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Effect of competition intensity and neighbor identity on architectural traits of *Fagus sylvatica*

Alice Penanhoat¹ · Nathaly Guerrero Ramirez^{2,3} · Méline Aubry-Kientz⁴ · Lucas Diekmann¹ · Sharath Paligi⁵ · Michela Audisio⁶ · Klara Mrak⁷ · Dominik Seidel¹

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Abstract

Key message Differences in architectural traits of European beech saplings submitted to different levels of competition intensity and neighborhood diversity show a shift toward lateral growth exploration for overtopped trees but less expressed apical control is maintained for beech grown with conifers.

Abstract Crown plasticity is a fundamental process to optimize the acquisition of light in forests, where it is often the limiting factor for growth. The processes leading to crown dynamics in response to biotic interaction are controlled by the competitive status of a tree, as well as the species diversity of the neighborhood. Yet, the ontogenic diversity of the different branches leading to crown structure makes it difficult to model crown plasticity. In this study, we used single-image photogrammetry and a semi-automatic topology reconstruction software to map the architecture of 3-year-old European beech trees (*Fagus sylvatica* L.) grown in pure pots or mixed with Douglas fir (*Pseudotsuga menziesii* (Mirbel) FRANCO) or Norway spruce (*Picea abies* L. H.KARST). Further, we investigated the effect of competition intensity (estimated with height rank) and neighbourhood diversity on architectural traits. To do so, we quantified the mean volume, slenderness, number of branches, branching rate, internode length, and diameter ratio for each stem and branch, up to the order three. Overtopped trees developed fewer branches and biomass but allocated more biomass to branches of a higher order than to the stem. The increase in the ramification of the stem and the diameter ratio of the first-order branches for overtopped trees indicate a shift in the growth strategy and a decrease in apical control. As competition intensity and neighbour identity have opposite effects on stem traits, it seems that the positive effect of plant diversity on growth can be attributed to the intrinsic effects of species identity rather than to competition release.

Keywords Juvenile · Saplings · Photogrammetry · Topology · Organizational level

Introduction

As climate change effects become more visible, mixed forests are a promising option to ensure the future provision of ecosystem functions and services, including forest

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productivity (Jucker et al. 2014; Toigo et al. 2015). Forests for which tree species differ in their strategies for resource acquisition may enable the plant community to maximize the use of available resources, i.e., through complementarity, resulting in higher ecosystem functioning (Barry et al. 2019; Pretzsch et al. 2013; Sapijanskas et al. 2014). In forests, where light is often the main limiting factor for growth and is asymmetrically distributed in space, the capability of a tree to access this resource is largely dependent on its height: overtopped trees have limited access to light and undergo a high competition intensity from the dominant higher trees. Different species have therefore developed different growth strategies and adapted architectural traits enabling them to deal with this issue (Rahman et al. 2013; Seidel et al. 2019).

Although individual crown shape and phenotype are bound to a genetic component, it is also determined by the environmental conditions experienced during ontogeny (Zimmer et al. 2015). Indeed, the shape of the crown is the result of the growth of each of the constituent branches, each branch responding to the conditions present in its micro-environment (Kawamura 2010; Osada 2021). However, individual branches are not completely independent in their growth pattern (Kawamura 2010; Rahman et al. 2014). Their development is controlled by internal signals integrating the resource availability at the plant scale as well as the light cues received from the environment (Hearn 2016; Stoll and Schmid 1998). These cues include the quantity and the quality of the transmitted light, which can be altered by the amount but also the properties of the surrounding foliage (Lintunen et al. 2013; Wang et al. 2020). Therefore, tree architecture may be shaped by the neighbourhood composition, for instance, the presence of conspecific or heterospecific competitors.

Previous studies have observed the response of tree species to different degrees of light, however, the studies were often realized using artificially set homogeneous gradients of light, when the penetration of light in the canopy is heterogeneous and determined by the canopy structure (Durand and Robson 2023). Moreover, studies targeting biomass allocation mainly focused on broad compartments such as above- and below-ground, or stem and branches, grouping all branch orders (Poorter 2001). Due to the technical difficulties of separating the different branch orders, the studies differentiating among branch orders include a small number of trees (Bayer et al. 2013; Lau et al. 2018), or focus on a subsample of branches and shoot (Mezghani et al. 2008; Toigo et al. 2021), limiting our understanding of intra-specific variation. For example, the smallest branches are usually left apart (Wilkes et al. 2021), despite their important role in displaying leaves and determining tree light interception capacity (Liu and Su 2016). Moreover, not only the sheer biomass of the organ, but also its geometry contributes to tree plasticity and acts as an indicator of the tree

growth strategy (de Haldat du Lys et al. 2023). Therefore, the development of growth models and precise allometric equations requires taking into account intraspecific variability by integrating the different tree compartments (Le Goff and Ottorini 2022).

Here, we mapped tree architecture and assessed the intra-specific variation for saplings growing under different biotic competition pressures, i.e., competition intensity and type. Specifically, we investigated the intraspecific variation of biomass allocation to the stem and branches, and the changes in their structural traits for European beech (*Fagus sylvatica* L.) saplings grown in pure pots or mixed with either Douglas fir (*Pseudotsuga menziesii* (Mirbel) Franco) or Norway spruce (*Picea abies* L. H.Karst). Further, we tested if single-image photogrammetry is a reliable method compared to traditional destructive biomass assessment.

