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Article

Does Slope Aspect Affect the Aboveground Tree Shape and Volume Allometry of European Beech (*Fagus sylvatica* L.) Trees?

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Abstract: In mountainous or hilly areas, the slope aspect affects the amount of solar radiation, with direct consequences on species distribution and tree growth. However, little is known on how the tree shape and volume allometry may be affected by contrasting environmental conditions driven by the slope aspect. This study aims to investigate whether the slope aspect affects the aboveground tree shape and volume allometry of European beech (*Fagus sylvatica* L.) trees. We used the data of scanned trees from two plots located on south- and respectively north-facing slopes and, additionally, an inventory dataset containing measurements of diameter at breast height (D) and tree height (H). To investigate the differences in tree shape, we used analysis of covariance. However, to assess the differences in volume allometry, we first predicted the volume of each individual tree within the inventory dataset using either the south- or the north-facing slope volume model, and then performed a paired t-test on the plot estimates based on the two volume models. Since the uncertainty originating from allometric volume model predictions was likely to affect the results of the paired t-test, we performed a Monte-Carlo simulation to assess the rate of null hypothesis acceptance with the paired t-test. The results showed that trees growing on the north-facing slope were significantly thinner ($p < 0.001$), with a significantly longer branching system ($p < 0.001$) compared to those on the south-facing slope. Correspondingly, the volume estimates per unit of forest area based on the south- vs. north-facing slope allometric volume models were significantly different ($p < 0.001$). The estimates of total aboveground volume per unit of forest area based on the north-facing slope allometric models were significantly larger compared to those based on the south-facing slope volume models, a difference driven by the significantly larger branch and stem volume for the north-facing slope. These differences in estimates per unit of forest area were larger when based on allometric models that only used D as a predictor of aboveground tree volume. The rates of null hypothesis acceptance within the paired t-test were generally low. For total aboveground volume estimated by D and H, the acceptance rate was 1.79%. Nevertheless, only using D to predict tree volume, the rates of null hypothesis acceptance were lower (i.e., 0.1%), suggesting that addition of H as a predictor of tree volume partly explains the differences caused by the slope aspect on volume allometry, but not enough to offset the differences entirely. In conclusion, slope aspect has significantly affected the tree shape and volume allometry of European beech trees.

Keywords: slope aspect; volume allometric model; tree shape; terrestrial laser scanning; European beech



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1. Introduction

Allometric models are widely used in forestry to predict tree-related parameters such as tree volume or biomass. Selection of allometric model was shown to considerably impact the biomass estimates [1,2], representing the largest source of uncertainty in biomass

estimates over large forest areas [3]. Typically, tree volume or biomass is predicted based on two predictor variables: diameter at breast height (D) and tree height (H). Therefore, the model would describe how tree volume or biomass vary with D and H. The relationship between size (e.g., volume or biomass) and shape (e.g., D and/or H) has long been studied, showing that a power function model describes the relationship well [4,5].

Allometric biomass or volume models were shown to be site specific [6,7] and species specific [6]. This means that the relationship between tree size and shape is affected by genotype and by the interaction between genotype and environmental conditions. It has been shown that the species (i.e., differences between species) was a stronger driver of variability in allometric models compared to site (i.e., differences between sites) [6]. However, the species specificity was shown to be highly reduced when including, among predictors, the wood density [8].

Besides site and species, inside closed-canopy stands, competition influences tree architecture and growth. The lateral shading stimulates trees to invest more in height growth than in diameter growth (being a lower priority in carbon allocation), making trees slenderer [9]. The environmental factors affecting the allometric relationships are related to climate and soil properties. Soil properties were shown to influence tree shape. For example, increasing the cation exchange capacity resulted in an increase in H/D ratio (i.e., the ratio between tree height and diameter at breast height); therefore, for any given D, the height was higher when cation exchange capacity was high [10]. However, despite the significant effects on H/D ratio, the effects of soil properties on allometric biomass models were shown to be not significant. Therefore, the relationship between aboveground biomass and its predictors D and H seems to be unaffected by soil properties [10]. When investigating the effects at the level of biomass per unit of area, the soil texture was shown to be an important factor affecting biomass stock [11]. Furthermore, since the growth is linked to climate, it was shown that climate significantly affects tree shape [12–14]. Investigating the effects of temperature gradient on tree allometry and biomass stock per unit of area is important because it may help to determine the effects of climate change on these tree and forest characteristics. Lines et al. [13] showed that trees in arid and colder conditions were much shorter for any given D, compared to those growing in wet and warmer conditions. However, the effect was observed among species and not within any species. Therefore, it was suggested that climate conditions tend to affect the spatial distribution of species more than the tree shape of individuals within the species. Nevertheless, in tropical trees, the precipitation, temperature, and dry season length emerged as key climate factors affecting the tree slenderness [15].

