



Tree growth as affected by stem and crown structure

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Abstract

Key message Prediction of tree growth based on size or mass as proposed by the Metabolic Scaling Theory is an over-simplification and can be significantly improved by consideration of stem and crown morphology.

Tree growth and metabolic scaling theory, as well as corresponding growth equations, use tree volume or mass as predictors for growth. However, this may be an over-simplification, as the future growth of a tree may, in addition to volume or mass, also depend on its past development and aspects of the current inner structure and outer morphology. The objective of this evaluation was to analyse the effect of selected structural and morphological tree characteristics on the growth of common tree species in Europe. Here, we used eight long-term experiments with a total of 24 plots and extensive individual measurements of 1596 trees in monospecific stands of European beech (*Fagus sylvatica* L.), Norway spruce (*Picea abies* (L.) Karst.), Scots pine (*Pinus sylvestris* L.) and sessile oak (*Quercus petraea* (Matt.) Liebl.). Some of the experiments have been systematically surveyed since 1870. The selected plots represent a broad range of stand density, from fully to thinly stocked stands. We applied linear mixed models with random effects for analysing and modelling how tree growth and productivity are affected by stem and crown structure. We used the species-overarching relationship $iv = a_0 \times v$ between stem volume growth, iv and stem volume, v , as the baseline model. In this model a_0 represents the allometric factor and α the allometric exponent. Then we included tree age, mean stem volume of the stand and structural and morphological tree variables in the model. This significantly reduced the AIC; RMSE was reduced by up to 43%. Interestingly, the full model estimating iv as a function of v and mean tree volume, crown projection area, crown ratio and mean tree ring width, revealed a $\alpha \cong 3/4$ scaling for the relationship between $iv \propto v^\alpha$. This scaling corresponded with Kleiber's rule and the West-Brown-Enquist model of the metabolic scaling theory. Simplified approaches based on stem diameter or tree mass as predictors may be useful for a rough estimation of stem growth in uniform stands and in cases where more detailed predictors are not available. However, they neglect other stem and crown characteristics that can have a strong additional effect on the growth behaviour. This becomes of considerable importance in the heterogeneous mixed-species stands that in many countries of the world are designed for forest restoration. Heterogeneous stand structures increase the structural variability of the individual trees and thereby cause a stronger variation of growth compared with monocultures. Stem and crown characteristics, which may improve the analysis and projection of tree and stand dynamics in the future forest, are becoming more easily accessible by Terrestrial laser scanning.

Keywords Growing area · Individual tree model · Legacy effect · Mixed-species stands · Structural diversity · Transitioning to uneven-aged stands

Introduction

In the past, many works have been published about the course of tree growth and its dependency on tree age or tree size (von Bertalanffy 1951; Richards 1959; Coomes and Allen 2007). Tree growth theory (von Bertalanffy 1951) and corresponding growth equations (Zeide 1993) used tree volume or mass as predictors for growth. Current stem volume or stem mass represent the accumulated past growth of a

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tree and are certainly better predictors for its current growth than tree age. Holding all other factors fixed, the bigger the present size of a tree the more extended the meristems for building new cells and the higher the growth rate. Thus the current size represents, together with other variables, the ecological legacy of the past individual tree growth. Other characteristics, such as the past tree ring pattern (Camarero et al. 2018) or crown morphology (Mäkelä and Valentine 2006), may further determine a tree's growth and vitality in the future. An estimation of the metabolic rate and growth of a tree, only based on body size or mass, as proposed by the metabolic scaling theory and model by West, Brown and Enquist (1997) (WBE model), may be useful for a rough species-overarching estimation of stem growth in uniform stands and if more detailed predictors are not available. The WBE model proposed the 3/4 scaling between plant growth and plant mass. It has been derived from the fractally structured internal pipe system of plants (West et al. 1997; Enquist et al. 1998). Based on the 3/4 scaling of allometric ideal plants Enquist et al. (2009) and West et al. (2009) later extended their scaling theory to the stand level and the self-thinning under demographic equilibrium conditions. Among others, Kozłowski and Konarzewski (2004) and Muller-Landau et al. (2006) argued that the WBE model is an oversimplification of tree allometry. Especially in heterogeneous stands with a wide variation of stem and crown allometries, tree growth may be co-determined by other tree attributes in addition to tree mass (Pretzsch 2014; Pretzsch et al. 2015).

A huge leap forward was the inclusion of individual tree-specific structural and morphological information for growth prediction. Well known exemplars for this approach are eco-physiological models (Landsberg 2011) and, in particular, structural–functional models (Sievänen et al. 2000, Grote and Pretzsch 2002) which use e.g., sapwood area, leaf area, or crown length as predictors of tree growth. Whereas eco-physiological processes and functions are often much more difficult to measure and less representative, structural and morphological traits are easier to access and may support the bridging of process-based and empirical approaches to modelling tree growth (Mäkelä and Valentine 2006). Structural and morphological traits, such as crown projection area, crown ratio and mean tree ring width, may contain ecological legacy information about the past of the tree that is relevant for its present and future growth. It can be made use of the fact that in seasonal forests tree ring pattern and crown structure store information about growth rhythm in trees (Lüttge and Hertel 2009). The tree ring pattern or crown structure can be harnessed for quantifying the tree's past development by appropriated metrics (Pretzsch 2021). Tree-ring, crown, or root morphology patterns represent a structural legacy imbedded in stem, crown, and root (Netzer et al. 2019; Ogle et al. 2015). This legacy may affect the tree's functioning and growth, e.g., via light interception,

hydraulic conduction, or water and nutrient uptake. In this way, the differences in structure may cause specific differences in the functioning and growth curve patterns. Such information about structural and morphological traits is often available for a larger number of trees and can be used for model parameterization or evaluation.

The objective of this study was to analyse the effects of selected structural and morphological characteristics on the growth of common tree species. Such detailed structural and morphological traits may contain information of the past growth that is “ecologically memorised” by the tree and determines its present and future growth (Berger and Hildenbrandt 2000; Camarero et al. 2018). Based on individual tree growth and allometric stem and crown characteristics of European beech (*Fagus sylvatica* L.), Norway spruce (*Picea abies* (L.) Karst.), Scots pine (*Pinus sylvestris* L.), and sessile oak (*Quercus petraea* (Matt.) Liebl.), we answer the following three questions:

Q1: how does tree volume growth depend on tree volume and tree age in general and at defined tree ages or in defined stand development phases?

Q2: how do stem and crown characteristics (e.g., mean annual growth in the past, crown ratio, crown projection area) determine individual tree growth?

Q3: how does the growing area efficiency (tree growth per crown projection area) depend on tree size and various stem and crown characteristics?

Finally, we discuss the implications of structure-growth relationships for forest ecology and management, and for silvicultural guidelines.