We hypothesize that the adaptive response and the consequent architectural traits will differ between pure and mixed planted communities. In particular, we expect an increase in biomass production for beech in mixed compared to monospecific tree communities as a result of species complementarity. Further, in monospecific tree communities, we expect an increase in lateral foraging compared to mixed communities, with a higher allocation to lateral branches due to higher intraspecific competition.

Methods

Experimental setup

The experiment was conducted at the Department for Plant Ecology and Ecosystems Research (51°33'N, 9°57'E; 177 m.a.s.l.), University of Göttingen, Germany. In May 2019, one-year-old European beech and Douglas fir saplings, and two-years-old Norway spruce saplings were brought from the Baumschule Willenbocke GmbH nursery, Walsrode, Germany. The saplings selection was done to ensure similar above- and below-ground lengths. The plants were transplanted outdoor, underneath a sheltered transparent plexiglass to allow natural light conditions and controlled water and nitrogen treatments. The pots were arranged in parallel rows with ~2 m between each row, and ~15 cm between each pot within a row. Each row had 35 pots, resulting in a total of 315 pots.

We established tree communities with either pure beech (BB), beech mixed with Douglas fir (DB), or beech mixed with spruce (SB) in 65 L volume pots. Pots were pierced, and the bottom was covered with dense fabric to enable water drainage while preventing leakage of the potting medium, which consisted of coarse gravel (up to 5 cm at the bottom) and pure sand. Each pot consisted of four plants, and in the mixed pots, two trees of each species were planted

diagonally. At the moment of transplantation, the pots location was randomly assigned using the R package *randomizr* (Coppock et al. 2023), with each of the species-combination repeated seven times in a row. For two years (2019–2021), plants were regularly watered and treated with fertilizers, insecticide, and fungicide to ensure their vigor. At the end of May 2021, once the leaves of the beech saplings were out, six treatments combining three soil moisture levels and two levels of nitrogen availability were established (see details on treatment levels in Supplementary Material). The plants were harvested between mid-August to mid-September 2021. Out of 315 pots, we randomly selected 53 pots to be destructively harvested using the *randomizr* R-package (Coppock et al. 2023) covering the full gradients of treatments and species combinations (Supplementary Table 1).

Biomass collection and measurements of heights and diameters

We harvested 23 pots of pure beech (BB), 13 pots of beech mixed with Douglas fir (DB), and 17 pots of beech mixed with spruce (SB), resulting in 152 harvested beech juvenile trees. In each pot (hereafter referred to as *Pot ID*), the height of all plants (hereafter referred to as *Tree ID*) was manually measured with a ruler vertically placed near the tree stem, with zero corresponding to the soil surface.

All trees were then harvested and their root systems were manually detangled and separated. The stem was cut at the junction between the belowground and aboveground parts, and both parts separated. We measured the diameter at the base of the stem as the mean of two perpendicular diameters measured with an electronic vernier calliper.

For beech trees, all the leaves were manually removed, and the architectural traits were measured on the deleafed tree. The biomass was divided between the woody elements, the leaves or needles, and the roots before being dried for ~72 h at 70 °C and weighed.

Architectural traits measurement

We measured the architectural traits of all harvested beech trees (Table 1). To do so, the aboveground part of the deleafed tree was placed in front of a white canvas, with the stem maintained inside a vice (Fig. 1). A scale bar was placed near the tree for conversion from pixel to meters. The pictures were taken using a smartphone (SAMSUNG A5) with a camera of 12 million pixels and saved in JPG format. We took pictures of the trees at around three meters from the canvas, which corresponded to at least two times the height of each tree. We captured the entirety of the tree, holding the camera parallel to the canvas and at the height at which the tree was fixed on the canvas to ensure orthographic projection and limit perspective distortion (Liu et al. 2021; Patterson et al. 2011). For each tree, we took pictures at two positions, with the first position corresponding to the one we visually considered as the best to be able to map all branches in the post-processing stage (Kędra et al. 2019) and the second perpendicular to the first one. We tested the effect of photograph position by comparing the reconstruction of the architecture on the two photographs. For a subset of twelve trees, we mapped all branches on the two photographs taken at orthogonal positions. For each tree and each photograph, all branches of the same order were grouped together to calculate the mean volume, diameter and length of the branches. We observed that these geometrical features were not sensitive to the point of view of the photograph (Supplementary Fig. 3).

Using the *SmartRoot* plugin in ImageJ (Lobet et al. 2011), we identified semi-manually all tree branches and recorded their topological relationship. The image was first transformed to a 8-bit grayscale image, before mapping the different branches. The output of the software provides for each identified axe its topology (order, parent segment, child segment) as well as its geometrical features (mean diameter, total length, estimated volume). The order of a given axis

Table 1 Variables used for the linear mixed model fitted on the stem or on the different branch orders

	Variable	Description	Stem	Branch order
Response variables	Share of volume	Ratio of volume of cumulated branches on total tree volume ($\text{cm}^3 \cdot \text{cm}^{-3}$)	X	X
	Volume	Volume (cm^3)	X	X
	No. branches	Number of branches at a branch order (count)		X
	Slenderness	Length to diameter ratio ($\text{cm} \cdot \text{cm}^{-1}$)	X	X
	Branching rate	Number of branches per length unit (cm^{-1})	X	X
	Internode length	Mean length of internodes (cm)	X	X
	Diameter ratio	Ratio between branch diameter and parent diameter at insertion ($\text{cm} \cdot \text{cm}^{-1}$)		X
Fixed effect	Comb	Species combination, categorical variable {BB; SB; DB}	X	X
	Height rank	Height Rank, categorical variable {1; 2; 3; 4}	X	X
Random effect	Pot ID	ID of the pot	X	
	Tree ID	ID of the tree	X	X