Since the environmental conditions affect the tree H/D ratio, it is to be expected that biomass allometry is also affected. Climate conditions were shown to modulate the relationship between size and biomass. However, the effect was present on only approximately 70% of species, with the allometry of annual species being generally less affected by climate than that of perennial species [14]. The relationship between aboveground biomass and its predictors D and H for Norway spruce (*Picea abies* L. Karst.) trees was shown to be significantly affected by mixture with other species [16]. In pure stands, due to a greater biomass of branches, the aboveground biomass was greater for trees of any D and H compared to trees in mixtures with European beech (*Fagus sylvatica* L.) [17].

In mountainous and hilly areas of the northern hemisphere, north-facing slopes receive less solar radiation, and therefore, the environmental conditions tend to be different compared to south-facing slopes, where the solar radiation is more abundant. It was shown that soil water evaporation on south-facing slopes was larger compared to north-facing slopes [18], affecting the composition, structure, and density of plant communities [19]. Despite significant differences in species composition, slope aspect was shown to have no significant effect on soil properties and carbon stock per unit of area, except for potassium, which was higher on the south-facing slope [20]. However, recent evidence has shown that trees from tropical treeline located on a south-facing slope grow faster compared to those on a north-facing slope [21].

European beech is one of the most widespread broadleaved trees in European forests [22]. The species grows on a wide range of soils [23] and, in terms of economic importance, is one of the most diversely used tree species in Europe [22]. In Romania, it is the most widespread forest tree species, covering roughly 30% of the entire forestland [24]. It usually makes pure stands on large and compact areas in hilly and mountainous regions, but also forms mixtures with silver fir (*Abies alba* Mill.) and Norway spruce in the mountains, and various broadleaves, e.g., sessile oak (*Quercus petraea* (Matt.) Liebl.) in the hilly region [25]. Since most of the areal species in Romania are in the mountain region, slope aspect is an important potential driver not only for forest growth, but also for tree shape and allometry. European beech has been extensively studied, with various allometric volume and biomass models reported for the species [26–33]. While the response of morphological plasticity to within and between species competition (i.e., European beech trees in pure vs. mixed species stands) was previously reported [16,34,35], little is known about the potential effect of slope aspect on European beech tree shape and allometry. Knowing more about the effects of slope aspect on species allometry can improve our understanding of local adaptation and phenotypic plasticity of the species in response to the contrasting environmental conditions (such as on the south- vs. north-facing slopes). Moreover, it can help with improving the prediction of forest volume and biomass, with positive consequences for the reliability of current and forthcoming climate change mitigation actions.

Developing site-specific and species-specific allometric models implies significant logistics and extended labor, since measuring tree volume or biomass usually involves destructive sampling of trees [36]. However, recent advances in sensors and algorithms for terrestrial laser scanning (TLS) have facilitated the acquisition of tree volume observations with less effort [37], and without cutting down the sample trees. The TLS is therefore considered a revolutionary tool for the study of tree allometry and tree architecture, making it possible to reconstruct tree shapes with unprecedented accuracy and detail [38]. Therefore, studies on allometric scaling can be more easily implemented with such technology [39,40].

In this paper, we aimed to answer the following research questions: (i) Does the slope aspect affect tree characteristics such as tree slenderness and the total length of branches? (ii) Does the slope aspect affect the allometric relationships between tree volume (i.e., total aboveground tree volume, stem volume, or branch volume) and its predictors (i.e., D and/or H)?

2. Materials and Methods

2.1. Location

The research was conducted in the central part of Romania, in a low-mountain area of the Carpathians (Postăvarul Mountain). Measurements were performed in two adjacent pure European beech forest stands in a community forest managed by Râșnov Forest District (Râșnov, Brasov County, Romania), located within the optimal range of the species. The selected forest stands were separated by a valley that was oriented east–west. Therefore, the slopes were oriented south and north. The following criteria were used for stand selection: (i) the age and the structure (e.g., diameter distribution and tree density) of the stands on the south- and north-facing slope are similar; (ii) the tree development stage is mature, because tree shape and allometry have already been defined by the contrasting environmental conditions on the south- and north-facing slopes; (iii) the stands show no signs of recent thinning that may have affected the shape and allometry of the sample trees. Within each stand, the location of the sample plot was selected to include a similar number of trees (i.e., 30 trees), thus assuming similar levels of competition in the two sample plots. The general characteristics of the stands are presented in Table 1.

Table 1. The characteristics of the two investigated forest stands.

