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Article

Long-Term Abandonment of Forest Management Has a Strong Impact on Tree Morphology and Wood Volume Allocation Pattern of European Beech (*Fagus sylvatica* L.)

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Abstract: The three-dimensional (3D) morphology of individual trees is critical for light interception, growth, stability and interactions with the local environment. Forest management intensity is a key driver of tree morphology, but how the long-term abandonment of silvicultural measures impacts trunk and crown morphological traits is not fully understood. Here, we take advantage of a long management intensity gradient combined with a high-resolution terrestrial laser scanning (TLS) approach to explore how management history affects the 3D structure of mature beech (*Fagus sylvatica* L.) trees. The management gradient ranged from long-term (>50 years) and short-term (>20 years) unmanaged to extensively and intensively managed beech stands. We determined 28 morphological traits and quantified the vertical distribution of wood volume along the trunk. We evaluated the differences in tree morphological traits between study stands using Tukey's HSD test. Our results show that 93% of the investigated morphological traits differed significantly between the study stands. Significant differences, however, emerged most strongly in the stand where forest management had ceased >50 years ago. Furthermore, we found that the vertical distribution of trunk wood volume was highly responsive between stands with different management intensity, leading to a 67% higher taper top height and 30% lower taper of beech trees growing in long-term unmanaged stands compared to those in short-term unmanaged or managed stands. These results have important implications for management intensity decisions. It is suggested that the economic value of individual beech trees from long-term unmanaged forests can be expected to be very high. This might also translate to beech forests that are extensively managed, but we found that a few decades of implementation of such a silvicultural system is not sufficient to cause significant differences when compared to intensively managed stands. Furthermore, TLS-based high-resolution analyses of trunk and crown traits play a crucial role in the ability to better understand or predict tree growth responses to the current drivers of global change.

Keywords: crown architecture; quantitative structure models; terrestrial laser scanning; tree taper; vertical distribution of trunk wood volume

1. Introduction

The three-dimensional (3D) architectural form of individual trees is critical for light harvesting and productivity, for biomechanical stability and survival, and for interactions with the local environment [1,2]. The 3D arrangement of the crown with its photosynthetically active foliage is of major importance for the carbon balance of an individual tree [2]. The crown as a whole tends to optimise light harvesting, leading to vertical and lateral crown expansion including light-related asymmetric growth. The local environmental conditions among the branches within a crown are the underlying cause for differential growth responses [2]. Radial increments of the trunk, however, are decisive for the physical stability of individual trees against disturbances and are of great economic value. Forest management aims at including different ecological (e.g., carbon sequestration and storage) and economical (e.g., timber quality, stability) facets in order to optimise individual-tree growth.

Until recently, quantifying the 3D tree structure of mature trees in situ has been time-consuming and of limited accuracy [3]. The introduction of high-resolution inventory tools for forest mensuration now provides the means to overcome these limitations. Terrestrial laser scanning (TLS), in particular, has been established for the non-destructive, efficient and accurate measurement of standard tree dimensions (e.g., [4,5]), and more recently for the investigation of 3D tree structure (for recent overviews see [3,6]).

In Central Europe, forests that are strongly dominated by European beech (*Fagus sylvatica* L.; in the following beech) represent, to a large extent, the natural vegetation, and beech forests are both economically and ecologically important [7]. TLS has recently been used to analyse the effects of tree species mixtures on the morphological traits of beech trees, specifically on crown displacement [8], branch angles [8], crown volume and crown surface area [9,10], vertical profiles of crown width [11], and external stem attributes [11]. There is, however, still a limited understanding of the impact of different intensities of forest management on beech tree morphology in pure stands.

It is well known that beech has a very high crown morphological plasticity not only in mixed [12,13], but also in pure stands [14,15]. From investigations using conventional measurement techniques, Fichtner et al. [16] found that crown morphology of beech responded sensitively to forest management intensity. With decreasing management intensity, the crown was positioned at higher heights and the crown volume decreased. Higher tree densities, which occurred in unmanaged stands, resulted in natural pruning and, thus, branch loss in the lower parts of the tree, reducing the crown length and shifting the crown towards a higher position. This was explained by the fact that the elimination of neighbouring trees in silvicultural interventions usually leads to rapid crown expansion of the remaining trees, bringing about higher crown volumes. Drivers of a larger crown volume were both a vertical and a lateral expansion of the crown, i.e., the crowns became deeper and wider with increasing management intensity [16]. Seidel et al. [17] used some of the same study sites as Fichtner et al. [16] for a comparison of crown morphological traits using both conventional and TLS-based measurement, and provide evidence that TLS-based measurements of crown dimensions are more reliable than conventional field measurements. However, it remains unclear how and to what extent forest management intensity impacts TLS-derived crown morphological traits, since Seidel et al. [17] did not differentiate between management intensities. We are aware of only one such study in pure beech forests that make use of TLS data: [18]. Along a management gradient that covered mature unmanaged stands and managed uneven-aged and even-aged stands, Juchheim et al. [18] determined 25 morphological traits of individual beech trees from TLS data. The authors found that different levels of forest management intensity significantly affected four of these 25 morphological traits: the height of the maximal horizontal crown extension, as well as the lean and the sweep of the tree trunks, decreased with increasing management intensity, while the crown surface area increased. Interestingly, many other important tree morphological traits, such as tree height, crown base height, crown radius, crown volume, wood volume or branch dimensions did not differ significantly among forest management intensity levels.

Based on the findings of Fichtner et al. [16], we expect that the length of the period without forest management might play a crucial role in determining the response of individual beech trees. Fichtner et al. [16] found significant differences in several morphological traits of beech trees only

after the long-term abandonment of forest management. Mausolf et al. [19] confirmed the impact of forest management on the radial growth of beech under fluctuating climatic conditions and found that beech trees in unmanaged stands were less sensitive to drought than those in managed stands. Importantly, the observed effect was most pronounced in the forest with the longest unmanaged period. The authors concluded that the longer the period since forest management cessation, the lower the drought sensitivity of mature beech trees. In studies using a gradient of forest management intensity, it is, therefore, not only relevant that forest stands are no longer managed—so as to cover the “low-intensity” end of the gradient—but rather that both short-term and long-term unmanaged stands should be included in such analyses [20,21].