Material and methods

Location and site characteristics of the selected stands

We used eight long-term experiments with 24 plots and extensive individual measurements of 1596 trees in mono-specific stands of European beech, Norway spruce, Scots pine, and sessile oak (Table 1). The experiments belong to a research network, which was established by far-sighted researchers in the late nineteenth century to procure growth and yield data as a quantitative basis for sustainable forest management (described, among others, by von Ganghofer (1881)). In the beginning, measurements on these experiments only included stem diameter, tree height and tree removal (Verein Deutscher Forstlicher Versuchsanstalten 1873, 1902). Later also tree coordinates, crown dimensions, and tree vitality have been measured (Pretzsch 2017; Pretzsch et al. 2019). Some of the experiments selected for

Table 1 Location, climate characteristics and site conditions of the eight long-term experiments included in this study

Experimental plot	No	Species	Age year ⁻¹	Longitude	Latitude	Elevation a.s.l	annual precipitation mmyear ⁻¹	Mean tempera- ture °C	Soil type	Substrate	Geology	Ecoregion
Sachsenried	607	N. spruce	66	10.82	47.87	760	1120	6.8	Parabrown soil	Loam	Günz-Mindel glacier	14.4.1
Denklingen	5	N. spruce	173	10.84	47.87	780	1120	6.8	Parabrown soil	Loam	alpine moraine	14.4.1
Weiden	611	S. pine	49	12.11	49.62	400	690	7.2	Braun soil	Sand	diluvial sand	9.1
Flachlanden	79	S. pine	133	10.54	49.38	485	680	8.0	Pseudogley	Sand	Coburg sandstone	5.3.1
Starnberg	91	E. beech	92	11.38	48.04	580	1000	7.8	Parabrown soil	Loam	Würm glacier material	14.4.1
Fabriktschleichach	15	E. beech	197	10.62	49.95	470	820	7.5	Braun soil	Sand	Coburg sandstone	5.2
Rohrbrunn	620	sessile oak	93	9.37	49.89	460	1120	7.0	Braun soil	Sand	Middle sandstone	2.2.1
Rohrbrunn	90	sessile oak	155	9.42	49.88	465	1120	7.0	Braun soil	Sand	Middle sandstone	2.2.1

The first two columns show the names and identification numbers of the experimental plots. The ecoregion numbers indicate the following units: 14.4.1 Westliche kalkalpine Jungmoräne, 9.1 Oberpfälzer Becken- und Hügelland, 5.3.1 Rangau-Hochfläche, 5.2 Steigerwald, and 2.2.1 Hochspessart (according to Arbeitskreis Standortskartierung (1985) Forstliche Wuchsgebiete und Wuchsbezirke in der Bundesrepublik Deutschland, 170 p.)

this study have been systematically surveyed since 1870. The selected 24 plots (three plots per experiment) represent a broad range of stand density, from fully to thinly stocked stands. Most of the stands were established by regular planting. To cover different tree ages, we selected one experiment in an earlier and one in an advanced stand development phase for each tree species. For details of the locations and site characteristics see Table 1.

The eight experiments represent growth conditions in the plains and highlands of Central and Southern Germany (Table 1). The experiments are located between 400 and 780 m a.s.l. The long-term mean temperature and mean annual precipitation exhibit a broad range of climate conditions (6.8–8.0 °C and 680–1120 mm year⁻¹, respectively). The distribution of the experiments over five eco-regions and seven geological zones is reflected in the spectrum of soil types. The poorest soils are pseudogley soils derived from Coburg sandstone, while the most fertile soils are parabrown soils from diluvial loess-loam in the pre-alpine highlands. Located mainly between Frankfurt, Regensburg and Garmisch-Partenkirchen, the majority of the experimental stands are stocking on soils of mediocre fertility in the Southern German gradual layer area “Schichtstufenlandschaft” and on soils of rich fertility in the pre-alpine highlands.

Table 2 provides an overview of all tree and stand variables, constants and coefficients used in this study. According to the standard of the International Union of Forest Research Organizations (Johann 1993; Kramer and Akça 1995) we used lowercase letters for tree variables and uppercase letters for stand variables.

Repeated surveys resulted in the data suitable for calculation of all common stand characteristics for each of the up to 21 successive survey periods. Table 3 gives an overview of the stand characteristics of the last survey. The reported stand-level data were derived from the successive inventories of the tree diameters, tree heights, and records of the removal trees. As explained in more detail further below, we included unthinned plots, where we recorded the natural mortality, and we also included thinned plots where we recorded the trees removed by heavy thinning. We used standard evaluation methods according to the DESER-norm recommended by the German Association of Forest Research Institutes (in German “Deutscher Verband Forstlicher Forschungsanstalten”) (Johann 1993; Biber 2013). For estimating the merchantable stem volume in dependence on tree diameter, tree height and form factor, we used the approach by Franz et al. (1973) with the equations and coefficients published by Pretzsch (2002, p. 170, Table 7.3) Table 4.

Each of the four species was represented by experimental plots in young and mature stands. The stand ages ranged from 44 to 188 years at the time of the last survey

Table 2 Overview of tree and stand variables, constants, and coefficients used in this study

Abbreviation	Explanation
$a_1, a_2 \dots$	Regression coefficients, fixed effects in the models 1–8
α	Metabolic constant, allometric exponent
$b_1, b_2 \dots$	Regression coefficients, random effects in the models 1–8
cl	Crown length, indicator of crown vitality
cpa	Crown projection area, representation of crown size and occupied area
cr	Crown radius, mean crown radius is used for calculating cpa
$d_{1.3}$	Stem diameter at breast height, proxy for tree size
d_q	Quadratic mean diameter of the forest stand
h	Individual tree height
hcb	Individual height of crown base, distance from ground to primary branch
h_q	Stem height of the tree with the quadratic mean diameter
Iv	stem volume increment, indication of tree growth per year
IV	Stem volume growth of the whole stand per year and hectare
iv/cpa	Crown area efficiency, volume per year and unit area
Mrw	Mean tree ring width from age zero to present
N	Tree number of the stand per hectare
TY	Total yield of stem volume of the whole stand per hectare
V	tree volume and proxy for individual size and tree development state
V	Standing stem volume per ha
v_{mean}	Mean tree volume of the tree in a stand, volume of the tree with d_q

Names, abbreviations, and explanations in alphabetic order

Table 3 Overview of the stand data of the eight long-term experiments in Norway spruce, Scots pine, European beech, and sessile oak underlying this study

