## Article

# Functional Crown Architecture of Five Temperate Broadleaf Tree Species: Vertical Gradients in Leaf Morphology, Leaf Angle, and Leaf Area Density 

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#### Abstract

The morphology, inclination, and spatial distribution of leaves in different parts of tree crowns are important determinants of the radiation, momentum, and gas exchange between the canopy and the atmosphere. However, it is not well known how these foliage-related traits vary among species differing in successional status. We measured leaf size, leaf mass area (LMA), leaf inclination (angle to the horizontal), leaf area density (LAD), total leaf area (leaf area index, LAI), and leaf area distribution across the crown in adult trees of five common, early to late-successional tree species (Betula pendula Roth, Quercus petraea (Matt.) Liebl., Carpinus betulus L., Tilia cordata Mill., and Fagus sylvatica L.) using different canopy access techniques and the harvest of foliated trees ( 29 trees in total). Leaf size increased continuously with crown depth in B. pendula and T. cordata but peaked at mid-crown in Q. petraea, C. betulus, and F. sylvatica to decrease toward the shade crown. By contrast, LMA and leaf angle decreased continuously with crown depth in all species, but the pattern of vertical change varied. The mid/late- and late-successional species had higher LAI, lower shade-leaf LMA, lower leaf angles (shade and sun crown), and higher LAD in the uppermost sun crown in comparison to early successional B. pendula. We assume that the most peripheral sun leaf layer is partly acting as a shield against excess radiation, with foliage properties depending on the structure of the shade crown. We conclude that the vertical change in leaf morphology, inclination, and spatial distribution in tree crowns is highly species specific, with partial dependence on the species' position in succession.


Keywords: adult trees; Betula pendula; Carpinus betulus; Fagus sylvatica; forest succession; leaf area density; leaf mass area; leaf inclination; Quercus petraea; Tilia cordata

## 1. Introduction

The size and shape of leaves and their three-dimensional position in crown space determine the exchange of radiation, gases, sensible heat, and momentum between forest canopies and the atmosphere. From the top to the bottom of a tree crown, radiation intensity decreases to less than $10 \%$, or even $1 \%$, of incident flux density while air humidity increases [1]. The foliage of a tree is thus exposed to highly variable environmental conditions along the vertical crown axis, triggering different acclimation processes of sun and shade leaves to radiation intensity and evaporative demand [2]. Changes with increasing crown depth in the size and morphology of leaves, leaf inclination, and the density of leaves per crown volume are thought to be adaptive responses to the light gradient in the crown, aimed at optimizing light interception of the whole crown [3]. Yet, changes in leaf size and orientation along the vertical axis could also be driven by other environmental factors that change from crown top to bottom, notably, atmospheric vapor pressure deficit (vpd), the load of excess radiation,
and the degree of foliar overheating, stressors that may impair leaf metabolism. In most broadleaf canopies that have been studied so far, leaf size increased and leaf angles became progressively more horizontal from the tree top toward lower crown strata [4-6], which is generally explained by the exponential decrease in light intensity. Lower leaf angles increase light capture when the sun is at high angles, which improves the cost-benefit ratio of leaf operation in the shade. Steeper leaf angles increase interception when the sun is at low angles (in the morning and evening hours and early and late in the season), and they can decrease the load of potentially harmful heat and excess radiation $[7,8]$. While various authors have studied leaf size and leaf morphology changes across tree crowns, only few detailed studies on leaf angle distribution and leaf area density exist for the crown of adult temperate trees [3,6,9-13].

The morphology and functionality of tree crowns in terms of radiation flux and matter exchange processing change markedly with forest succession from early to late-successional species [14]. Early successional trees are typically shade intolerant, while late-successional species often cast deep shade and are able to tolerate low light intensities by their shade leaves and own offspring [15]. Correspondingly, at fertile and moist sites, early successional trees should develop an acquisitive growth strategy directed toward rapid capture of light and canopy space with cheap-to-construct leaves and high photosynthetic activity, while late-successional species should tend more to a conservative growth strategy with expensive-to-construct leaves that have lower photosynthetic rates, are more tolerant of shade, and typically are longer lived [16-18].

Changes in plant functional traits with forest succession have frequently been investigated in tree seedlings and saplings but rarely in adult trees. From a compilation of literature data, we assume that the shift from acquisitive to conservative traits should mostly be confined to the lower crown of adult trees, where light regimes depend largely on crown architecture, while this gradient is less distinct in the exposed sun crowns [15]. Niinemets, Ü suggested that leaf functional changes with succession should relate to tree species differences in foliage distribution, with early successional trees typically having short crowns and late-successional species more extended crowns with longer vertical gradients in leaf mass per area (LMA) [2]. Canopy structural data compiled by [8] further indicate that late-successional trees have higher leaf area densities (LAD, leaf area per canopy volume) in the sun crown than early successional trees, resulting in a steeper light intensity decline with crown depth in the former. There is some evidence that temperate tree species shift their crown architecture from a monolayer type (sensu [19]) in high-light environments toward a multilayer type in low light, as observed, for example, by [20] in conifers. Such a modification enhances light capture under low light while maximizing canopy carbon gain under high light.