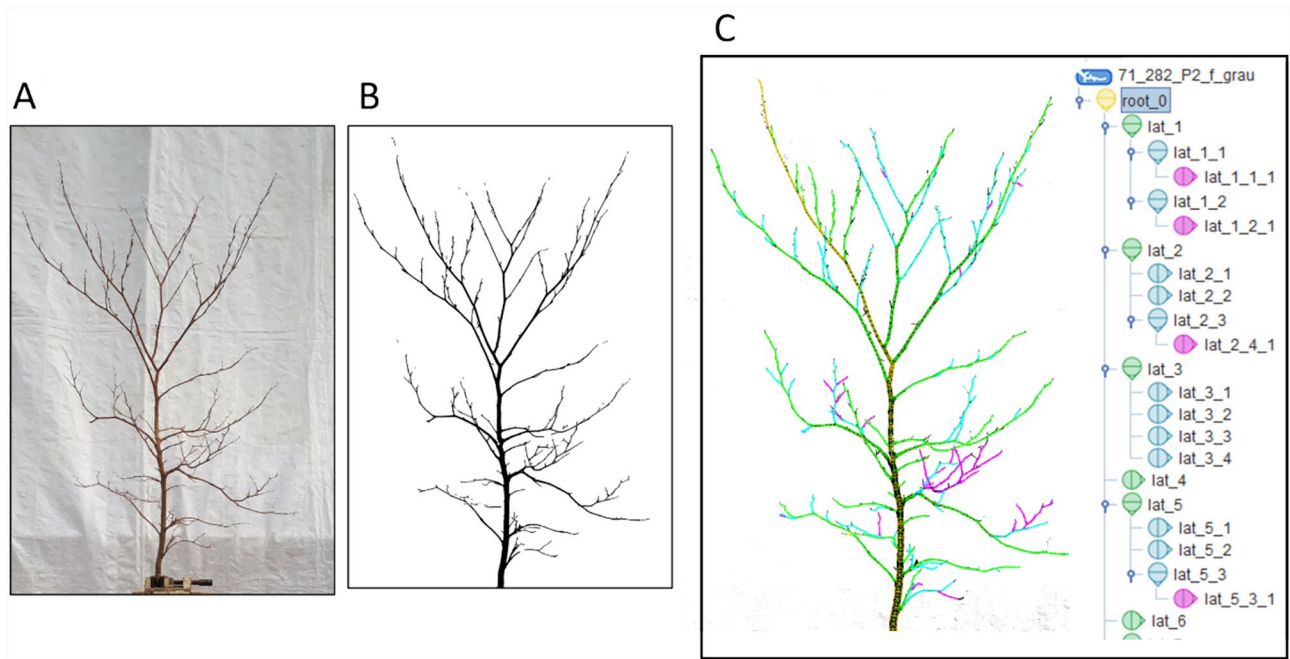


Fig. 1 Illustration of the measurement of the architectural traits. **(A)** Raw image of the tree. **(B)** Binarization of the image. **(C)** Reconstruction of the topology in SmartRoot

corresponded to one unit more than that of its parent, with the minimal order corresponding to zero. The mapping of the branches was done manually, using one axis per branch, and one for the stem. We identify branches as the longest path between a furcation and a tip (Wilkes et al. 2021). If the stem presented a fork with the two ramifications having similar diameter, we identified the longest ramification as the continuation of the stem. Identifying the parent-branch segment closest to the first child-branch segment, we calculated the diameter ratio as the ratio between the diameter at the insertion of the child segment and the diameter of the parent segment at the insertion point. The branching rate of a given branch corresponded to the number of ramifications per length unit. Identifying an internode as the segment of a branch between two ramifications, we calculated for each branch the mean internode length using the node coordinates.

Data analysis

We validated the performance of the image analysis by comparing the estimation of total shoot volume, stem basal diameter and stem length to manual measures of total tree dry biomass, stem diameter and total tree height. For each estimate, we used a linear model (estimated using ordinary least square) and calculated the coefficient of determination R^2 , the root-mean-square deviation (RMSD), and the mean absolute error (MAE). At the tree scale, we grouped

branches belonging to the same branching order and calculated the total cumulated volume as the sum of the volume of all branches, the mean diameter as the average branch mean diameter, and the mean length as the average branch length.

Within each pot, we ranked the trees by height from one (the highest) to four (the smallest) and used this height rank as an indicator of the competitive status of a tree. The species combination within a pot is an indicator of the competition type received by a target tree. We modelled the effect of the height rank and neighbourhood diversity on stem and branch traits using linear mixed effect models calculated with the “lme4” R-package version 1.1 (Bates et al. 2015). For measurements at the tree or stem scale, we included the Pot ID as a random effect. For measurements at the branch order scale, we included the Tree ID nested in the Pot ID as random effects. As fixed effects, we ran a first model with the height rank as the explaining categorical variable (Table 2, Model 1), followed by a second model using the model residuals with species combination as the explaining variable (Table 2, Model 2). In neither of the models, we included the other treatments implemented at the end of the experimental phase because changes in tree architecture are not expected in response to changes in nitrogen and water availability occurring after the start of the growing season (Fender et al. 2011; Nielsen and Jørgensen 2003; Simon et al. 2011), which was the case here (see Supplementary results).

