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Light-Induced Height Growth in Tree Regeneration: A Study of Thirteen Species in Swiss Forests

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Abstract

Natural regeneration is crucial for sustainable forest development, and light availability significantly influences the growth and survival of young trees. Different tree species respond in distinct ways to varying light conditions, particularly in terms of height growth. This ability to adapt, alongside shade tolerance, plays a key role in determining species survival in competitive environments. Understanding species-specific responses to changes in canopy openness is essential for forest management and for promoting specific tree species compositions. However, a comprehensive comparison of main tree species in Swiss forests under different light conditions has been lacking. To address this gap, an extensive field study was conducted, sampling more than 2’000 saplings (±30 - 600 cm in height) of different tree species distributed across various light conditions in 39 forest districts. During data collection, special attention was given to covering different elevations and ensuring high biogeographical diversity representative of Swiss forests. Canopy openness was modelled using a recently developed canopy radiative transfer model. A linear mixed-effects model was applied to analyse the relationship between canopy openness and height growth for each species. The model accounted for tree height variability and site characteristics such as understory woody density, productivity, elevation, and forest district differences.

The results revealed significant interspecific differences in growth responses to varying canopy openness. *Picea abies* (L.) H. Karst. demonstrated a strong relative growth response to increased light availability, meaning that this species was able to multiply its height growth by the highest factor with increasing canopy openness. *Acer pseudoplatanus* L., *Fagus sylvatica* L., *Pseudotsuga menziesii* (Mirb.) Franco, and *Tilia cordata* Mill. & *Tilia platyphyllos* Scop. exhibited the largest absolute height growth differences between high and low canopy openness. Moderate growth differences were observed in *Prunus avium* L., *Betula pendula* Roth, and *Quercus petraea* Liebl. & *Quercus robur* L., which already exhibited relatively high growth rates under shaded conditions. In contrast, *Abies alba* Mill., *Pinus sylvestris* L., and *Larix decidua* Mill. showed only a slight increase in height growth in response to improved light conditions. A widely discussed concept in the literature suggests that shade tolerance can be understood as a trade-off between survival probability under low-light conditions and growth potential under high-light conditions. Shade-tolerant tree species are therefore expected to exhibit a high survival probability in shaded environments but relatively low growth rates under favourable light conditions. In contrast, shade-intolerant species are assumed to have lower survival chances in shaded conditions but higher growth rates in high-light environments. In this study, the relationship between species-specific shade tolerance, as documented in the literature, and height growth under high-light conditions was examined. While the expected patterns were confirmed for some tree species, considerable deviations were observed in many cases. Notably, *Fagus sylvatica* L. exhibited a surprisingly high height growth under high-light conditions, despite its well-documented shade tolerance. This indicates that the modelled height growth under high-light conditions does not always align with the species-specific shade tolerance documented in the literature. The substantial differences between species in their height growth response to canopy openness provide valuable insights into their competitive strategies. This knowledge is highly relevant for forest management, as it facilitates the prediction of species-specific responses to canopy interventions and supports decision-making in silvicultural practices.

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Acronyms and Abbreviations

AI	Artificial Intelligence
AIC	Akaike Information Criterion
BIC	Bayesian Information Criterion
FD	Forest District
GAMM	Generalizes Additive Mixed Model
GLMM	Generalized Linear Mixed Model
LMM	Linear Mixed Model
NFI	Swiss National Forest Inventory
RMSE	Root Mean Squared Error
R^2c	conditional R^2
R^2m	marginal R^2
SD	Standard Deviation
SE	Standard Error
UWD	Understory woody density

Tree species:

A. alba	*Abies alba* Mill.
A. pseudoplatanus	*Acer pseudoplatanus* L.
B. pendula	*Betula pendula* Roth
F. sylvatica	*Fagus sylvatica* L.
L. decidua	*Larix decidua* Mill.
P. abies	*Picea abies* (L.) H. Karst.
P. sylvestris	*Pinus sylvestris* L.
P. avium	*Prunus avium* L.
P. menziesii	*Pseudotsuga menziesii* (Mirb.) Franco
Q. petraea	*Quercus petraea* Liebl.
Q. robur	*Quercus robur* L.
T. cordata	*Tilia cordata* Mill.
T. platyphyllos	*Tilia platyphyllos* Scop.

1 Introduction

Natural regeneration is essential for the sustainable persistence of Swiss forests and significantly influences the perception of their ecosystem services (Bachofen, 2009; Brang & Duc, 2002; Bundesamt für Umwelt BAFU, 2022). Light availability affects the survival and growth of tree regeneration and is primarily regulated by canopy density and the composition of the surrounding trees, which determine the degree of shading (Pretzsch et al., 2005). Canopy management, through targeted thinning or gap creation, offers a direct way to influence light conditions, setting it apart from other site factors that are less manageable. Additionally, canopy openness impacts microclimatic conditions, such as temperature and soil moisture, which further influence seedling establishment and growth (Kimmins, 2004). Depending on the extent of canopy cover by larger trees, the competitive pressure on regenerating saplings varies. High canopy openness leads to a dense regeneration layer, where only the most competitive saplings thrive. In contrast, a closed canopy results in sparse regeneration, where limited light conditions can negatively affect the growth of young trees (Ward & Stephens, 1993). Annual height growth is a key and easily measurable indicator to assess the vitality of regeneration. Furthermore, height growth data can provide insights into the growth strategies and competitive abilities of tree species, as tree height, which is directly influenced by height growth, is often a decisive factor for tree survival in regeneration (Macek et al., 2016; Petrovska et al., 2022).

Different tree species show varying occurrence probabilities depending on light conditions. Moreover, it has been observed that the height growth of different tree species depends to varying degrees on light availability. A popular scientific definition that allows for a classification based on shade tolerance considers the growth achieved under high light conditions and mortality rates under low light conditions. It is assumed that there is a trade-off between these two traits: shade-tolerant species exhibit relatively slow growth under favourable light conditions but have low mortality under limited light. In contrast, shade-intolerant species show rapid growth under high light conditions but suffer high mortality under low light (Kobe et al., 1995; Kobe & Coates, 1997; Löf et al., 2007; Pacala et al., 1994; Petritan et al., 2007). This differentiation among tree species is also linked to their distinct niches in the successional process: shade-intolerant species colonize open areas immediately following natural disturbances, whereas shade-tolerant species gradually replace them as the succession progresses (Brzeziecki & Kienast, 1994; Whitmore, 1989).

Silvicultural measures can be used to influence light availability and, in turn, tree regeneration. In Swiss forestry practice – particularly in mountainous regions – it is common to apply regeneration cuts that are specifically adapted to the site conditions and the respective forest community. Brang et al. (2014) describe this management approach as a combination of various close-to-nature silvicultural methods, where interventions are defined based on the specific forest type and its current condition. While in the Swiss lowlands, decision-making authority largely rests with forest owners and local authorities, a significant portion of forests in hilly and mountainous regions—such as the Jura and the Swiss Alps—serve a protective function. This accounts for nearly 50% of Switzerland's forest area (Losey & Wehrli, 2013), where measures are implemented according to both the protective role and the specific forest site to ensure the long-term sustainability of this function (Bundesamt für Umwelt BAFU, 2024; Frehner et al., 2005).

Climate change poses a profound challenge for forest management, with models predicting significant shifts in the distribution of tree species, including potential declines in widespread species such as spruce and beech (Frehner et al., 2018; Zimmermann et al., 2014). In addition to direct impacts, indirect effects like pests, diseases, and forest fires present significant risks

(Rigling et al., 2008). In response to these challenges, research and Swiss forest policy emphasize enhancing species diversity as one out of five key adaptation principles (Allgaier Leuch et al., 2017; Brang et al., 2016; Bundesamt für Umwelt BAFU, 2023). However, in the widely practiced close-to-nature silviculture in Switzerland, particularly under the use of single-tree selection cutting, regenerating shade-intolerant species remains challenging as the created canopy gaps often fail to provide sufficient light, leading to maintained dominance of shade-tolerant species that were often pre-established before cutting (Brang et al., 2014; Brüllhardt et al., 2022; Ligot et al., 2013; Pommerening & Murphy, 2004; Wagner et al., 2010). Given these challenges, a comprehensive understanding of the light-dependent growth responses of various tree species is essential to promote regeneration of a tree species composition adapted to changing climate conditions.

Several studies have already examined the influence of light conditions on the growth of natural regeneration. For the more common and widespread species among the target tree species defined in this study, a solid knowledge base exists regarding their light responses. For instance, Schmid et al. (2021) in the Swiss Alps and Hökkä & Mäkelä (2014) in Finland demonstrated that, in addition to tree height, gap size has a significant impact on the height growth of *Picea abies* (L.) Karst (*P. abies*). Brüllhardt et al. (2020) found in their study on *Acer pseudoplatanus* L. (*A. pseudoplatanus*) and *Fagus sylvatica* L. (*F. sylvatica*) across various Swiss forests that height growth in both species is similarly influenced by light availability. For *Abies alba* Mill. (*A. alba*), Kupferschmid et al. (2013) observed a linear increase in height growth with increasing light availability across three sites in Switzerland. This selection provides only a glimpse into the research focusing on one or two tree species regarding the effects of light conditions on height growth.

In contrast, studies comparing three or more of the target tree species defined in this study are relatively rare. Löf et al. (2007) investigated five of the species included in this study (*F. sylvatica, P. abies, Prunus avium* L. (*P. avium*), *Quercus robur* L. (*Q. robur*) and *Tilia cordata* Mill. (*T. cordata*)) and found that height growth increased in all species with reduced canopy cover. Additionally, for all species except *P. avium*, the observed growth patterns aligned with their shade tolerance ranking. However, it is important to note that this study was conducted as a planting experiment under a *P. abies* plantation rather than on naturally regenerating trees. Ligot et al. (2020) examined the responses of *A. alba*, *P. abies*, and *Pseudotsuga menziesii* (Mirb.) Franco (*P. menziesii*) to varying light conditions alongside other species not included in this study. However, the findings for *P. menziesii* should be interpreted with caution, as growth was severely impaired by pest and pathogen pressure. When comparing *A. alba* and *P. abies*, their study showed that *P. abies* exhibited greater height growth across nearly all light conditions and tree heights. Furthermore, Bebre et al. (2021) conducted a controlled pot experiment with seedlings up to 56 cm in height, including *F. sylvatica*, *P. abies*, and *P. menziesii*. Their results indicated that *P. menziesii* achieved higher relative height growth across all light conditions compared to the other two species. However, the extent to which these ex situ findings can be extrapolated to natural forest conditions remains uncertain.

Despite the valuable insights gained from previous research, most studies have been limited by their local scope, making it difficult to generalize findings across different forest types and regions. Additionally, the light-dependent growth responses of less common tree species remain insufficiently explored. Comparative studies that assess growth responses to light availability across multiple species are also rare. This study seeks to fill these gaps by providing a comprehensive analysis of the growth responses to varying light conditions across a broad range of species distributed across differing environmental areas of Switzerland, thereby contributing to a more nuanced understanding of regeneration dynamics in Swiss forests. Specifically, this study seeks to answer the following research question:

How does light availability, as measured by the degree of canopy openness, affect the height growth of the following 13 tree species in Switzerland: *A. alba, A. pseudoplatanus, Betula pendula* Roth (*B. pendula*), *F. sylvatica, Larix decidua* Mill. (L. decidua), *P. abies, Pinus sylvestris* L. (*P. sylvestris*), *P. avium, P. menziesii, Quercus petraea* Liebl. (*Q. petraea*), *Q. robur, T. cordata and Tilia platyphyllos* Scop. (*T. platyphyllos*)?