In the absence of multiple-species studies on leaf traits and crown properties of adult trees, it is unclear whether the acquisitive-conservative trait dichotomy in leaf traits and crown structure is applicable to temperate trees. For example, the assumption of early successional trees having mostly monolayered crowns with large, acquisitive, short-lived leaves may be valid for tropical moist forests $[21,22]$ but seems not to apply to Europe's temperate tree flora. Here, large-leaved pioneer trees are absent and the crowns of early successional trees do not represent monolayers. The typical early successional trees (e.g., Betula, Populus, and Pinus species) rarely have horizontal leaf inclinations, and the leaves of late-successional species are, due to climatic constraints, not longer lived than those of early successional species. This may question the validity of the concept of acquisitive and conservative strategies in leaf operation in this tree flora, when considering adult trees. Testing this concept and predictions on changes in crown functionality with succession requires information on leaf properties and crown architecture of adult trees, which is rarely available.

Here, we present a comprehensive analysis of leaf traits and foliage distribution in the crown of adult trees of five temperate broadleaf tree species. The species represent abundant early (Betula pendula), mid- or mid-/late- (Quercus petraea, Carpinus betulus), and late-successional species (Tilia cordata, Fagus sylvatica) of the Central European tree flora. Leaf size, LMA, leaf angles, LAD, and cumulative leaf area were measured in dependence on height in crown in living or harvested trees to
search for patterns of successional change in foliage properties. The objectives were to find out whether (i) leaf size increases, and LMA decreases, from the uppermost crown to the lower shade crown in all species; (ii) leaf inclination angles become increasingly horizontal with increasing depth in the crown [3]; (iii) the difference in leaf size and leaf angles between sun and shade leaves is greater in latethan early or mid-successional species; (iv) LAD is higher in late- than early successional species [8]; and (v) total leaf area increases from early to late-successional species. The three-dimensional analysis of foliage structure in this study builds the foundation for a forthcoming study on leaf optical properties and the resource economy of crown space occupation in the five species.

## 2. Materials and Methods

### 2.1. Study Sites

Each of two mature stands of the five tree species B. pendula Roth, Q. petraea (Matt.) Liebl., C. betulus L., T. cordata Mill., and F. sylvatica L. were selected for study in the lowlands (80-230 m a.s.l.) of northwestern and central Germany in level terrain on sandy-to-loamy glacial soil (Table 1). The stands had a closed canopy (canopy closure $>0.9$ ) and were monospecific or at least dominated by the target species in terms of stem numbers (Table 2). If other species were admixed, we selected individuals of the target species with conspecific neighbors. Mean tree height was 20-27 m, and mean diameter at breast height (dbh) varied between 19 and 44 cm depending on species. Most trees were 80-120 years old, with the pioneer species (Betula) being somewhat younger and the Quercus trees older than this range. The stem density of the studied stands varied with the crown dimensions of the species (Table 3); it was particularly low in the Q. petraea stands.

Table 1. Functional and morphological traits of the five studied tree species according to [23-28] and others.

|  | Betula <br> pendula | Quercus <br> petraea | Carpinus <br> betulus | Tilia <br> Cordata | Fagus <br> sylvatica |
| :--- | :---: | :---: | :---: | :---: | :---: |
| Family | Betulaceae | Fagaceae | Betulaceae | Malvaceae | Fagaceae |
| Successional status | early | mid/late | mid/late | late | late |
| Shade production of adults ${ }^{1}$ | V | III | I | II | I |
| Shade tolerance of saplings $^{2}$ | V | IV | II | III | I |
| Light demand of shade leaves $^{3}$ | 20 | 7 | 2.5 | 3 | $<1$ |
| Drought tolerance $^{4}$ | mid | high | mid/high | mid | low |
| Type of mycorrhiza |  | ECM | ECM | ECM | ECM |
| Xylem anatomy ${ }^{6}$ | diffuse | ring | diffuse | diffuse | diffuse |

${ }^{1}$ From various literature sources and personal observations of Ellenberg (1996). Relative categorization of species (I-very high, II—high, III-medium, IV-low, V—very low). ${ }^{2}$ From various literature sources and personal observations of Ellenberg (1996). Relative categorization of species (I—very high, II—high, III-medium, IV—low, V-very low). ${ }^{3}$ Relative PAR flux density (in percent of incident flux density around noon at overcast sky) measured at the level of lowest shade leaves inside closed stands ( $56-136$ individual measurements per species).
${ }^{4}$ Drought tolerance ranking based on distribution range and habitat preference data in [25], dendrochronological information of drought-induced growth reductions (after [29] and other sources), $\mathrm{P}_{50}$ values of embolism resistance, and records of drought damage (e.g., pre-senescent leaf loss) of the species. ${ }^{5} \mathrm{ECM}=$ ectomycorrhizal. ${ }^{6}$ Ring-porous, diffuse-porous.

Table 2. Some physiographic characteristics of each of the two study sites per species in northern and central Germany.

| Species | Site \# | Location | Coordinates | Slope | Elevation <br> (m a.s.l.) | Soil <br> Substrate | Admixed <br> Species |
| :--- | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Betula <br> pendula | 1 | Lehrer Wald <br> (Helmstedt county), <br> Lower Saxony | $10^{\circ} 42^{\prime} \mathrm{E}$ <br> $52^{\circ} 19^{\prime} \mathrm{N}$ | level | 95 | Loamy <br> sand | Alnus <br> glutinosa |
| Betula <br> pendula | 2 | Lappwald <br> (Helmstedt county), <br> Lower Saxony | $11^{\circ} 01^{\prime} \mathrm{E}$ |  |  |  |  |
| $52^{\circ} 16^{\prime} \mathrm{N}$ | level | 147 | Loamy <br> sand | Pinus <br> sylvestris |  |  |  |