Characteristic	South-Facing Slope	North-Facing Slope
Species composition	100% European beech	100% European beech
Area (ha)	34.6	32.5
Slope (%)	25	26
Altitude range (m)	750–1000	730–970
Soil type	Alisols	Alisols
Coordinates	45.588, 25.498	45.585, 25.499

2.2. Scanning of Sample Trees and Data Processing

In each of the two forest stands, we scanned the trees from a sample plot of 1000 m² using a terrestrial laser scanner (TLS) produced by Faro, USA (Faro Focus 70 s). Twenty stations were performed in each sample plot, to generate sufficient returns. A total of 60 trees were scanned: 30 trees located on the south-facing slope and 30 trees on the north-facing slope. Since the number of trees per plot were the same, competition among trees in both plots was assumed similar.

We used Faro Scene (Faro, Lake Mary, FL, USA, v. 2018.0.0.648) to pre-process the data. The separation of individual trees was performed in CloudCompare (v. 2.11 beta). After separation, using the ASCII cloud type, each tree was saved as a txt. file. Further analysis was performed in Matlab (MathWorks, Natick, MA, USA v. R2017b), using the integrated TREEQSM procedure [41]. For each tree, the following characteristics were derived:

- Diameter at breast height, D (in cm), determined as the diameter of a cylinder fitted to the height 1.1–1.5 m.
- Total tree height, H (in m), determined as the vertical distance between ground level and the extremity of the highest branch detected.
- Total length of branches (in m), determined as the sum of the lengths of all branches remaining after stem identification.
- Branch volume (in m³), determined as the sum of all individual branch volumes.
- Stem volume (in m³).
- Total aboveground tree volume (in m³), determined as the sum of branch and stem volumes.

The characteristics of the scanned trees are presented in Table 2. Despite a slightly larger mean D on the south-facing slope compared to north-facing slope, the differences were not significant (independent samples *t*-test: $p = 0.807$). However, the mean H was significantly larger for the north-facing slope (independent samples *t*-test: $p < 0.001$). The basal areas for the two plots were comparable (Table 2).

Table 2. The characteristics of the scanned sample trees.

Characteristic	South-Facing Slope	North-Facing Slope
Mean D [and range of D] (cm)	54.9 [35.2–81.4]	53.5 [33.3–70.5]
Mean H [and range of H] (m)	30.3 [25.3–33.8]	33.5 [27.2–39.0]
Number of trees scanned	30	30
Basal area (m ² ha ⁻¹)	63.7	61.4

2.3. Data Analysis

2.3.1. Testing the Differences in Tree Shape between South and North Facing Slope

We tested the differences in tree shape (*TS*) between south- and north-facing slope using the following ANCOVA model:

$$TS = \beta_0 + \beta_1 \cdot D + \beta_2 \cdot ASP + \varepsilon, \quad (1)$$

where TS is the predictor variable, which can either be (i) the ratio between tree height and diameter at breast height (H/D ratio), or (ii) the total length of branches; D is the diameter at breast height; and ASP is the slope aspect.

2.3.2. Development of Allometric Volume Models

Observations from each of the two plots were used further to develop allometric volume models. Because the limited number of observations did not allow us to model the heteroscedasticity, we adopted a logarithmic transformation of all variables to develop the models:

$$\ln(V) = \beta_0 + \beta_1 \cdot \ln(D) + \varepsilon, \quad (2)$$

$$\ln(V) = \beta_0 + \beta_1 \cdot \ln(D) + \beta_2 \cdot \ln(H) + \varepsilon, \quad (3)$$

where β_0 , β_1 , and β_2 are the model parameters to be estimated; $\ln(V)$ is the natural logarithm of the dependent variable, volume (V , which can be the total aboveground tree volume, the stem volume, or the branch volume); $\ln(D)$ is the logarithm of diameter at breast height; $\ln(H)$ is the logarithm of total tree height; ε is the residual term, assumed to be normally distributed with mean zero. The coefficient of determination (R^2) was further reported, showing the goodness of fit.

2.3.3. The Effects of Differences in Allometric Models on Volume Estimates over Large Forest Areas

Allometric volume models are typically used to estimate the volume of individual trees; therefore, a more appropriate assessment of differences between south- and north-facing slopes would be to investigate the differences at the level of large forest area estimates. For this purpose, we extracted all plots where European beech occurred from the Romanian National Forest Inventory (NFI). Each plot in the Romanian NFI was established at an intersection of a 4 by 4 km grid. Within a 500 m² subplot, D and H were measured for all trees with D larger than 28.5 cm; in a smaller 200 m² concentric subplot, the trees with D smaller than 28.5 cm (but larger than 5.6 cm) were also measured. Because an allometric model should be applied to predict volume for trees roughly within the range of covariates used to develop the model, we further restricted the range of diameter at breast height to be between 30 and 100 cm. Therefore, those plots containing trees with $D < 30$ cm or $D > 100$ cm were excluded. A total of 134 plots, containing 674 European beech trees in total, were identified, called hereafter the “inventory dataset”. The volume of these trees was estimated using the allometric models developed in this study for (i) the south-facing slope and (ii) the north-facing slope. For each tree in the inventory dataset, we calculated the individual tree volume using the back-transformed form of Equation (2) and respectively Equation (3):