Furthermore, certain aspects with high relevance for forestry and forest ecosystem dynamics have not yet been studied in pure beech forests by means of high-resolution TLS data. In particular, the amount of merchantable wood volume (woody material > 7 cm in diameter) and the wood volume of the branch-free trunk, as well as the vertical distribution of wood volume within the branch-free trunk (i.e., the tree trunk taper), are key characteristics of the economic value, as well as the biomechanical stability, of individual trees. However, the effects of different management intensities in beech forests on merchantable wood volume and tree trunk taper are not well understood.

In this study, we used 28 different traits of individual-tree morphology and the vertical distribution of wood volume along the trunk, each inferred from high-resolution TLS data, to analyse how different intensities of silvicultural management impact the 3D architecture of beech trees. The gradient of forest management intensity covered long-term and short-term unmanaged stands, as well as extensively and intensively managed stands.

2. Materials and Methods

2.1. Study Sites

This study analysed four mature beech stands located in south-eastern Schleswig-Holstein and in north-western Mecklenburg-Western Pomerania at a mean altitude of 20–90 m above sea level (North Germany, 53°35′–53°47′ N, 10°30′–10°47′ E). The study area is characterised by a suboceanic climate (annual precipitation is about 800 mm, mean annual temperature 8.3 °C [22]). The geological substrate originates from the last (Weichselian) glaciation, the dominant soil texture is till, with the associated soil types luvisols, pseudogleyic luvisols and stagnic gleysols. The forest vegetation of the study area is naturally dominated by meso- to eutrophic beech forests (*Asperulo-Fagetum* beech forests, Natura 2000 code 9130) and oligotrophic beech forests (*Luzulo-Fagetum* beech forests, Natura 2000 code 9110). All selected stands were dominated by beech and belonged to the *Asperulo-Fagetum* beech forest type, the mean stand age ranged from 105 to 121 years (Table 1).

Three of the four stands (Schattiner Zuschlag, SZ, Hevenbruch, HEV, Berkenstrüken, BKS) belong to the municipal forest of the city of Lübeck. The fourth stand (Sirksfelder Zuschlag, SIR) is located in the forests of the Duchy of Lauenburg County. The stands cover a gradient of management intensity ranging from long-term unmanaged (SZ), short-term unmanaged (HEV), extensively managed (BKS) to intensively managed (SIR) stands. In SZ, all forest management interventions ceased in 1950 due to its location near the former border between the German Democratic Republic and the Federal Republic of Germany. In 1994, this forest became part of the unmanaged reference areas of the city of Lübeck. The latter was also the case for HEV, i.e., these are long-term (>50 years; SZ) and short-term (>20 years; HEV) unmanaged beech forests. The managed stand BKS is subjected to a nature-oriented management approach (“minimal intervention system”), which aims at (i) approximating natural dynamics, structures and species compositions in the managed forests, (ii) setting and accomplishing appropriate economic targets that do not overcharge ecosystem capability and resilience, and (iii) following the principle of minimal intervention [23,24]. In beech forests, this management approach involves exclusively single-tree selection harvest based on the target diameter at breast height (DBH) of trees (70 cm for beech); once individual beech trees have

a DBH > 40 cm, they are not subjected to thinning operations any more [24]. Finally, the managed stand SIR was established in 1972 as a demonstration site for the usual high-intensity thinning regime for pure beech stands in this area, i.e., heavy thinning from above. This approach includes an early reduction of stem density at an age of about 30 to 40 years, and continuous maintenance of low stem densities and stand basal areas by heavy thinning from above at intervals of five to seven years. At a target DBH > 60 cm, the beech trees are harvested by single-tree selection. As a result of the different management intensities applied, high values for stem densities, stand volume and stand basal area were found in SZ (369 stems ha⁻¹; 903 m³ ha⁻¹; 59 m² ha⁻¹), intermediate values in HEV and BKS (HEV: 194 stems ha⁻¹; 690 m³ ha⁻¹; 34 m² ha⁻¹; BKS: 188 stems ha⁻¹; 652 m³ ha⁻¹; 39 m² ha⁻¹), and low values in SIR (104 stems ha⁻¹; 392 m³ ha⁻¹; 25 m² ha⁻¹). An overview of the characteristics of the four study stands is given in Table 1. In all stands, the soil type was (pseudogleyic) luvisol. Mausolf et al. [19] analysed the soil chemical properties of the upper mineral soil horizon (A-horizon) in three of the four stands (SZ, HEV, BKS). In general, similar values were found, though a trend towards slightly higher soil fertility at SZ and BKS was observed than at HEV. Forest site mapping yielded the same site factor codes for SZ, HEV and BKS (37.5.8.5) and only a slightly different code for SIR (37.5.8.3).

Table 1. Characteristics of the four study stands. Stand dendrological data for Schattiner Zuschlag (SZ), Hevenbruch (HEV) and Berkenstrücken (BKS) are taken from [19]. Data for Sirksfelder Zuschlag (SIR) are from G.M. Böbinger (unpubl.).

	Schattiner Zuschlag (SZ)	Hevenbruch (HEV)	Berkenstrücken (BKS)	Sirksfelder Zuschlag (SIR)
Management intensity	Unmanaged > 50 years	Unmanaged > 20 years	Extensively managed	Intensively managed
Elevation (m a.s.l.)	58	75	80	65
Soil type	(pseudogleyic) luvisol	(pseudogleyic) luvisol	(pseudogleyic) luvisol	(pseudogleyic) luvisol
Age (years)	109	121	105	110
Stem density (n ha ⁻¹)	369	194	188	104
Stand volume (m ³ ha ⁻¹)	903	690	652	392
Stand basal area (m ² ha ⁻¹)	59	34	39	25
Mean diameter at breast height (cm)	44	45	47	54
Mean tree height (m)	41	36	39	34

2.2. TLS Data Acquisition and Registration

In March 2017, TLS data was recorded at two circular plots of 1000 m² each (i.e., plot radius of 17.82 m) in each stand using a Riegl VZ-400i terrestrial laser scanner (Riegl, Horn, Austria). Each plot was scanned from six scanner positions in a multiple scan mode [6], with one scanning position in the centre of the plot and the other positions spread in the four cardinal directions at a distance of 20 to 25 m from the centre (the exact position depended on stand structure and was selected to reduce occlusions). The angular resolution was 0.04° (corresponding to a resolution of 7 mm at 10 m). At all positions, the scanner was also tilted by 90° to overcome the limitation of the panoramic field of view. The instrument was mounted on a tripod and operated at a height of 1.30 m. All scans were performed under clear skies and nearly windless conditions.