Table 2. Cont.

| Species | Site \# | Location | Coordinates | Slope | Elevation (m a.s.l.) | Soil Substrate | Admixed Species |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Quercus petraea | 3 | Breitenhees, Lüneburg Heath, Lower Saxony | $\begin{gathered} 10^{\circ} 30^{\prime} \mathrm{E} \\ 52^{\circ} 49^{\prime} \mathrm{N} \end{gathered}$ | level | 120 | Loamy sand | Picea abies |
| Quercus petraea | 4 | Breitenhees, Lüneburg Heath, Lower Saxony | $\begin{gathered} 10^{\circ} 30^{\prime} \mathrm{E} \\ 52^{\circ} 49^{\prime} \mathrm{N} \end{gathered}$ | level | 123 | Loamy sand | Picea abies |
| Carpinus betulus | 5 | Ziegelrodaer Forst (near Mansfeld), Thuringia | $\begin{gathered} 11^{\circ} 32^{\prime} \mathrm{E} \\ 51^{\circ} 26^{\prime} \mathrm{N} \end{gathered}$ | 5\% NW | 225 | Sandy loam | Tilia cordata, Acer ssp. |
| Carpinus betulus | 6 | Ziegelrodaer Forst (near Mansfeld), Thuringia | $\begin{aligned} & 11^{\circ} 32^{\prime} \mathrm{E} \\ & 51^{\circ} 26^{\prime} \mathrm{N} \end{aligned}$ | 11\% N | 235 | Sandy loam | Fraxinus excel., Tilia cordata |
| Tilia cordata | 7 | Colbitz-Letzlinger Heide (county of Wolmirstedt), Saxony-Anhalt | $\begin{aligned} & 11^{\circ} 32^{\prime} \mathrm{E} \\ & 52^{\circ} 21^{\prime} \mathrm{N} \end{aligned}$ | level | 85 | Loamy sand | Quercus robur, Fraxinus excel. |
| Tilia cordata | 8 | Colbitz-Letzlinger Heide (county of Wolmirstedt), Saxony-Anhalt | $\begin{aligned} & 11^{\circ} 33^{\prime} \mathrm{E} \\ & 52^{\circ} 20^{\prime} \mathrm{N} \end{aligned}$ | level | 78 | Loamy sand | Quercus robur, Fraxinus excel. |
| Fagus sylvatica | 9 | Unterlüss, Lüneburg Heath, Lower Saxony | $\begin{aligned} & 10^{\circ} 16^{\prime} \mathrm{E} \\ & 52^{\circ} 50^{\prime} \mathrm{N} \end{aligned}$ | level | 115 | sand | Quercus petraea |
| Fagus sylvatica | 10 | Unterlüss, Lüneburg Heath, Lower Saxony | $\begin{gathered} 10^{\circ} 19^{\prime} \mathrm{E} \\ 52^{\circ} 49^{\prime} \mathrm{N} \end{gathered}$ | level | 113 | Loamy sand | - |

Table 3. Stand structural characteristics of each of the two studied stands of the five species.

| Species | Site \# | Stand Age (year) | Basal <br> Area $\left(\mathrm{m}^{2} h \mathrm{a}^{-1}\right)$ | Stem <br> Density (ha ${ }^{-1}$ ) | Abundance of Main Species (\% of Stems) | Mean <br> Height (m) | $\begin{gathered} \text { Mean } \\ \mathrm{dbh}^{1}(\mathrm{~cm}) \end{gathered}$ |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Betula pendula | 1 | 45 | 25.2 | 880 | 85 | $20 \pm 3$ | $19 \pm 6$ |
| Betula pendula | 2 | 67 | 28.5 | 420 | 98 | $25 \pm 3$ | $25 \pm 3$ |
| Quercus petraea | 3 | 154 | 27.5 | 260 | 94 | $23 \pm 3$ | $37 \pm 6$ |
| Quercus petraea | 4 | 149 | 23.8 | 190 | 95 | $23 \pm 2$ | $44 \pm 6$ |
| Carpinus betulus | 5 | 116 | 31.5 | 345 | 68 | $27 \pm 5$ | $29 \pm 1$ |
| Carpinus betulus | 6 | 95 | 37.0 | 420 | 77 | $26 \pm 3$ | $32 \pm 9$ |
| Tilia cordata | 7 | 83 | 35.9 | 370 | 96 | $23 \pm 4$ | $23 \pm 9$ |
| Tilia cordata | 8 | 65-81 | 37.7 | 780 | 81 | $22 \pm 4$ | $22 \pm 9$ |
| Fagus sylvatica | 9 | 95-115 | 30.8 | 445 | 92 | $26 \pm 2$ | $38 \pm 7$ |
| Fagus sylvatica | 10 | 96 | 24.2 | 375 | 100 | $26 \pm 2$ | $38 \pm 6$ |

${ }^{1}$ arithmetic mean.

