



Tamm reviews

The course of tree growth. Theory and reality

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ABSTRACT

The course of tree growth, especially the level and persistence until advanced age, indicates the competitiveness and fitness of trees and determines stand structure and dynamics. The velocity of size growth and aging affects many other plants and animals living at and from trees. Thus forestry and many ecosystem functions and services are depending on the course of tree growth.

First, novel empirical findings of particular persisting tree growth in various parts of the world were presented and motivated this review. The revealed increasing, mostly positive, deviations of observed from theoretically expected tree growth directed this review to be based on literature and own long-term experiments, stem analyses, and increment cores from temperate forests. Second, the common growth theory and respective growth equations were revisited; they later were used for analyzing observed courses of dominant trees' mass growth and productivity. Third, tree developments over size and age were analyzed as affected by tree species, site conditions, thinning, and fertilization and environmental changes. Stem analyses and increment core analyses of Norway spruce (*Picea abies* (L.) KARST.) representing the growth from 1560 to 1882 indicated a persistence of volume growth beyond age of 300 years even in this historic period of comparatively steady environmental conditions. The mass growth of 735 dominant trees revealed mean culmination ages between 211 and 480 years with the ranking sessile oak (*Quercus petraea* (MATT.) LIEBL.) > European beech (*Fagus sylvatica* L.) > Norway spruce > Scots pine (*Pinus sylvestris* L.). Trees on sites with high site index grew quicker, peaked, and decreased earlier in annual growth, whereas trees on poor sites culminated later in terms of age. The courses of annual growth in dependence on tree mass ran more synchronous on different sites. They differed much more in the level than in the rhythm. A total of 910 Scots pines on combined thinned and fertilized compared with control plots revealed for both groups a continuous increase of growth until high ages and no preponed size-related growth decrease of the treated trees.

For analyzing any modification of the course of growth by environmental changes I used a dataset of 591 cored European beeches and for corroboration 580 permanently surveyed tree from long-term experiments of the four above mentioned main tree species in Europe. On top of their long-lasting growth all species together showed a strong acceleration of annual growth. Their growth acceleration was obviously caused by environmental changes and the highest in 1850 to 1900. It lessened in the last 50 years, and did not trigger any preponed age- or size related decrease. Finally, I discussed the consequences of the amazingly high and long-lasting tree growth for forest ecology, management and future research.

1. Introduction

An important empirical basis for the perception of the course of tree growth in forests is the extensive stem analyses study of Norway spruce by von Guttenberg (1915) in mountain forests in Tyrol (at present Austria and Italy). His 125 analyzed stems covered a period from 1560 to 1882 and the visualized results of 30 trees determine textbook and experiential knowledge till present (e.g. Assmann 1970, Kramer 1988, Wenk et al. 1990). Von Guttenberg showed the unimodal course of annual stem volume increment over age, the S-shaped bending and

asymptotic behaviour of the growth curves, and the dependence of the shape on site conditions and social status of the trees within the stand (see von Guttenberg 1915, panels I-XXI).

For the present theoretical understanding of the course of tree growth von Bertalanffy von (1951) was most influential by formulating his growth equation

$$d\text{mass}/dt = \eta \times \text{mass}^{2/3} - \kappa \times \text{mass} \quad (1)$$

based on first eco-physiologically principles of anabolism and catabolism (Kleiber 1947, Rubner 1931). By using the tree mass rather than

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tree age as predictor variable he used aspects of the individual's history (accumulated mass) rather than age for predicting its further development. The metabolic scaling theory (West et al. 1997) revised this approach, used Kleiber's 3/4 instead of Rubner's 2/3 and Bertalanffy's scaling exponent and came with a mechanistic explanation for this scaling based on the fractal structure of the tree's internal pipeline system (Enquist et al. 1998). However, the prediction of growth just based on mass may be an over-simplification (Kozłowski and Konarzewski 2004, Muller-Landau et al., 2006), especially in heterogeneous stands with a wide variation of stem and crown allometries (Pretzsch and Schütze 2005, Pretzsch 2014). Using mass or size is better than using only age, however, prediction of growth by age is still state-of-the-art in many models (Zeide 1993, Albrecht and Mißbach 2009).

Bertalanffy developed and tested Eq. (1) for animals and micro-organisms which have mainly living and respiring tissue inside similar to herbaceous plants. With increasing age trees, in contrast, may no longer actively maintain the internal parts but use the core of stable heart wood as non-respiring low-cost scaffolding for the rest of their body. Despite of these differences the function may be flexible enough as its allometric factors η and κ in $dmass/dt = \eta \times mass^{2/3} - \kappa \times mass$ consider such low respiration compared with other organisms. Due to its theoretical foundation and flexibility latter function will be applied in this study.