TLS point clouds were co-registered using the registration tools “Automatic Registration 2” and “Multi Station Adjustment” of Riegl RiSCAN Pro 2.6.1, resulting in a registration accuracy between 2.2 and 3.0 mm. Stray and noise points with a so-called surface reflectance less than −25 dB or a pulse shape deviation greater than 15, both terms defined by the scanner manufacturer Riegl, were removed to achieve a higher quality point cloud [25,26]. The reflectance value in dB ranges from −25 up to 5,

with positive values indicating retro-reflecting targets and negative values diffusely reflecting targets. For the TLS registration, the point cloud captured in the plot centre was used as the project (Cartesian) coordinate system and the other scanning positions were registered to the centre position.

2.3. TLS Data Post-Processing

In the post-processing process, only dominant trees of Kraft classes I and II (dominant and co-dominant [27]) were included. The tree segmentation was performed in two steps. First, the trees of the TLS point cloud were automatically segmented with the SimpleTree (4.33.06) software, a plugin of Computree (5.0.054b) [28]. The automatically extracted trees were then visually inspected, and falsely classified tree segments were manually corrected using RiSCAN PRO software. In total, 131 trees were extracted and analysed (number of trees in two 0.1 ha plots per stand: SZ: 61; HEV: 24; BKS: 28; SIR: 18). Figure 1 displays the point clouds of two beech trees as examples.

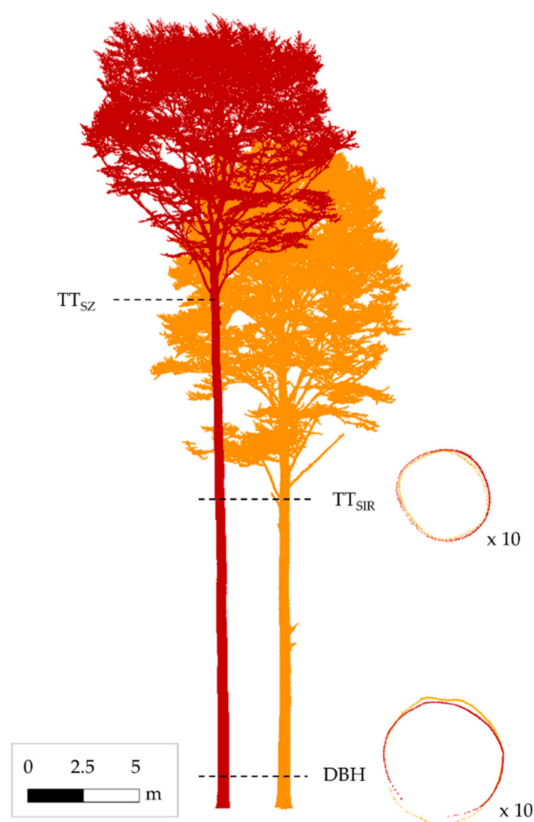


Figure 1. Filtered point clouds from terrestrial laser scanning (TLS) of two exemplary European beech trees with approximately the same total wood volume. The left tree (red) is a representative individual growing in a long-term unmanaged stand, Schattiner Zuschlag (SZ; diameter at breast height (DBH): 53.6 cm; tree height: 37.2 m; taper top height (TT): 23.4 m; total wood volume (V_{tot}): 6.5 m³; wood volume of the branch-free trunk (V_{bft}): 3.6 m³). The right tree (orange) is growing in an intensively managed stand, Sirksfelder Zuschlag (SIR; DBH: 56.1 cm; tree height: 31.7 m; TT: 13.9 m; V_{tot} : 6.7 m³; V_{bft} : 2.4 m³). The circles display the contours at DBH and at taper top height in SIR (red cycles: SZ; orange cycles: SIR).

We quantified the classical forest inventory parameters and aboveground wood volumes for each extracted tree individual using quantitative structure models (QSMs). QSMs are a state-of-the-art approach [29] to quantify the 3D structure of a tree including its branch topology. In contrast to common allometric equations which mainly use DBH and tree height, QSMs can deliver a much more accurate estimate of the aboveground wood volume [30,31]. They are a description of the tree as a hierarchical collection of geometric primitives (here: cylinders) that are fitted into the point cloud

from which topological and geometric tree characteristics can be derived. To generate the QSMs, we used the TREEQSM (2.30) software developed by Raumonen et al. [29], which runs in Matlab® (MathWorks, Natick, MA, USA) version R2016a on the Taurus high-performance cluster (HPC) of the TU Dresden. The method first segments the point cloud of a tree into stem and individual branches and simultaneously determines its topological branching structure. In a second step, the method creates a surface and volume model of the segments by fitting cylinders. The segmentation and modelling process is sensitive to specific method parameters [32,33] that, for instance, define the size and number of segments (patches of points) or the minimum/maximum branch diameters that are allowed in the modelling. Therefore, we conducted a parameter optimisation test using a subset of three trees (small, medium and large) by comparing the modelled QSMs with the original point cloud. This led to the following parameter values: first minimum patch size: 8 cm; second minimum patch size: 3 cm; second maximum patch size: 6 cm; relative cylinder length: 4; relative radius for outlier removal: 5.

The outputs of the TREEQSM software are DBH, tree height, total wood volume (V_{tot}), number of branches, branch length, trunk volume and branch volume. For the branch traits we considered the total as well as the first two branch orders. The height-to-diameter ratio (H/D ratio) was calculated from tree height and DBH. In addition to the total wood volume, we determined the merchantable wood volume (V_{mw}), defined as all aboveground woody structures with a diameter > 7 cm (i.e., the trunk and the larger branches). The volume of fine woody material (V_{fwm}) was calculated as the difference between V_{tot} and V_{mw} . Table 2 provides an overview of all measured morphological traits.

Table 2. Morphologic traits measured for each sample tree.