### 2.2. Stand Structure and Crown Volume

In each of the 10 stands, two circular plots of $1000 \mathrm{~m}^{2}$ in size (radius of 17.9 m ) were installed in stand sections with high canopy closure. The degree of canopy closure was assessed visually for every plot by estimating gap fraction vertically upwards from the ground at about 10 locations per plot. Canopy gaps larger than about $25 \mathrm{~m}^{2}$ were avoided. Dbh) was measured at $1.3-\mathrm{m}$ height for all trees in the plots with a dendrometer tape, and tree height for the majority of trees (32-46 per plot) was measured with a height meter (PM-5/1520; Suunto, Vantaa, Finland). For the remaining stems, we calculated dbh-height relationships for every plot and tree species using different polynomial or logarithmic equations and derived the height of the unmeasured trees from recorded dbh. We always selected the equation with the best fit. Leaf area index (LAI) was measured in the 10 stands with

10 circular litter buckets of $0.287-\mathrm{m}^{2}$ aperture that were installed in the plots at fixed distances of 2.2 m . The litter was collected on two dates (November/December and February/March) and the material was sorted for leaves, twigs, and fruits. The leaves were separated by species. Each of the 50 randomly collected leaves per bucket were immediately scanned for leaf area and the mass determined to obtain the LMA. The total mass of dry leaf litter $\left(70^{\circ} \mathrm{C}, 48 \mathrm{~h}\right)$ was converted to leaf area with the LMA values and related to the aperture of the litter buckets to calculate stand LAI for the target tree species and the admixed species, if present.

Crown projection area was derived with the Suunto height meter by determining the stem distance of eight points of the crown periphery. For visualizing and analyzing the three-dimensional shape and volume of the crown, we applied the crown window approach. With the window, we took drawings of the crown silhouette at scale at a height of 1.8 m from four directions in the stand. The four drawings were overlaid using the software WinDig, version 2.5 [30] and CrownShape (M. Hagemeier, unpubl.) for calculating individual polyhedrons that visualized the shape of the crown in good approximation of the natural conditions (see Figure S1 in the Supplement). The software also allowed quantifying total crown volume and crown extension at different heights. The crown radius at different relative heights in the canopy was averaged over all directions and the means expressed over height in percentage of the maximum canopy radius recorded for that tree.

Leaf angles (i.e., leaf inclination relative to the horizontal) were measured for a large number of leaves per species from the shade to the sun crown using a mobile elevator van or scaffolding towers for canopy access. We constructed an electronic protractor according to [31] that allowed determining and storing the inclination values of individual leaves (i.e., the blade's departure from the horizontal) by means of resistance measurement. We aligned the protractor with the fall line of the blade (roughly in the middle of the blade) and determined the angle to the horizon $\left(0^{\circ}\right)$. The measurements were conducted only in windless conditions. Angles below the horizon (hanging leaves) were considered negative, but the value was multiplied by -1 to calculate with positive values in the statistical analysis. We refrained from measuring leaf azimuth due to frequent compass needle misreadings in the vicinity of the scaffolding towers. Each several hundred individual leaves (in most cases 200-1000 per height level) were measured between June and August in five height levels in the canopy ( $<0.25,0.25-0.50$, $0.50-0.75,0.75-0.875$, and $0.875-1.0$ relative height) of several trees per species to obtain means and frequency distribution plots of leaf angle. In case of Betula, Quercus, and Fagus, scaffolding towers in the vicinity of site \#9 were used for canopy access. The mobile elevator van served for reaching the crown of the Carpinus and Tilia trees.

The vertical distribution of leaf area in the crown was determined by harvesting each four mature trees of Quercus, Carpinus, and Tilia in the plots during midsummer; in case of Betula and Fagus, 6 and 11 trees, respectively, were harvested. All trees had characteristic dbh and height values of those trees reaching the upper canopy layer in the respective stands. The trees selected for harvest were analyzed for crown shape and crown volume in the preceding winter in order to relate leaf area to crown volume. The felled trees were sliced into $2-\mathrm{m}$ height layers and all leaves in a layer were sampled quantitatively for mass determination after drying at $70^{\circ} \mathrm{C}$ for 48 h . In every height layer of a tree, five samples with about 25 leaves were collected randomly for determining leaf size and LMA using a scanner and the software WinFolia (Régent Instruments, Quebec, QC, Canada). The fraction of total area contained in the different 2-m height layers was plotted against relative canopy height to obtain vertical leaf area distribution for every tree. Further, the total leaf area in the 2-m height layers was related to the volume of the respective layer to calculate leaf area density (in $\mathrm{m}^{2} \mathrm{~m}^{-3}$ ) in dependence on height in the canopy.

### 2.3. Statistical Analyses

In all figures, means and standard deviation are given. All data were tested for normal distribution with a Shapiro-Wilk test. Exponential, quadratic, or linear regression equations were calculated to express the dependence of leaf parameters on relative height in the canopy. The regression analyses
were conducted with the software Xact (SciLab, Hamburg, Germany). As the study focus was on the vertical change in foliage parameters in the crown, we did not compare species means in most of the traits. However, plot means of leaf area index (litter bucket data) were compared between the two sampling years and among the five species using a Scheffé test for unbalanced samples. These analyses were conducted with SAS software (SAS Institute, Cary, NC, USA). A significance level of $p<0.05$ was used throughout the study.

## 3. Results

### 3.1. Leaf Size and Leaf Mass Area

Our investigation of 22-26-m-tall adult trees in the upper canopy showed that mean leaf lamina size increased linearly from the upper sun crown to the lowermost shade crown in Betula and Tilia, while it peaked at 0.5-0.6 relative canopy height in Quercus, Carpinus, and Fagus and decreased toward the shade crown again (Figure 1). The leaf area minimum was reached in Betula, Quercus, and Tilia in the uppermost sun crown, while in Carpinus and Fagus, the lowermost shade leaves were as small as, or even smaller than, the uppermost sun leaves.