This review starts with empirical findings re-questioning the commonly assumed early S-shaped bending and asymptotic behaviour of the growth curves of trees (von Guttenberg 1915, Pretzsch et al. 2020, Stephenson et al. 2014). Then I clarify the essential difference between the course of individual tree growth and tree productivity; latter is also called as area-related growth or stand growth (Pretzsch and Schütze 2005, Sterba 1999, 2019, Webster and Lorimer 2003). Background of this review are empirical findings of the course of old and especially big trees that contradict existing textbook theory and knowledge. I start with three examples and Table 1 with an overview of the main variables used in this review.

The first example is based on the above-mentioned stem analysis data by von Guttenberg (1915) introduced in Table 2. The stem analyses by von Guttenberg (1915) in Fig. 1a show hardly any S-shaped trend and asymptotic behavior even at ages beyond 300 years (see Table 3), which is a high age for Norway spruce in view of maximum ages of 200–400 reported by Ellenberg and Leuschner (2010, p. 104). The annual growth plotted over tree age and tree volume (Fig. 1b) reflect a long lasting annual growth till advanced tree age (see also Büntgen et al. 2019). In order to calculate the tree productivity in terms of the growth per growing area I calculated the average stem volume-tree crown projection allometry visualized in Fig. 1c (see parameters for cpa v in Table 4). Tree productivity can be calculated based on annual

stem volume growth, iv , per crown projection area, cpa , as a substitute for growing area (Sterba 1999, 2019, Webster and Lorimer 2003). As the cpa increases continuously with stem volume the productivity (iv/cpa) peaks and decreases earlier than iv . I also show tree productivity (iv/cpa) for the Guttenberg trees (Fig. 1d) which culminates early and is sometimes confounded with annual growth (iv) which culminates much later, if at all (Fig. 1b). Compared with other methods for measuring stem volume or tree mass growth (such as increment coring, repeated measurements on long-term plots) stem analyses as applied by von Guttenberg (1915) and in this review (section 3) for analysing tree growth are destructive but most accurate (Sillett et al. 2015a and b). Based on tree ring analyses using stem disks from 10 to 20 different stem heights and a retracing of the height growth they precisely reconstruct the annual stem volume and the respective volume growth back to the early juvenile phase of the tree (see Pretzsch 2009, p. 115–118).

In a phase when old trees were mainly valued because of their ecosystem services such as wildlife habitat provision (Brunet et al. 2010, Dieler et al. 2017, Lindenmayer 2017) or landscape esthetics (Pukkala et al. 1988, Tyrväinen et al. 2005), Stephenson et al. (2014) increased the attention to old trees by their finding that for most species mass growth rate increased continuously with tree size (Fig. 2). The findings of this and other reports about the persistence of individual growth of old trees (Sillett et al. 2015a and b) motivated for this review. The high mass growth rates of big Sitka spruces in USA (Fig. 2a) and persisting growth rates of various species on inventory plots in Spain and USA (Fig. 2, b and c) underpin that there is no early and inevitable and inherent downregulation of growth with size due to the prevalence of respiratory losses compared with the gains by assimilation.

When concluding that big trees actively fix large amounts of carbon compared to smaller trees one should consider the difference between growth per individual and growth per unit of growing area (i. e. productivity) explained in the previous section (Fig. 1b versus Fig. 1d). As the growing area requirement per tree continuously increases with size, tree productivity and contribution to carbon fixation per unit area decreases although the growth may continue till advanced age and big size.

In addition to the commonly underestimated growth at advanced ages, as introduced above, even under steady state conditions, environmental changes may contribute to a persistence or increase of the growth of old trees. This hypothesis was corroborated by the change of the relationship between stem diameter growth and age in the last several hundred years shown in Fig. 3 (see also Pretzsch et al. 2020).

Stem diameter and tree mass plotted over age for $n = 577$ European beeches (see Table 2). The growth trajectories are represented in grey, green, and red for years < 1900, 1900–1950, and > 1950. They show that at present defined diameters or masses are reached much earlier than in the past. The reference lines in the background of (a) represent proportional diameter growth of $0.1\text{--}0.6\text{ cm yr}^{-1}$ (lowest to steepest).

For Fig. 3 I pooled diameter growth records from European beech long-term experiments, stem analyses, and increment cores (see Table 2). The comparison of the observed growth trajectories with the grey reference lines (diameter development proportional to age) reveals a rather linear development although textbooks assume an asymptotic course after age 100–200 (Schober 1972). Mass even increases in a J-shaped way till high tree ages. Both diameter and mass development show that in the last decades, size growth was significantly higher at defined tree ages than in historical times ($\ll 1900$). It means that trees achieve defined diameters or masses at much younger ages at present than in the past. It also means that trees of a given advanced diameter have higher growth rates at present compared with the past. Latter growth trends apply for European beech and other tree species (see section 3.5) growing in Germany but should not be transferred to other regions without further review. However, they underpin the hypothesis that tall trees not necessarily reduce growth because of inefficient allometric assimilation/respiration or surface/volume ratios as assumed,

Table 1
Main variables used in this review and their description.