2 Methods

2.1 Study sites

Measurements were conducted in a total of 39 different forest districts, covering elevations ranging from 327 to 1'797 meters above sea level (Figure 2). The selection of forest districts was made to ensure a comprehensive representation of the biogeographical diversity of Swiss forests. Additionally, care was taken during site selection to include enough locations where the rarer tree species within the target species group could be measured. When selecting forest areas for measurements, it was ensured that no interventions in the tree layer had taken place since the acquisition of LiDAR data, which were used for modelling light conditions. The same criterion applied to natural events that might have led to changes in the canopy structure. Depending on the region, the LiDAR data were acquired at some point between 2017 and 2023. It was assumed that if no interventions or natural events leading to changes in the canopy had occurred, the canopy structure remained unchanged since the LiDAR acquisition.

With the support of knowledgeable local foresters, specific areas within each forest district were identified to maximize the coverage of different sub-canopy light conditions and to represent the local species diversity as comprehensively as possible. The expertise of the foresters also facilitated the measurement of individuals from less common species that occur only sporadically or in localized populations.

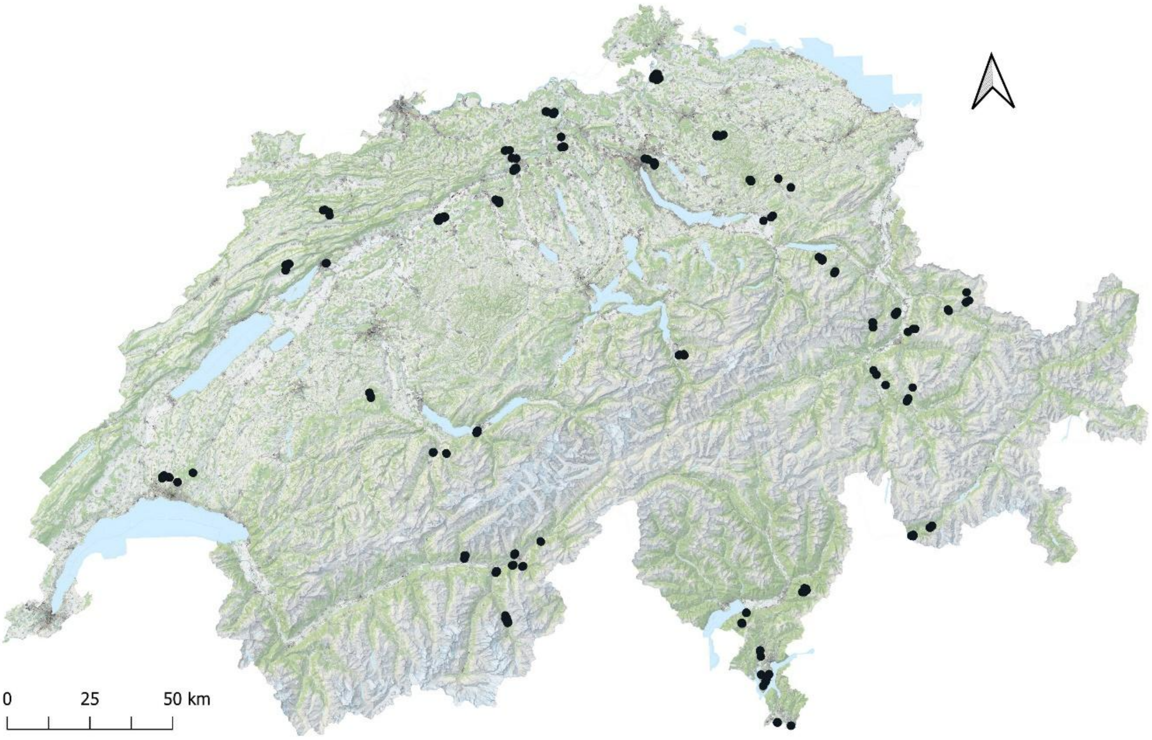

Figure 2: Map showing the distribution of study sites. Basemap from Federal Office of Topography swisstopo (2024a).

2.2 Sampling design

For the measurements, dominant tree individuals were selected, ensuring that the sampled trees exhibited straight growth and showed no visible damage. If individuals with minor damage or other irregularities were measured, this was recorded and later considered in the outlier analysis. Additionally, only trees primarily influenced by competition from the canopy layer were included. Trees affected by strong competitive influences in the understory were excluded, as this type of competition could not be fully captured by the applied light modelling approach.

For the selected individuals, tree height and the terminal shoot length of the current year, and if possible, the last two years were measured. Additionally, coordinates and local productivity values were recorded, and the understory woody density was determined. Tree height and terminal shoot length were measured using a ruler. The effective tree height was measured from the tree base to the tip of the terminal shoot, including the terminal bud. Only trees with a minimum height of 30 cm were measured, and measurements were conducted using a standard folding ruler, with only trees whose height could be accurately determined with this tool included in the dataset. Trees exceeding the measurable height limit were excluded from the analysis. The tallest measured tree was 635 cm. The current year's terminal shoot growth was determined using the scar of the previous year's terminal bud and for deciduous trees the presence of leaves directly emerging from the stem. The height growth of previous years was measured if clearly identifiable through bud scale scars. If lammas growth was present, it was considered in the current year's growth measurement. In such cases, the growth increments of previous years were not recorded due to the high likelihood of measurement errors. Coordinates were recorded using the ppm10xx GNSS receiver, which usually achieves positional accuracy in the range of decimetres (ppm - Precise Positioning Management GmbH, n.d.). If precise coordinates could not be obtained due to poor signal reception, this was noted and considered during outlier analysis. The same procedure was followed when the LiDAR-based canopy height model, which was later used for light modelling, deviated from the actual forest situation due to unrecorded natural or anthropogenic canopy interventions. The foresters provided information on local productivity values, also known as increment values. In the forest districts surveyed in the canton of Ticino, such data were not available, so a value published by the National Forest Inventory (NFI) for the corresponding region was used instead (Abegg et al., 2023). Understory woody density was assessed within a 2-meter radius around the sampled tree by estimating the proportion of the area covered by woody vegetation. A rating of 1 was assigned if coverage was <5%, 2 for 5 - 25% coverage, and 3 for >25% coverage (Table 2). Data collection was conducted from August to October 2024.

The number of forest districts in which individuals were measured varies depending on tree species, as does the number of data points per species. This variation is due to differences in species distribution and abundance (Table 1).

Table 1: Summary statistics for each species showing number of observations (n), number of forest districts (FD n) and averaged values for each fixed effect and response variable including ranges. Predictor abbreviations: FD (Forest district), UWD (Understory woody density). Species abbreviations: A. alba (Abies alba), A. pseudoplatanus (Acer pseudoplatanus), B. pendula (Betula pendula), F. sylvatica (Fagus sylvatica), L. decidua (Larix decidua), P. abies (Picea abies), P. sylvestris (Pinus sylvestris), P. avium (Prunus avium), P. menziesii (Pseudotsuga menziesii), Q. petraea & Q. robur (Quercus petraea & Quercus robur), T. cordata & T. platyphyllos (Tilia cordata & Tilia platyphyllos).

Species	n	FD n	Height growth [cm]		Canopy openness [%]		Elevation [m]		Productivity [m^3/ha/year]		Tree height [cm]		UWD	
			mean	range	mean	range	mean	range	mean	range	mean	range	mean	range
A. alba	207	33	16.0	0.5 - 55.7	22	4 - 87	981.9	397.8 - 1744.2	7.96	1.5 - 13.4	121.6	31 - 362	2.45	1 - 3
A.pseudoplatanus	254	34	35.8	0.5 - 172	23	4 - 84	813.6	343.9 - 1651.9	8.55	1.5 - 13.4	196.6	31 - 543	2.52	1 - 3
B. pendula	151	32	51.9	2 - 147	39	10 - 80	948.2	367 - 1718.4	7.00	1.5 - 13.4	218.1	39 - 582	2.40	1 - 3
F. sylvatica	299	33	23.7	0.2 - 125	19	5 - 84	822.9	365.2 - 1519.4	8.72	3.25 - 13.4	189.4	36 - 431	2.38	1 - 3
L. decidua	157	24	27.7	0.1 - 125	39	8 - 86	1138.7	367.2 - 1750.2	5.84	1.5 - 12.5	152.1	37 - 400	2.28	1 - 3
P. abies	336	37	12.7	0.5 - 89	24	4 - 84	986.9	365.6 - 1797	7.50	1.5 - 13.4	126.0	31 - 635	2.35	1 - 3
P. sylvestris	102	19	17.5	2.2 - 57	37	11 - 81	1057.9	366.9 - 1743.7	5.21	1.5 - 12.5	129.6	31 - 377	2.26	1 - 3
P. avium	111	28	42.4	0.3 - 136	26	7 - 79	666.6	349.3 - 1577.1	8.18	1.5 - 12.5	196.1	34 - 432	2.67	1 - 3
P. menziesii	87	13	28.4	5 - 98	26	7 - 79	588.2	367.4 - 1150.4	10.30	3.5 - 13.4	122.7	35 - 373	2.56	1 - 3
Q. petraea & Q. robur	174	25	38.2	1.2 - 211	30	6 - 89	641.7	333.4 - 1417.4	8.72	2 - 13.4	134.9	31 - 415	2.49	1 - 3
T. cordata & T. platyphyllos	99	20	25.7	0.5 - 100	22	6 - 87	521.5	365.3 - 1202	8.28	2.5 - 13.4	157.7	31 - 441	2.46	1 - 3

2.3 Data preparation

Height growth was calculated as the mean terminal shoot growth across all measured years. If measurements were available for only a single year, that value was used instead.

The elevation of each data point was determined based on the recorded coordinates and a digital height model (DHM25) provided by Federal Office of Topography swisstopo (2024b). Growth increment values (expressed in m^3/ha/year) provided by foresters were sometimes expressed as ranges rather than precise values. To convert this categorical data into a continuous variable, the arithmetic mean of the given range was calculated.

Field data were collected for the following tree species: *A. alba*, *Acer platanoides* L., *A. pseudoplatanus*, *B. pendula*, *Castanea sativa* Mill., *F. sylvatica*, *L. decidua*, *P. abies, P. sylvestris, P. avium*, *P. menziesii*, *Q. petraea*, *Q. robur*, *T. cordata* and *T. platyphyllos*. Due to insufficient sample sizes, *Acer platanoides* and *Castanea sativa* were excluded from further analysis. For the same reason, both *Quercus* species (*Q. petraea* and *Q. robur*) were grouped into a single category. Similarly, *T. cordata* and *T. platyphyllos*, were analysed together.

The following calculation steps were not carried out by me but were provided by my supervisor, Florian Zellweger, in the context of my master's thesis. For light modelling, the enhanced CanopyHeightModel2Radiation (C2R) by Webster et al. (2023) was applied. This model calculates below canopy light conditions at each data point's coordinates based on a high-resolution canopy height model and was shown to represent the light conditions very well (Webster et al., 2023; Zellweger et al., 2019). The Canopy Height Model was derived from LiDAR data collected nationwide by Federal Office of Topography swisstopo (2024b) and processed by the NFI (Ginzler, 2021). Two key light variables were extracted: *Canopy openness,* an indicator of total incoming radiation reaching the sub-canopy and potential direct solar radiation, which represents the proportion of direct solar radiation reaching the ground, accounting for the time-dependent solar position. To obtain a standardized measure of potential direct solar radiation, an average daily value between 10am and 4pm was computed for June. Additionally, to correct for spatial differences in potential radiation, the modelled values were adjusted by multiplying them with local potential radiation estimates (Zimmermann & Roberts, 2001). This resulted in an indicator for *potential direct solar radiation*, which was used as an explanatory variable as described below.