Experi-ment	Species	Age last survey	Site index	N	d_q	h_q	v_{mean}	V	IV	TY
		Year	age 100							
SAC 607	N. spruce	60	39.4	822	31.3	26.6	0.81	665	24.5	923
DEN 5	N. spruce	143	36.9	384	53.5	40.3	3.66	1404	15.9	2141
WEI 611	S. pine	44	27.8	2702	14.4	15.0	0.08	211	9.7	294
FLA 79	S. pine	134	24.2	378	38.0	29.6	1.53	579	6.7	933
STA 91	E. beech	92	34.4	319	36.1	33.0	1.55	496	12.6	767
FAB 15	E. beech	188	28.7	192	58.6	39.0	4.63	888	10.5	1367
ROH620	sessile oak	92	29.2	352	32.9	28.0	1.11	389	9.0	666
ROH 90	sessile oak	149	25.7	244	43.8	30.6	2.28	557	11.1	1039

The variable abbreviations (see also Table 2) are N tree number per hectare, d_q quadratic mean diameter h_q height of the tree with the quadratic mean diameter, v_{mean} mean tree volume, V standing volume per hectare, IV mean annual stem volume growth per hectare in the last survey period, TY total yield stem volume until the last survey. The site index was based on the yield tables by Assmann and Franz (1963,1965), Wiedemann (1943), Schober (1967,1975) and Jüttner (1955). Volume and volume growth were given in merchantable stem volume ≥ 7 cm at the smaller end

(Table 3). From each of the eight experiments, we included plots without thinning, with moderate, and with heavy thinning. The plots without active thinning represented the stand development under self-thinning conditions. Compared with the stand basal area of the unthinned plots (100%), the density of the moderately thinned plots was kept at a level of about 70%. The stand basal area on the heavily thinned plots was kept at a level of about 50%.

The setpoint stand basal areas of about 70 and 50% of the unthinned plots were achieved by continuously removing trees in the course of the successive surveys. The broad variation of stand ages and stand densities covered by the 24 plots (four species \times two stand ages \times three stand density variants) was important for the representativeness of the results. We were aiming at general species-, age-, and stand density-overarching results and tried to avoid a case

Table 4 Overview of the tree characteristics (mean, minimum and maximum values) of the eight long-term experiments in Norway spruce (N.sp.), Scots pine (S pi.), European beech (E. beech), and sessile oak (s. oak) underlying this study

Experiment	Species		<i>N</i>	$d_{1.3}$ cm	<i>h</i> m	<i>v</i> m ³	<i>cd</i>	<i>cpa</i> m ²	<i>cl</i> m	<i>iv</i> dm ³ year ⁻¹
SAC 607	N. sp.	Mean	3581	16.65	15.92	0.025	3.47	10.05	9.56	12.21
		Min		2.80	3.51	0.001	1.53	1.83	0.10	0.01
		Max		47.30	30.06	0.211	5.21	21.34	17.63	97.01
DEN 5	N. sp.	Mean	6229	34.86	30.89	0.164	5.07	21.14	11.72	24.96
		Min		5.80	8.30	0.001	1.78	2.48	2.80	0.22
		Max		88.80	44.30	1.018	8.11	51.65	20.20	164.97
WEI 611	S. pi	Mean	7848	7.31	9.09	0.003	2.36	5.49	5.34	1.90
		Min		1.30	1.43	0.001	0.51	0.20	0.10	0.01
		Max		29.00	19.23	0.058	5.01	19.70	11.69	26.58
FLA 79	S. pi	Mean	5272	20.27	18.14	0.040	4.23	14.66	6.43	8.61
		Min		4.30	7.33	0.001	2.27	4.06	0.10	0.02
		Max		60.00	32.92	0.425	7.27	41.49	13.41	73.97
STA 91	E. be	Mean	1709	21.15	22.16	0.053	5.20	23.79	14.21	17.67
		Min		6.10	10.16	0.001	1.15	1.04	3.09	0.05
		Max		47.60	34.02	0.317	10.75	90.76	25.22	108.07
FAB 15	E. be	Mean	5509	34.89	29.09	0.183	6.79	39.50	16.30	26.48
		Min		11.30	14.95	0.006	0.01	0.01	2.69	0.18
		Max		97.50	42.83	1.590	13.97	153.29	35.74	208.06
ROH620	s. oak	Mean	1995	21.60	21.44	0.046	3.87	12.66	8.52	14.87
		Min		6.80	12.10	0.002	1.49	1.75	0.00	0.02
		Max		50.00	30.50	0.298	6.76	35.92	18.90	95.41
ROH 90	s. oak	Mean	4221	25.58	22.19	0.075	7.24	43.40	9.25	15.87
		Min		8.90	12.20	0.003	0.75	0.44	0.90	0.01
		Max		71.00	31.30	0.691	11.75	108.43	20.70	144.24

The variable abbreviations were *n* number of observations, $d_{1.3}$ stem diameter at breast height, *h* tree height, *v* stem volume, *cd* crown diameter, *cpa* crown projection area, *cl* crown length and *iv* mean annual volume growth in the survey period after measurement of the tree characteristics. Volume and volume growth were given in merchantable stem volume ≥ 7 cm at the smaller end

study character, focussed on one or just a few selected stands, only.

Table 3 reports the mean stand characteristics of the three differently thinned plots per each experiment. To quantify the site quality of the included experimental stands we used the site index based on the species-specific yield tables by (Assmann and Franz 1963, 1965); Wiedemann (1943); (Schober 1967, 1975) and Jüttner (1955). Based on the stand ages and the dominant tree heights of the last survey and based on the height-age-relationships of the abovementioned yield tables we calculated the dominant heights of the stand age of 100 years by extrapolation. This standard procedure of site indexing (Skovsgaard and Vanclay 2008) resulted in site indices of 24.2–39.4 m at age 100. Notice, that the site indexes are rather similar within the pairs of young and old stands of each species. Certainly, the tree number per hectare decreases with age and is much higher for conifers with mostly slim crowns compared with deciduous species with more extended and more space requiring crowns. Mean stem diameters ranged between 14.4 and 58.6 cm and mean heights between 15.0 and 40.3 m. The standing stem

volumes reached maximum values of 1404 m³ha⁻¹ at the last survey. In the last survey periods, the mean periodic stem volume growth ranged between 6.7–24.5 m³ha⁻¹year⁻¹ and the total yield until the last survey was 767–2141 m³ha⁻¹. The density on the three plots per site ranged between unthinned conditions to heavy thinning. Thus the plots represent fully to thinly stocked conditions. All stands were without canopy gaps, caused by damages.

The broad variation of growth and yield characteristics due to species, age and site conditions was intentional, as we aimed at generalisable results regarding the effect of the stem and crown structure on individual tree growth. In summary, the dataset covered ecologically different tree species (light demanding to shade tolerant), different site conditions (average to excellent sites), different tree ages (middle-aged to old), varying stand densities (unthinned to heavily thinned), and a broad range of social tree positions (dominated to predominant trees). Any spatial and temporal autocorrelations due to the nested data levels, experiment, plot, and tree, were taken into account by the random effects in models 1–8 (see Sect. “Statistical analyses and models”).