Abbreviation	Description
A_m, A_d	Asymptotic final tree mass and tree diameter, respectively
CAI	Current annual stand growth
cpa	Crown projection area, based on 8 crown radii measurements
d_{culm}	Stem diameter at the time of mass growth culmination
id	Stem diameter increment \equiv diameter growth
ih	Tree height increment \equiv height growth
ir	Stem radius increment \equiv annual ring width
iv_{stem}	Stem volume increment \equiv stem volume growth
iv/cpa	Stem volume growth per growing area \equiv tree productivity
m	Above ground tree mass
MAI	Mean annual growth at the stand level
mai	Mean annual mass increment in a given survey period \equiv mean annual tree mass growth
m_{culm}	Tree mass at the age of mass growth culmination
SI	Site index in terms of height at age 100
t_{culm}	Age at the time of tree mass growth culmination
V_{stem}	Stem volume of the individual tree

Table 2

Data base for analyzing the course of growth of trees and any deviation between observation and theory. The von Guttenberg data (1915) was digitized for this review. The data for European beech comes from data from own stem analyses, increment coring, and long-term experiments. Age, stem diameter, tree height, stem volume, stem and branch mass represent the final values when the trees were sampled. The calendar years represents the time span covered by the tree ring data. The von Guttenberg data set includes predominant to suppressed trees, the European beech data set predominant to dominant trees.

data		sample	age	calendaryear	d	h	v (m ³)m (Mg)	social class
Guttenberg (1915)	mean	n	yr	years	cm	m	1.96 v	predom.
	min	30	172	1710	38.84	31.20	0.50 v	to
	max		320	1882	59.30	40.70	5.39 v	supp.
E. beech pooled	mean	577	224	1927	55.32	26.68	3.08 m	predom.
	min		45	1603	24.97	15.93	0.40 m	to
	max		744	2017	124.50	45.99	18.61 m	dom.

among others, by Assmann (1970, pp 120-129). Another reason for the very common misjudgement of the growth of big trees may be their rarity and the technical and ethical obstacles to analyzing their growth (Sillett et al. 2015a and b). The growth trends revealed for European beech suggest that part of the amazingly prolonged growth trend may be caused by environmental changes. That large-sized trees continue growing till high ages suggests that for trees size is not as growth restricting as predicted by theory (von Bertalanffy 1951) for micro-organism, animals, or herbaceous plants.

The overarching goal of this review was to contrast common assumptions and theory of tree growth with new empirical findings. In particular, I (i) introduce the ecological theory of tree growth over age and size, its mechanistic substantiation and biometrical formulation, I (ii) show empirical finding on tree growth and its dependency on, among others, species, site conditions, thinning, fertilization and

environmental changes, and (iii) draw conclusions from the revealed secular increase of growth over age for ecological science, forest management, and future research. The analyses were mainly based on data from forest trees in Europe; though the results and consequences derived from this review should be validated for species other than the European context, and environmental conditions different from Europe.

2. Theoretical considerations

In this section the theory and biometrical basis of tree mass growth will be introduced that shaped our perception of size-age and size growth-size development of trees. It will be shown that the mechanistically grounded growth function by von Bertalanffy von (1951) both based on the 2/3 or 3/4 scaling described well the mass and volume growth of trees. It also corroborated the empirical finding that mass