Measure	Abbreviation	Origin	Reference/Calculation
Diameter at breast height (cm)	DBH	QSM	Raumonen et al. (2013)
Tree height (m)	TH	Point cloud	$Z_{\text{max}} - Z_{\text{min}}$
Total wood volume (m ³)	V_{tot}	QSM	Raumonen et al. (2013)
Total branch number		QSM	Raumonen et al. (2013)
Height-to-diameter ratio	H/D-ratio	Point cloud	TH/DBH 100
Merchantable wood volume (m ³)	V_{mw}	QSM	See Section 2.3. this publication
Volume of fine woody material (m ³)	V_{fwm}	QSM	See Section 2.3. this publication
Crown base height (m)	CBH	Point cloud	See Section 2.3. this publication
Crown volume (m ³)	CV	Point cloud	See Section 2.3. this publication
Crown projection area (m ²)	CPA	Point cloud	See Section 2.3. this publication
Crown surface area (m ²)	CSA	Point cloud	See Section 2.3. this publication
Crown ratio	CR	Point cloud	CL/TH
Crown length (m)	CL	Point cloud	TH-CBH
Crown openness (°)		Point cloud	Martin-Ducup et al. (2016)
Crown sinuosity		Point cloud	Martin-Ducup et al. (2016)
Taper (cm m ⁻¹)		Point cloud	See Section 2.3. this publication
Taper top height (m)	TT	Point cloud	See Section 2.3. this publication
Volume of branch-free trunk (m ³)	V_{bft}	QSM	See Section 2.3. this publication
Mean branch length sum (m)		QSM	Raumonen et al. (2013)
Mean maximum branch order		QSM	Raumonen et al. (2013)
Mean branch number 1st order		QSM	Raumonen et al. (2013)
Mean branch number 2nd order		QSM	Raumonen et al. (2013)
Branch volume 1st order (m ³)		QSM	Raumonen et al. (2013)
Branch volume 2nd order (m ³)		QSM	Raumonen et al. (2013)
Branch length 1st order (m)		QSM	Raumonen et al. (2013)
Branch length 2nd order (m)		QSM	Raumonen et al. (2013)
Crown length-width ratio		Point cloud	$CL / (\sqrt[4]{CPA \cdot 4 \pi^{-1}})$
Crown roughness		Point cloud	Martin-Ducup et al. (2016)

Furthermore, we determined several crown morphological traits. The crown base height (CBH) was defined as the height of the lowest living primary branch and measured in RiSCAN Pro. The crown volume (CV), crown projection area (CPA) and crown surface area (CSA) for each tree were computed

with a concave hull (alpha-shape with α -value = 0.3) using the Point Cloud Library [34] and the Computational Geometry Algorithms Library [35]. We calculated crown ratio (CR) as crown length (CL = tree height minus CBH) divided by tree height. Crown openness (i.e., the angle between the symmetry axis of the crown and the outer limit of the shade crown), crown sinuosity (i.e., the vertical crown asymmetry) and crown roughness (i.e., the ratio between the surface of a modelled crown and the surface of the 3D alpha-shape) were derived according to Martin-Ducup et al. [36].

We also determined the taper of each tree trunk. Tree trunk taper is defined as the decrease in diameter with height (expressed as cm m^{-1}). For each trunk, DBH was used as the lower diameter, and the diameter at the taper top height as the upper diameter. Taper top height (TT) is defined as height of the bifurcation point of the first major branch minus 50 cm (Figure 2). For forked trees, however, the TT is the height of the thinnest diameter just beneath the fork (max. 2 m below; Figure 2). For the stem section up to TT, we calculated the trunk volume (i.e., the wood volume of the branch-free trunk, V_{bft}). Please note that V_{bft} is different from the wood volume, which is given as the output “trunk volume” (also termed “tree stem volume”, see [18]) by the TREEQSM software. To make this difference more explicit, we marked the trunk, as defined by TREEQSM, in blue in Figure 2. In our study, we decided to use V_{bft} instead of ‘trunk volume’ because V_{bft} is of paramount economic importance in forestry. As morphological traits we used TT, the taper along the trunk up to the TT, and V_{bft} . Additionally, we analysed the vertical profile of the taper up to a standardised trunk height of 10 m by measuring the taper of 2.5 m sections along the trunk. Finally, we determined the vertical profiles of mean wood volume per 1 m trunk section up to a height of 20 m.

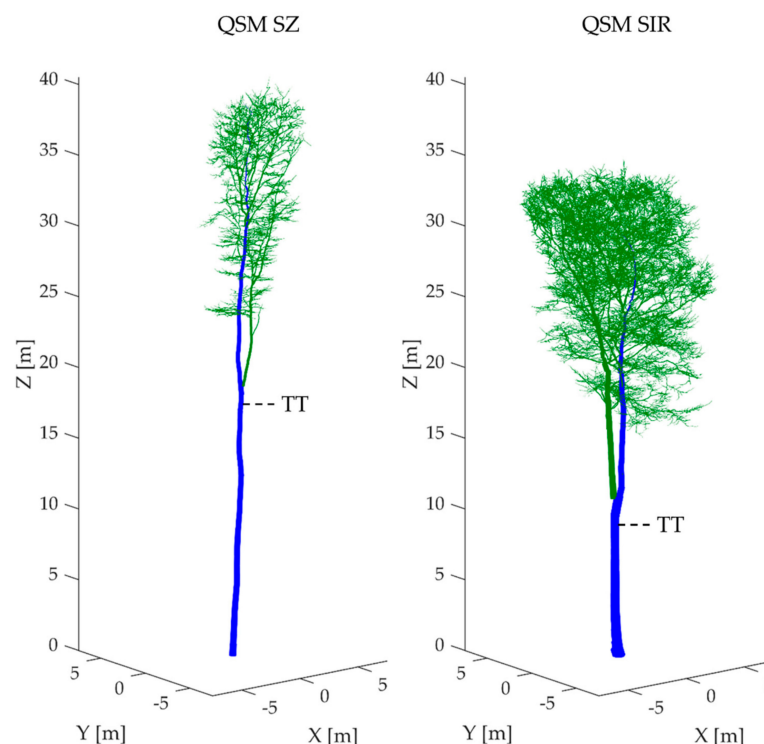


Figure 2. Quantitative structure models (QSM) of European beech trees to illustrate the measuring point for the taper top height (TT). The tree on the right displays an example for the TT measurement in forked trees. The wood volume of the branch-free trunk (V_{bft}) was determined for the stem section up to TT. The trunk, as determined by the TREEQSM software, is shown in blue. The branches of different orders as defined by TREEQSM are shown in green. The left tree is growing in the long-term unmanaged stand Schattiner Zuschlag (SZ; TT: 18.0 m), the right tree in the intensively managed stand Sirksfelder Zuschlag (SIR; TT: 9.1 m).