Table 2 Equations of the models

	Stem level	Branch orders
Model 1	$Y_i = \alpha_{\text{Pot}_i} + \beta \times \text{HR}_i + \varepsilon_i$	$Y_i = \alpha_{\text{Pot}_{\text{Tree}_i}} + \beta \times \text{HR}_i + \varepsilon_i$
Model 2	$\varepsilon_i = \alpha'_{\text{Pot}_i} + \beta' \times \text{Comb}_i + \varepsilon'_i$ with $\alpha_{\text{Pot}_i} \sim N(\alpha_{\text{Pot}}, \sigma_{\text{Pot}}^2)$	$\varepsilon_i = \alpha'_{\text{Pot}_{\text{Tree}_i}} + \beta' \times \text{Comb}_i + \varepsilon'_i$ with $\alpha_{\text{Pot}_{\text{Tree}_i}} \sim N(\alpha_{\text{Pot}}, \sigma_{\text{Pot}}^2)$ and $\alpha_{\text{Pot}_j} \sim N(\alpha_{\text{Pot}}, \sigma_{\text{Pot}}^2)$

For a given element i (branch or stem), Y_i is the corresponding value of the architectural trait (response variable), α_{Pot_i} is the random effect of the PotID on the response, $\alpha_{\text{Pot}_{\text{Tree}_i}}$ is the random effect of the Pot ID:Tree ID interaction on the response, which represents the deviation of each PotID:TreeID combination from the PotID mean; ε : The residual error term, representing the random variation not explained by the model. The models assume a normal distribution of variances, an independence of the random effects and a normal distribution of the random effects

HR is the Height Rank, *Comb* is the species combination

We used the same model structure for all response variables across branching orders (Table 2). All variables were modelled using a Gaussian distribution, except for the number of branches which as a count variable was modelled using a Poisson distribution. We tested the assumption of normality of the residuals in models using the “Dharma” R-package (Hartig 2017). To assure the normality of the residuals, the volume was log-transformed. All models were computed with the “lme4” package and the marginal and conditional R^2 were calculated using the *get_gof* function of the “modelsummary” R-package (Arel-Bundock 2022). The marginal R^2 describes the proportion of variance explained only by the fixed effect (Height Rank or neighbourhood) and the conditional R^2 describes the proportion of variance explained by both fixed and random effects (TreeID, PotID)(Nakagawa and Schielzeth 2013). The statistical analyses were done using the R software (R version 4.0.5 (2021-03-31)).

Results

Validity of the method: comparison with manual measurements

The dry woody aboveground biomass of the beech plants ranged from 7.9 g to 153.67 g, with a median of 56.23 g and a mean of $57.77 \pm \text{SE } 3.17$ g. The woody aboveground volume of the beech plants ranged from 7.9 cm³ to 150.6 cm³, with a median of 57.3 cm³ and a mean of $59.0 \pm \text{SE } 2.33$ cm³. The positive relationship between the volume and the dry biomass of the beech trees was statistically significant ($R^2 = 0.85$, $p < 0.001$, $\beta = 1$, 95% CI [0.92, 1.06], Std. $\beta = 0.92$, 95% CI [0.86, 0.98], Fig. 2A). Yet, there was a tendency for variance to increase towards bigger trees, with an MAE of 8.9 (14%) and a RMSD of 12.1 (20%).

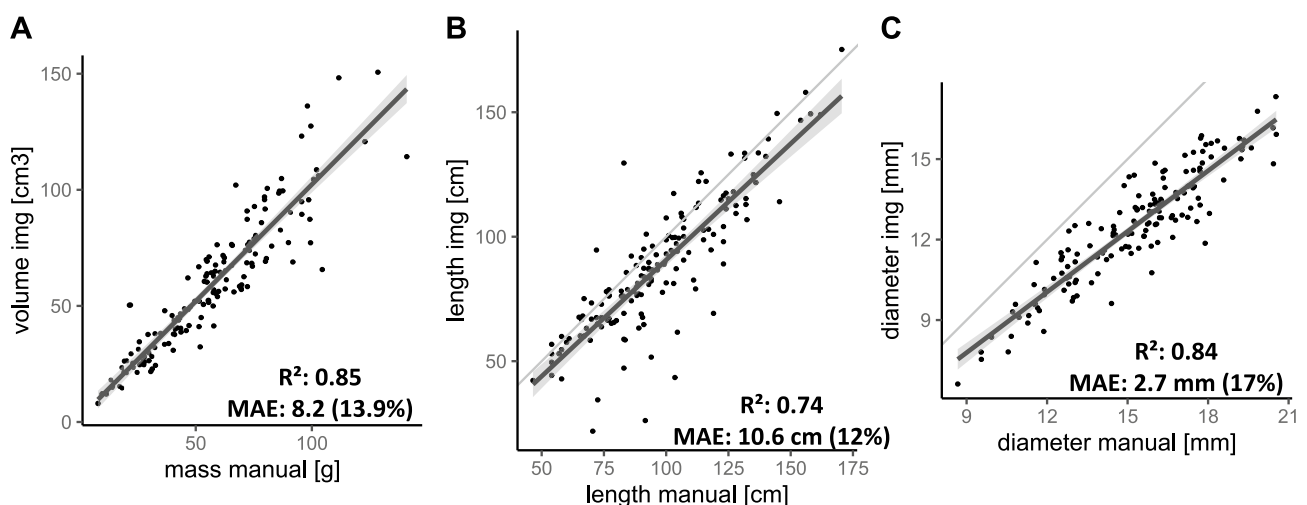


Fig. 2 Linear relation between measures from image analysis and from manual measurements. **A** Relation between total tree shoot volume and total shoot dry mass; **B** stem length; **C** stem base diame-