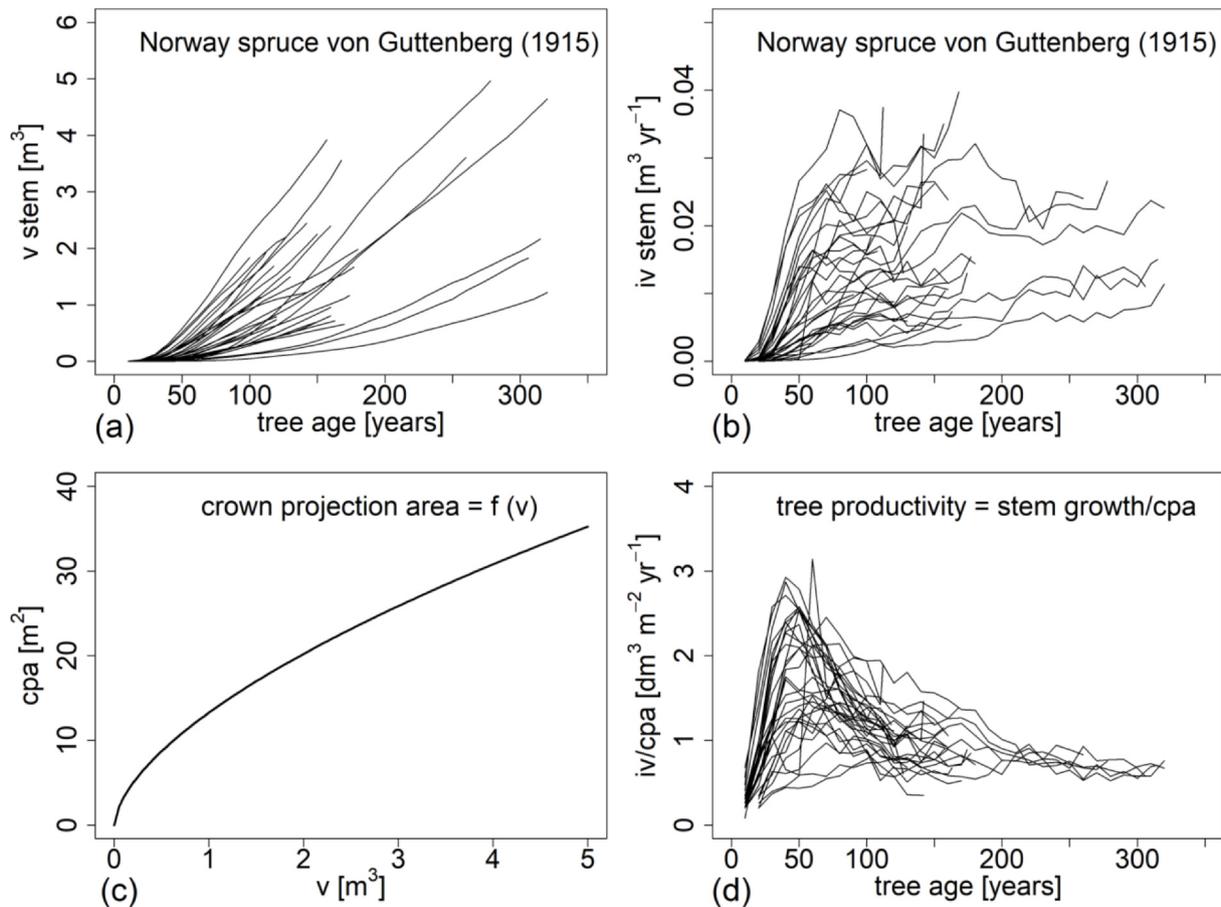


Fig. 1. Tree volume growth of 30 up to 320-years-old Norway spruces analysed by von Guttenberg (1915). (a) stem volume plotted over tree age, (b) annual stem volume growth plotted over tree age, (c) allometric relationship between crown projection area, cpa, and stem volume, v, and (d) development of tree productivity in terms of annual volume growth per crown projection area of the respective trees. For underlying data see Table 2.

Table 3
Results of the fit of the von Guttenberg (1915) trees to the model $d_{mass}/dt = \eta \times mass^{2/3} - \kappa \times mass$.

data	species	n	measure	t _{culm}	m _{culm}	A _m	d _{culm}	A _d
				yr	Mg	Mg	cm	cm
von Guttenberg	N. sp.	8	mean	308	1.870	6.316	54.9	93.1
	predom.		min	85	0.388	1.311	32.2	54.7
			max	1073	7.479	25.266	116.5	197.6
	N. sp.	19	mean	142	0.707	2.387	40.7	68.9
	dom.		min	72	0.239	0.806	26.1	44.3
			max	427	1.868	6.310	63.8	108.2
	N. sp.	3	mean	86	0.229	0.774	25.7	43.5
	subdom.		min	52	0.201	0.678	24.3	41.1
			max	121	0.257	0.86	27.0	45.7

$t_{culm} = -\ln(1/3)/(\kappa/3)$; $m_{culm} = A_m \times (2/3)^3 = A_m \times 0.296$; $A_m = (\eta/\kappa)^3$; the diameter at culmination age and the asymptotic diameter were calculated by $d_{culm} = e^{(\ln(m_{culm})-a)/b}$; $A_d = e^{(\ln(A_m)-a)/b}$ with species-specific coefficients by Forrester et al. (2017) (see text in section 2.2).

growth can continue until much higher tree ages or tree sizes as assumed in most common textbooks (Assmann 1961, Kramer 1988, Mitscherlich 1970, Wenk et al. 1990).

2.1. One-, two- and three dimensional tree characteristics

First, it will be explained why the focus was on the volume or mass growth of dominant trees when analyzing their course of growth and aging. The stem analyses trees by von Guttenberg (1915) (see Table 2) were used again as a basis for this purpose. When growing in dominant position within the stand, tree height and diameter increase, culminate and decrease at earlier tree ages than stem volume or tree mass (Fig. 4, a-c). Accordingly, the accumulative curves of height and diameter are earlier regrading increase, point of inflexion and asymptotic bending. The volume or mass growth curves flatten the latest, if at all, during normal rotation periods.