2.4. Statistical Analysis

Because the individual trees were not independent samples each from different stands, we evaluated the differences in tree morphological traits at the level of the study stands using a Tukey-HSD test. This test, just as a one-way analysis of variance, assumes independent data drawn from normal distributions with equal variances of group-specific means, but is optimised to detect differences between pairs of those means. The assumption of equal variances, tested with the rough Levene's test, was not fulfilled for few parameters. A simulation conducted for further data review indicated a slight underestimation of p-values for our sample size. We therefore adjusted the confidence level to 0.97 to make sure the error probabilities stayed within the conventional significance level of 0.05. All statistical data analysis was performed with R (3.4.2) [37].

3. Results

We found distinct differences in almost all (26 out of 28) tree morphological traits between the stands along the management intensity gradient (Figures 3–5; Table A1). Several morphological traits of the whole tree and the branches, for example DBH, H/D ratio, V_{tot} , V_{fwm} and the number of branches, were significantly lower in the long-term unmanaged stand SZ compared to short-term unmanaged and managed stands (Figure 3; Table A1). By contrast, tree height was largest in SZ and decreased in the stands along with an increasing management intensity. V_{mw} was lowest in SZ and highest in the short-term unmanaged stand HEV and in the extensively managed stand BKS, but subsequently decreased again in the intensively managed stand SIR. The mean relative proportion of V_{mw} to V_{tot} was 72%, 57%, 53% and 52% in SZ, HEV, BKS and SIR, respectively.

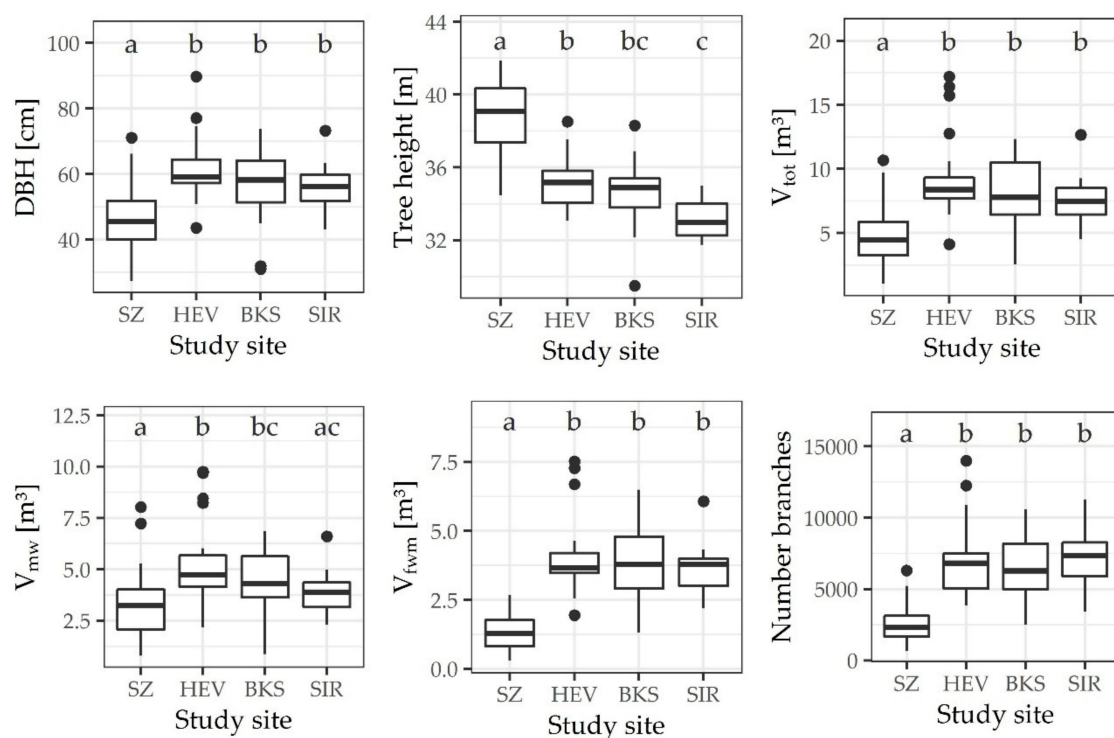


Figure 3. Variation in tree metrics between the stands along the management gradient. Different letters indicate significant differences (Tukey-HSD, $p < 0.03$) between study sites. DBH = diameter at breast height, V_{tot} = total wood volume, V_{mw} = merchantable wood volume, V_{fwm} = volume of fine woody material. SZ = Schattiner Zuschlag (long-term unmanaged), HEV = Hevenbruch (short-term unmanaged), BKS = Berkenstrücken (extensively managed), SIR = Sirksfelder Zuschlag (intensively managed).