Repeated measurements at the tree and stand level

In addition to the diameter at breast height ($d_{1.3}$, cm) and tree height (h , m), the height to crown base (hcb, m) and the crown radii in eight cardinal directions were measured according to standards described by Pretzsch (2009, pp. 115–118). All variables were repeatedly measured in the past. Based on these variables we calculated the crown length (cl, m) and crown ratio (cr, m) ($cr = cl/h$). The eight radii were used to calculate the crown projection area in m^2 $cpa = cr \times \text{with } cr^{-2} = \sqrt{(r_1^2 + r_2^2 + \dots + r_8^2)/8}$. We further calculated the mean tree ring width in cm/year as $mrw = d_{1.3}/2/\text{tree age}$ (Fig. 1). These were the main structural and morphological variables that we used as predictors for estimating the tree growth in the respective following periods. For overview of the individual tree characteristics on the eight long-term experiments see Table 4.

Statistical analyses and models

To analyse the effect of characteristics such as tree age, mean ring width and crown size on tree growth, we applied linear mixed effect models with nested random effects. In this way, we account for any spatial and temporal autocorrelation

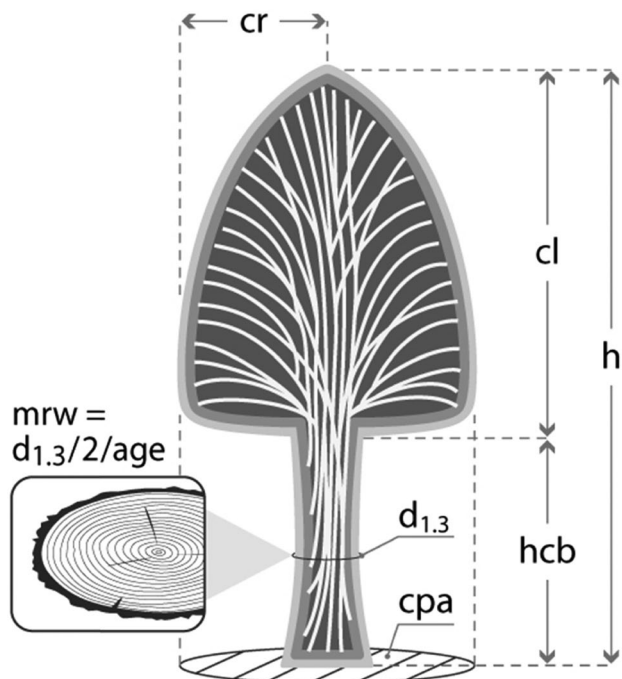


Fig. 1 Visualisation of variables used in this study for quantifying tree structure and crown morphology. $d_{1.3}$ stem diameter at height 1.3 m, h tree height, hcb height to crown base, cl crown length, cr crown radius, cpa crown projection area, mrw mean ring width ($=d_{1.3}/2/\text{tree age}$)

effects. The fixed effect variables such as stem volume, tree age, crown projection area, crown ratio, and mean ring width represented the influence of the trees' past and present characteristics on its growth. The fixed effects were covered by the parameters a_0 – a_n . The random effects on a_0 (intercept) at the experiment, plot, survey, and tree level took into consideration any spatial (several plots per experiment, several trees per plot) and temporal (several successive surveys, repeated measurements at the same tree) autocorrelations. The random effect $b_i, b_{ij}, b_{ijk}, b_{ijkl}$ covered the level of the experiment, the plot, the survey and the tree. We described the respective model alternatives and selected the variable combinations based on the root mean square error, RMSE, and the AIC criterion (Akaike 1981). The following numbers of the models referred to the results in the text (Models 1–8). In Table 5 we restricted the results to the characteristics of the fixed effects.

Model 1

$$\ln(iv_{ijklm}) = a_0 + a_1 \times \ln(v_{ijklm}) + b_i + b_{ij} + b_{ijk} + b_{ijkl} + \epsilon_{ijklm}$$

was fitted to annual stem volume increment, iv , of trees on long-term experiments with known stem volume, v , at the beginning of the respective measurement period. This model reflected the general dependency of tree growth on tree size. By pooling the data of all four tree species and different tree and stand development phases we addressed the overarching allometric relationship $iv \sim v^\alpha$.

Model 2

$$\ln(iv) = a_t + \alpha_t \times \ln(v)$$

Using this model we analysed the relationship between stem volume growth and stem volume for each plot and survey separately. In this way, we analysed the drift of the $iv \sim v^\alpha$ allometry with progressing stand development (see Supplement Table 1).

Models 3.1 and 3.2

$$a_t = a_0 + a_1 \times \text{age} \text{ and } \alpha_t = a_0 + a_1 \times \text{age}$$

Models 4.1 and 4.2

$$a_t = a_0 + a_1 \times v_{\text{mean}} \text{ and } \alpha_t = a_0 + a_1 \times v_{\text{mean}}$$

The models 3a and 3b and 4a and 4b revealed the drift of the allometric factor a and allometric exponent α with progressing stand development. The progressing stand development was represented by stand age and mean stem volume of the stand, respectively.

Table 5 Statistical characteristics of the models of the models 1 and 3–8 for analysing the relationships between stem volume growth and stand and tree characteristics

Model	Variables	N	a_0	Std (a_0)	p value	a_1	Std (a_1)	p value	a_2	Std (a_2)	p value	a_3	Std (a_3)	p value	a_4	Std (a_4)	p value	a_5	Std (a_5)	p value	
1	$iv \sim v$	1596	-3.73	0.651	<0.001	1.44	0.022	<0.001													
2	$iv \sim v$, see Supplement Table 1																				
3.1	$a_t \sim age$	25	-1.28	0.227	<0.001																
3.2	$\alpha_t \sim age$	25	1.29	0.121	<0.001																
4.1	$a_t \sim v_{mean}$	25	-2.79	0.243	<0.001																
4.2	$\alpha_t \sim v_{mean}$	25	1.38	0.031	<0.001																
5	$iv \sim v, age$	1596	3.67	0.249	<0.001	1.22	0.020	<0.001	-1.68	0.053	<0.001										
6	$iv \sim v, v_{mean}$	1596	-4.00	0.016	<0.001	1.45	0.026	<0.001	-0.96	0.030	<0.001										
7	$iv \sim v, v_{mean}, cpa, cr, mrw$	1596	-2.45	0.352	<0.001	0.77	0.084	<0.001	-0.34	0.080	<0.001	0.21	0.031	<0.001	-0.18	0.043	<0.001	1.29	0.043	<0.001	
8.1	$cpa \sim v$	1596	2.95	0.016	<0.001	0.49	0.015	<0.001													
8.2	$cr \sim v$	1596	-1.06	0.010	<0.001	0.11	0.009	<0.001													
8.3	$mrw \sim v$	1596	-1.96	0.08	<0.001	0.08	0.008	<0.001													