When stereometric bodys increase, their 1-dimensional measures (e.g., diameter, height) increase linearly, their 2-dimensional measures (e. g., basal area, leaf area) quadratically, and 3-dimensional measures (e. g., stem volume, tree mass) cubically (Prodan 1965). Both height

Table 4

Statistical characteristics of the main models used in this review. The model numbers refer to section 3.1.2 where the models are introduced in detail. For the result of model 1 see Supplement Tables 1-2. For reasons of space the table reports only the fixed effect parameters of the respective models. Variable explanations are cpa, crown projection area; v stem volume; mai, mass increment; group, dominant and subdominant trees; SI, site index; m, tree mass; tculm, time of growth culmination; massculm, tree mass at time of culmination; dculm, diameter at time of culmination; d, stem diameter; year, calendar year.

Model	group	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
2	N. sp	cpa ~ v	3765	2.587	0.011	0.000	0.606	0.011	0.000						
2	S. pi	cpa ~ v	493	2.628	0.032	0.000	1.024	0.047	0.000						
2	E. be	cpa ~ v	3420	3.462	0.017	0.000	0.560	0.015	0.000						
2	s. oak	cpa ~ v	2105	2.946	0.016	0.000	0.935	0.016	0.000						
3	N. sp	mai ~ age, SI	3350	-12.28	0.23	0.000	1.18	0.01	0.000	2.57	0.06	0.000			
3	S. pi	mai ~ age, SI	1520	-8.82	0.15	0.000	1.04	0.01	0.000	1.71	0.04	0.000			
3	E. be	mai ~ age, SI	2330	-18.41	0.36	0.000	1.61	0.02	0.000	3.76	0.06	0.000			
3	s. oak	mai ~ age, SI	390	-10.29	0.15	0.000	1.27	0.02	0.000	1.97	0.04	0.000			
4	N. sp	mai ~ mass, SI	3350	-4.82	0.13	0.000	0.55	0.01	0.000	1.08	0.03	0.000			
4	S. pi	mai ~ mass, SI	1520	-3.54	0.08	0.000	0.51	0.01	0.000	0.75	0.02	0.000			
4	E. be	mai ~ mass, SI	2330	-6.56	0.11	0.000	0.65	0.01	0.000	1.42	0.02	0.000			
4	s. oak	mai ~ mass, SI	390	-3.80	0.06	0.000	0.54	0.01	0.000	0.85	0.02	0.000			
5	all	tculm ~ SI	57	718.75	104.26	0.000	-12.34	3.13	0.000						
5	all	massculm ~ SI	57	4631.98	4141.73	0.268	0.60	0.12	0.000						
5	all	d culm ~ SI	57	48.91	23.09	0.039	0.85	0.69	0.225						
6	ref	mai ~ m	870	-0.42	0.11	0.000	0.41	0.12	0.000						
6	treat	mai ~ m	7030	0.56	0.06	0.000	0.25	0.01	0.000						
7a	E. beech, stem	d ~ age, year	78,547	-167.43	1.70	0.000	22.25	0.34	0.000	22.23	0.23	0.000	-2.87	0.05	0.000
7b	E. beech, stem	m ~ age, year	78,547	-408.68	4.05	0.000	53.16	0.81	0.000	53.13	0.54	0.000	-6.86	0.11	0.000
7a	E. beech, exp.	d ~ age, year	4240	7.70	17.38	0.658	-23.54	4.05	0.000	-0.97	2.29	0.672	3.19	0.54	0.000
7b	E. beech, exp.	m ~ age, year	4240	9.78	41.53	0.814	-56.25	9.69	0.000	-2.32	5.48	0.672	7.62	1.28	0.000
7a	all species	d ~ age, year	19,750	21.85	7.67	0.004	-12.04	1.91	0.000	-2.98	1.01	0.003	1.71	0.25	0.000
7b	all species	m ~ age, year	19,750	82.37	17.89	0.000	-39.03	4.46	0.000	-12.25	2.36	0.000	5.43	0.59	0.000

growth and stem diameter growth curves (Fig. 4, a and b) bend relatively early. However, the diameter growth has, via basal area, a quadratic influence and becomes the main driver of volume and mass growth in advanced ages. Fig. 4 shows the stem volume growth as measured by von Guttenberg (1915); notice that the course of mass growth would yield similar results as it develops proportional to volume ($mass \propto volume$) (Enquist et al. 1998, Niklas 1994).

Fig. 4, d-f shows relationships between the different measures of tree growth that deserve special interest. With increasing stem diameter, tree height growth and tree ring width and diameter growth decrease early (Fig. 4, d and e). However, height determines stem volume and tree mass only linearly, whereas diameter growth has a quadratic effect. Thus, although annual diameter growth, id, and ring width, ir, decrease with size at middle ages, stem volume and mass growth may still increase. The reason for this is that a given ring width is generated by an increasing meristemic surface and coats an increasing volume of the tree (Fig. 4e). Therefore, the volume growth may persist at a high level until advanced ages, even if the height and diameter growth are stagnating or decreasing (Fig. 4f).