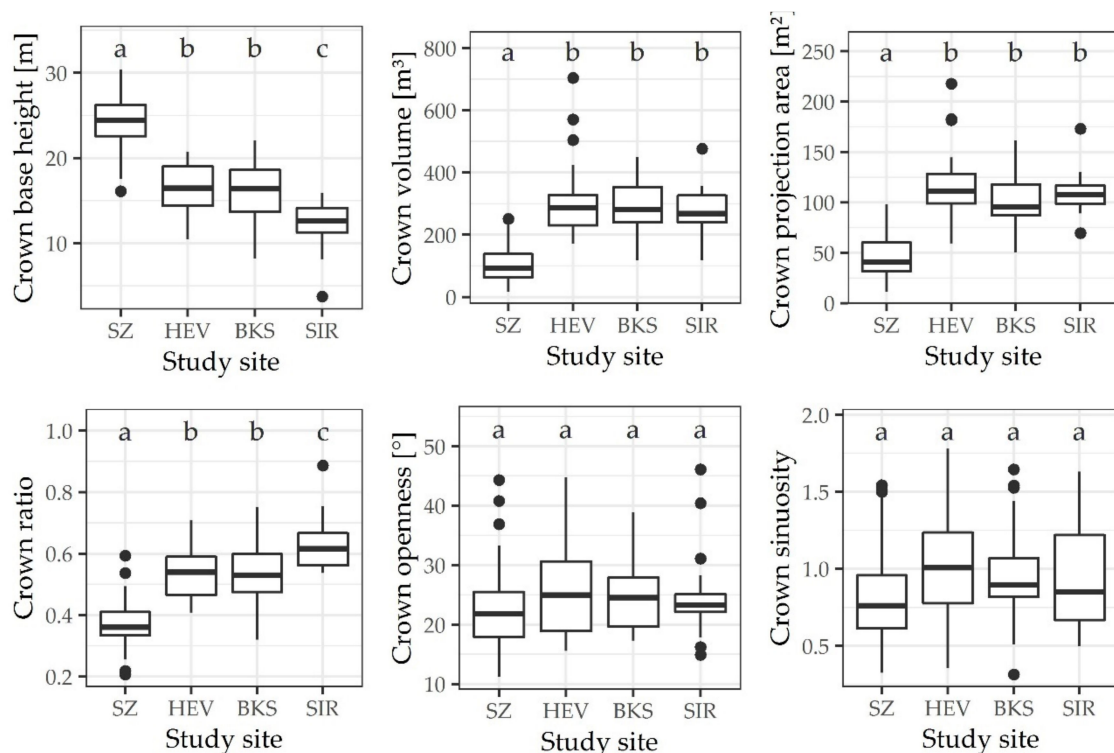


Figure 4. Variation in crown morphological traits between the stands along the management gradient. Different letters indicate significant differences (Tukey-HSD, $p < 0.03$) between study sites SZ = Schattiner Zuschlag (long-term unmanaged), HEV = Hevenbruch (short-term unmanaged), BKS = Berkenstrücken (extensively managed), SIR = Sirksfelder Zuschlag (intensively managed).

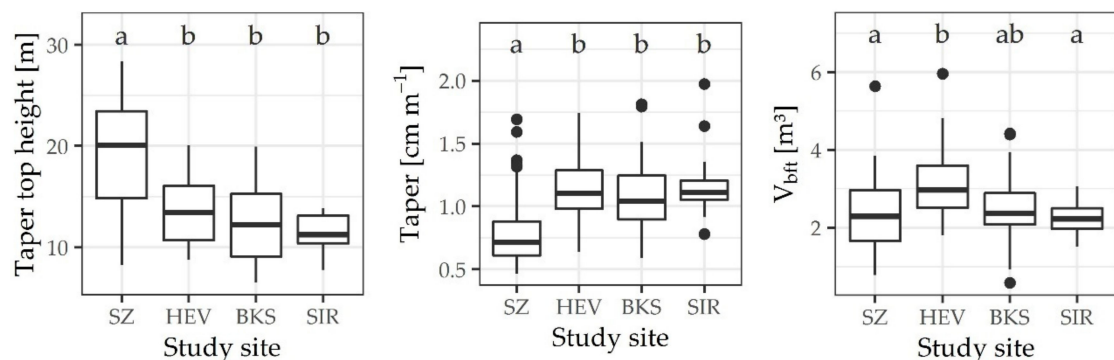


Figure 5. Variation in taper top height, taper and the wood volume of the branch-free trunk between the stands along the management gradient. Different letters indicate significant differences (Tukey-HSD, $p < 0.03$) between study sites. V_{bft} = Volume of branch-free trunk. SZ = Schattiner Zuschlag (long-term unmanaged), HEV = Hevenbruch (short-term unmanaged), BKS = Berkenstrücken (extensively managed), SIR = Sirksfelder Zuschlag (intensively managed).

Of the crown morphological traits, CV, CPA, CSA, CL and CR were significantly lower in SZ compared to the other three stands (Figure 4; Table A1). Whereas these other stands showed similar values for CV, CPA, CSA and CL, CR was significantly higher in the intensively managed stand SIR than in HEV and BKS. For CBH, the same pattern was found as for tree height: the largest values occurred in SZ and subsequently decreased in the stands along with an increasing management intensity. By contrast, crown openness and crown sinuosity did not differ between the four stands (Figure 4). Figure 1 illustrates the differences in the architectural structure of individual beech trees growing in the long-term unmanaged stand SZ and in the intensively managed stand SIR.

TT and trunk taper were significantly higher and lower, respectively, in SZ than in the other three stands (Figure 5). The V_{bft} was similar in SZ and SIR, and significantly higher in HEV (Figure 5). The vertical profiles of the taper up to a trunk height of 10 m were very similar for HEV, BKS and SIR, whereas it was considerably different for SZ (Figure 6). In HEV, BKS and SIR the initial taper at the trunk base amounted to about 2.25 cm m^{-1} and decreased to values around 1.20 cm m^{-1} at a trunk height of 10 m. In SZ, the initial taper was much lower (1.52 cm m^{-1}), and the decrease was much weaker (0.89 cm m^{-1} at 10 m height). The vertical profiles of mean wood volume per 1 m trunk section were almost identical in BKS and SIR, but diverged to a higher level in HEV and to a lower level in SZ (Figure 7). Again, the decrease in wood volume was considerably smaller in the long-term unmanaged stand SZ than in the other three stands (i.e., shallower course of the curve in SZ).

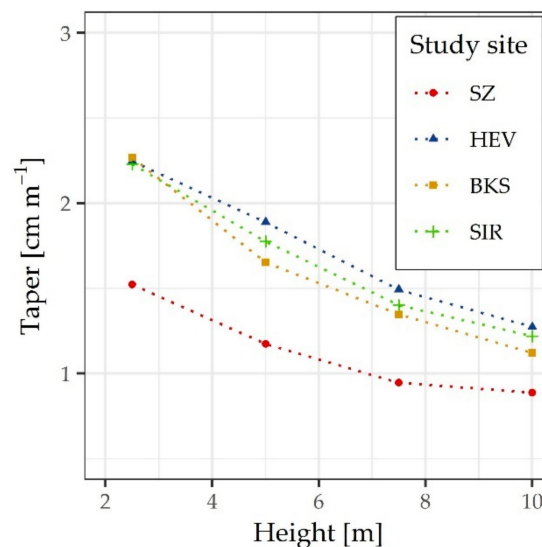


Figure 6. Vertical profile of the taper along the trunk every 2.5 m up to a height of 10 m. SZ = Schattiner Zuschlag (long-term unmanaged), HEV = Hevenbruch (short-term unmanaged), BKS = Berkenstrücken (extensively managed), SIR = Sirksfelder Zuschlag (intensively managed).

