundance increases. In contrast, medium palatable species such as Fagus sylvatica show a more gradual decline in browsing pressure than less palatable species such as Picea abies.

This interaction suggests that an abundance of browse resources plays a critical role in modulating ungulate foraging behavior. When browse is abundant, ungulates distribute their foraging more evenly across available species, potentially reducing the intense pressure on highly palatable species. Conversely, when browse is scarce, highly palatable species bear the brunt of browsing pressure, likely due to their preferred nutritional qualities.

4.3.2. Comparison of browse abundance across study sites and among tree species

The comparison of browse abundance between the two national parks shows differences for each tree species. In particular, the higher browse abundance of *Picea abies, Sorbus aucuparia, Abies alba,* and *Acer pseudoplatanus* in the TNP compared to the RNP can be attributed to differences in forest gaps. In the TNP, most of the transects (95.5%) contain *Sorbus aucuparia,* which thrives in large canopy gaps and open areas, although they are also able to survive under forest canopy, but in stunted form (Hamberg et al., 2015; Petritan et al., 2009; Zywiec et al., 2013; Żywiec and Ledwoń, 2008). The TNP has much larger gaps due to the historic large-scale natural disturbances that have occurred since 2004 on the spruce-dominated forest stand (Pajtík et al., 2015; Sproull et al., 2015). On the other hand, the saplings of *Fagus sylvatica* are distributed in all transects in the RNP (Fig. 1). This shade-tolerant and highly competitive species is also less browsed than the other deciduous tree species and dominates the young generation of trees. In TNP it is less abundant, due to a combination of environmental and historical factors (Pielech et al., 2021). The lower browse abundance of *Sorbus aucuparia* in the RNP may be associated with a high browsing pressure due to the higher herbivore density in the area. Chronic impacts from ungulate browsing can reduce the abundance of palatable tree species by reducing the population density and structural development (Didion et al., 2009). When comparing tree species in the TNP, *Picea abies*, followed by *Sorbus aucuparia* and *Abies alba*, provides a substantial amount of browse, while *Acer pseudoplatanus* contributes the least.

4.3.3. Comparison of ungulate browsing pressure across study sites and between tree species

The ungulate browsing pressure varies across the study sites in the case of Fagus sylvatica and Sorbus aucuparia. The higher browsing pressure on Fagus sylvatica in the RNP may be related to the differences in the distribution of browse and species composition between the study sites following the differences in the canopy gaps. Despite the negative relationship between browse abundance and browsing pressure, the shadetolerant Fagus sylvatica saplings dominate most of the transects in the study area in the RNP and remain the main browse source for ungulate herbivores. Similarly, the highly palatable Sorbus aucuparia experienced more browsing pressure in the TNP than in the RNP, which may be because the distribution of the species was limited to a few transects in the RNP. Different findings show that browsing pressure on tree species in a given site is influenced by the interacting factors, mainly the ungulate population and browsing preference, and the browse abundance and diversity (Bohdan et al., 2020; Candaele et al., 2023; Churski et al., 2017).

However, when comparing ungulate browsing pressure between the tree species, a higher impact was observed on species such as *Acer pseudoplatanus* and *Sorbus aucuparia* in the TNP and *Carpinus betulus* in the RNP. According to Kupferschmid et al. (2019), densities of all species fall when annual browsing surpasses a threshold of 5%–10%. Our findings are also in line with other research (D'Aprile et al., 2020; Konôpka et al., 2018; Sample et al., 2023) which indicates that browsing pressure is especially high on palatable species.

In contrast, *Fagus sylvatica* and *Picea abies* face much lower browsing pressure within each study site than the highly palatable focal tree species. However, the actual loss of twig dry mass due to ungulate browsing is significant for these species at both study sites. This suggests that the moderate and less palatable species contribute considerably to high browse in forest ecosystems, even more than the more heavily browsed palatable species. Thus, this implies that browsing pressure is distributed across all available food resources among tree species, with ungulates exploring a broad range of feeding options regardless of their selectivity.

4.4. Post-browsing remnants: consequences for palatable tree regeneration

Despite the substantial browsing pressure on the tree saplings, the results indicate that some twig dry mass survives the browsing loss in all species, albeit to different extents. Among tree species, Picea abies retains the greatest browse after ungulate browsing in the TNP. Similarly, Fagus sylvatica retains the greatest browse in the RNP. This is likely due to the overall abundance of these species in their respective habitats (Fig. 5). On the other hand, Carpinus betulus and Acer pseudoplatanus were the least abundant, resulting in the smallest residual browse among the species. Although there are differences among forest communities, the high palatability of certain tree species results in greater browsing pressure, and significantly lower the residual browse. This suggests that such browsing pressure may hinder ecological succession, and suppress the growth of young generations following disturbance in natural ecosystems (Didion et al., 2009; Ramirez et al., 2019). Ungulates control the forest composition of regenerating trees by selectively browsing palatable broadleaved trees, leading to the competitive release of conifers (Rooney and Waller, 2003). For example, in TNP, the remaining browse from most broad-leaved deciduous species is less abundant than that of coniferous species after intense browsing. The ungulate browsing pressure may limit changes in species composition following natural disturbance and slow the transition from a historically conifer-dominated forest to one with diverse stands with deciduous species dominance.