The course of annual growth culminates and decreases in the temporal order $d < h < ba < v$. The volume or mass growth integrates the 3D stem size components (height, diameter, basal area), it culminates later than the other components, and was used for the following analyses of the course of growth with increasing size and age.

2.2. Growth theory

A widely-used explanation for the uni-modally shaped curve of the current annual growth and the S-shaped curve of the accumulated size comes from von Bertalanffy (1951, p. 282). He assumed a 2/3 scaling between assimilation and body mass ($iv \propto v^{2/3}$) and a proportional relationship ($iv \propto v$) between respiration and mass, resulting in $iv = dv/dt = \eta v^{2/3} - \kappa v$ (Bertalanffy von, 1951, pp 282–283). Other growth equations analogously derive the growth from expansion and reduction components (Zeide 1993). West et al. (1997) and Enquist et al. (1998) called the 2/3 scaling into question and suggested its replacement by a 3/4 scaling, i. e. $iv \propto v^{3/4}$. Subsequently I applied both approaches for modelling the stem growth of the 30 stems (Table 2) of

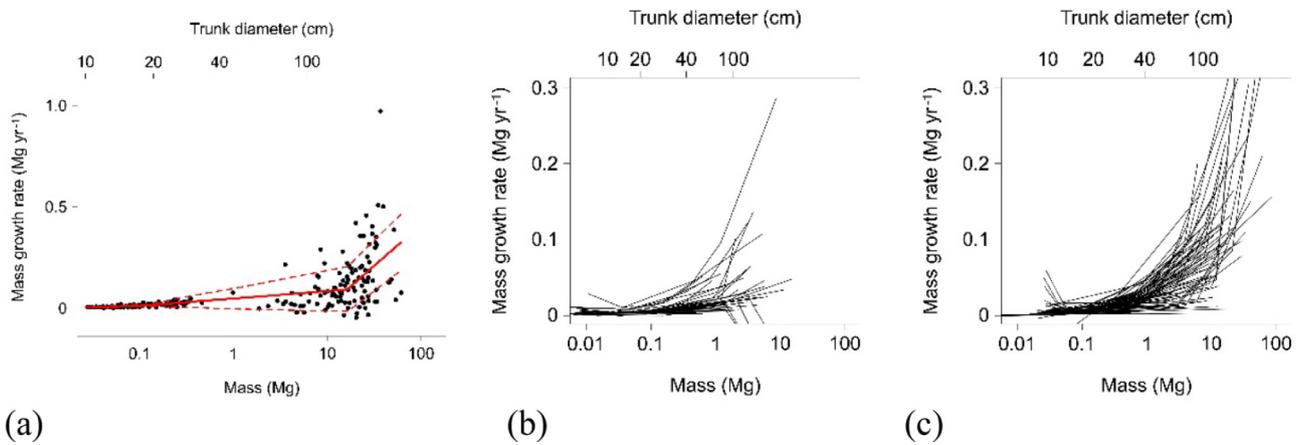


Fig. 2. Evidence of continuously high growth rates of individual trees despite of advanced tree age and size. Above ground dry mass growth plotted over mass of (a) 409 big Sitka spruces (*Picea sitchensis* (BONG.) Carrière) in USA (b and c) various tree species on forest inventory plots in Spain and USA, respectively (modified after Stephenson et al. (2014)). As a reference for forest science the upper abscissa shows the respective trunk diameters.

Norway spruce analyzed by von Guttenberg (1915). Notice, that mass growth develops proportional to volume ($mass \propto volume$) and that analyses based on tree mass and volume will yield similar results. In the following I will repeatedly switch between the two measures; for some trees mass was available, in other cases just stem volume, however, the relationships and the conclusions are analogous.

As this review used Bertalanffy's function $dmass/dt = \eta \times mass^{2/3} - \kappa \times mass$ repeatedly for analyzing the course of tree growth, e.g., for the quantification of growth culmination, it will be briefly introduced first. The equation derives the mass growth of an individual depending on mass, so it takes into consideration the present state or the organism for its development in the future. This is equivalent to a memory effect of the tree's history. In this equation the driver of growth is tree body mass, not age. However, integration in respect to age results in $mass = A \times (1 - e^{k \times t})^3$, with $A = (\eta/\kappa)^3$ and $k = \kappa/3$. The resulting description of size growth over age is the result, not the underlying principle. Latter function allows among others the quantification of the time of growth culmination $t_{culm} = -\ln(1/3)/(\kappa/3)$, equivalent with the point of inflexion of the mass growth. The equation was used furthermore to quantify the body mass at the time of culmination $m_{culm} = A \times (2/3)^3 = A_m \times 0.296$, and the asymptote of the curve $A = (\eta/\kappa)^3$, i. e., the final body mass (see Table 1).