ter. The solid black line corresponds to the linear regression, and for length (**B**) and diameter (**C**) the grey line corresponds to the $y = x$ line

The height of the trees manually measured ranged from 48 cm to 170.5 cm, with a median of 93 cm and a mean of $96.3 \pm \text{SE } 2.03$ cm. The relationship between the length of the stem manually measured on the actual tree and the measurements from image analysis was positive (slope = 0.91) and statistically significant ($R^2 = 0.74$, $p < 0.001$, Fig. 2B). The length of the stem from the image analyse was slightly underestimated compared to the actual length. The MAE was 10.6 cm (12%), and the RMSD of 16.7 cm (17%).

The diameter of the stems manually measured ranged from 0.87 cm to 2.19 cm, with a median of 1.55 cm and a mean of $1.52 \pm \text{SE } 0.02$ cm. The relationship between the diameter of the stem manually measured and the measurements from image analysis was positive (slope = 0.75) and statistically significant ($R^2 = 0.84$, $p < 0.001$, Fig. 2C), with a constant underestimation of the diameter from the image analysis. The MAE was of 2.7 mm (17%), and the RMSD of 2.9 mm (19%).

Biomass allocation

Beech plants grown in the monospecific neighbourhood had an average woody aboveground biomass of 51.9 ± 1.9 g, significantly lower than the biomass of beech

grown in mixtures. Beech woody aboveground biomass was 58.0 ± 3.5 g in the mixture with Douglas fir and 72.4 ± 3 g in the mixture with spruce (Fig. 3, Table 3). This represented an increase of dry aboveground biomass of ~11% in the Douglas fir and ~40% in the spruce neighbourhood compared to the pure neighbourhood. Likewise, beech plants grown in pure neighbourhoods had lower total shoot volume (53.4 ± 1.4 cm³) compared to the total shoot volume of beech growing with Douglas fir (59.7 ± 2.1 cm³) or spruce (73.2 ± 2.4 cm³). We observed no significant difference in the shoot:root biomass ratio of beech in response to the composition of the neighbourhood (Fig. 3). Within the aboveground compartment, on average, the stem represented 63.4% of the total tree volume, the first-order branches 28%, the second order branches 7.5% and higher order branches less than 1% (Table 3).

Effect of height rank on architectural traits

The height rank of a tree influenced at least one architectural trait for each stem or branch order. The effect of height rank was linear and overtopped trees (HR = 4) displayed the strongest differences with the reference (HR = 1) in terms of architectural traits. Generally, the total volume of trees

Fig. 3 Aboveground biomass (A), aboveground volume (B) and shoot:root biomass ratio (C) of European beech in the different species combinations. DB Douglas–Beech, BB pure Beech, SB Spruce–Beech. Stars indicate significant differences (tested with linear mixed model)

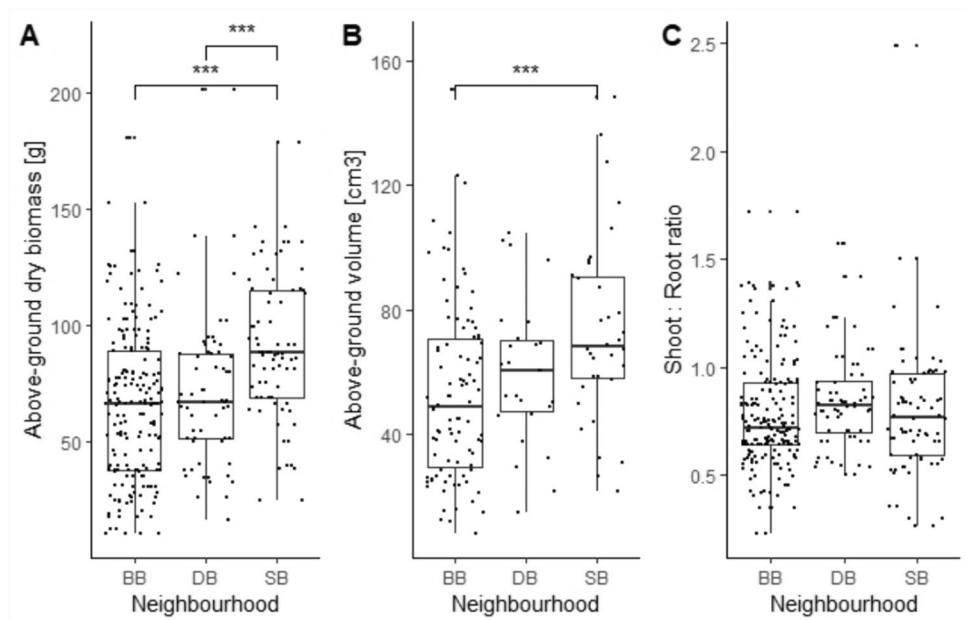


Table 3 Mean share in volume of different branch orders to the total tree volume of beech [%] and standard error SE