The LMA showed an exponential increase with height in all five species, but the species differed considerably with respect to the shape of the curve (Figure 2). Early successional Betula had the smallest absolute LMA difference between lowermost shade and uppermost sun crown. In Carpinus and Tilia, LMA changed only a little at lower and middle height in the crown to show a steep increase in the uppermost quartile of stem length. In contrast, Fagus and Betula revealed a more gradual LMA increase over the entire leafy crown, while Quercus took an intermediate position (parameter c in Table 4). The (mid) late-successional species Carpinus, Tilia, and Fagus had lower absolute LMA values not only in the shade but also in the sun crown than the early to mid-successional species Betula and Quercus (parameter a in Table 4).


Figure 1. Size of leaf laminas in dependence on height in the canopy of the five tree species. Every point stands for the mean and SD of 125 measurements each taken at a given crown height (different trees from two sites per species). Note different $y$-axis scaling in the graphs.

Table 4. Parameters $a, b$, and $c$ of exponential regression equations of the form $y=a+b x^{c}$ for the dependence of leaf mass area (LMA) on relative height in the crown for the five species. Correlation coefficients $r$, $p$-values, and degrees of freedom are also given. Each data point refers to the mean of five sets of measurements on branches where each of the 25 leaves were investigated.

| Species | a | b | c | r | $\boldsymbol{p}$ | df |
| :--- | :---: | :---: | :---: | :---: | :---: | :---: |
| Betula | 50.5 | 38.7 | 3.3 | 0.94 | $<0.001$ | 26 |
| Quercus | 59.9 | 65.2 | 4.9 | 0.94 | $<0.001$ | 32 |
| Carpinus | 30.7 | 71.3 | 5.9 | 0.91 | $<0.001$ | 29 |
| Tilia | 30.3 | 60.5 | 7.4 | 0.91 | $<0.001$ | 21 |
| Fagus | 23.2 | 59.9 | 1.8 | 0.79 | 0.011 | 18 |



Figure 2. LMA in dependence on height in the canopy of the five tree species. Given are means of each five datasets with 25 leaves each taken per height level and tree ( $n=4-11$ trees per species).

### 3.2. Leaf Angles and Leaf Area Distribution in the Crown

All five species showed exponential increases in mean leaf angles (degrees from horizontal) from the mid-stem position to the crown top. In the late-successional species Carpinus, Tilia, and Fagus, angles varied only a little across the lower half of the stem (Figure 3). These species had similar angles in the shade crown with means in the range of $18^{\circ}-21^{\circ}$ (parameter a in Table 5). Fagus and (to a lesser degree) Carpinus differed from the other species in that the leaves with lowest angle (ca. $13^{\circ}$ and $17^{\circ}$ ) occurred in the middle and not the lowermost shade crown. Early successional Betula differed from the other four species by maintaining relatively steep leaf angles (typically $\geq 30^{\circ}$ ) also below a relative canopy height of 0.5 . Thus, Betula had the largest leaf angles in both the shade and the sun crown; in the uppermost sun crown, means of about $55^{\circ}$ were measured (Figure 4). Differences between shadeand sun-crown leaf angles were largest in Quercus and Tilia ( $\sim 110 \%$ and $100 \%$ greater angles in the uppermost than the lowermost leaves), followed by Fagus ( $\sim 75 \%$ ). The vertical leaf angle gradient was smallest in Betula and Carpinus ( $\sim 25 \%$ and $40 \%$ difference). Due to a large leaf angle increase with height in the uppermost crown (parameter c in Table 5), Tilia reached its steepest leaf angles ( $40^{\circ}-50^{\circ}$ ) only in the most exposed sun crown (Figure 3). The frequency distribution of leaf angles at five height levels, as displayed in Figure 4, shows that the three late-successional species and Quercus were characterized by a more left-skewed distribution pattern in all height levels (i.e., a higher abundance of leaves with low angles). In contrast, early successional Betula was characterized by a normal or, in the upper crown, right-skewed angle distribution, indicating that leaves with steeper inclination are relatively more abundant than leaves with low angles; most Betula leaves hang downward. Weighted by the total leaf area in the different height levels and averaged over the whole crown, we found mean leaf angles of $49^{\circ}$ for Betula, $25^{\circ}$ for Quercus, $22^{\circ}$ for Carpinus, $24^{\circ}$ for Tilia, and $22^{\circ}$ for Fagus in the closed stands.

Table 5. Parameters $\mathrm{a}, \mathrm{b}$, and c of exponential regression equations of the form $y=a+b x^{\mathrm{c}}$ for the dependence of leaf angle on relative height in the crown for the five species. Correlation coefficients $r$, $p$-values, and degrees of freedom are also given.

| Species | a | b | c | r | $\boldsymbol{p}$ | df |
| :--- | :---: | :---: | :---: | :---: | :---: | :---: |
| Betula | 29.0 | 34.5 | 2.13 | 0.84 | $<0.001$ | 28 |
| Quercus | $(0)$ | 45.4 | 1.73 | 0.86 | $<0.001$ | 24 |
| Carpinus | 19.2 | 18.8 | 6.44 | 0.72 | 0.035 | 20 |
| Tilia | 20.7 | 36.8 | 10.2 | 0.79 | 0.022 | 16 |
| Fagus | 17.0 | 27.7 | 3.61 | 0.75 | 0.001 | 30 |



Figure 3. Leaf angles (degrees from horizontal) in dependence on height in the canopy of the five species. Means and SD of each ca. 90 individual measurements taken in early summer (May to early June; filled symbols) or mid to late summer (end of June to early September; open symbols). The influence of season was not significant in any of the species.