The model numbers refer to Sect. 2.3 where the models were introduced in detail. For the results of model 2 see Supplement Table 1. For reasons of space the table reported only the fixed effect variables of the respective models. iv stem volume growth, v stem volume, α_t and a_t intercept and slope of the relationships between iv and v ; age, tree age; cpa , crown projection area; cr , crown ratio; mrw , mean ring width; a_0 – a_5 , regression coefficients; $std(a_0$ – $a_5)$ standard error of the regression coefficients

Model 5

$$\ln(iv_{ijklm}) = a_0 + a_1 \times \ln(v_{ijklm}) + a_2 \times \ln(\text{age}_{ijklm}) + b_i + b_{ij} + b_{ijk} + b_{ijkl} + \varepsilon_{ijklm}$$

Model 5 was similar to model 1 but included tree age as a predictor variable. Using this model we tried to reveal how the allometric $iv \sim v^\alpha$ relationship was co-determined by tree age.

Model 6

$$\ln(iv_{ijklm}) = a_0 + a_1 \times \ln(v_{ijklm}) + a_2 \times \ln(v_{\text{mean } jklm}) + b_i + b_{ij} + b_{ijk} + b_{ijkl} + \varepsilon_{ijklm}$$

Model 6 was similar to model 2 but included mean stem volume as a predictor variable instead of tree age. Using this model we tried to reveal how the allometric $iv \sim v^\alpha$ relationship was co-determined by mean tree stem volume as a proxy for the stand development phase.

Model 7

$$\ln(iv_{ijklm}) = a_0 + a_1 \times \ln(v_{ijklm}) + a_2 \times \ln(v_{\text{mean } jklm}) + a_3 \times \ln(\text{cpa}_{ijklm}) + a_4 \times \ln(\text{cr}_{ijklm}) + a_5 \times \ln(\text{mrw}_{ijklm}) + b_i + b_{ij} + b_{ijk} + b_{ijkl} + \varepsilon_{ijklm}$$

By this model, we tried to reveal how the allometric $iv \sim v^\alpha$ relationship was co-determined by mean tree stem volume (as a proxy for the stand development phase), by crown projection area and crown ratio (as indicators for the current tree structure), and by mean ring width (as a proxy for the tree's past growth).

Models 8.1–8.3

$$\ln(\text{cpa}) = a_0 + a_1 \times \ln(v),$$

$$\ln(\text{cr}) = a_0 + a_1 \times \ln(v),$$

$$\ln(\text{mrw}) = a_0 + a_1 \times \ln(v).$$

These three models represented auxiliary relationships which reflected how crown projection area, crown ratio and mean tree ring width depended on the current stem volume. By insertion of these auxiliary allometric relationships (relationships between cpa and v , cr and v , and mrw and v) model 7 may be transformed to model 1, and vice versa.

The statistical software R 3.4.1 (R Core Team 2018) was used for all calculations, in particular the function lme from the package nlme (Pinheiro et al. 2018).

Results

Stem volume growth depending on stem volume and tree age (Q1)

The regression analysis of the relationship between stem volume growth and stem volume (model 1) yielded an allometric exponent $a_1 = 1.44 \pm 0.02$ (see Fig. 2a and Table 5). Interestingly this is not at all in accordance with the general $\alpha = 3/4$ scaling rule proposed by Kleiber (1947) and the metabolic scaling theory by West et al. (1997).

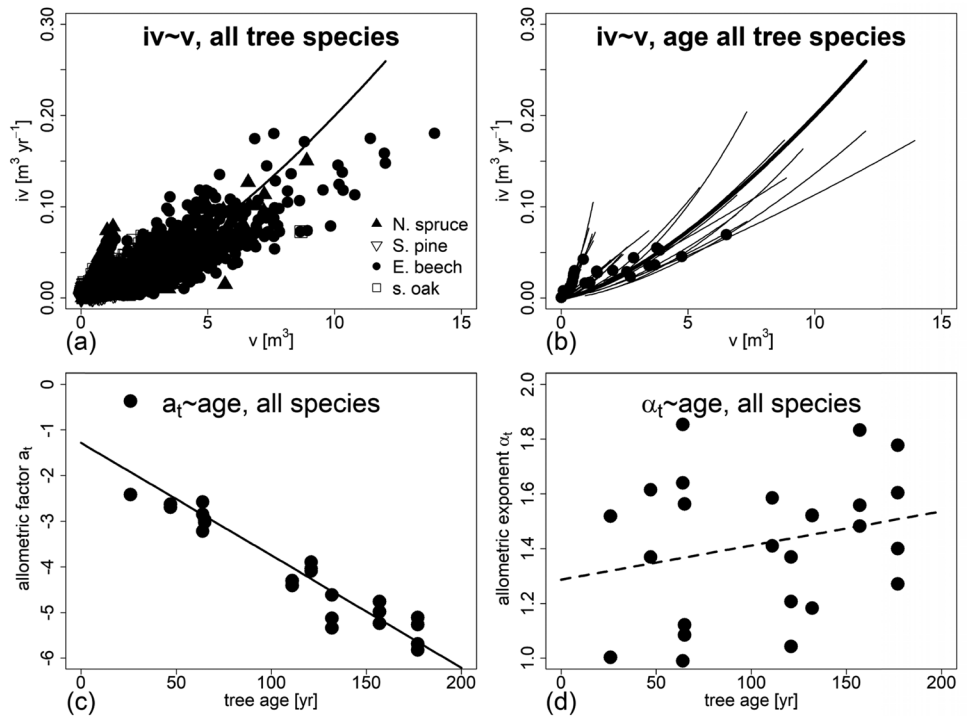
To trace the $iv \sim v$ relationship to the level of the single survey and the inter-individual relationship between iv and v at a given point in time, we fitted the regression $\ln(iv) = a_t + \alpha_t \times \ln(v)$ to the stem growth and stem volume data of every individual survey separately (see model 2 and statistical characteristics in Supplement Table 1). The results were visualised by the delogarithmic relationships $iv = a_t \times v^{\alpha_t}$ in Fig. 2b. The temporal $iv \sim v$ relationships were also progressive ($\alpha_t \gg 1$). Obviously at a given point in time, the tall trees benefit overproportionally in growth due to their preferential access to light and their outcompeting effect on lower neighbours. Supplement Table 1 shows that all temporal inter-individual $iv \sim v$ relationships were highly significant regarding their intercepts a_t and slopes α_t . The slopes ranged mainly between $\alpha_t = 0.99 - 1.85$.