Combination	Monospecific beech				Douglas fir/beech mixture				Spruce/beech mixture				Mean			
	Stem	1	2	3	Stem	1	2	3	Stem	1	2	3	Stem	1	2	3
Share volume [%]	63.2	28.4	7.4	0.93	62.98	28.24	7.63	1.14	64.12	26.95	7.83	1.04	63.4	28.1	7.56	0.83
SE	1.07	0.73	0.38	0.14	2.67	1.86	0.85	0.26	1.44	1.01	0.56	0.17				

decreased with a lower height rank. In particular, the sheer volume of the stem, the number of branches, and their mean volume decreased with increasing overtopping. Yet the decrease in volume was steeper for the stem than for the branches. We found a significant effect of the height rank on the share of total woody volume that each branch order represented: overtopped trees allocated significantly less volume to the stem and more to the higher branch orders. In particular, the share of volume allocated to second-order branches was significantly higher for trees of height rank 3 and 4 compared to height rank 1 (Fig. 4A).

The slenderness of the stem significantly decreased with increasing height competition (conditional $R^2=0.27$, marginal $R^2=0.18$, p -value <0.05). The primary and secondary branches of overtopped trees, height rank three and four, were also significantly less slender than trees of height rank one. The stem branching rate increased for increasing height ranks, but the effect was only significant for the overtopped trees of height rank four (p -value = 0.008, conditional $R^2=0.16$, marginal $R^2=0.04$). Contrastingly, the mean internode length of the stem and first-order branches decreased, again with

the effect being significant only for overtopped trees (stem: p -value = 0.01, first branch order: p -value = 0.009) and with the model having a stronger explanatory power for the stem (conditional $R^2=0.13$, marginal $R^2=0.04$) than for the first order branch (conditional $R^2=0.06$, marginal $R^2=0.01$). Finally, the ratio of first order branch diameter to stem diameter at insertion (diameter ratio) increased significantly and linearly for all height ranks (conditional $R^2=0.04$, marginal $R^2=0.01$) (Fig. 4A).

Effect of neighbourhood type on architectural traits

When assessing the influence of neighbourhood type, we only found a significant effect on the architectural traits of the stem. In comparison with the beech in monospecific pots, beech mixed with conifers presented a lower branching rate of the stem, and higher internode length (Fig. 4B). Beech saplings mixed with conifers had a higher stem volume compared to saplings in monospecific pots, although only significant for the mixture with Douglas fir, and a slenderer stem than in monospecific pots, only significantly different for beech mixed with spruce.

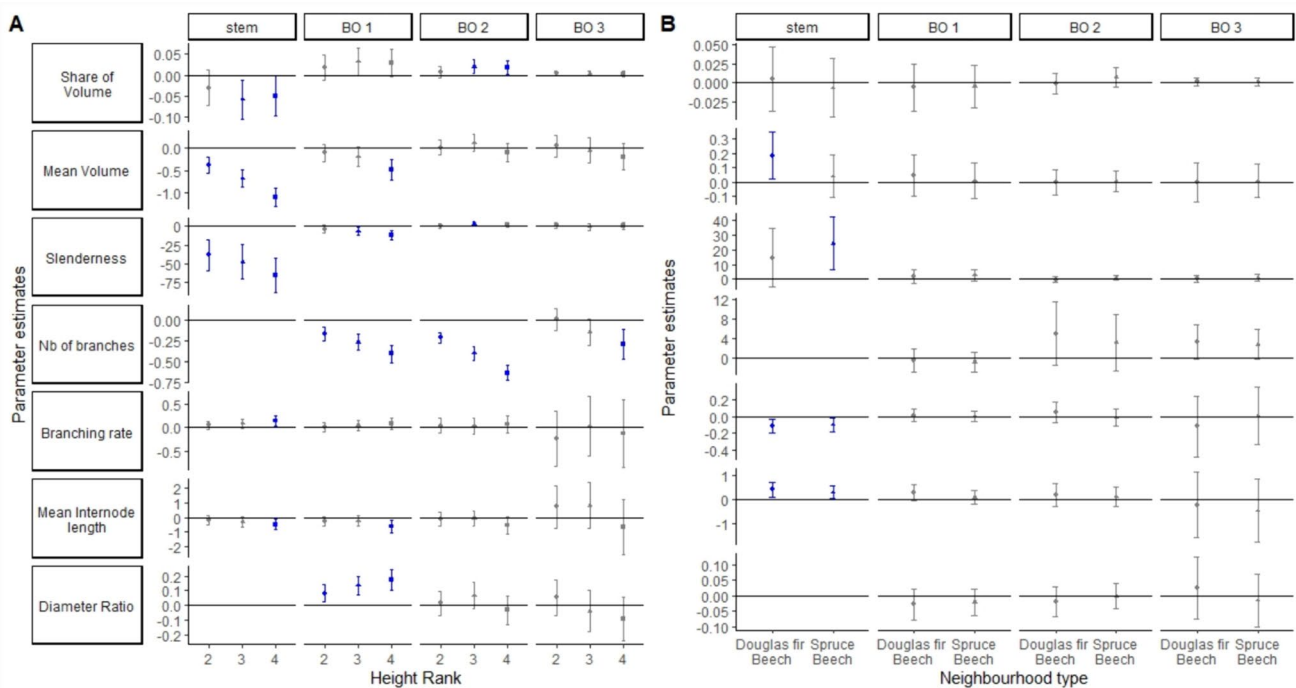


Fig. 4 Parameter estimates and 95% confidence intervals based on linear mixed models assessing the effects of height rank and neighbourhood type on Share of Volume, Volume (log transformed), Number of branches, Slenderness, Branching rate, Internode length, Diameter ratio for stem and across branch orders (BO) 1, 2, and 3. **A** Results of the first model, effect of height rank from