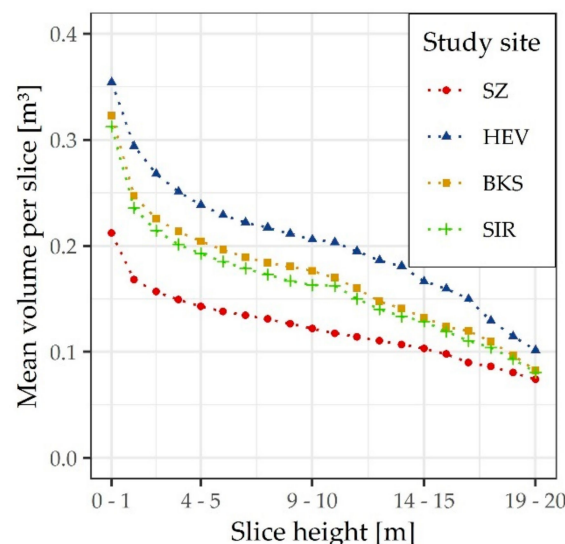


Figure 7. Vertical profile of the mean wood volume per 1 m trunk section up to a height of 20 m. SZ = Schattiner Zuschlag (long-term unmanaged), HEV = Hevenbruch (short-term unmanaged), BKS = Berkenstrücken (extensively managed), SIR = Sirksfelder Zuschlag (intensively managed).

4. Discussion

Our analysis of 28 morphological traits and of the vertical distribution of wood volume in the trunk, both derived from TLS data, revealed strong differences of the 3D morphology of individual beech trees between the stands. This is in agreement with the general statement by Juchheim et al. [18] that morphological traits of beech were significantly modified by different levels of silvicultural management intensity. In their study, however, this was only substantiated for four of 25 morphological traits. The overall outcome of our results, thus, differs from that of Juchheim et al. [18] because we observed significant differences between the stands in 26 of 28 morphological traits. To explain this inconsistency, we suggest that the most important driver for the occurrence of differences in morphological traits is the forest management history and specifically the length of the gradient in management intensity. For the unmanaged stands, the length of the gradient is determined by the length of the period since management cessation. An important finding in our study is that the long-term and the short-term unmanaged stands, SZ and HEV, respectively, showed major differences in morphological traits, whereas we did not find any significant differences between HEV and the extensively managed stand, BKS. Juchheim et al. [18] used only one class of unmanaged stands, which corresponds to the short-term unmanaged stand HEV in our study.

In the long-term unmanaged stand, SZ, very high values of stand basal area and stand volume accumulated ($59 \text{ m}^2 \text{ ha}^{-1}$, and $903 \text{ m}^3 \text{ ha}^{-1}$, respectively [19]). It is well known that a high growing stock, accompanied by high stand densities and a closed canopy, strongly impacts crown dimensions [16,38,39]. This explains the significantly different values in several crown morphological traits in SZ compared to the other stands. Crown dimensions, in turn, are one of the most important drivers of tree growth [17,40]. Mausolf et al. [19] found that radial growth rates increased significantly with increasing management intensities (SZ: $23.6 \text{ cm}^2 \text{ year}^{-1}$; HEV: $33.3 \text{ cm}^2 \text{ year}^{-1}$; BKS: $43.4 \text{ cm}^2 \text{ year}^{-1}$) as a result of decreasing intraspecific competition. As a consequence, we observed a significantly lower DBH and wood volume of individual beech trees in SZ than in the other stands. Under the condition of high competition due to high stand densities, height growth has the highest priority for biomass allocation [27]. Preferential carbon investments in height growth are, therefore, to be expected in the long-term unmanaged stand SZ, resulting in significantly higher tree heights than in the other stands. The significantly lower tree height in the intensively managed stand SIR might be explained by the very early and severe reduction of stem density at an age of <40 years, and enduring maintenance of low stem densities by heavy thinning from above every five to seven years.

There might be other possible reasons underlying the inconsistency between the findings of Juchheim et al. [18] and our study, for example methodological differences in data recording and determination of morphological traits. However, like Juchheim et al. [18], we used TLS for data recording, and direct point cloud analysis (e.g., tree height, CV, CL) as well as QSMs (e.g., wood volume, branch traits) for data processing. Differences in abiotic environmental conditions (in particular climate and soil) and in tree age might also be an explanation. We cannot rule out the former, because of differences in climate (suboceanic in our study area vs. transition zone between suboceanic and subcontinental in the study area of Juchheim et al. [18]) and edaphic conditions (moraine soils originating from the last glaciation vs. shell lime sediments originating from the period of the Upper Muschelkalk). However, both study areas provide excellent growing conditions (with regard to nutrient and water supply) for beech. We therefore expect that these differences between the study areas probably played a minor role. In Juchheim et al. [18] tree age per study plot ranged from 104 to 186 years and is, thus, often higher than in our study (age range 105 to 121 years, Table 1). However, in one of the three management intensity classes, the mature even-aged beech stands, the age of the trees only ranged from 104 to 119 years and was considerably lower than in the other study plots. Given that age-related changes in the 3D morphology of beech trees emerge at an age between 100 and 190 years, then a higher number of significant relationships between management intensity and morphological traits would have been expected to occur in the study by Juchheim et al. [18]. We therefore assume that differences in tree age are of minor importance in explaining the different findings.

We found that the amount of V_{mw} peaked in the short-term unmanaged stand HEV, and that there was no significant difference in V_{mw} of trees growing in long-term unmanaged (SZ) and intensively managed (SIR) stands. There are possibly two main reasons for this. Firstly, due to the large increments in DBH in SIR, the largest beech trees already reached the target DBH of >60 cm and had recently been harvested. Such large trees are still present in the short-term unmanaged stand HEV (cf. Figure 3), and in the extensively managed stand BKS only a small number of large diameter trees have been harvested due to the higher threshold DBH of 70 cm for selection harvest according to the principles of the applied silvicultural system (see Methods).