2.4 Statistical analysis

To examine the effect of a light variable on height growth while accounting for other influencing factors, a Linear Mixed Model (LMM) was applied, following the structure outlined in equation (1) (Bigler, 2021).

$$y_i = \beta_0 + \sum_{j=1}^{p} \beta_j \cdot V_{j,i} + b_i + \varepsilon_i \qquad (1)$$

Here, y_i represents the dependent variable for observation i, β_0 is the fixed intercept, and β_j are the fixed effects for the predictors $V_{j,i}$. Additionally, b_i represents the random effect, assuming a random intercept for the grouping variable, and $\varepsilon_i \sim N(0, \sigma^2)$ is the residual error.

In the model used in this study, the dependent variable was height growth, while the fixed effects included a light variable, elevation, productivity, tree height, and understory woody density (Table 2). The selection of the specific light variable is discussed in a later section. Understory woody density was treated as an ordinal variable, assuming a linear distance between the three categories. Forest district and species were included as random effects. In cases where species-specific models were formulated, species was omitted as a random effect.

The response variable, height growth, exhibited a right-skewed distribution and violated assumptions of normality and homoscedasticity, with strong heteroscedasticity observed in the residuals. Additionally, the initial model formulation allowed for potentially negative predictions of height growth, which are biologically unrealistic. To address these issues, two alternative models were tested: A Generalized Linear Mixed Model (GLMM) with a Gamma distribution and log-link function was examined as a potential alternative. Additionally, a log-transformed LMM, in which the dependent variable height growth was log-transformed, was tested. The models were compared using Akaike Information Criterion (AIC), Bayesian Information Criterion (BIC), marginal R^2 (R^2m), and conditional R^2 (R^2c). The log-transformed LMM was selected as the final model due to its superior AIC and BIC values. Therefore, the following specific model was used:

$$\log(heigth\ growth_i) = \beta_0 + \sum_{j=1}^{5} \beta_j \cdot V_{j,i} + u_i + v_i + \varepsilon_i \qquad (2)$$

Where $V_{1,i}$ represents the light variable, $V_{2,i}$ productivity, $V_{3,i}$ elevation, $V_{4,i}$ tree height, and $V_{5,i}$ understory woody density. The random effect $u_i \sim N(0, \sigma_u^2)$ defines the random intercept for each forest district, and $v_i \sim N(0, \sigma_v^2)$ defines the random intercept for each species.

Model formulation was performed using the `lmer()` function from the *lme4* package in R, version 4.4.1 (Bates et al., 2015; R Core Team, 2024). Model assumptions were reassessed using residual distribution plots, residuals vs. predicted values plots, and Q-Q plots comparing sample and theoretical quantiles. To assess collinearity among fixed effects, variance-inflation factors and pairwise Pearson correlation coefficients were computed.

A comparison of the two light variables – canopy openness and potential direct solar radiation - revealed that canopy openness explained a greater portion of the variance in height growth. The comparison was conducted using estimates, t-values, root mean squared error (RMSE), R^2, and AIC values from LMM models incorporating either canopy openness or potential direct solar radiation as predictors. To examine whether the influence of light variables varied by altitude, the dataset was split into high-elevation (>1000 m a.s.l.) and low-elevation (<1000 m a.s.l.) subsets. The performance of the model with canopy openness as explanatory variable was consistently superior in both elevation ranges. To assess redundancy between light variables, the correlation between canopy openness and potential direct solar radiation was calculated, yielding r = 0.85. Including potential direct solar radiation in a model alongside canopy openness resulted in a marginal increase in R^2 by 0.0015, indicating minimal additional explanatory power. Consequently, potential direct solar radiation was excluded from further analyses, and only the effect of canopy openness was considered.

Outliers were identified using Cook's distance, defining data points exceeding the threshold 4/n as outliers. With an initial dataset of 2154 observations, this led to a threshold of 0.0019, resulting in 48 identified outliers. All outliers flagged for potential data inconsistencies during data collection (n=18) due to potential tree damage, abnormal growth patterns, or uncertainties regarding recorded coordinates or LiDAR data were excluded from further analyses. Cook's distance was recalculated for the reduced dataset, and again, 43 outliers were identified. An additional flagged outlier (n=1) was removed. All remaining outliers were re-evaluated for potential errors that occurred during data collection and processing. Identified errors (n=4) were corrected, while remaining outliers were retained for impact assessment. Removing the remaining outliers had no substantial effect on model coefficients, direction of effects, or significance levels. The exclusion resulted in a moderate increase in R^2 (from 45% to 50%). The remaining 38 outliers accounted for only 1.8% of the dataset (final n = 2135) and did not significantly impact model performance, they were considered biological variation and retained in the dataset for further analysis.

To facilitate interpretation, back-transformation was applied to log-transformed height growth values presented in plots and tables in the results section, restoring them to their original scale (cm). Since back-transformation produces asymmetric confidence intervals, the mean of both back-transformed confidence bounds was reported as the standard error (SE) in Table 3. The asymmetric confidence intervals for the effect of canopy openness are visualized in Figure 3. To calculate the model results presented in Table 3, fixed effects were standardized by centering variables at zero and scaling them so that one standard deviation corresponds to ±1, enhancing comparability of estimates across predictors.

Model predictions for Figure 4 und Figure 5 were generated using the `predict()` function in *lme4* with `re.form = NA`, excluding random effects from predictions. Figure 3 presents model-based predictions generated using `ggpredict()` from the *ggeffects* package (Lüdecke, 2018), providing marginal predictions based on fixed effects while excluding random effects. In both cases, predictions were made by setting tree height to 150 cm for all species, while the other fixed effects were assigned the species-specific mean value. For Figure 4 the range between 10% and 50% was selected to represent an interval where model predictions show a relatively narrow confidence interval. Furthermore, the comparison between 10% and 50% canopy openness is expected to serve as an example of light conditions before and after canopy layer intervention.

To assess overall model fit, R^2m and R^2c values were computed using the `r.squaredGLMM()` function from the *MuMIn* package in R (Kamil Bartoń, 2024). The variance explained by each fixed effect (Figure 7) was determined using separate models, where each predictor was the sole fixed effect while retaining the random effects structure. The contribution of random effects to the total variance of the model was analysed by determining the variance components for each random factor — namely, forest district and species. The total variance consists of the variance attributed to forest districts, species, and the remaining unexplained variability. The proportion of variance explained by each random factor was calculated as the ratio of its variance component to the total variance. This approach follows the variance partitioning framework in mixed-effects models described by Nakagawa & Schielzeth (2013). The variance components were determined using the `VarCorr()`function from the *lme4* package.

Artificial intelligence (AI)-assisted tools were used in parts of the code generation, literature search and during the writing process. All AI-generated content was manually reviewed and refined to ensure accuracy and scientific integrity. A detailed documentation of the AI tools used and their specific contributions can be found in the Appendix Table A. 1.

Table 2: Description of the explanatory and grouping variables used to build the statistical model.

Type	Name	Description	Unit/Levels
Fixed Effects	Canopy openness	Proportion of total incoming radiation reaching the sub-canopy based on Webster et al. (2023)	Percentage
	Elevation	Elevation above sea level	Metres
	Productivity	Expected increase in wood volume per year and hectare, also known as increment	m^3/ha/year
	Tree height	Sapling height at the end of the growing season	Centimetres
	Understory woody density	Index based on proportion of a 2-meter radius around the sampled tree covered by woody vegetation	Index consisting of three levels: 1 (coverage <5%), 2 (5-25% coverage), 3 (>25% coverage)
Random Effects	Forest district	Study sites	39
	Species	Tree species	11; based on 13 species, with two pairs of species being grouped together

3 Results

3.1 Species-specific responses of height growth to canopy openness

The way height growth depends on canopy openness varies between species, as seen in Figure 3. *A. pseudoplatanus* and *F. sylvatica* exhibit moderate growth under low canopy openness compared to other species, but their growth increases significantly as canopy openness increases. A similar curve is observed for *P. menziesii* and *T. cordata & T. platyphyllos*, though the growth increase is less pronounced. For *B. pendula*, *P. avium*, and *Q. petraea & Q. robur*, growth is already relatively high at low canopy openness, with only a slight increase as canopy openness increases. Both *L. decidua* and *A. alba* show relatively average growth at low canopy openness, with moderate increases as the canopy openness increases. *P. sylvestris* starts with fairly average growth but do not increase much as the canopy openness rises. *P. abies* exhibits low growth under low canopy openness but can achieve higher growth at higher canopy openness. While each species exhibits an individual growth response to different levels of canopy openness, the growth curves of certain species show similar patterns.

The following section presents the results on the influence of canopy openness on height growth based on species-specific modelling. Since the dependent variable, height growth, was log-transformed in the model formulation, it is important to note that the values discussed in this section represent relative rather than absolute differences. These results indicate the proportional change in height growth as canopy openness increases but do not specify the absolute magnitude of this change. The absolute change in height growth resulting from a given relative difference depends on the average growth rate of the tree species, which can be derived from the intercept in Table 3.

For the majority of species, an increase in canopy openness results in a significant increase in height growth (Table 3). However, this relationship was not significant for *P. avium*. When the species were arranged according to the relative effect of canopy openness on their main shoot growth, the following order from high to low was identified: *P. abies, F. sylvatica, A. pseudoplatanus, T. cordata & T. platyphyllos, L. decidua, P. menziesii, A. alba, P. avium, Q. petraea & Q. robur, P. sylvestris, B. pendula*. *P. abies* demonstrates the most substantial relative increase in growth, with height growth increasing by 1.77 times (a 77% increase) when the canopy openness is elevated by one standard deviation (which corresponds to a 17% increase), compared to the lowest increase of 1.20 times (a 20% increase) estimated for *B. pendula*. As explained in the previous section, the model used for the analysis was log-transformed, meaning it highlights relative differences rather than absolute ones. This is the reason why *P. abies* exhibits the highest relative growth increase due to canopy openness: Under shady conditions, this species exhibits very low growth, leading to high relative increases in growth under better light conditions, although absolute height growth is much lower than for other species.