1 to 4 on response variables. **B** Results of the second model, effect of neighbourhood identity on architectural traits. The horizontal line represents the intercept (**A**: Height rank = 1, **B**: Neighbourhood type = monospecific beech). In blue the effect size for which the difference was significant

Discussion

In this study, we used architectural information derived from single-image photogrammetry to evaluate the changes in growth strategy in saplings of beech grown in pure or mixed neighbourhood. We showed the importance of considering the different branching orders when addressing the response of a tree to competition, as the amplitude—and even the direction—of their response varied considerably. This goes along with recent work by Toigo et al. (2021), who also observed differential growth of the stem and branches in response to species mixing in adult beech trees. We found that branch traits and the resulting tree architecture were influenced by the intensity of the competition as well as by the species identity of the neighbour. All the observed architectural traits were significantly affected by the height rank of a tree, in particular traits of the stem and the first-order branches.

Single image photogrammetry to reconstruct sapling architecture

Ours results showed that image-derived architectural and geometrical traits were in agreement with those obtained from manual measurements. Indeed, the length of the stem was well estimated with an MAE of 10.6 cm (12%). This is similar to the relative error of 12% (1.03 m) found by Lau et al. (2019) in the estimation of the length of 10–20 cm diameter branches using a laser scanner. With additional steps including a taper-function calibrated on manual measurements, Wilkes et al. (2021) reduced the bias to 1.3% (17 cm). When considering each individual branch, the error in length estimation was higher (MAE: 2.1 cm, 23.5%) (Supplementary Fig. 4), as branches, contrary to the stem, were not always in a plane parallel to the one of the camera, which could lead to deformation in the visualisation of their length. The stem diameter was systematically underestimated in the image analysis. This could be due to the sensitivity of diameter measurement to measurement location, especially on the base of the stem where the tapering is steep. However, the error we observed (MAE: 2.7 mm, 17%) was still much lower than the estimation from laser scanning, of 5.14 cm (40%) for example in the study by Lau et al. (2019). Indeed, the similar size of laser beam width and branch leads to echoes on the object edges, resulting in noise in the point cloud, which often leads to an overestimation of the diameter (Abegg et al. 2021). Finally, the comparison of total aboveground dry biomass to estimated volume also led to a low error (MAE: 8.2, 13.9%), but became higher when we included the comparison of each single branch (MAE:

0.2, 35.3%, Supplementary Fig. 4). However, because the elements observed were highly heterogeneous (stem, branches of different orders etc.), and would have required the measurement of several wood density parameters, we were here comparing two different measurements, mass and volume.

The addition of post-processing steps and manual calibration enables the usage of LiDAR for small elements reconstruction, however, major drawbacks of laser scanning are the cost of a scanning device, the time of scanning which takes up to ten minutes per individual (Wilkes et al. 2021), and the additional processing of the point-cloud before any measurement can be realized. Moreover, an increasing number of studies point out the limitation of LiDAR applicability for elements smaller than two cm in diameter, calling for the development of a new alternative for the mapping of saplings or small branches (Abegg et al. 2021; Martin-Ducup et al. 2020). In our case, setting up the tree and taking two pictures of a tree took less than one minute. The most time-consuming step was the semi-automatic image analysis. However, it was still faster than manual measurements: we needed 40 min to manually measure all branches diameter and lengths of one three-year-old beech sapling (Supplementary method). The method presented here is fast, affordable and its applicability was validated for the architecture reconstruction of European beech saplings.

Structural response to competition intensity

In our study, we observed that the total tree volume was correlated with the competition index, here: the height rank. However, the usage of ratio enabled us to compare the sheer effect of competition beyond the tree size. In particular, the shared volume that each branch order represented highlighted the changes in growth strategies between the different competitive statuses of the saplings. We observed a decrease in apical control or prioritization of the growth of the stem, to the benefit of lateral ramifications for overtopped trees, in line with the foraging behaviour theory (Stoll and Schmid 1998; Van de Peer et al. 2017). Indeed, as the height rank (or competition) increased, the share of volume of the stem decreased, while the share of volume of the higher branches increased (Fig. 4A, Table 3). The ramification of the stem also increased with Height Rank. A possible explanation is the interruption of axillary bud dormancy, as a strategy to increase the number of lateral exploring shoots. This is in line with earlier work demonstrating that the number of primary branches increases with neighbourhood competition in young trees of *Fagus sylvatica* (Van de Peer et al. 2017). According to the optimal foraging theory, branching frequency should increase when a plant encounters high local resource availability (Stoll and Schmid 1998; Sutherland and Stillman 1988). Thus, for saplings grown in the tropics, it

was found that trees in clearings had a higher branching ratio than in the understorey (Poorter and Werger 1999). In our case, we can expect that overtopped trees will find higher light availability with lateral exploration. Moreover, we also identified an increase of primary branches diameter ratio with competition (Fig. 4), meaning that the more the competition increased, the more the diameter of a ramification increased compared to the stem. This either shows a limited radial growth of the stem, an increase of radial growth of first-order branches or a combination of both mechanisms.