$$\hat{V}_{ij} = \exp(\hat{\beta}_0 + 0.5 \cdot RSE_1^2) \cdot D_{ij}^{\hat{\beta}_1}, \quad (4)$$

$$\hat{V}_{ij} = \exp(\hat{\beta}_0 + 0.5 \cdot RSE_2^2) \cdot D_{ij}^{\hat{\beta}_1} \cdot H_{ij}^{\hat{\beta}_2}, \quad (5)$$

where \hat{V}_{ij} is the volume estimate of tree i from plot j ; D_{ij} and H_{ij} are the diameter at breast height and respective height of tree i from plot j within the inventory dataset; $\hat{\beta}_0$, $\hat{\beta}_1$, and $\hat{\beta}_2$ are the parameter estimates of Equation (2) or (3), for either the south- or north-facing slope trees; and RSE_1 and RSE_2 are the residual standard error of Equations (2) and (3), respectively, fitted on either the south- or north-facing slope observations.

The mean volume per hectare and the standard error of the mean were calculated using the following formulae:

$$\hat{\mu} = \frac{1}{n} \sum_{j=1}^n \hat{V}_j \quad (6)$$

$$SE(\hat{\mu}) = \sqrt{\frac{1}{n(n-1)} \sum_{j=1}^n (\hat{V}_j - \hat{\mu})^2} \quad (7)$$

where n is the total number of plots ($n = 134$) and \hat{V}_j is the plot volume estimates, based on the sum of individual tree predictions within each plot.

2.3.4. Testing the Differences in Volume Allometry between South- and North -Facing Slopes

Because testing the differences directly at the level of allometric volume models is challenging due to their nonlinear model form, we examined the differences between south- and north-facing slopes at the level of large area volume estimates. Each of the two models derived for the south- and respectively north-facing slope were used to estimate the volume of each tree in the inventory dataset. Therefore, two sets of plot level estimates (V_j in Equation (6)) were obtained: one based on the south-facing slope (i.e., allometric volume model) and another one based on the north-facing slope. Specifically, we used the allometric volume models (for the south- and north-facing slope) as two different treatments applied to the inventory dataset. We used a paired t-test (two-tailed) to test whether the mean differences between plot estimates were significantly different from zero.

2.3.5. Determining the Rate of H_0 Acceptance within the Paired t -Test

The uncertainty originating from the allometric model predictions (i.e., residual variance and allometric model parameters) is likely to affect the uncertainty of plot estimates, with direct consequences on the results of paired t-test. To determine the rate of H_0 (null hypothesis) acceptance within the paired t-test due to uncertainty in the allometric model predictions, we performed a Monte-Carlo error propagation procedure as follows:

- Step 1. Select a set of random model parameters from a bi-variate (for Equation (2)) or tri-variate (for Equation (3)) normal distribution for the south-facing slope.
- Step 2. Select a set of random model parameters from a bi-variate (for Equation (2)) or tri-variate (for Equation (3)) normal distribution for the north-facing slope.
- Step 3. Select 674 random values (one for each tree in the inventory dataset) from a normal distribution with mean zero and standard deviation equal to the residual standard error of Equation (2) or (3), fitted to the south-facing slope observations.
- Step 4. Select another set of 674 random values from a normal distribution with mean zero and standard deviation equal to the residual standard error of Equation (2) or (3), fitted to the north-facing slope observations.
- Step 5. Calculate the predicted volume for each tree in the inventory dataset based on the south-facing slope model. The volume of each tree was calculated using the model parameters selected at step 1 (i.e., $\hat{\beta}_{0m}$, $\hat{\beta}_{1m}$ and/or $\hat{\beta}_{2m}$). To each tree prediction, a random residual (i.e., r_{ijm} from step 3) was added. The back-transformation correction factor was then used to account for the transformation bias (RSE_{s1} is the residual standard error of Equation (2) fitted to the south-facing slope observations; RSE_{s2} is the residual standard error of Equation (3) fitted to the south-facing slope observations):

$$\hat{V}_{ij} = \exp(\hat{\beta}_{0m} + \hat{\beta}_{1m} \cdot \ln(D_{ij}) + r_{ijm}) \cdot \exp\left(\frac{RSE_{s1}^2}{2}\right) \quad (8)$$

$$\hat{V}_{ij} = \exp(\hat{\beta}_{0m} + \hat{\beta}_{1m} \cdot \ln(D_{ij}) + \hat{\beta}_{2m} \cdot \ln(H_{ij}) + r_{ijm}) \cdot \exp\left(\frac{RSE_{s2}^2}{2}\right) \quad (9)$$