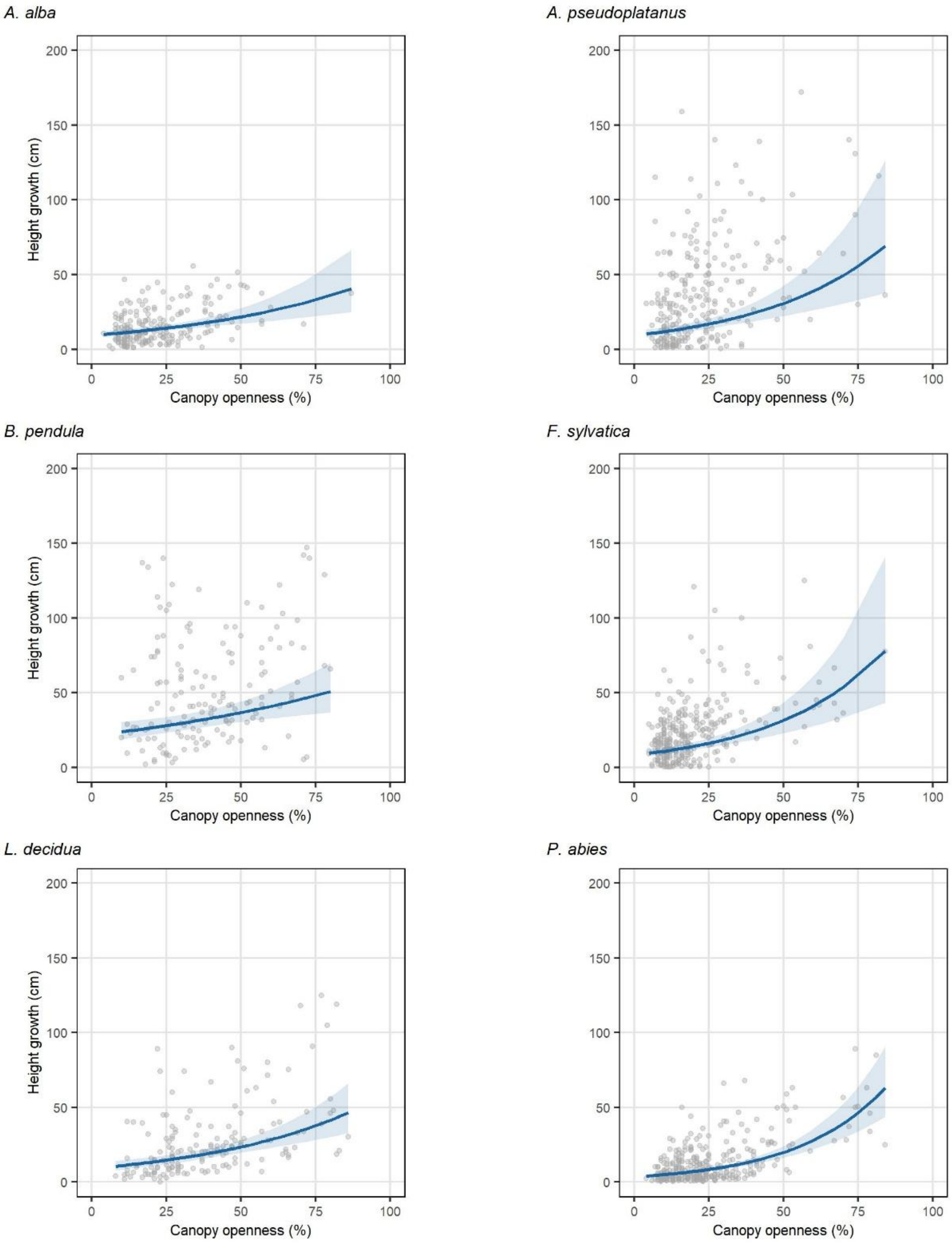

Figure 3: Response curves illustrating the species-specific relationship between canopy openness and height growth. Data points represent raw observations, while lines show predictions from a Linear Mixed Model (LMM) with 95% confidence intervals. For model predictions, tree height is set to 150 cm, while all other fixed effects—except for canopy openness—are held at their species-specific mean values. The random effect of the forest district is excluded. Species in this figure: A. alba (Abies alba), A. pseudoplatanus (Acer pseudoplatanus), B. pendula (Betula pendula), F. sylvatica (Fagus sylvatica), L. decidua (Larix decidua), P. abies (Picea abies).

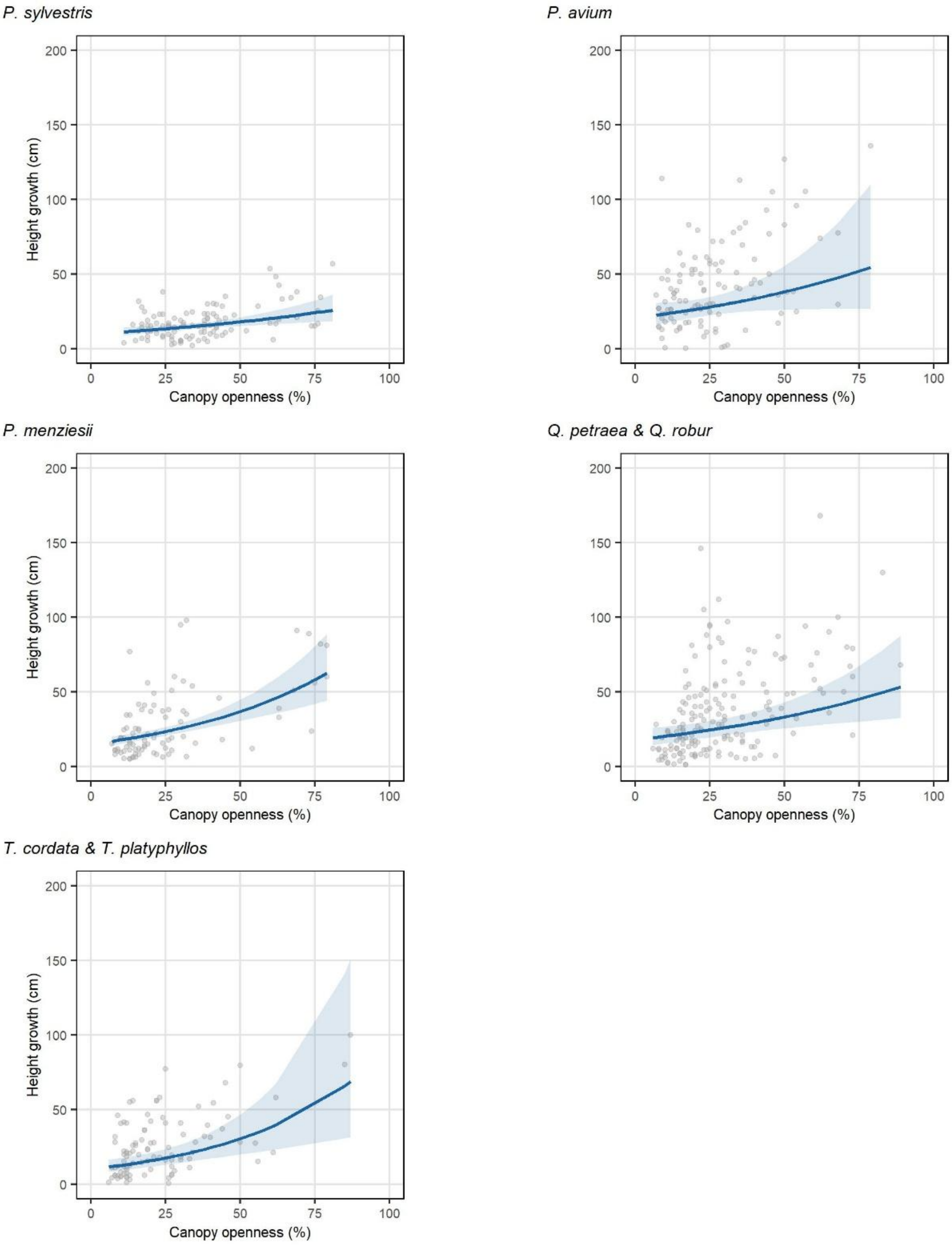

Figure 3: (continued) Sepcies in this figure: P. sylvestris (Pinus sylvestris), P. avium (Prunus avium), P. menziesii (Pseudotsuga menziesii), Q. petraea & Q. robur (Quercus petraea & Quercus robur), T. cordata & T. platyphyllos (Tilia cordata & Tilia platyphyllos).

The tree species exhibited varying responses in absolute additional height growth when the canopy openness increased from 10% to 50% (Figure 4). The height increase resulting from these 40% additional canopy openness ranges from 20.68 cm for *F. sylvatica* to 6.74 cm for *P. sylvestris*. Thus, the increase in absolute height growth due to higher canopy openness varies between tree species. The significant disparities between the species configurations in this section and the preceding one with regard to the impact of canopy openness on height growth can be elucidated as follows. The preceding abstract (based on Table 3) concentrated on relative growth, whereas the latter (based on Figure 4) focuses on absolute growth. Due to the variation in species with respect to their intercept, the analysis of relative and absolute growth yields distinctly divergent results when comparing species to each other.

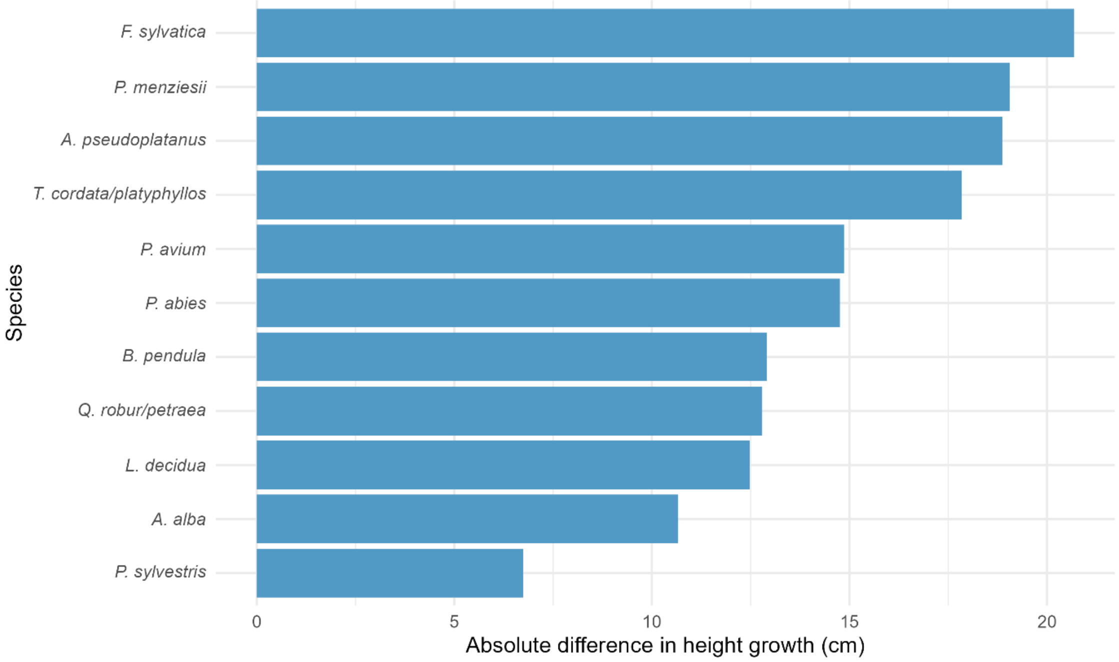

Figure 4: Barplots showing the absolute difference in predicted height growth between canopy openness 50% and 10%. Species abbreviations: F. sylvatica (Fagus sylvatica), P. menziesii (Pseudotsuga menziesii), A. pseudoplatanus (Acer pseudoplatanus), T. cordata & T. platyphyllos (Tilia cordata & Tilia platyphyllos), P. avium (Prunus avium), P. abies (Picea abies), B. pendula (Betula pendula), Q. petraea & Q. robur (Quercus petraea & Quercus robur), L. decidua (Larix decidua), A. alba (Abies alba), P. sylvestris (Pinus sylvestris).

For the different tree species, the modelled height growth at a canopy openness of 60% varies (Figure 5). The highest height growth is observed in *P. menziesii*, reaching 44.20 cm, while the lowest growth is recorded for *P. sylvestris* at 20.25 cm. With the exception of four tree species, all others exhibit a height growth exceeding 35 cm.