Based on the species-specific tree mass-stem diameter relationships by Forrester et al. (2017) I also calculated the diameter at the time of annual mass growth culmination and the asymptotic diameter, $d_{culm} = e^{(\ln(m_{culm})-a)/b}$, and $A_d = e^{(\ln(A_m)-a)/b}$, respectively, as stem

diameter is more conceivable and common in forest practice (Tables 3 and 5). For Norway spruce the tree mass-stem diameter relationships by Forrester et al. (2017) was for example $\ln(mass) = -2.0464 \times 2.3048 \times \ln(d)$ and its inversion yielded $d = e^{(\ln(m)-a)/b}$. It enabled to get from tree mass back to the stem diameter at breast height $d = e^{(\ln(m)+2.0464)/2.3048}$.

2.3. Examples of empirical application and evaluation

For exemplification of the von Bertalanffy function the von Guttenberg (1915) data, introduced in Table 2, were digitized. This historical data covering the growth period from 1560 to 1882 was chosen to avoid any superimposition of the growth by climate change but reflect steady state environmental conditions. The analyses shown in Fig. 5 was based only on predominant and dominant trees, i. e., on trees with only minor inhibition of size growth by competition.

Fig. 5a shows the $iv \ v$ courses of 27 predominant and dominant Norway spruces as measured by von Guttenberg (1915); they were fitted using the Bertalanffy model by the Gauss-Newton algorithm. Supplement Tables 1 and 2 show the statistical characteristics for both regressions applying 2/3 and 3/4 as allometric exponent in the expansion component of the resulting equations $iv = dv/dt = \eta v^{2/3} - \kappa v$ and $iv = dv/dt = \eta v^{3/4} - \kappa v$, respectively. Fig. 5, b and c visualize the results in terms of the $iv \ v$ and $iv \ age$ courses, respectively. In Fig. 5d the model prediction (2/3 scaling) was used as reference (1.0-line) and the observed courses of growth were plotted against the predicted

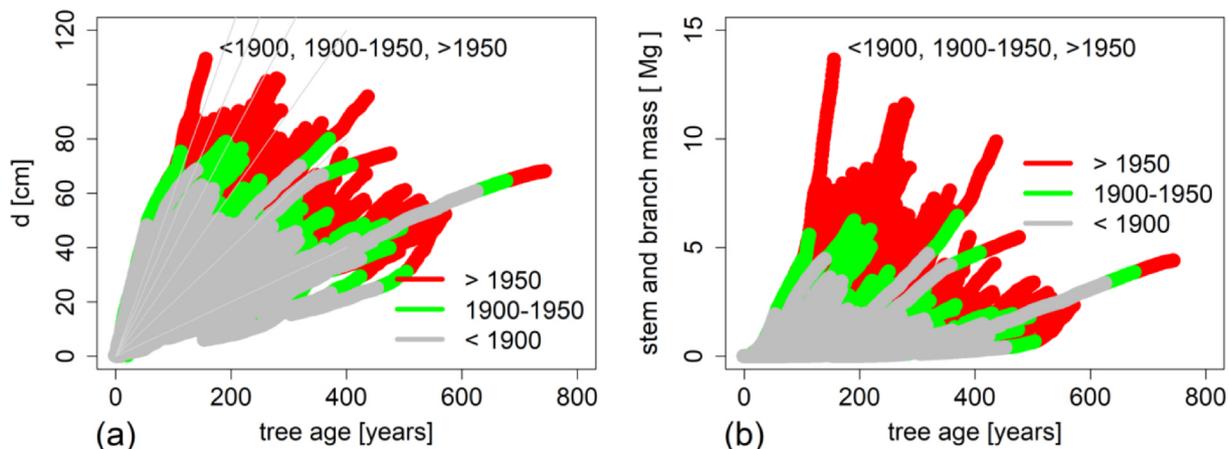


Fig. 3. Stem diameter growth (a) and above ground mass growth of dominant European beech trees in Germany from 1650 to presence (< 1900, 1900–1950, and > 1950).