- Step 6. Calculate the predicted volume for each tree in the inventory dataset based on the north-facing slope model. The volume of each tree was calculated using the model parameters selected at step 2 (i.e., $\hat{\beta}_{0m}$, $\hat{\beta}_{1m}$ and/or $\hat{\beta}_{2m}$). To each model prediction, a random residual (r_{ijm} from step 4) was added. The back-transformation correction factor was used to account for the transformation bias (RSE_{n1} is the residual standard error of Equation (2) fitted to the north-facing slope observations; RSE_{n2} is the residual standard error of Equation (3) fitted to the north-facing slope observations):

$$\hat{V}_{ij} = \exp(\hat{\beta}_{0m} + \hat{\beta}_{1m} \cdot \ln(D_{ij}) + r_{ijm}) \cdot \exp\left(\frac{RSE_{n1}^2}{2}\right) \quad (10)$$

$$\hat{V}_{ij} = \exp(\hat{\beta}_{0m} + \hat{\beta}_{1m} \cdot \ln(D_{ij}) + \hat{\beta}_{2m} \cdot \ln(H_{ij}) + r_{ijm}) \cdot \exp\left(\frac{RSE_{n2}^2}{2}\right) \quad (11)$$

Step 7. Calculate the plot volumes extrapolated to hectare for the inventory dataset based on the south-facing slope model, using the individual tree predictions from step 5. To extrapolate the plot volume to hectare, a factor of 20 was used for those trees measured within the 500 m² sample plot, and a factor of 50 for trees within the smaller 200 m² sample plot.

Step 8. Perform similar calculations as in step 7, but for the north-facing slope, using the individual tree predictions from step 6.

Step 9. Apply a paired t-test comparing the 134 plot estimates based on the allometric volume model for the south-facing slope (from step 7) with the 134 plot estimates based on the allometric volume model for the north-facing slope (from step 8). Retain the *p*-value of the test.

Step 10 Repeat steps 1–9 for *m* = 100,000 times and further report the proportion of repetitions with *p* > 0.05 out of the total number of repetitions.

3. Results

3.1. The Differences in Tree Shape between South- and North-Facing Slope

3.1.1. H/D Ratio

For the analyzed samples, the H/D ratio decreased with D (Figure 1), meaning that slenderness decreased with tree size. The ANCOVA results (Equation (1)) showed that trees growing on the north-facing slope had a significantly higher H for the same D (*p* < 0.001), regardless of tree size. The interaction between regression lines was not significant (*p* = 0.408), thus meeting the assumption of homogeneity of regression slopes. Therefore, the decrease of tree slenderness by tree size was similar on the north- and south-facing slope; however, the tree slenderness was systematically larger (significantly) on the north-facing slope. This result has further implications on volume allometry, since trees with a higher height for the same D will usually exhibit a larger stem volume.

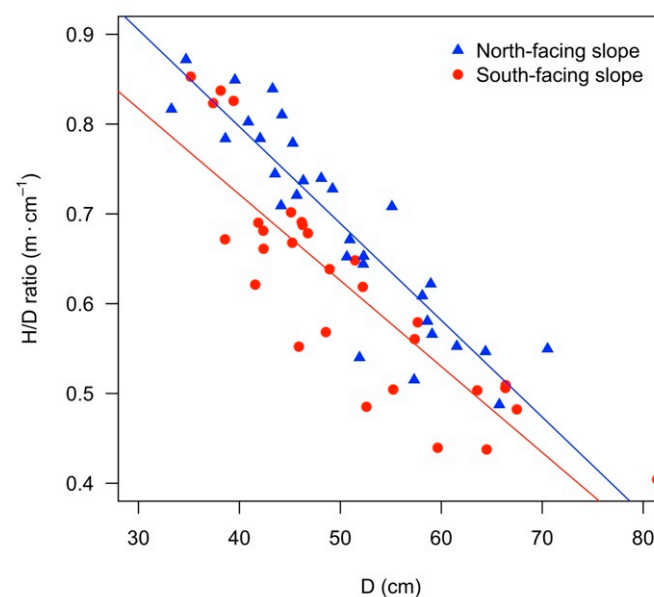


Figure 1. The relationship between H/D ratio and D for trees growing on the north-facing slope (blue triangles) and on the south-facing slope (red dots). The regression lines for the two groups follow the same color differentiation.

3.1.2. Total Length of Branches

The total length of branches was also dependent on tree size (Figure 2). However, the north-facing slope trees exhibited a significantly longer branching system length compared to south-facing slope trees. The ANCOVA results confirmed the significant differences ($p = 0.0016$) and the lack of interaction between ASP and D variables ($p = 0.430$). Therefore, the total length of branching system increased with D, similarly for the south-facing slope trees and the north-facing slope trees, but with a systematic longer branching system for trees on the north-facing slope, regardless of tree size.