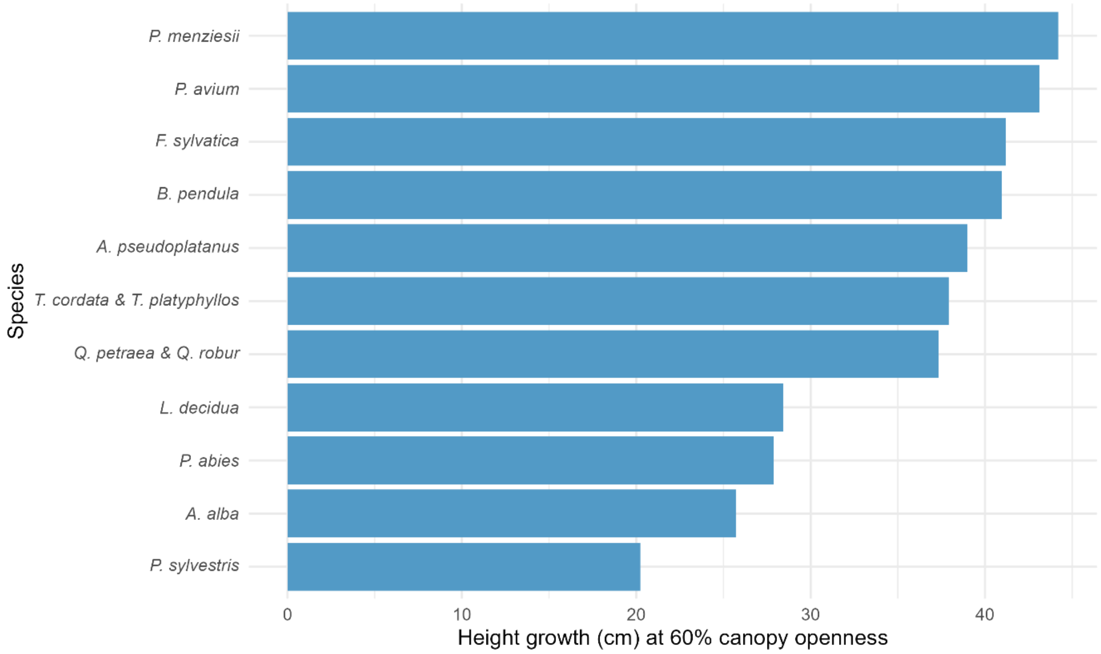

Figure 5: Barplots showing the predicted height growth at 60% canopy openness. Species abbreviations: P. menziesii (Pseudotsuga menziesii), P. avium (Prunus avium), F. sylvatica (Fagus sylvatica), B. pendula (Betula pendula), A. pseudoplatanus (Acer pseudoplatanus), T. cordata & T. platyphyllos (Tilia cordata & Tilia platyphyllos), Q. petraea & Q. robur (Quercus petraea & Quercus robur), L. decidua (Larix decidua), P. abies (Picea abies), A. alba (Abies alba), P. sylvestris (Pinus sylvestris).

3.2 Model performance and influence of other predictors

To assess potential collinearity correlations between fixed effects were assessed. A moderate correlation between elevation and productivity was detected; however, both variables were retained in the final model, as their influence and significance varied across species. No strong correlations were observed among the remaining variables (Figure 6).

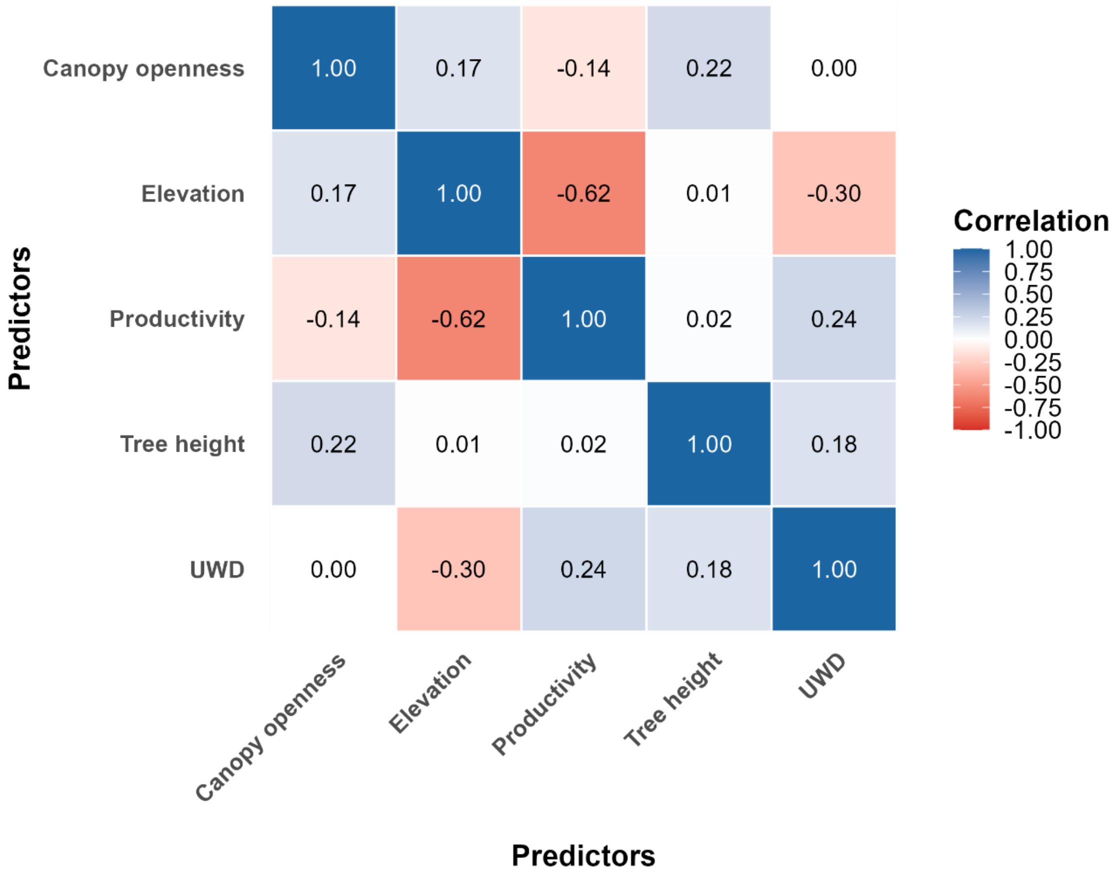

Figure 6: Correlation matrix displaying the pairwise correlations among fixed effects used in the model. Predictor abbreviation: UWD (understory woody density).

For the model based on the entire dataset across all tree species, the explanatory power of the predictors was analysed. The largest proportion of variance is explained by tree height (20%), followed by canopy openness (17%), understory woody density (7%), productivity (2%), and elevation (1%) (Figure 7). Forest district accounts for 11%, while species distinction explains 9% of the variance.

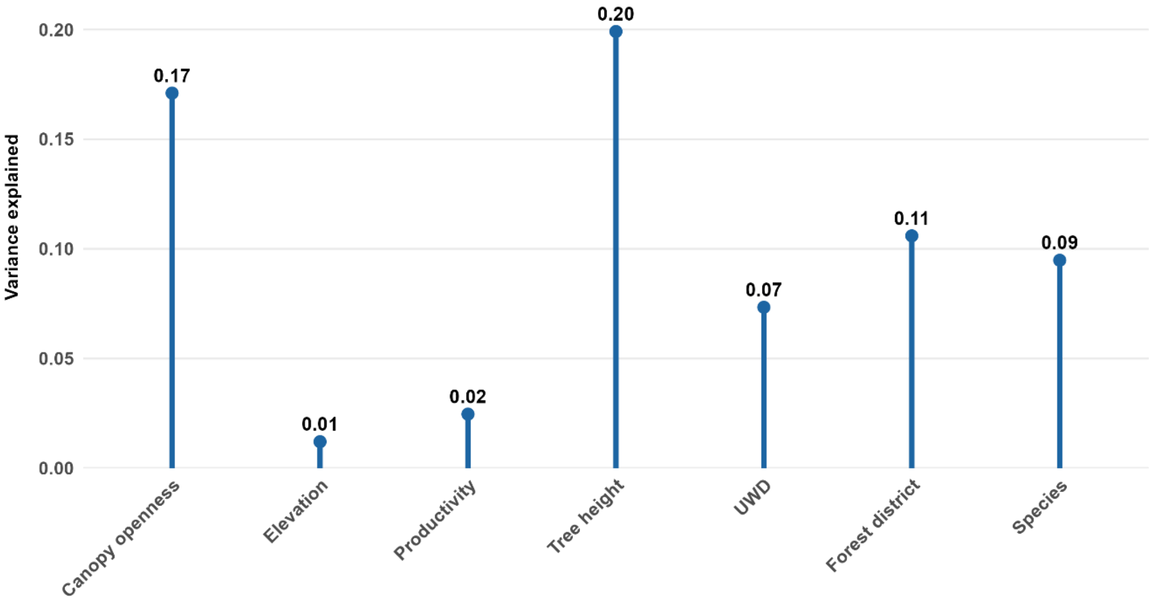

Figure 7: Proportion of variance explained by fixed and random effects in the Linear Mixed Model (LMM) using data from all species. The explained variance for fixed effects was determined using separate models with only one predictor, while the variance explained by random effects was derived from the model's variance components. Predictor abbreviation: UWD (understory woody density).

When an individual model is formulated for each tree species, it becomes evident that the influence of individual predictors varies depending on the species. For nearly all studied tree species, elevation does not have a significant impact on height growth (Table 3). However, in *L. decidua*, an increase in elevation by one standard deviation (equivalent to 368.10 m) results in a relative decrease in growth of 0.82 of the initial value, corresponding to a reduction of 18%. In contrast, productivity has a significant effect on height growth in several species. A one standard deviation increase in productivity, corresponding to 3.44 m^3/ha/year, results in a relative height growth increase of 1.32 in *L. decidua*, 1.29 in *A. alba*, 1.24 in *B. pendula*, and 1.20 in *P. sylvestris*. Understory woody density is positively associated with height growth across multiple species. The strongest effect is observed in *A. pseudoplatanus*, where an increase in understory woody density by one standard deviation, equivalent to 0.74, results in a relative height growth increase of 1.46. In contrast, *Q. petraea* & *Q. robur* show the smallest effect, with an increase of only 1.13. Tree height is positively correlated with height growth across all species. The strongest response is found in *A. alba*, where an increase in tree height by one standard deviation (99.18 cm) leads to a relative height growth increase of 1.73. The weakest effect is observed in *P. avium*, with an increase of only 1.20. Variation in height growth across forest districts is most pronounced in *T. cordata* & *T. platyphyllos*, where the standard deviation across districts corresponds to a relative variation of 1.26. In contrast, *P. menziesii* exhibits no variation across forest districts (1.00), indicating consistent growth across different locations.

The predictive accuracy of the model varied among tree species. The best agreement between observed and predicted values was found for *P. sylvestris*, with a RMSE of 1.59 cm, whereas the highest RMSE was observed for *A. pseudoplatanus* (2.46 cm). The marginal R^2 values ranged from 0.57 for *P. menziesii* to 0.20 for *P. avium*. The conditional R^2 reached its highest value for *Q. petraea & Q. robur* (0.66) and its lowest for *P. avium* (0.29).