Secondly, we provide the first evidence that the vertical distribution of wood volume along the trunk (and thus the major part of the merchantable wood volume of a tree) differs between the long-term unmanaged stand SZ and the other stands (Figures 5–7). A significantly higher CBH and TT (i.e., a longer branch-free trunk) and a significantly lower taper in SZ mean a strong concentration of coarse woody material in the trunk. In concert with the larger tree heights and smaller crowns in SZ (i.e., less V_{fwm} ; see the large differences in the relative proportion of V_{mw} to V_{tot} between SZ (72%) and the other stands (cf. 55%)) this explains the lack of significant differences in the amount of V_{mw} between SZ and SIR. Furthermore, we observed that the wood volume of the branch-free trunk was almost identical in SZ and SIR, despite significant differences in DBH. Again, this can be attributed to the large differences in tree morphology, in particular to the longer branch-free trunk and the lower taper in SZ compared to SIR.

These results may have very important implications for several issues: the economic value of individual beech trees from forests which have not been managed over the long term can be expected to be very high. This might also translate to extensively managed beech forests, because the abandonment of thinning interventions above a DBH of 40 cm leads to high stand densities and high growing stocks in the long term. Our study shows, however, that a few decades of implementation of such a silvicultural system in the study stands are not sufficient to cause significant differences in the vertical distribution of wood volume along the trunk when compared to intensively managed stands (cf. BKS and SIR in Figures 5–7). Furthermore, the biomechanical stability of individual beech trees in long-term unmanaged beech stands might be high due to a strong radial growth of the whole trunk (and, additionally, a relatively small crown; [16]), which is important in the face of more frequent and intense extreme weather events due to climate change (in particular wind and ice storms). Also, the long-term sequestration of carbon is advantageous in such stands because these coarse woody materials can either be used for longstanding products or are more resistant to decomposition when left in the forest.

It is important to note that we focused in this study on individual-tree morphology and wood volume distribution. To transfer findings to the stand level, the density and the spatial distribution patterns of stems are decisive factors. The stem density is by far the highest in the long-term unmanaged stand SZ, and therefore the stand basal area increment is also high in SZ, despite a relatively low individual-tree radial increment [19]. Accordingly, a very high stand wood volume of $1416 \text{ m}^3 \text{ ha}^{-1}$ exists in SZ, compared to 1120, 1142, and $680 \text{ m}^3 \text{ ha}^{-1}$ in HEV, BKS and SIR, respectively (wood volumes calculated on the basis of our sample trees). It should be noted, however, that the differences are even more pronounced with respect to the V_{mw} ($1018, 633, 607, 350 \text{ m}^3 \text{ ha}^{-1}$ in SZ, HEV, BKS, SIR, respectively) and, in particular, the economically most valuable wood quantity, the V_{bft} : $722 \text{ m}^3 \text{ ha}^{-1}$ in SZ versus 375, 346 and $200 \text{ m}^3 \text{ ha}^{-1}$ in HEV, BKS and SIR, respectively. This points to the potential that a long-term reduction in management intensity might have in terms of a high economic yield. However, our study design was developed for the analysis of individual trees, and was not aimed at the estimation of the stand volume (due to the limited number of trees located in two 0.1 ha plots). Further research is required to attempt such estimations.

5. Conclusions

Because tree communities are the sum of co-occurring individuals, they can be considered as networks of locally interacting individuals [41]. The outcome of different forest management approaches is, thus, strongly affected by tree interactions at the local neighbourhood level. These tree neighbourhood interactions, in turn, constitute a key factor determining a tree's architecture and, ultimately, growth, and productivity patterns [42,43]. Our study highlights the relevance of a long-term perspective on the impact of forest management intensity on local neighbourhood interactions and, thus, 3D tree structure. There are some morphological traits of trees which are highly responsive to silvicultural interventions, such as tree height or CBH. Also, the lateral expansion of the crown is very sensitive to the elimination of neighbouring trees [14,18]. However, the majority of morphological traits of individual trees in pure beech stands seem to be quite insensitive to a short-term change in management intensity, as reflected by a narrow gradient length (here: stands unmanaged or extensively managed for a few decades). Differences emerge only after a prolonged period of time (either since the cessation or the intensification of management). Studying the facilitative-competitive interactions in a long-term unmanaged old-growth beech forest in northeastern Germany, Fichtner et al. [44] concluded that competition seemed to become less important in stands with a high growing stock and in tree communities with a long continuity of anthropogenic undisturbed population dynamics. Also, drought-induced growth decline is lower in long-term unmanaged stands [19]. Further research is needed that covers a long gradient of management intensities (including long-term unmanaged stands), different tree species and various environmental conditions in order to further advance our understanding of the legacies of silvicultural management impact on 3D tree architecture, growth, and productivity. Such knowledge may be crucial in the face of ongoing environmental change, which is predicted to have unprecedented consequences for growth and coexistence of European tree species.

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Appendix A

Table A1. Additional tree morphological traits. Different letters indicate significant differences (Tukey-HSD, $p < 0.03$) between study sites. SZ = Schattiner Zuschlag (long term unmanaged), HEV = Hevenbruch (short term unmanaged), BKS = Berkenstrücken (extensively managed), SIR = Sirksfelder Zuschlag (intensively managed).

Study Site	SZ	HEV	BKS	SIR
Height-diameter ratio	0.86 a	0.58 b	0.63 b	0.60 b
Mean branch length sum [m]	1515.6 a	4391.9 b	4072.7 b	4479.9 b
Mean maximum branch order	8.3 a	9.5 b	9.5 b	9.2 b

Table A1. Cont.

Study Site	SZ	HEV	BKS	SIR
Mean branch number 1st order	44.7 ab	39.1 a	44.9 ab	53.8 b
Mean branch number 2nd order	274.6 a	389.9 b	407.3 b	559.6 c
Branch volume 1st order [m ³]	638.9 a	1213.0 b	948.1 ab	898.6 ab
Branch volume 2nd order [m ³]	392.4 a	949.0 b	902.3 b	901.9 b
Branch length 1st order [m]	110.8 a	165.0 b	158.2 b	200.9 c
Branch length 2nd order [m]	302.1 a	586.9 b	569.5 b	729.1 c
Crown surface area [m ²]	574.9 a	1640.3 b	1437.8 b	1669.9 b
Crown length [m]	14.7 a	19.3 b	19.2 b	21.4 b
Crown length-width ratio	2.09 a	1.62 b	1.71 b	1.83 ab
Crown roughness	0.33 a	0.25 b	0.25 b	0.23 b

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