Both a_t and α_t were used for exploring the development of these coefficients with progressing stand development via models 3.1 and 3.2. The results were shown in Fig. 2c, d and Table 5. We also carried out analogous regression analysis on the basis of the variable v_{mean} instead of tree age. The calculations yielded similar results as the regressions analyses based on tree age (see Supplement Fig. 2).

We found a highly significant ($p < 0.001$) negative correlation between the allometric factor a_t and tree age (corr = -0.94) and also between the allometric factor a'_t and mean tree volume, v_{mean} , (corr = -0.80) (Fig. 2c and Supplement Fig. 2a). In contrast, the allometric exponent α'_t was independent of both tree age (Fig. 2d and Supplement Fig. 2b) and mean tree volume. The respective Pearson correlation coefficients were $r = 0.24$ and $r = 0.14$ (both non-significant).

The results of the $a_t \sim \text{age}$ and $\alpha_t \sim \text{age}$ regression and the analogous regressions based on v_{mean} were shown in Table 5 and Supplement Fig. 2. Both evaluations showed that the allometric factor may decrease with tree age. This means that the scaling remained similar but the level of the curves decreased with increasing age (Fig. 2c, d, Supplement Fig. 2).

Fig. 2 Dependency of stem volume increment, iv , on stem volume and tree age at the beginning of the respective growth periods visualised for a pooled dataset of Norway spruce, Scots pine, European beech and sessile oak. **a** Measurement and model of the $iv \sim v$ relationship (see Table 5, model 1), **b** overall relationship $iv \sim v$ compared with the $iv \sim v$ relationship of each included survey period. The black dots represent the mean iv and mean v values for each survey, **c** allometric factor a_t and **d** allometric exponent α_t plotted over tree age; the relationship $a_t \sim \text{age}$ was highly significant (solid black line in (c)) whereas there was no significant relationship $\alpha_t \sim \text{age}$ (broken black line in (d))



To scrutinize the contribution of tree age or mean tree volume to the estimation of iv we analysed the relationships $iv = f(v, \text{age})$ and $iv = f(v, v_{\text{mean}})$, in addition to the baseline relationship $iv = f(v)$ (see models 5 and 6). For model parameters see Table 5. The RMSE was 0.67 in case of $iv = f(v)$, 0.48 for $iv = f(v, \text{age})$, and 0.40 also for $iv = f(v, v_{\text{mean}})$. Thus the RMSE could be reduced by 28–40% by adding the tree age or mean tree volume as a predictor. It was an important finding that mean tree size had a similar predictive power as tree age (see Supplement Fig. 2 and Table 5). Tree or stand age is often not available but mean tree volume is rather easy accessible and mostly

available when monitoring, inventorying, or modelling tree and stand growth.

Figure 3a showed the dependency of stem volume increment, iv , on stem volume and tree age at the beginning of the respective growth periods. Here, we visualised the results of the overarching evaluation for all species and how it developed with progressing tree age (see Table 5, Model 5). Figure 3b showed the dependency of stem volume increment, iv , on stem volume and mean stem volume at the beginning of the respective growth periods (see Table 5, Model 6).

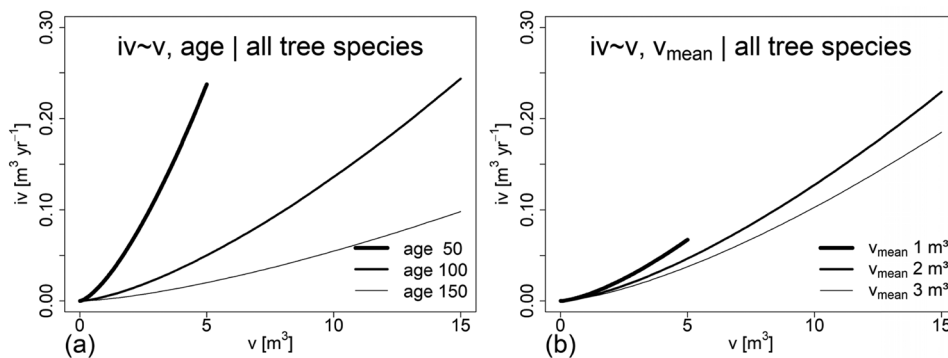


Fig. 3 Dependency of stem volume increment, iv , on **a** stem volume and tree age and **b** stem volume and mean stem volume of the stand at the beginning of the respective growth periods. Overarching analysis for all species. **a** Model of the $iv \sim v, \text{age}$ relationship (see Table 5,

model 5) for tree ages of 50, 100, and 150 years, and **b** model of the $iv \sim v, v_{\text{mean}}$ relationship (see Table 5, model 6) for stands with mean tree volume of $v_{\text{mean}} = 1, 2, \text{ and } 3 \text{ m}^3$

Stem volume growth depending on stem and crown characteristics (Q2)

Based on the model $iv = f(v, v_{\text{mean}})$, we included variables of the individual tree structure and morphology to further improve the prediction of iv . The inclusion of cpa , cr , and mrw (see Table 5, model 7) showed the best results regarding the reduction of the AIC criterion and RMSE. Compared with the baseline relationship ($iv = f(v)$), the relationships $iv = f(v, v_{\text{mean}})$ and $iv = f(v, v_{\text{mean}}, cpa, cr, mrw)$ further reduced the AIC and RMSE, respectively. Interestingly, the tree species added as categorical variable, and the site index did not significantly contribute to the model.

Figure 4 visualised the full model (see Table 5, model 7) $iv = f(v, v_{\text{mean}}, cpa, cr, mrw)$. According to this overarching model, the exponential relationship $iv \propto v^{3/4}$ remained close to $\alpha \cong 3/4$ during the whole stand development. However, stem structure and crown morphology modified this basic relationship as shown in Fig. 4. With progressing stand development, indicated by v_{mean} in Fig. 4a, individual growth of trees with defined stem volume decreased (indicated by $a_2 = -0.34$ in model 7, see Table 5). The crown projection area had a strong positive effect on tree volume growth (Fig. 4b) (indicated by $a_3 = 0.21$ in model 7, see Table 5). Increasing crown ratios slightly decreased stem volume growth (Fig. 4c) (indicated by $a_4 = -0.18$ in model 7, see Table 5). The past mean tree ring width, mrw , indicated the tree's growth potential (combination of site index, neighborhood conditions, inner stem hydraulic).