Table 3: Results and performance of the model for each tree species. The model used was a Linear Mixed Model (LMM) with a log-transformed dependent variable, height growth. For better interpretability, the table values were back-transformed and can be understood as relative changes. Fixed effects were scaled, meaning their reference values correspond to standard deviations (SD), which also applies to the random effect. Due to this scaling, the intercept represents height growth under average conditions (Canopy openness=26.33%, Elevation=855.91 m, Productivity=7.78 m^3/ha/year, UWD=2.42, Tree height=159.15 cm). Additionally, the table includes the number of data points and the number of sampled forest districts per species. Predictor abbreviations: UWD (understory woody density), FD (forest district). Species abbreviations: A. alba (Abies alba), A. pseudoplatanus (Acer pseudoplatanus), B. pendula (Betula pendula), F. sylvatica (Fagus sylvatica), L. decidua (Larix decidua), P. abies (Picea abies), P. sylvestris (Pinus sylvestris), P. avium (Prunus avium), P. menziesii (Pseudotsuga menziesii), Q. petraea & Q. robur (Quercus petraea & Quercus robur), T. cordata & T. platyphyllos (Tilia cordata & Tilia platyphyllos).

		Fixed Effects					Random Effect		Model Statistics		
	Intercept	Canopy openness	Elevation	Productivity	UWD	Tree height	FD SD	FD n	RMSE	R^2m	R^2c
A. alba (n=207)											
Coefficient	14.78	1.33	1.07	1.29	1.16	1.73	1.08	33	1.73	0.44	0.54
SE	1.14	0.09	0.10	0.12	0.06	0.12					
t-value	34.87	4.45	0.71	2.75	3.11	8.27					
A. pseudoplatanus (n=254)											
Coefficient	17.34	1.49	0.97	0.99	1.46	1.48	1.18	34	2.40	0.37	0.48
SE	1.72	0.12	0.13	0.13	0.11	0.08					
t-value	28.82	5.09	-0.21	-0.05	5.10	7.29					
B. pendula (n=151)											
Coefficient	31.53	1.20	0.89	1.24	1.02	1.28	1.10	32	1.73	0.36	0.51
SE	2.97	0.07	0.08	0.13	0.06	0.06					
t-value	36.70	3.33	-1.20	2.11	0.40	4.85					
F. sylvatica (n=298)											
Coefficient	17.78	1.57	0.99	0.95	1.38	1.25	1.18	33	2.30	0.28	0.40
SE	1.75	0.12	0.13	0.12	0.08	0.08					
t-value	29.25	6.02	-0.12	-0.46	5.33	3.48					
L. decidua (n=157)											
Coefficient	21.20	1.37	0.82	1.32	1.02	1.37	1.09	24	1.83	0.49	0.58
SE	2.38	0.08	0.08	0.15	0.06	0.10					
t-value	27.20	5.36	-2.02	2.36	0.29	4.29					
P. abies (n=336)											
Coefficient	9.96	1.77	0.90	1.08	1.29	1.58	1.11	37	1.93	0.50	0.59
SE	0.73	0.09	0.07	0.09	0.06	0.09					
t-value	31.50	11.61	-1.41	0.94	5.88	8.38					

		Fixed Effects					Random Effect		Model Statistics		
	Intercept	Canopy openness	Elevation	Productivity	UWD	Tree height	FD SD	FD n	RMSE	R^2m	R^2c
P. sylvestris (n=102)											
Coefficient	16.95	1.22	0.91	1.20	1.01	1.32	1.03	19	1.59	0.41	0.47
SE	1.58	0.07	0.07	0.10	0.05	0.08					
t-value	30.42	3.33	-1.26	2.14	0.22	4.30					
P. avium (n=111)											
Coefficient	28.65	1.23	1.18	1.26	1.24	1.20	1.09	28	2.21	0.20	0.29
SE	3.79	0.13	0.21	0.17	0.14	0.11					
t-value	25.35	1.97	0.94	1.73	1.96	2.04					
P. menziesii (n=87)											
Coefficient	22.15	1.36	0.94	1.07	1.18	1.58	1.00	13	1.66	0.57	0.57
SE	2.51	0.07	0.12	0.08	0.08	0.13					
t-value	27.51	5.75	-0.45	0.95	2.54	5.74					
Q. petraea Q. robur (n=172)											
Coefficient	23.98	1.23	0.96	1.16	1.13	1.58	1.25	25	1.72	0.44	0.66
SE	3.17	0.08	0.15	0.14	0.06	0.10					
t-value	23.99	3.12	-0.26	1.25	2.24	7.42					
T. cordata T. platyphyllos (n=99)											
Coefficient	25.40	1.45	1.46	1.04	1.30	1.23	1.26	20	1.95	0.30	0.51
SE	6.31	0.14	0.41	0.16	0.10	0.11					
t-value	13.17	3.89	1.35	0.27	3.31	2.23					

4 Discussion

4.1 Light response

4.1.1 Strategies in low-light conditions

An interesting observation in the growth response curves is that certain tree species react similarly to changing light conditions, whereas others exhibit highly divergent responses. For instance, the growth response curves of *B. pendula* and *P. avium* share a very similar shape. Both species maintain relatively high growth even under low-light conditions. This characteristic is often described in the literature as typical for pioneer species, as they strive to maximize light capture and photosynthesis even in shaded conditions. In contrast, shade-tolerant species reduce their height growth under low-light conditions and invest their resources in non-photosynthetic tissues, which increases their survival probability in shaded environments (Song & Jin, 2023).

Various studies confirm the differences in responses to low-light conditions among tree species. Ameztegui & Coll (2011) describe how *P. abies* and *P. sylvestris* adopt different strategies: *P. abies* reduces height growth under low-light conditions, whereas *P. sylvestris* maintains high height growth to escape shade, albeit at the cost of a reduced survival rate. Similarly, the present study's results indicate that *P. sylvestris* exhibits greater height growth under low-light conditions than *P. abies*. Additionally, Petritan et al. (2009) demonstrated how the greater shade tolerance of *F. sylvatica* compared to *Fraxinus excelsior* and *A. pseudoplatanus* is achieved through specific architectural and leaf morphological adaptations. These include leaf distribution throughout the tree height, radial growth patterns, and plagiotropic growth.

4.1.2 Shade tolerance and high-light growth

Based on the classification of shade tolerance proposed by Matter & Schütz (2002), the tree species analysed in this study can be categorized as follows: a five-tier classification distinguishes between strongly light-demanding species, light-demanding species, semi-light-demanding species, semi-shade-tolerant species, and shade-tolerant species. *B. pendula* and *L. decidua* are classified as strongly light-demanding species. Semi-shade-tolerant species include *A. pseudoplatanus*, *P. abies*, *P. sylvestris*, *P. avium*, and *Q. petraea* & *Q. robur*. Shade-tolerant species include *A. alba*, *F. sylvatica*, and *T. cordata* & *T. platyphyllos*. However, shade tolerance decreases for certain species as they develop thicker stems. *A. pseudoplatanus* is then considered semi-light-demanding, while *P. sylvestris* and *Q. petraea* & *Q. robur* transition to light-demanding species, and *P. avium* becomes strongly light-demanding. Additionally, *P. menziesii* is classified as a semi-light-demanding species based on Ammann et al. (2024).

A widely accepted and discussed concept in forest ecology explains shade tolerance through a trade-off between high-light growth potential and survival in low-light conditions (Kobe et al., 1995; Kobe & Coates, 1997; Löf et al., 2007). Shade-tolerant species are expected to exhibit lower height growth in high-light conditions while achieving higher survival rates in shaded environments. When ranking species based on the height growth under high-light conditions achieved in this analysis, the order of decreasing shade tolerance is as follows: *P. menziesii*, *P. avium*, *F. sylvatica*, *B. pendula*, *A. pseudoplatanus*, *T. cordata* & *T. platyphyllos*, *Q. petraea* & *Q. robur*, *L. decidua*, *P. abies*, *A. alba*, *P. sylvestris*.

This ranking does not entirely align with the expected shade tolerance classification. Only *A. alba* and *P. abies*, which exhibit relatively low height growth, and *B. pendula*, with high height growth, match the expected results. The placement of *A. pseudoplatanus* and *P. avium* does not significantly deviate from literature-based shade tolerance classifications, particularly when considering the decline in shade tolerance with increasing developmental stage. Notably, *P. menziesii*, *F. sylvatica*, and *T. cordata* & *T. platyphyllos* exhibit unexpectedly high height growth under high-light conditions. In contrast, *L. decidua* and *P. sylvestris* show relatively low growth rates despite their classification as strongly light-demanding and semi-shade-tolerant species.

A possible explanation for the unexpectedly low height growth of *L. decidua* and *P. sylvestris* is that their survival strategy does not primarily rely on competitiveness under either shaded or high-light conditions, which is an implicit assumption of the trade-off theory. Instead, these species are naturally adapted to habitats with minimal competition from other tree species (Rudow, 2024). This physiological specialization for low-competition environments may come at the cost of reduced competitiveness in more productive sites, which could explain their relatively sparse natural distribution in other habitats.

Due to the large differences between the literature and the ranking established here, the approach of quantifying shade tolerance solely based on growth performance under high-light conditions may not be universally applicable across a diverse range of forest communities. It can be assumed that the forest sites considered here are simply too different from one another.

4.1.3 The beech advantage, species comparisons, and suppression

F. sylvatica stood out in the analysis due to its relatively high growth rates under high-light conditions, which is atypical for a shade-tolerant species. This suggests that the trade-off between performing well in shaded environments and competing effectively under high-light conditions may not be as pronounced for this species. This observation is further supported by the widespread and dense distribution of *F. sylvatica* in the study area.

A study by Ligot et al. (2013) examined the dominance of *F. sylvatica* in continuous cover silviculture in Belgium. They found that, when comparing height growth between *Q. petraea* and *F. sylvatica*, the latter consistently exhibited greater height growth across all light conditions. They concluded that in this forest community, controlling canopy openings alone is insufficient to promote the regeneration of *Q. petraea*. In the present analysis, *F. sylvatica* did not always show higher growth across all light conditions, but it was able to achieve greater increments when canopy openness exceeded 50%. This contrasts with the findings of Lüpke & Hauskeller-Bullerjahn (2004), who observed that *Q. petraea* achieved greater growth under high-light availability.

Several studies have compared the light response and shade tolerance of *F. sylvatica* and *A. pseudoplatanus*. Petritan et al. (2009) found that *A. pseudoplatanus* exhibited greater growth than *F. sylvatica* under high-light conditions. This aligns with the findings from this analysis, where *A. pseudoplatanus* showed slightly higher height growth at high-light conditions. In the growth response curves modelled in this study, both species appear to have very similar growth responses across different light conditions. These results align with those of Brüllhardt et al. (2020) who attributed their findings to the suppression effect on *A. pseudoplatanus* during early development. Their study found that the annual height increment of *A. pseudoplatanus* decreases with age, a pattern not observed for *F. sylvatica*. This suggests that suppression, which is common in continuous forests, has a stronger negative effect on *A. pseudoplatanus* than on *F. sylvatica*. Under open light conditions and given the same young age, *A. pseudoplatanus* would theoretically achieve greater height growth than *F. sylvatica*. However, due to past suppression, this advantage could not be fully realized, resulting in both species exhibiting similar height growth patterns. If the height growth potential of other tree species also decreases with age, suppression could similarly lead to reduced competitive ability compared to *F. sylvatica*.