The vertical distribution of leaf area along the stem revealed marked differences between the five species. Early successional Betula and late-successional Tilia concentrated their leaf area entirely in the upper half of the stem, while Quercus, Carpinus, and Fagus extended their leaves downwards to a relative height of 0.30 or even 0.25 in the studied trees, which were all part of the upper canopy layer (Figure 5). The height of the highest amount of leaf area increased from Fagus (ca. 0.70) to Quercus (ca. 0.78), to Betula and Carpinus (ca. 0.80), and peaked at Tilia (ca. 0.88). Thus, late-successional Fagus had the lowest center of gravity of its leaf area in the crown. The vertical extension of leaf area along
the stem and the relative height of the highest amount of leaf area were not related to each other in the species and showed no clear difference between early and late-successional taxa. As expected, the vertical change in mean crown radius as derived from the crown window observations mirrored the vertical change in leaf area per height level in the five species.


Figure 4. Frequency distribution of leaf angles (degrees from horizontal) in five height levels in the canopy of the five species. Width of angle classes: $10^{\circ}$. Given are the number of measured leaves and the arithmetic mean $(M) . \mathrm{n}=0$ indicates a lack of leaves at this height level or the absence of suitable twigs that could be accessed for measurement.

Leaf area density (i.e., leaf area per crown volume) was the parameter with largest difference between early/mid- and late-successional species. While leaf area density in the lowermost shade crown was similar for the five species $\left(0.3-0.5 \mathrm{~m}^{2} \mathrm{~m}^{-3}\right)$, it reached much higher values in the uppermost sun crown in Carpinus and Tilia (10-20 $\mathrm{m}^{2} \mathrm{~m}^{-3}$ ) than in Betula and Quercus (about $3 \mathrm{~m}^{2} \mathrm{~m}^{-3}$; Figure 6; only incomplete data available for Fagus). The steepest leaf area density increase occurred in the uppermost crown (ca. 0.9-1.0 relative height) of the latter two species, while the increase was much weaker in Betula and Quercus. According to litter bucket measurements in each of the two stands per species, leaf area index increased from Betula (3.6 and 5.4) to Quercus (5.4 and 5.5) and further to Tilia (5.9 and 8.2), Carpinus (7.7 and 8.9), and Fagus (8.0 and 8.8; Figure 7). Closed stands of the late-successional species thus had higher mean LAIs than stands of the early/mid-successional species (admixed species are included in the figures).


Figure 5. Leaf area distribution in dependence on height in the canopy in the five tree species (black bars) (leaf-area-per-height level in percent of the tree's total). Also indicated is the relative volume of the canopy along the stem axis (black line), that is the mean canopy radii in percent of maximum canopy radius. Based on the analysis of each of the four tree individuals per species with typical dbh and height in the canopy that were analyzed for their crown dimensions with the canopy window and were subsequently harvested with their foliage.


Figure 6. Leaf area density (leaf area per crown volume) in dependence on height in the crown of the five tree species. The data were calculated from measured crown volume (crown window data) and the corresponding leaf areas per volume and height level as determined for each of the four harvested tree individuals per species. No data available for Fagus. Parameters of the exponential equations of the form $y=\mathrm{a}+\mathrm{b} x^{\mathrm{c}}$ : Betula: $\mathrm{a}=0.142, \mathrm{~b}=2.91, \mathrm{c}=9.02$; Quercus: $\mathrm{a}=0.524, \mathrm{~b}=3.93, \mathrm{c}=17.78$; Carpinus: $\mathrm{a}=3, \mathrm{~b}=36.9, \mathrm{c}=42.1$; Tilia: $\mathrm{a}=0.447, \mathrm{~b}=13.8, \mathrm{c}=36.4$.


Figure 7. Leaf area indices of the five tree species in two years (1998 and 1999) according to litter bucket measurements in two sites per species (each 10 litter buckets per site). Given are means and SD. Only the Betula and Quercus stands were monospecific; a small proportion of other tree species were admixed in the Carpinus, Tilia, and Fagus stands. The leaf area of these admixed species is indicated by cross-hatching on top of the bars. Significant species differences in 1998 are indicated by different small letters, and in 1999, by different capitals (Scheffé test, $p<0.05$ ). Significant differences between years are indicated by *.

## 4. Discussion

### 4.1. Sun Crown Foliage

Our study is among the few that compared the foliage properties of the uppermost sun crown among tree species differing in successional status. We measured particularly steep leaf angles in the sun crown of Betula, with most leaves hanging, which is also the case in Populus species, another important genus of temperate early-successional tree species (Table 6). Early and late-successional species have in common leaf angles being steepest in the uppermost sun crown and decreasing with crown depth, independently of species differences in leaf size. Decreasing leaf angles with crown depth are commonly observed in temperate tree crowns [3,4,32] (see Table 6), but our results reveal considerable species differences in the pattern of leaf angle change from sun to shade crown. The inclination decrease was more or less continuous in Betula and Quercus but restricted to the upper crown third or half in the case of Carpinus, Tilia, and Fagus, while leaf angles changed little across the shade crown. All species also had in common that the most exposed sun leaves had the highest LMA and reached the greatest leaf area density in the crown. In three of the five species, these leaves were also the smallest in the crown. Leaf size increased with crown depth either linearly (Betula, Tilia) or curvilinearly (Carpinus and Fagus), with a peak in mid-crown.