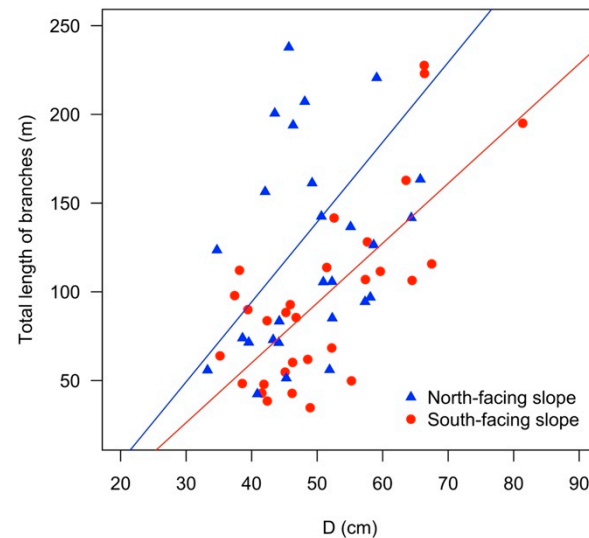


Figure 2. The relationship between total length of branches and D for trees growing on the north-facing slope (blue triangles) and on the south-facing slope (red dots). The regression lines for the two groups follow the same color differentiation.

3.2. Allometric Volume Models for South- and North-Facing Slope

The allometric volume models for trees on the south- and north-facing slopes are presented in Table 3. The coefficient of determination (R^2) values were generally larger for south-facing slope trees, denoting a smaller residual variability (RSE) and a better capacity of D and H to explain volume variability. The models predicting branch volume presented higher RSE and lower R^2 values. Also, for the north-facing slope model, H proved to be a non-significant predictor of branch and stem volume (Table 3).

3.3. Volume Estimates Per Unit of Forest Area and the Differences between South- and North-Facing Slopes

The estimates of aboveground volume were systematically larger when based on the north-facing slope model compared to the south-facing slope model (Table 4). The total aboveground volume estimate based on the north-facing slope model was 12.8% larger (i.e., by $41.8 \text{ m}^3 \text{ ha}^{-1}$) when using only D as a predictor (i.e., Equation (4)) and 5.1% larger (i.e., by $16.6 \text{ m}^3 \text{ ha}^{-1}$) when H was added into the allometric volume model (using D and H as predictors of total aboveground tree volume, as in Equation (5)). The differences at the level of volume compartments were smaller for stem volume. The estimates of stem volume per hectare (i.e., Equation (6)) based on the north-facing slope allometric model were larger by 7.2% (i.e., $19.2 \text{ m}^3 \text{ ha}^{-1}$) for Equation (4) and by 1.2% (i.e., $3.3 \text{ m}^3 \text{ ha}^{-1}$) for Equation (5). Nevertheless, the branch volume estimates per unit of forest area based on the north-facing slope model were larger by 38.4% (i.e., $25.7 \text{ m}^3 \text{ ha}^{-1}$) for Equation (4) and by 22.5% (i.e., $15.6 \text{ m}^3 \text{ ha}^{-1}$) for Equation (5) compared to the estimates based on the south-facing slope.

Table 3. The parameter estimates of Equations (2) and (3), for different response variables and datasets.

Response Variable	Predictors	Eq.	β_0	β_1	β_2	RSE	R ²
South facing slope model							
Total aboveground volume	D	Equation (2)	−6.8388	2.0531 ***	-	0.1088	0.9415
	D and H	Equation (3)	−9.0429	1.9505 ***	0.7647 ***	0.0863	0.9645
Stem volume	D	Equation (2)	−6.0327	1.7964 ***	-	0.1397	0.8821
	D and H	Equation (3)	−9.0670	1.7174 ***	0.5896 *	0.1318	0.8988
Branch volume	D	Equation (2)	−13.2380	3.1950 ***	-	0.6773	0.5015
	D and H	Equation (3)	−17.0814	3.0163 ***	1.3337 ns	0.6790	0.5169
North facing slope model							
Total aboveground volume	D	Equation (2)	−8.2148	2.4273 ***	-	0.1285	0.9286
	D and H	Equation (3)	−9.8582	2.3018 ***	0.6075 *	0.1223	0.9376
Stem volume	D	Equation (2)	−7.0782	2.0764 ***	-	0.1653	0.8518
	D and H	Equation (3)	−8.4681	1.9702 ***	0.5138 ns	0.1636	0.8600
Branch volume	D	Equation (2)	−15.958	3.9170 ***	-	0.8070	0.4619
	D and H	Equation (3)	−18.3236	3.7366 ***	0.8746 ns	0.8191	0.4655

Levels of significance: * $p < 0.05$; *** $p < 0.001$; ns $p > 0.05$.