The approach used in this study assumes that light-driven height growth is determined by the current canopy openness, disregarding previous light conditions. While the long-term effects of early suppression on later growth remain largely unclear, this represents a potential limitation. In uneven-aged forests, many seedlings likely grow under shaded conditions in their early years, leading to initial suppression. For *P. abies*, it has been observed that height growth only began to increase five years after a significant canopy opening (Hökkä & Mäkelä, 2014). Collet et al. (2011) studied the response of *F. sylvatica* and *A. pseudoplatanus* to canopy openings and found that *F. sylvatica* responded immediately with increased height growth, whereas *A. pseudoplatanus* showed a delayed response of two years.

4.2 Other predictors

A positive effect of tree height on height growth was observed for all tree species. Similar relationships have been documented in previous studies, such as for *P. abies* (Hökkä & Mäkelä, 2014) and *F. sylvatica* (Collet & Chenost, 2006; Feldmann et al., 2020).

The fact that understory woody density exhibited a positive relationship with height growth across all species suggests that this variable can be interpreted as an indicator of site productivity. The benefits of greater site productivity may outweigh potential negative effects of competition. It is important to note that the trees analysed in this study were dominant individuals, and care was taken to ensure that their light conditions were not influenced by neighbouring shrubs or regeneration. However, root competition, and thus competition for nutrients from adjacent vegetation, cannot be ruled out. Interestingly, understory woody density showed no correlation with canopy openness (Figure 6). This suggests that understory woody density is correlated with other site characteristics that promote strong height growth. An alternative explanation could be that seedlings and saplings increase their height growth as a response to high competition in the understory. However, no direct evidence supporting this hypothesis could be found in the literature.

When comparing the standard deviation of height growth across different forest districts by species, it is notable that *Q. petraea & Q. robur* and *T. cordata & T. platyphyllos* exhibit the greatest variability across different forest regions. A possible explanation is that in many cases, only one of the two grouped species was found and measured within a given forest district. Consequently, a portion of the variability between forest districts may actually reflect the inherent variability between the combined species.

4.3 Model performance

4.3.1 Limitations in model formulation

A comparison of R^2 values by species reveals that the chosen modelling approach fits some species better than others. This suggests that an alternative model considering different relationships and possibly incorporating additional factors—such as climatic conditions, soil properties, exposure, or substrate variables—might be more suitable for certain species.

During model development, a Generalized Additive Model (GAM) was also tested but was not used further to prevent overfitting and to allow for a numerical comparison across species (Appendix Figure A.1). A comparison of the GAM results with the primary model used in this study showed that the model fit varied by species. For example, *A. alba, L. decidua,* and *Q. petraea & Q. robur* displayed a curve shape in the GAM models that resembled an asymptotic growth response curve, indicating saturation in the growth response to light availability. Other studies have found that, for A. alba, canopy openness above 30% or 50% negatively affects growth (Kučeravá et al., 2013; Stancioiu & O'hara, 2006). Although our analysis does not confirm a negative effect of too much light, an asymptotic growth response curve appears to be a more appropriate assumption for *A. alba* than the exponential growth model applied here. Petritan et al. (2009) observed that an asymptotic growth response curve effectively described the growth response of *F. sylvatica* under different light conditions. Although such a response curve is not possible in the model formulation used in this study, a visual inspection of the data distribution and the GAM model suggests that this relationship is possible but rather unlikely.

As described in the methods section, the second light variable, potential direct solar radiation, was excluded from this study due to its limited additional explanatory power compared to canopy openness when considering the entire dataset. However, Schmid et al. (2021) demonstrated that, for *P. abies* at higher elevations, potential direct solar radiation had a greater influence on height growth than canopy openness. While the exclusion procedure used in this study accounted for differences across elevation gradients, a species-specific analysis of the influence of potential direct solar radiation may be worthwhile.

4.3.2 Variability among species

A closer examination of the distribution of data points, the modelled response curves, and the associated confidence intervals for each tree species reveals that some species exhibit clearer patterns, while others show greater variability among individuals. This variance is also reflected in the RMSE, which was highest for *A. pseudoplatanus*. Brüllhardt et al. (2020) compared the light-dependent growth of *F. sylvatica* and *A. pseudoplatanus* and also found that models *for A. pseudoplatanus* yielded higher RMSE values than those for *F. sylvatica*. This suggests considerable variability among individuals of this species. Whether this variability is driven by genetic factors, site-specific conditions, or previous developmental history remains unclear. However, Caspersen & Kobe (2001) and Kobe & Coates (1997) found that shade tolerance in certain species is linked to site-specific soil moisture conditions. This implies that, depending on the species, interactions between the effect of light availability and the effect of site conditions on growth may play a crucial role in growth dynamics.

4.4 Limitations in data collection

4.4.1 Varying data distribution across species

One limitation of the data collection method used in this study is that the various light conditions were not equally represented for all tree species. It remains unclear to what extent this is due to the varying light-dependent occurrence of tree species or whether it results from inconsistencies in data collection. However, this leads to variations in the accuracy of model predictions depending on the tree species.

Furthermore, the distribution of tree height among individuals varied by species, and the average tree height differed between species. This is problematic because shade tolerance in certain tree species changes as they progress through different developmental stages. Kneeshaw et al. (2006) even found that, among all seven tree species examined, significant differences in shade tolerance emerged during development, even in individuals between 0 and 400 cm in height. Kunstler et al. (2009) also observed varying classifications of shade tolerance when comparing seedlings (tree height <100 cm) and saplings (tree height >100 cm). Since the height distribution of measured individuals differs between species, comparability across species in this regard is not ensured.

4.4.2 Dominant tree individuals

It is important to highlight that the restriction to dominant individuals reduces the ecological representativeness of this study and its comparability with other research. Instead of capturing the entire range of individuals, the focus was placed on those individuals that performed best within a given group. This limitation enhances the relevance of the findings for forestry, as it aligns with the selection of future dominant trees (Z-Bäume) that are likely to be promoted in forest management strategies.

4.5 Management implications

With the goal of forestry to maintain or even increase species diversity in forests, it is often argued that larger canopy gaps are necessary to promote the regeneration of less shade-tolerant species (Annighöfer et al., 2019; Brüllhardt et al., 2022). In some cases, however, large gaps alone appear to be necessary but not sufficient for the promotion of light-demanding species. Collet et al. (2008) investigated regeneration in a forest dominated by *F. sylvatica* and *A. pseudoplatanus* and highlighted the importance of advance regeneration in these species. Even within gaps, a significant portion of regeneration consisted of advance regeneration of *F. sylvatica* and *A. pseudoplatanus*. This challenges the classical gap theory, which suggests that large canopy disturbances primarily facilitate the regeneration of light-demanding pioneer species. They concluded that controlling advance regeneration is essential for ensuring the successful recruitment and establishment of light-demanding species.

Model predictions by Zimmermann et al. (2014) indicate that *F. sylvatica* will lose its competitiveness and dominance in lower elevations of Switzerland in the future. Oak species (*Quercus* spp.), in particular, are regarded as promising future tree species and are being actively promoted (Pluess et al., 2016). At present, however, the regeneration of *F. sylvatica* remains highly competitive. This study has demonstrated that, in addition to its well-documented shade tolerance (Petritan et al., 2009; Wagner et al., 2010), *F. sylvatica* is also capable of competitive height growth under high-light conditions. When considered alongside the previously mentioned significance of advance regeneration and the anticipated shifts in species distribution due to climate change, these findings highlight the importance of early silvicultural interventions in beech-dominated stands. Such interventions should occur shortly after gap formation to prevent excessive competition and the potential suppression of light-demanding species such as *Quercus* spp.

Advance regeneration also plays a significant role in spruce-dominated forests. In a *P. abies* stand affected by a bark beetle outbreak, it was found that although advance regeneration comprised only a small portion of total regeneration, it exhibited an above-average survival rate (Macek et al., 2016). In the management of protection forests, which are often dominated by *P. abies*, advance regeneration is frequently promoted to enhance forest resilience and enable faster recovery following disturbances (Brang et al., 2015; Bundesamt für Umwelt BAFU, 2024; Pluess et al., 2016). This is done by avoiding large-scale interventions to maintain the protective function of the forest, resulting in relatively small gaps and limited light availability for regeneration.

It is generally assumed that, due to climate change, vegetation zones will shift upward by approximately 500 to 700 meters by the end of the 21st century (Frehner et al., 2018). Specifically, it is predicted that several shade-tolerant species, such as *A. alba*, *F. sylvatica*, and *P. abies*, will find favourable environmental conditions at higher elevations (Pluess et al., 2016; Zimmermann et al., 2014). Consequently, promoting advance regeneration in protection forests at these elevations does not necessarily conflict with fostering climate-adapted tree species. Their shade tolerance enables them to establish and persist under low-light conditions, contributing to advance regeneration. However, given the uncertainties surrounding these projections, particularly regarding extreme weather events and indirect effects of climate change, maintaining a high degree of tree species diversity remains essential. Therefore, the promotion of light-demanding species should also be a priority in higher elevations. Achieving this goal requires careful planning of silvicultural interventions that consider the presence of potential seed trees for future climate-adapted species and, where stand conditions allow, favor the creation of larger canopy openings. Additionally, thinning and tending operations can contribute to species diversity following both planned interventions and natural disturbances (Bebi et al., n.d.; Pluess et al., 2016).

Depending on the site, other factors beyond light availability can significantly influence regeneration dynamics. In particular, browsing pressure has a significant impact on species composition in regeneration in certain regions and should therefore be carefully considered (Bundesamt für Umwelt BAFU, 2010; Kupferschmid et al., 2015).

5 Conclusion

For all thirteen investigated tree species, it was possible to model how height growth of regeneration depends on canopy openness, using data from various forest sites across Switzerland. In all cases, a significant effect of canopy openness on height growth was observed. However, the shape and magnitude of the growth response curve varied among species.

A correlation between growth under high light availability and shade tolerance could only be confirmed for a subset of species. This suggests that testing such relationships across diverse forest communities with varying site conditions may not be meaningful. As previously reported in other studies, the shade-tolerant *F. sylvatica* exhibited remarkable height growth under high-light conditions. This finding reinforces the challenge of regenerating light-demanding species in beech-dominated forests.

Overall, the performance of the selected model formulation— which accounted for factors such as tree height, site productivity, elevation, competition from the understory, and forest district— was satisfactory for most species. However, applying the same model structure to all species introduces limitations. The model's fit varied between species, suggesting that a species-specific model selection could provide more differentiated insights into species-specific light-dependent growth response curves.

There remain unresolved questions regarding the impact of suppression, as well as the effects of different episodes of canopy opening and closure on an individual’s long-term growth potential. Future research could focus on how quickly and effectively various tree species recover from prolonged shading and subsequently benefit from improved light conditions. Additionally future research could investigate how the height growth potential of different tree species changes with age, and how this may influence the competitiveness of individuals that have grown under suppressed conditions.

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7 Appendices

Table A. 1: Overview of generative AI and AI-assisted technologies used in this study.