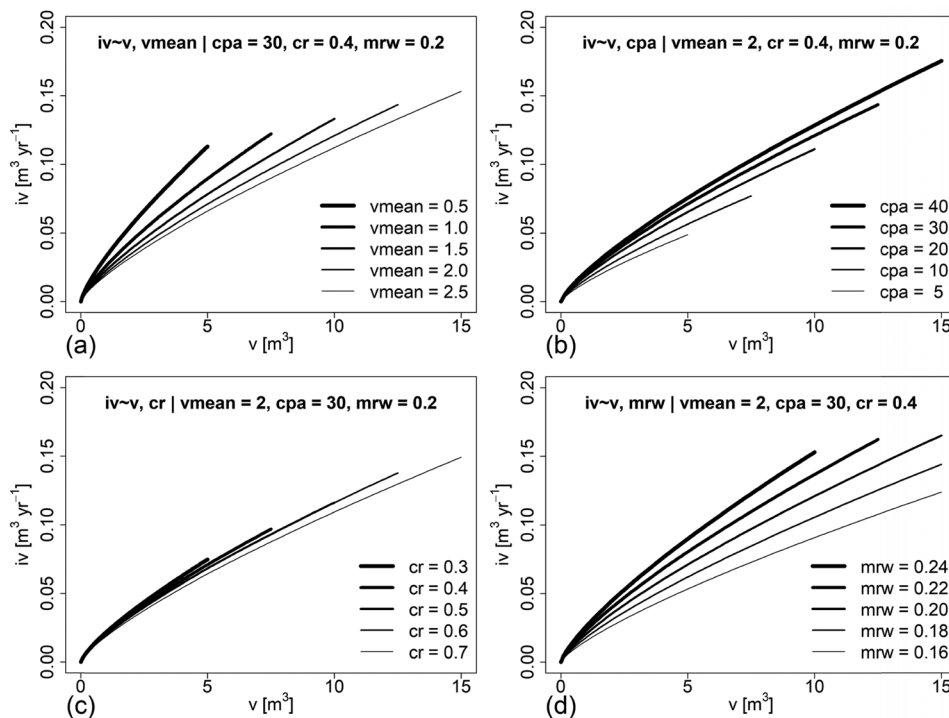
The variable mrw had a strong positive effect on tree volume growth (Fig. 4d) (indicated by $a_5 = 1.29$ in model 7, see Table 5). Notice, that when showing the effects of different structural and morphological traits on growth in Fig. 4a, b, c, d, we set the other variables constant on their overall mean level as provided by the dataset.

In summary, when analysing Q2 we started with the $\ln(iv) \sim \ln(v)$ relationship (see model 1, Table 5) as a baseline model with AIC = 1830 and a root mean square error of the prediction of RMSE = 0.67. Inclusion of the tree age (see model 2, Table 5) reduced both, the AIC to 1807 and RMSE to 0.40, which meant a strong reduction of the RMSE by 39%. Inclusion of the mean stem volume v_{mean} (see model 3, Table 5) also reduced both, the AIC to 1820 and RMSE to 0.48, which meant a reduction of the RMSE by 29% compared with the baseline model 1. The use of v_{mean} as a predictor was of special interest, as in contrast to the tree age, the mean stem volume is more readily available as a predictor. Inclusion of structural and morphological tree attributes reduced both statistical measures to AIC = 1761 and RMSE = 0.38. In the case of RMSE this means a reduction by 43% compared with the baseline model $\ln(iv) \sim \ln(v)$.

Stem growth per crown projection area (Q3)

The transition from individual tree growth to productivity shown in Figs. 4, 5 was based on the relationships $iv = f(v, v_{\text{mean}}, cpa, cr, mrw)$ and

Fig. 4 Dependency of stem volume increment, iv , on stem and crown characteristics shown for Norway spruce, Scots pine, European beech and sessile oak in one overarching evaluation (see underlying model 7 in Table 5). Stem volume growth plotted over the individual stem volume (a) for stands with different mean tree volumes as an indication for progressing stand development, (b) for trees with different crown projection areas, (c) for trees with different crown ratios, cr , and (d) for trees with a different mean ring width, mrw , in their development so far



$iv/cpa = f(v, v_{mean}, cpa, cr, mrw)$. By rearrangement of model 7 $iv = e^{a_0} \times v^{a_1} \times v_{mean}^{a_2} \times cpa^{a_3} \times cr^{a_4} \times mrw^{a_5}$, we arrived at the equation.

$iv/cpa = e^{a_0} \times v^{a_1} \times v_{mean}^{a_2} \times cpa^{a_3} \times cr^{a_4} \times mrw^{a_5} / cpa$. The latter equation represented a description of tree productivity in dependence on stem and stand attributes. Its visualisation (Fig. 5) showed how the crown projection area affected tree productivity (Fig. 5a, b). For this evaluation, we kept mrw and cr constant at the overall mean level ($mrw = 0.2, cr = 0.3$). The figure visualized that in general the smaller the crown projection area of trees, the higher their growing area efficiency. Figure 5a showed the iv/cpa plotted over v for different cpa -level. It revealed that productivity increased on average with increasing stem volume. However, the level was lower in the case of trees of large crown compared to small-crowned trees. Figure 5b corroborated this finding by showing the continuous decrease of tree productivity with increasing cpa values. This decrease applied for trees of all stem volume level. We found no interaction that would suggest a steeper decrease of productivity for larger stems compared to smaller ones.

On the one hand, we revealed a progressive relationship ($\gg 1$) between iv and v , [$iv = f(v)$] by model 1 (see Fig. 2). On the other hand, we found a degressive relationship between iv and other tree attributes in addition to v , $iv = f(v, v_{mean}, mrw, cpa, cr)$ using model 7 (see Fig. 4). These two relationships are not contradictory. By insertion of the basic allometric relationships between cpa and v , cr and v , and mrw and v (Supplement Fig. 3) the degressive relationship of model 7 may be transformed to the progressive relationship of model 1.

Discussion

Stem structure and crown morphology measurements can improve the understanding, modeling, and prediction of tree growth and can bridge the gap between statistical and eco-physiological modelling approaches (Mäkelä and Valentine 2006). Classical approaches of growth projection were mainly based on tree age (Richards 1959; Assmann and Franz 1965). Simple allometric approaches and metabolic scaling at least included the current total size or mass in the prediction of future growth (King 2005; Nord-Larsen and Johannsen 2007). However, generic allometric relationships neglected other tree attributes that better consider the individual tree’s status, growing space, or crown structure (e.g., Coates et al. 2003). Individual eco-physiological models (Korol et al. 1995; Grote and Pretzsch 2002) and structural–functional models (Lacointe et al. 2000; Sievänen et al. 2008) conceptualized tree growth based on basic physiological mechanisms such as photosynthesis, respiration, partitioning, and allometric principles (Mäkelä et al. 2000; Landsberg 2003; Valentine and Mäkelä 2005). Latter models for the estimation of tree growth were often calibrated by annual growth rates at the tree level since information of carbon and nutrient flows as well as forest structure at higher levels of the resolution were rare (Jonard et al. 2020). This study emphasized that various aspects of stem and crown structure and morphology which strongly affect tree growth may deserve special consideration when building, initiating, calibrating or evaluating individual tree models.