Table 4. The mean volume per hectare (Equation (6)) and standard error of the mean (Equation (7)) based on south- and north-facing slope allometric models, the p -values of the paired t -test, and the rates of H_0 acceptance within the paired t -test, by volume pool estimated and allometric model form.

Volume Pool Estimated	Predictors of Tree Volume	Allometric Model Form	Mean Volume per Hectare ($m^3 ha^{-1}$), Based on Allometric Model for		SE of the Mean ($m^3 ha^{-1}$), Based on Allometric Model for		p -Value of Paired t -Test	Percentage of H_0 Acceptance at $p > 0.05$
			South-Facing Slope	North-Facing Slope	South-Facing Slope	North-Facing Slope		
Total aboveground volume	D	Equation (4)	327.43	369.28	18.77	21.94	<0.001	0.10%
	D and H	Equation (5)	326.42	342.99	18.53	21.72	<0.001	1.79%
Stem volume	D	Equation (4)	265.80	285.00	15.00	16.37	<0.001	0.96%
	D and H	Equation (5)	263.93	267.24	14.99	16.25	<0.001	1.68%
Branch volume	D	Equation (4)	67.08	92.82	5.47	7.12	<0.001	0.93%
	D and H	Equation (5)	69.47	85.11	5.36	6.96	<0.001	6.47%

The results of the paired t -test showed significant differences between plot estimates based on the south- and north-facing slope models, for all estimated volume pools (Table 4). Therefore, the volume allometry for trees growing on the south facing-slope differs significantly from that of trees growing on the north-facing slope. The acceptance rate of null hypothesis (i.e., H_0) within the paired t -test due to uncertainty in allometric model predictions was generally low. The rates of H_0 acceptance were lower when using only D as a predictor of tree volume (when the absolute differences between estimates were large; see Table 4) and increased when including H as additional predictor of tree volume (when the absolute differences between estimates were smaller). For total aboveground volume, the rate was 0.1% when using only D and 1.79% when using both D and H. Therefore, the addition of H reduced the differences (and increased the likelihood for H_0 acceptance) in volume allometry for the south- vs. north-facing slopes, but it was not sufficient to offset the differences entirely.

4. Discussion

The results showed significant differences in tree shape traits (i.e., H/D ratio and the total length of branches) and volume allometry between south- and north-facing slopes in our study sites.

The H/D ratio is a well-established measure of stand stability [41], being affected by competition with the neighboring trees. In our study, despite the sample plots containing the same number of trees (i.e., similar competition among trees assumed), the H/D ratio

was larger on the north-facing slope. This result may be the consequence of the lower amount of solar radiation on the north-facing slope, which allows for better soil moisture during the growing season (with European beech being adapted to moist rather than dry environments) [22]. A negative correlation between tree height and solar radiation (which could limit soil moisture) was also found by Saremi et al. [42], thus justifying our results. On the other hand, the diameter growth, which is more active towards the end of the vegetation season, may be stimulated by the higher amount of solar radiation available on the south-facing slope (i.e., a longer growing season) [43]. However, as European beech is deciduous, such differences are not expected to play an important role (especially for adjacent slopes).

The longer branching system on the north-facing slope may have also been caused by the lower solar radiation. Lower radiation requires trees to be more effective in intercepting light; therefore, the trees need to invest more in crown branch development in order to develop an effective leaf system [44–46]. Moreover, where moisture is less limiting (i.e., the case of northern slopes), transpiration and respiration costs are easier to cover, and more respiring tissue could be supported. Therefore, a larger branch area allowing for better light interception is not a disadvantage as it would be on warmer and drier south-facing slopes.

The parameters of volume allometric models in Table 3 were slightly different for the south- and north-facing slope trees, suggesting that 1% increase in D , while keeping H constant, produces more tree volume on the north-facing slope (i.e., 2.3018% compared to 1.9505%). The cause for this difference may originate in the way trees allocate biomass during growth. First, the increase in D on the north-facing slope may generate an increase in branch volume. Another potential explanation for the stronger main effect of D on the north-facing slope is related to a more sustained D growth towards the treetop (at the base of the live crown), resulting in a more cylindrical stem taper as D increases. Nevertheless, the main effect of H (Table 3) was lower on the north-facing slope (i.e., $\beta_2 = 0.6075$) than on the south-facing slope (i.e., $\beta_2 = 0.7647$). Since the model parameters in any allometric model are correlated [47], it was expected that a stronger main effect of D would yield a lower main effect of H . The main effect of H represents the relative increase in aboveground tree volume generated by 1% increase in H , while keeping D constant. Therefore, a 1% increase in H produced more aboveground tree volume on the south-facing slope. Again, there are two potential causes explaining this result: (i) for trees with similar D , increasing H generates a modification of stem taper, making the stem more cylindrical, and/or (ii) an increase in H generates an increase in tree branch volume. However, considering that increasing H while keeping D constant means an increase of H/D ratio (trees become slender), it may be suggested that as the trees become slenderer, the branch volume increases more on the south-facing slope. While this second assumption might not seem completely unrealistic, it is unlikely to be the main cause for the differences in the main effects of H (for the south- vs. north-facing slope models). The ratio between the parameter estimates of D and parameter estimates of H [48] was also different for the south- and north-facing slope models (i.e., 2.55 on the south-facing slope and 3.79 on the north-facing slope), which also suggests that compared to D , on the south-facing slope, H has a stronger effect on aboveground tree volume.