Steep leaf angles are usually interpreted as an adaptation to optimize whole-canopy carbon gain because light transmission to lower layers is increased, while steep sun leaf angles typically should cause only a slight reduction in carbon gain, as light intensities remain above light saturation in the sun crown most of the time. The shade crown could profit from steep sun leaves by extending its leaf area and thereby increasing carbon gain. Our results question this interpretation, as the steepest sun leaves were found in early-successional B. pendula, which maintains only a small leaf area in lower crown strata and has by far the highest light transmission to the ground [15] (see Table 1) (i.e., much of the transmitted light is not used). If the amount of light transmitted to lower foliage layers were decisive, we instead would have expected steeper sun leaf angles in late-successional species, which typically produce larger leaf areas in the shade crown. There are several possible explanations why pioneer trees often produce sparse crowns with more vertically oriented leaves. Wind drag and frequent mechanical
interference with neighbor trees could play a role. However, strong winds are not a major site factor for Central European forests, and late-successional trees are also subject to frequent mechanical crown interactions with neighbors [33]. As an alternative explanation, we assume that the pioneer tree B. pendula is unable to produce shade leaves with low light demand due to physiological reasons and thus is dependent on higher light transmission to its demanding lower crown layers. Steep sun leaf angles would then mainly be a consequence of shade leaf physiology. Steep leaf angles could also help to avoid damage by excess radiation [34]. More speculative is the interpretation that early successional trees such as the Betula species, which often grow in nutrient-poor soils, use vertical leaf angles to avoid high radiation and heat loads in the sun crown, because chemical protection from excess radiation and heat damage may be less affordable for these species.

The small size of the leaves in the uppermost crown matches observations in other studies [35]. This phenomenon may best be interpreted as an adaptation to meet the constraints of the tree's hydraulic system, targeted at reducing the water loss of the most sun-exposed leaves. However, leaf size effects on radiation transmission through the crown may also be important, as a top layer of small leaves does expose a smaller fraction of the crown volume to direct shade than would a sun crown with larger (but fewer) sun leaves. By forming a layer of small, steeply inclined leaves in the peripheral crown, the penumbra effect is used to expose large inner-crown areas to sufficiently high levels of diffuse radiation which allow fairly high photosynthetic rates while minimizing the burden of excess radiation and heat load [36,37]. An interesting phenomenon in this context is the marked LAD increase from crown bottom to top, which was observed in all four studied species. It may be interpreted as further indication that the top layer of relatively small and steeply inclined leaves plays an important functional role by shielding the highly productive inner parts of the crown from excess radiation and heat damage [7]. In accordance, [38] found lower nitrogen contents and a reduced photosynthetic capacity in the uppermost leaves of a beech (F. sylvatica) crown, while the leaves of the lower sun crown (3-6 m below the top) were richer in N and photosynthetically more active. In contrast, leaf xanthophyll content decreased from the top to the crown interior. This suggests that the small size and step orientation of the uppermost leaves is a compromise to balance the need for intercepting as much light as possible in periods of excess light with the goal of transmitting sufficient radiation to lower layers during low-light periods. As we found a much greater LAD increase in the mid- to late-successional species C. betulus and T. cordata than in B. pendula and Q. petraea, we assume that the need for protection is larger in the former species with a well-developed shade crown. The small, upwards or downwards inclined sun-canopy leaves of Betula and Populus species flutter even in a light wind [39], which may represent another adaptation to improve the light regime in the crown interior. Flutter decreases the amount of light intercepted by upper-canopy leaves, while it increases the number of light flecks in the lower crown and creates a spatially more even light distribution at relatively high mean flux densities [40], which may enhance overall canopy carbon gain.

Our finding of decreasing leaf angles with proceeding succession seems to contrast with patterns observed in tropical forest successions, where many pioneer trees such as the Macaranga and Cecropia species have monolayered crowns with low leaf angles, while late-successional trees often have multilayered sun crowns with steeper leaf inclination [21]. In tropical environments with high radiation intensities, steep leaf angles obviously are not required for achieving a high carbon gain, as direct sun light hits the crown at steeper angles to the horizontal. This is demonstrated by the mentioned tropical pioneer trees, which are capable of monopolizing light access by building monolayered crowns, while they do not possess a typical shade crown. This should be different for early successional trees in energy-limited temperate and boreal forests, for which the productivity of lower leaf layers may be more important.

Table 6. Leaf angles (inclination in degrees relative to the horizontal) in the shade and sun crown of various temperate broadleaf trees according to literature sources. Mid = crown at mid height. Values were partly read from plotted data or calculated from ellipsoidal functions describing leaf angle distribution. Crown average stands for weighted means of the crown (if not indicated otherwise).

| Species/Community | Shade Crown | Crown Average | Sun Crown | Source |
| :---: | :---: | :---: | :---: | :---: |
| Betula pendula | 30 | 49 | 53 | This study |
| Populus deltoides | 32.3 |  | 75.7 | McMillen and McClendon (1979) [9] |
| Quercus petraea | 21 | 25 | 41 | This study |
|  | 29 | 37 | 38 | Schlünder (unpubl.) |
| Quercus robur and petraea | 26 |  | 46 | Kull et al. (1999) [6] |
| Quercus rubra | 11 |  | 10.1 | McMillen and McClendon (1979) [9] |
| Oak-hickory forest | 10 | 33 | 38 | Hutchison et al. (1986) [4] |
| Carpinus betulus | 21 | 22 | 26 | This study |
|  | 13 | 21 (mid) | 42 | Elias (1990) [5] |
| Tilia cordata | 18 | 24 | 34 | This study |
| Acer saccharum | 7.8 |  | 14.6 | McMillen and McClendon (1979) [9] |
| Fagus sylvatica | 20 | 22 | 37 | This study |
|  | 15 | 34 | 53 | Schlünder (unpubl.) |
|  | 22.2 | 26 (mid) | 34 | Planchais \& Sinoquet (1998) [41], Planchais \& Pontailler (1999) [42] |