However, the findings also show that intense browsing pressure has not eliminated the highly palatable tree species such as *Carpinus betulus* and *Acer pseudoplatanus*. Despite the significantly lower amount of browse remnants of these palatable species, their regeneration can still be found, although in most cases restricted to the lower height classes. This is because the higher abundance of potential fodder provided by less palatable focal tree species mitigates the impact of browsing pressure on palatable trees. Escaping a year of ungulate browsing could enhance survival and recruitment prospects, even though sapling recruitment success is strongly influenced by canopy gap conditions. This is particularly notable because most browsing loss on the saplings for all species, as observed in our study sites, occurs at heights below 1 m and is stronger in RNP.

5. Conclusion

This study presents a novel approach to assess tree regeneration in forest ecosystems by measuring browse abundance and browsing pressure. A relationship was established between the browsing intensity index (BI) and ungulate browsing pressure on tree saplings, allowing the BI to estimate actual browsing pressure on different tree species. Across all species, saplings in the lower height classes exhibit the greatest browse abundance and twig dry mass loss due to ungulate browsing. The impact of ungulate browsing varies greatly between tree species within forest ecosystems. In the TNP, Acer pseudoplatanus and Sorbus aucuparia experienced higher browsing pressure than other species, while Carpinus betulus experienced more intense browsing in the RNP, resulting in a significantly lower dry mass of twigs remaining. In contrast, species such as Picea abies and Fagus sylvatica tend to retain more twigs after browsing, which increases their potential for recruitment into the forest canopy. Despite high browsing pressure, palatable species can thrive and regenerate in forest ecosystems. This resilience is due to the abundant alternative food sources provided by less palatable focal species, which mitigate the effects of ungulate browsing. Because, increasing the overall browse abundance is associated with reducing browsing pressure, particularly for highly palatable species, where this effect is more pronounced compared to less palatable species. The findings have important implications for forest management, particularly in areas where ungulates threaten tree regeneration. Increasing browse abundance may reduce browsing pressure on palatable species, promoting balanced regeneration and biodiversity. From a methodology perspective, previous studies, such as Rhodes and St. Clair (2018) and Sample et al. (2023), have linked ungulate abundance to browsing intensity, with higher browsing intensities associated with higher deer densities. In contrast, this study evaluates ungulate browsing pressure based on twig dry mass loss per species, independent of ungulate abundance. This approach provides a simpler method for estimating browsing pressure and assessing tree regeneration potential, with applications to large-scale forest ecosystem studies. Finally, we suggest a long-term study to examine the combined effects of canopy gaps and species vulnerability levels, strengthening our argument that browse abundance plays a critical role in protecting palatable species from ungulate browsing pressure in natural forest ecosystems.

CRediT authorship contribution statement

Aklilu Bajigo Madalcho: Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. Anna Gazda: Writing – review & editing, Validation, Software. Jerzy Szwagrzyk: Writing – review & editing, Validation, Supervision, Project administration, Methodology, Funding acquisition, Conceptualization.

Data availability

Data will be made available on request.

Funding

This research was funded by Polish National Science Foundation (NCN) (grant No. 2018/31/B/NZ8/02786, project title: "How do largescale disturbances influence the relationship between ungulate herbivory and natural regeneration in temperate forests?") from the Ministry of Science and Higher Education of the Republic of Poland within the framework of statutory activities SUB/040011-D019/2020 of the Department of Forest Biodiversity, University of Agriculture in Krakow.

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Jerzy Szwagrzyk reports financial support was provided by Polish National Science Foundation (NCN), grant No. 2018/31/B/NZ8/02786 (project title: "How do large-scale disturbances influence the relationship between ungulate herbivory and natural regeneration in temperate forests?") from the Ministry of Science and Higher Education of the Republic of Poland within the framework of statutory activities SUB/040011-D019/2020 of the Department of Forest Biodiversity, University of Agriculture in Krakow. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://do i.org/10.1016/j.fecs.2024.100288.

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Publication 3: Madalcho, A. B., Gazda, A., & Szwagrzyk, J. (2025). Ungulate browsing patterns and forage abundance determine the regeneration of palatable tree species: Using new perspectives in assessing ungulate browsing pressure in temperate forests. *Forest Ecosystems*, *12*(November 2024), 100288. <u>https://doi.org/10.1016/j.fecs.2024.100288</u>

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Publication 1: Madalcho, A. B., Szwagrzyk, J., Maciejewski, Z., Gazda, A., & Bodziarczyk, J. (2023). Allometric scaling models for tree saplings: Assessing potential fodder for ungulate herbivores. *Trees, Forests and People, 13*. <u>https://doi.org/10.1016/j.tfp.2023.100424</u>

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