In forestry, allometric models are typically used to predict the volume (or biomass) of individual trees within forest inventory plots [8]. Since the estimates of interest are expressed in volume (or biomass) per unit of forest area, the allometric models affect the plot estimates. Testing the differences at the level of the developed model is challenging because the models are non-linear. Therefore, in this study, our approach was to consider the models as different treatments for the inventory dataset in order to better emulate reality. When only using D to predict tree volume, the differences between south- and north-facing slopes were more pronounced (i.e., larger) compared to estimates based on models that used both D and H . This was observed not only for total aboveground volume, but also for its components (i.e., stem and branch volume). Therefore, the addition of H did explain the differences between treatments of inventory data (i.e., south- vs. north-facing

slope models), but it was not sufficient to entirely mask the differences. The explanation is related to the H/D ratio differences. We showed that on the north-facing slope, the trees were thinner, with a higher H for trees of similar D (compared to the south-facing slope). Since for the same D, the trees were higher, it can be assumed they have a larger stem volume. Indeed, the estimates per unit of forest area based on the north-facing slope model only using D as a predictor were larger (Table 4). Including H as additional predictor, the most substantial decrease in differences between volume estimates per unit of forest area was observed for stem volume, thus resulting in fairly small differences (1.2%, or $3.3 \text{ m}^3 \text{ ha}^{-1}$). Although small, the mean differences between the two treatments (south- vs. north-facing slope models) was still significantly different from zero ($p < 0.001$).

The longer branching system of trees on the north-facing slope was also reflected into a larger branch volume estimate when based on the north-facing slope model compared to the south-facing slope model. Adding H as a branch volume predictor resulted in a reduction in differences. However, the reduction was not substantial, suggesting that H addition cannot offset the effect of slope aspect on branch volume allometry as efficiently as for stem volume.

To improve the robustness of our results, we presented the rates of H_0 acceptance within the paired t-test due to allometric model prediction uncertainty. Accepting the H_0 in the paired t-test would mean non-significant differences between south- and north-facing slope models (or treatments for the inventory dataset). A large acceptance rate would be associated with a higher probability for a type I error (false positive) in the paired t-test. This is because, given the possible combinations of model parameters for the south- and north-facing slopes, if those combinations that produce non-significant differences at the level of inventory dataset are frequent, it increases the likelihood that differences between south- and north-facing slope are not significant. However, the rates of H_0 acceptance were relatively small. When using both D and H to predict aboveground tree volume, the H_0 was accepted for less than 2% of repetitions. This result suggests that it is unlikely that differences in volume allometry between the south- and north-facing slope are significant. The rates of H_0 acceptance within the paired t-test depend not only on the level of uncertainty originating from allometric model predictions, but also on the actual differences between estimates of volume per unit of forest area. The H_0 acceptance rate becomes smaller as the model prediction uncertainty is reduced, while the differences between means becomes larger. In our analysis, the models only using D as a predictor (Equation (2)) presented larger prediction uncertainty, reflected by the lower R^2 (Table 3) but also by the higher standard error of the mean (Table 4). Despite the larger model prediction uncertainty, the rates of H_0 acceptance were smaller compared to models using both D and H, because the actual differences between means of volumes per hectare (Table 4) were larger for models only using D (Equation (2)).

5. Conclusions

The conclusions of this study can be summarized as follows: (i) north-facing slope trees were significantly slenderer (higher H for any given D) than the south-facing slope trees (ANCOVA: $p < 0.001$); (ii) the north-facing slope trees had significantly longer branching systems compared to south-facing slope trees (ANCOVA: $p < 0.001$); (iii) the differences between the estimates of volume per unit of forest area based on the south-facing slope model and the north-facing slope model were significant (paired t-test: $p < 0.001$) for all volume pools tested (i.e., total aboveground tree volume, stem volume, and branch volume); (iv) the differences between estimates of volume per unit of forest area based on the south- and north-facing slope models were larger when only using D as a predictor in allometric models; (v) including H as additional predictor of tree volume partly explained the effect of slope aspect on volume allometry, but it was not sufficient to offset the differences between the estimates entirely.

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