This study revealed a high significance of selected structural and morphological stem and tree characteristics for the growth of common tree species in Central Europe. For this purpose, we started with the models $iv = f(v)$ and $iv = f(v, v_{mean})$, which only took into account the stem

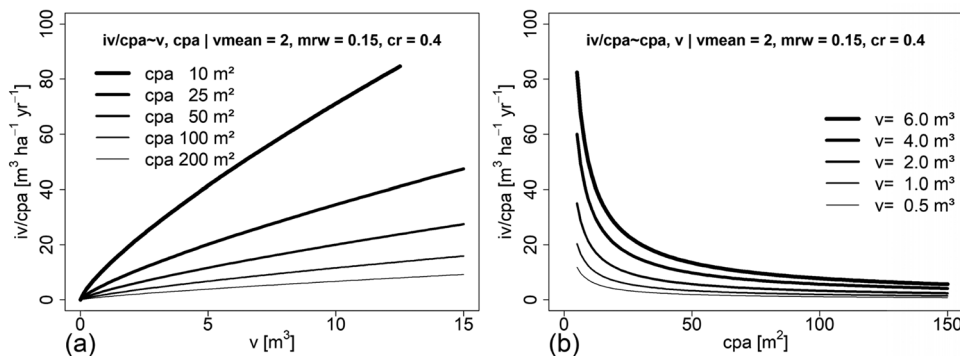


Fig. 5 Dependency of tree growth per crown projection area, iv/cpa , on stem volume and crown characteristics according to a species-overarching evaluation for Norway spruce, Scots pine, European beech and sessile oak (model 7). **a** iv/cpa depending on stem volume, shown for various levels of cpa . **b** iv/cpa depending on cpa , shown

for various levels of v . For (a, b) cpa and v were varied and the other independent variables v_{mean} , mrw , and cr were set constant. Variables are v stem volume, cpa crown projection area, v_{mean} mean stem volume of the stand, mrw mean ring width, cr crown ratio

volume for the prediction of tree growth in the following period. The surveys in different stand development phases showed a strong inter-individual variation of iv due to size-asymmetric competition. The rather simple double logarithmic equation $\ln(iv) = a_0 + \alpha \ln(v)$, which becomes $iv = a'_0 \times v^\alpha$, explained about 60% of the variation of annual growth (iv). However, these relationships considered neither the stand structure and species nor the individual tree's structural and morphological attributes. So, they also neglected information about the past of the tree, e.g., information about the tree structure and morphology as adapted to the social status of the tree within the stand.

Our sequence of models for estimating tree volume growth, iv , showed a continuously increasing accuracy from models including only stem volume, to models with mean stem volume or tree age, to the model including crown projection area, crown ratio and mean tree ring width. This underlined the relevance of structure and morphology for growth prediction. The inclusion of stem and crown information reduced the RMSE by 43% compared with the bivariate scaling. The reduction of AIC and the RMSE after the inclusion of further tree characteristics indicated that those attributes represent important additional information, affecting tree growth. We hypothesised that the structural and morphological traits contain relevant information of a tree's past that are relevant for current and future growth. Interestingly, the inclusion of tree species via a categorical variable and site index did not improve the accuracy. Apparently, the structural and morphological traits already contain such information.

Inclusion of the crown projection area, cpa , crown ratio, cr , and mean ring width, mrw , even changed the relationship between tree attributes and growth from progressive to degressive (compare Fig. 3 with 4). Interestingly, the inclusion of further stem and crown characteristics beyond stem volume led to a scaling close to $= 3/4$ ($iv \propto v^{3/4}$) (see Table 5, model 7, regression coefficient $a_1 = 0.77 \pm 0.084$). This meant that the revealed scaling was close to the overarching $= 3/4$, predicted by the constant of Kleiber (1947) and the metabolic scaling theory by West et al. (1997). Notice that the underlying regression analysis was based on 1596 trees of various ages, tree species, and stand densities; i.e., the resulting coefficients were quite well substantiated by data. This meant that the $3/4$ scaling was modified by other stem and crown characteristics (Fig. 4). This substantiated the notion, that for a rough estimation of tree growth, the $3/4$ scaling approach may suffice. However, for a more accurate estimation of tree growth the full model, encompassing a broader set of tree variables, representing the past and present state of structure and morphology of the tree, should be applied.

For analysing and predicting growth at the tree or stand level, information about the stand or tree characteristics (e.g., by classical inventory or TLidar) might be applied for a more accurate estimation of the growth depending on stand and tree characteristics. Stand characteristics such as age or mean tree size of the stand may be sufficient for growth predictions in uniform monospecific stands. However, individual tree information such as crown width, crown length or relative tree size may become even more relevant in heterogeneous stands with trees varying strongly in social status, crown sizes and growth (Pretzsch and Rais 2016; Pretzsch 2019).

Tree productivity can be calculated based on annual stem volume growth per crown projection area, cpa . Cpa may be used as a substitute for the growing area (Webster and Lorimer 2003). Crown projection area translated tree growth (iv) to productivity (iv/cpa). As the cpa increases continuously with stem volume, the productivity (iv/cpa) peaks and decreases earlier than iv . In contrast to tree growth, tree productivity decreased continuously with tree size. As crowns may overlap or stay in distance to each other (Pretzsch 2014), the real tree growing area may be lower or higher than the cpa . This may change the level of the relationship between stem and crown size, but not the continuous increase of cpa with stem size. When concluding that big trees actively fix larger amounts of carbon compared to smaller trees (e.g., Stephenson et al. 2014), one should consider those differences between growth per individual and growth per unit of growing area (i.e., productivity). As the growing area requirement per tree continuously increases with size, tree productivity and contribution to carbon sequestration per unit area decreases although the growth may continue until advanced age and big size (Schütz 2002; Sillett et al. 2015).

Conclusions

The species- and site-overarching analyses of tree growth data showed that stem volume as a predictor allowed only a rough estimation of tree growth. However, the inclusion of stem structure and crown morphology variables significantly improved the prediction of tree growth. Simplifying approaches that mainly rely on stem diameter or tree mass for growth estimation may be useful for rough species-overarching upscaling in uniform stands and in cases where more detailed predictors are not available. Stem and crown characteristics, and maybe other internal stem traits (e.g., heartwood area portion, embolism, narrow ring series caused by damages or suppression phases) may become of considerable importance for assessing and better predicting tree growth in the more heterogeneous stands of the future, where tree structure varies and may cause a strong variation of the course of growth.

Author contributions statement HP initiated and conceptualised the study, evaluated the data, wrote, and revised the manuscript.

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Compliance with ethical standards

Conflict of interest The author declares that he has no conflict of interest.

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