### 4.2. Shade Crown Foliage

Even though the definition of criteria for distinguishing sun- and shade-crown foliage is somewhat arbitrary, the LMA decrease with crown depth may serve as a useful parameter. The mid/late- and late-successional species ( $C$. betulus, $T$. cordata, and $F$. sylvatica) all had shade leaves with low LMA values between 20 and $30 \mathrm{~g} \mathrm{~m}^{-2}$, while the lowermost leaves of B. pendula and $Q$. petraea reached higher values between 50 and $60 \mathrm{~g} \mathrm{~m}^{-2}$. Another difference was the minimum leaf angle reached in the lowermost shade crown, which averaged at $18^{\circ}-21^{\circ}$ in the former species but was as high as $30^{\circ}$ in early successional B. pendula. In this respect, $Q$. petraea $\left(21^{\circ}\right)$ tended more to the late-successional species, but the total area of leaves with low angles was small in oak. The late-successional species had not only thinner, more horizontal leaves in the shade crown, but their total leaf area per ground area (LAI) was also larger than in the early/mid-successional species. We found an LAI increase from ca. 4 in B. pendula to ca. 8 in F. sylvatica, in accordance with the LAI increase that characterizes the succession from early to late-successional species in the temperate forest biome [15,28]. The increase is mostly due to the more extended shade crown of late-successional trees, which are able to produce shade leaves with greater shade tolerance than the early/mid-successional species and thus can maintain larger leaf areas with a positive carbon balance under low-light conditions. However, the existence of an extended shade crown is not necessarily linked to a specific crown morphology, notably, a larger vertical crown extension with more deep-reaching lowermost leaf layers. This was demonstrated by T. cordata, which concentrated, in contrast to C. betula and F. sylvatica, the bulk of its leaf area above 0.6 relative canopy height but nevertheless formed typical shade leaves with low LMA and low angles. We did not find a positive relation between LAI and vertical crown extension in these five species.

It is well known that leaf size generally increases with crown depth and decreasing light intensity in temperate broadleaf trees in parallel with the LMA decrease [35]. The lowermost shade leaves are often the largest in the crown with lowest LMA. Large, thin, and horizontally oriented leaves maximize the surface area projection and optimize the cost-benefit ratio of leaf operation under low-light conditions. A decrease in the evaporative demand of the air toward deeper crown layers may also drive the leaf area and specific leaf area increase. In our sample, however, leaf size decreased from a mid-crown peak toward the lower shade crown in three of the species ( $Q$. petraea, C. betulus, and F. sylvatica), in a similar manner as found by [4,5]. This suggests that the efficiency of light absorption is not the only determinant of leaf size in the shade crown. However, leaf support costs in terms of biomass investment in petioles increase as leaves become more horizontal [3]. It is possible that the ratio between the costs of leaf construction (which increase) and the benefits in terms of $C$ gain (which decrease) become increasingly unfavorable toward deeper crown layers, so that leaf size is reduced in the deepest shade due to a shortage in carbohydrates (and nutrients) for building leaves.

## 5. Conclusions

The five investigated broadleaf tree species are typical representatives of the groups of early, $\mathrm{mid} /$ late- or late-successional species in the European temperate tree flora. We found marked species differences in foliage properties and leaf distribution and orientation in the crown of adult trees, but the sample size (five species) is too small to draw more general conclusions on trends over successional time. However, with reference to other published work, some interesting insights into crown functioning and its change with forest succession are possible. Even though all species experience the same light environment in the upper sun crown, they differ considerably in leaf size, LMA, leaf inclination, and LAD of sun and shade foliage. Part of this variation is certainly related to different phylogenies (five genera, three families) and thus may reflect adaptation to past environments, but the position in succession also seems to shape foliage properties. The mid/late- and, in particular, the late-successional species have a significantly larger total leaf area (LAI) due to the formation of extended leaf layers with low LMA and nearly horizontal leaf orientation in the lower crown, which are absent in B. pendula, the only true early-successional species of this study. The existence of morphologically distinct shade foliage is not necessarily associated with large vertical crown extension, in contradiction to the assumption of [2]. We present some evidence in support of the assumption that the structure of the uppermost sun leaf layer is partly determined by the existence of distinct shade foliage, which is sensitive to excess radiation. More comparative multiple-species studies with adult trees are needed to draw conclusions on successional trends in foliage and crown structural properties and to explore differences between temperate and tropical broadleaf trees.

Supplementary Materials: The following figure demonstrating the use of the crown window is available online at http:/ /www.mdpi.com/1999-4907/10/3/265/s1, Figure S1. The three-dimensional shape of a crown and its volume were determined with the crown window approach. From four directions in the stand, we took drawings of the crown silhouette at scale at the observer height of 1.8 m . The four drawings were digitized and overlaid using the software WinDig, version 2.5 (Lovy 1996) and CrownShape (M. Hagemeier, unpubl.) for calculating individual polyhedrons that visualized the shape of the crown in good approximation of the natural conditions.
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