AI-based tool	Use case	Scope	URL
Claude 3.7 Sonnet by Anthropic	R code generation for data analysis and visualization	Methods & Results	https://claude.ai/
Connected papers	Literature search	Introduction & Discussion	https://www.connectedpapers.com/
Scite	Literature search	Introduction & Discussion	https://scite.ai/
ChatGPT (GPT-4) by OpenAI	Translation and Revision of text	Entire work	https://chatgpt.com/
DeepL	Translation and Revision of text	Entire Work	https://www.deepl.com/

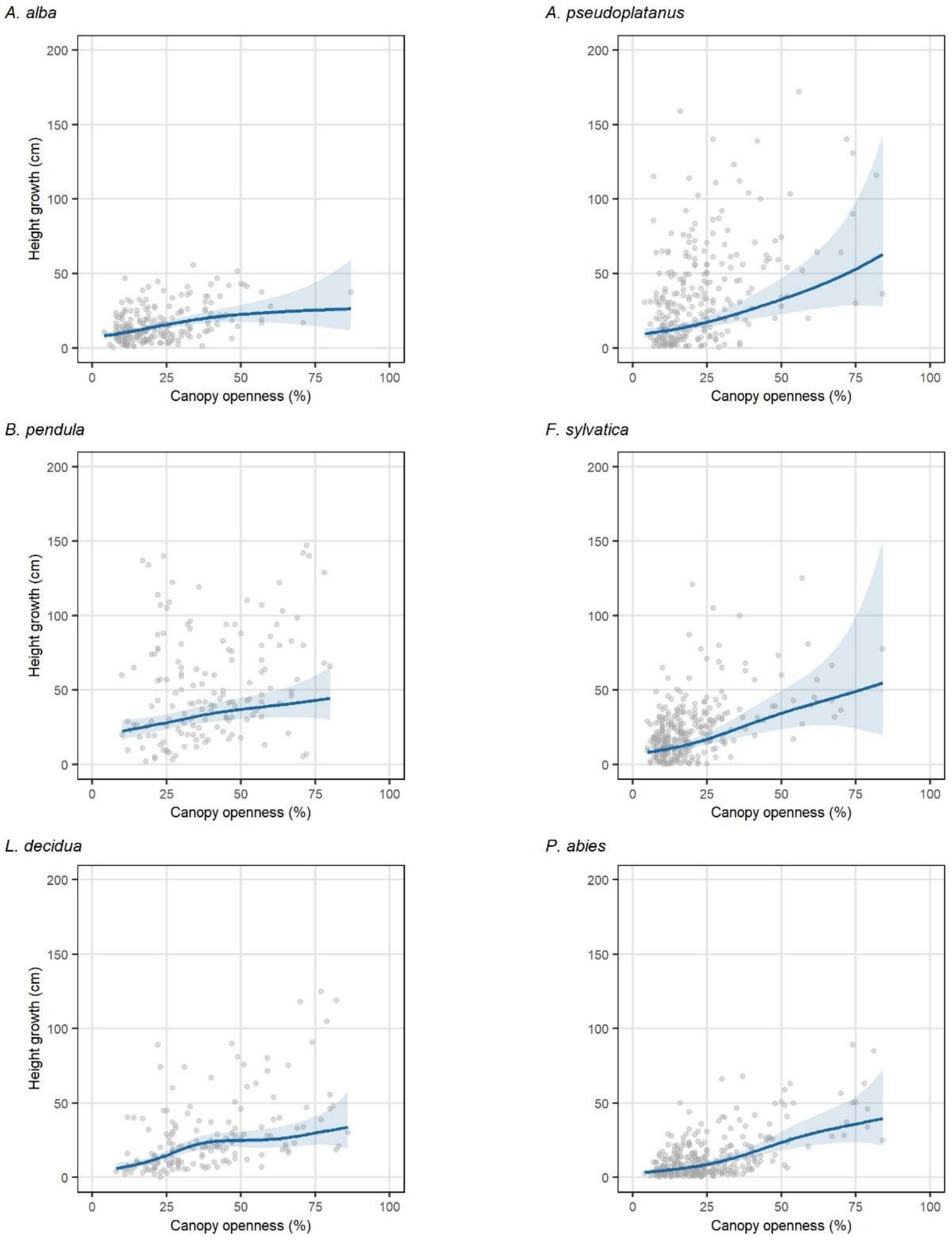

Figure A.1: Response curves based on a Generalised Additive Mixed Model (GAMM) illustrating the species-specific relationship between canopy openness and height growth. Data points represent raw observations, while lines show prediction from a GAMM with 95% confidence intervals. For model predictions, tree height is set to 150 cm, while all other fixed effects—except for canopy openness—are held at their species-specific mean values. The random effect of the forest district is excluded. Species in this figure: A. alba (Abies alba), A. pseudoplatanus (Acer pseudoplatanus), B. pendula (Betula pendula), F. sylvatica (Fagus sylvatica), L. decidua (Larix decidua), P. abies (Picea abies).

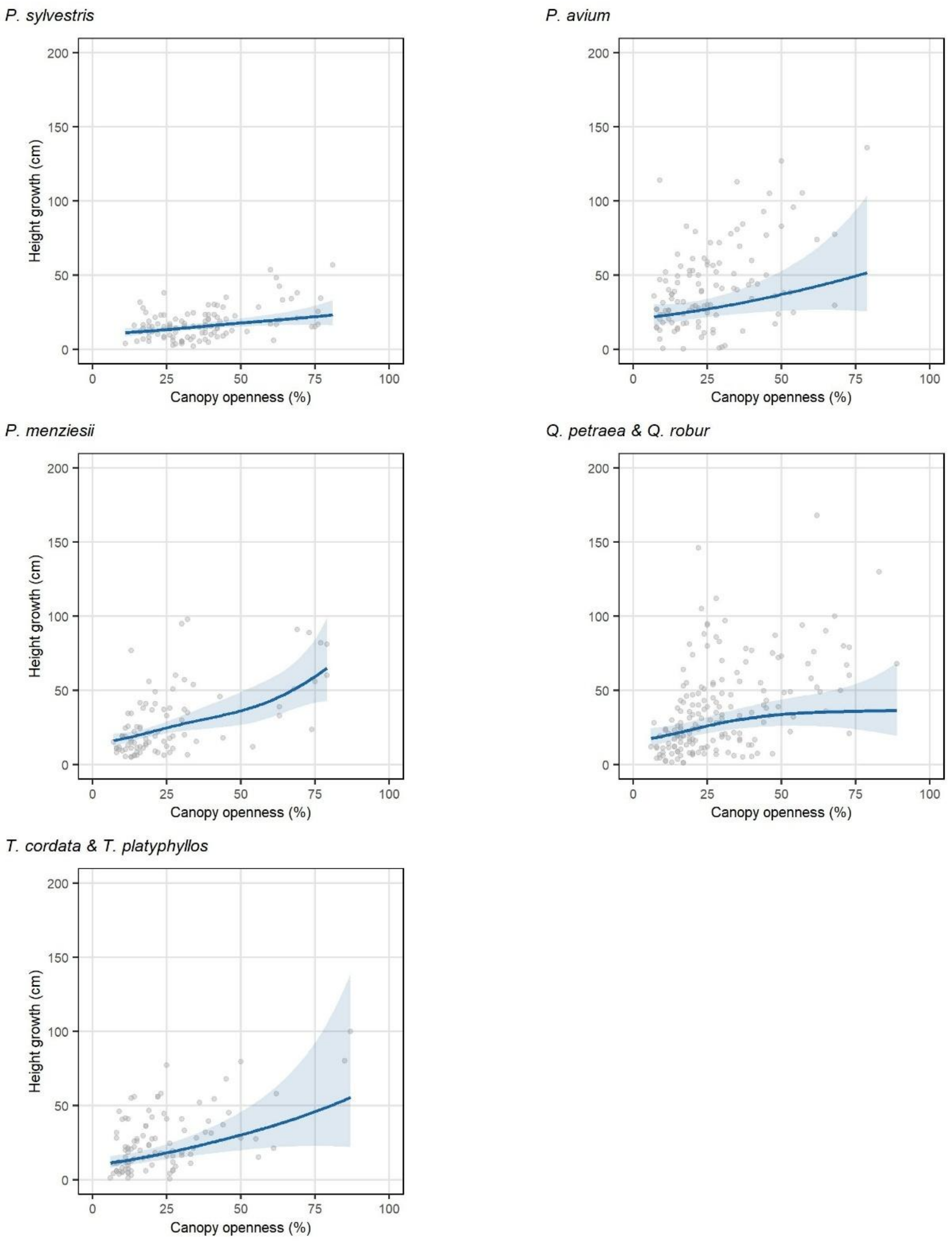

Figure A. 1: (continued) Sepcies in this figure: P. sylvestris (Pinus sylvestris), P. avium (Prunus avium), P. menziesii (Pseudotsuga menziesii), Q. petraea & Q. robur (Quercus petraea & Quercus robur), T. cordata & T. platyphyllos (Tilia cordata & Tilia platyphyllos).

Eidgenössische Technische Hochschule Zürich
Swiss Federal Institute of Technology Zurich

Eigenständigkeitserklärung

Die unterzeichnete Eigenständigkeitserklärung ist Bestandteil jeder während des Studiums verfassten schriftlichen Arbeit. Eine der folgenden drei Optionen ist in Absprache mit der verantwortlichen Betreuungsperson verbindlich auszuwählen:

○ Ich bestätige, die vorliegende Arbeit selbständig und in eigenen Worten verfasst zu haben, namentlich, dass mir niemand beim Verfassen der Arbeit geholfen hat. Davon ausgenommen sind sprachliche und inhaltliche Korrekturvorschläge durch die Betreuungsperson. Es wurden keine Technologien der generativen künstlichen Intelligenz[1] verwendet.

● Ich bestätige, die vorliegende Arbeit selbständig und in eigenen Worten verfasst zu haben, namentlich, dass mir niemand beim Verfassen der Arbeit geholfen hat. Davon ausgenommen sind sprachliche und inhaltliche Korrekturvorschläge durch die Betreuungsperson. Als Hilfsmittel wurden Technologien der generativen künstlichen Intelligenz[2] verwendet und gekennzeichnet.

○ Ich bestätige, die vorliegende Arbeit selbständig und in eigenen Worten verfasst zu haben, namentlich, dass mir niemand beim Verfassen der Arbeit geholfen hat. Davon ausgenommen sind sprachliche und inhaltliche Korrekturvorschläge durch die Betreuungsperson. Als Hilfsmittel wurden Technologien der generativen künstlichen Intelligenz[3] verwendet. Der Einsatz wurde, in Absprache mit der Betreuungsperson, nicht gekennzeichnet.

Titel der Arbeit:

Light-Induced Height Growth in Tree Regeneration: A Study of Thirteen Species in Swiss Forests

Verfasst von:
Bei Gruppenarbeiten sind die Namen aller Verfasserinnen und Verfasser erforderlich.

Name(n):	**Vorname(n):**
Braun	Angela

Ich bestätige mit meiner Unterschrift:

- Ich habe mich an die Regeln des «Zitierleitfadens» gehalten.
- Ich habe alle Methoden, Daten und Arbeitsabläufe wahrheitsgetreu und vollständig dokumentiert.
- Ich habe alle Personen erwähnt, welche die Arbeit wesentlich unterstützt haben.

Ich nehme zur Kenntnis, dass die Arbeit mit elektronischen Hilfsmitteln auf Eigenständigkeit überprüft werden kann.

Ort, Datum	**Unterschrift(en)**
Zürich, 27.03.25	A. Braun

Bei Gruppenarbeiten sind die Namen aller Verfasserinnen und Verfasser erforderlich. Durch die Unterschriften bürgen sie grundsätzlich gemeinsam für den gesamten Inhalt dieser schriftlichen Arbeit.

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[1] z. B. ChatGPT, DALL E 2, Google Bard
[2] z. B. ChatGPT, DALL E 2, Google Bard
[3] z. B. ChatGPT, DALL E 2, Google Bard