The slenderness of the stem and the first-order branches decreased with increasing Height Rank (Fig. 4A). This contrasts with the observations of MacFarlane & Kane, who reported a positive non-linear effect of competition on slenderness, with overtopped trees having a slenderer stem than dominant trees (MacFarlane and Kane 2017). However, this study was realized on adult trees and included light-demanding species, and for young European beech saplings the observed increase in stem slenderness with competition was not significant (Van de Peer et al. 2017). Slenderness is part of the shade avoidance syndrome, with trees increasing their growth in height to reach for more light. In our results, we also observe a decreased internode length for the overtopped trees. Our results therefore indicate that the growth was overall reduced, but the primary growth more than the secondary.

Changes in architecture in response to competition type

The mixture with conifer species had an effect on competition type, but also competition intensity as both conifers were not equal in terms of competition status. Douglas fir was overrepresented in the dominant tree category ($HR = 1$), while spruce was overrepresented in the overtopped tree category (Supplementary Fig. 1), confirming previous observations made on adult trees, namely that non-native Douglas fir has a higher competitiveness than native Central European forest tree species such as Norway spruce or European beech (Thomas et al. 2022). Thus, we observed that in average beech saplings mixed with spruce developed significantly more aboveground biomass than in pure pots (Fig. 3). However, for beech mixed with Douglas fir, there was no significant difference in the total aboveground biomass, and the mean volume of the stem was significantly higher (Fig. 4B). Thus, our hypothesis that beech mixed with conifers will develop more biomass than in monoculture due to complementarity in resource acquisition and architectural display was partially confirmed.

The identity of the competitor only had an effect on architectural traits of the stem. The mixture with conifers, compared to monospecific pots, influenced the architectural traits in the same direction but was not always significant for

the same species. Compared to beech grown in pure pots, the stem of the beech grown with conifers had a higher volume, was slenderer and less ramified (Fig. 4B). This suggests a shade avoidance syndrome in beech when grown with conifers, also observed in adult trees (Thurm and Pretzsch 2016). The decrease in stem ramification partially agrees with earlier findings showing that beech trees submitted to interspecific competition had a lower number of first-order branches than those exposed to intra-specific competition (Van de Peer et al. 2017). However, we attribute the significant decrease in stem branching rate (the number of child branches per length unit) mostly to the significant increase in stem length, as the decrease in the number of first-order branches was small and not significant. Moreover, for adult beech trees mixed with spruce, Bayer et al. observed a significant increase in the number of second, third and fourth-order branches (Bayer et al. 2013), which we also observed here (although not significant).

The contrasting patterns of competition intensity and type can be explained by different mechanisms underlying the growth. For example, the mean length of stem internodes increased with neighbourhood diversity but decreased with higher competition intensity. The decrease in internode elongation with increased competition intensity can be explained by an overall decrease in growth, when the increase due to neighbourhood diversity may be due to differences in light spectra transmitted by allo- or conspecific neighbours. Indeed, in the case of annual plants, it was shown that internode elongation was triggered by a decrease in red/far-red ratio (Kurepin et al. 2007; Xu et al. 2020).

Conclusion

We showed that single-image photogrammetry can be used for the accurate characterization of architectural pattern of three-years-old tree saplings. The detailed consideration of branches of different branch orders revealed differences in the growth strategy of trees subjected to different competition intensity and neighbourhood diversity. After only two years of interaction, beech trees already displayed differences in architectural traits depending on their competitive status and neighbour's identity, in particular at the stem and first-order branch scales. Stem and branch traits were mostly influenced by the intensity of the competition, which led to an overall reduction of growth, and a limitation of primary growth and apical control. However, beech saplings grown in heterospecific neighbourhood displayed bigger and slenderer stems than beech grown in pure neighbourhood. Although we studied here juveniles trees, this could have implications for forestry applications and the planning of forest composition in the future. We argue that the non-destructive photogrammetric method presented here could

help future research involving juvenile trees with respect to the analysis of their shape or detailed architecture. Image acquisition is fast, simple and cheap and while there is no full three-dimensional assessment, our data shows that a reliable estimation of tree biomass and architecture is possible. Despite our method being the most adapted to juvenile beech trees, considering their size and beech architecture, we encourage further studies to expand and validate this method across tree architecture types.

Author contribution statement Study design: Sharath Paligi, Alice Penanhoat; Data collection, Alice Penanhoat, Sharath Paligi, Michela Audisio, Klara Mrak, Lucas Diekmann; Data analysis, Alice Penanhoat, Méline Aubry-Kientz, Nathaly Guerrero Ramirez; Supervision, Dominik Seidel; Writing—original draft preparation: Alice Penanhoat, Writing—review and editing: Alice Penanhoat, Nathaly Guerrero Ramirez, Dominik Seidel. All authors have read and agreed to the final version of the manuscript.

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Data availability Data will be made available upon acceptance via gro. data (<https://data.goettingen-research-online.de/>).

Declarations

Conflict of interest The authors have no relevant financial or non-financial interests to disclose.

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