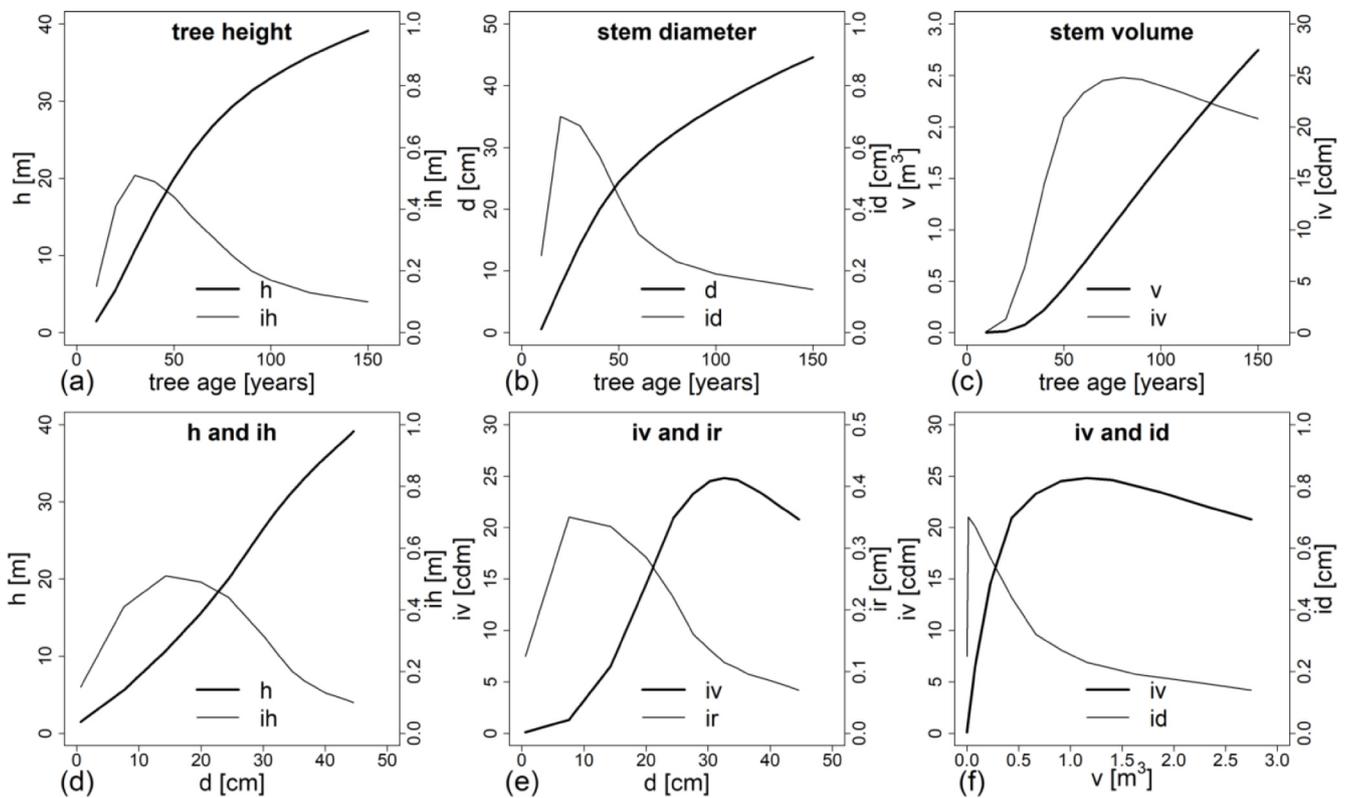


Fig. 4. The development of tree height, diameter, and volume shown by example for a 320 years old model stem growing under good site conditions according to von Guttenberg (1915, p. 142). I chose tree Tree No. XXX, $d = 58.5\text{ cm}$, $h = 38.1\text{ m}$, $v = 4.64\text{ m}^3$.

Table 5

Characteristics of annual mass growth depending on mass and age of Norway spruce, Scots pine, European beech, and sessile oak in Central Europe. Results of the parameterization of the model $d_{mass}/dt = \eta \times mass^{2/3} - \kappa \times mass$ based on trees of the pooled datasets 1–3.

species	n	measure	t_{culm}	m_{culm}	A_m	d_{culm}	A_d
			yrs	Mg	Mg	cm	cm
Norway spruce	333	mean	226	3.310	11.182	73.34	124.37
		SE	6.2	0.178	0.602	1.74	2.95
Scots pine	182	mean	211	1.575	5.320	57.82	98.90
		SE	9.4	0.162	0.547	2.00	3.42
European beech	174	mean	466	15.344	51.839	90.39	150.45
		SE	16.18	2.732	9.229	4.73	7.87
sessile oak	46	mean	480	26.629	89.962	121.57	197.33
		SE	16.9	10.230	34.559	8.60	13.96

$t_{culm} = -\ln(1/3)/(\kappa/3)$, age of culmination of annual mass growth; $m_{culm} = A_m \times (2/3)^3 = A_m \times 0.296$, tree mass at the age of culmination of mass growth; $A_m = (\eta/\kappa)^3$, asymptote of mass growth; d_{culm} the diameter at culmination age of mass growth; A_d , asymptotic diameter (for details of the formulas see Method sections 2.2 and 2.3).

developments. This comparison between observed and predicted growth underlines reasonable suitability of the von Bertalanffy model for the description of the courses of individual tree growth.

The RMSE (Supplement Tables 1 and 2, mean RMSE 0.00150124 versus 0.00150456) showed that von Bertalanffy's equation with Rubner's 2/3 scaling performed slightly better than with the 3/4 scaling by Kleiber (1947) and West et al. (1997). So, I used the original 2/3 scaling introduced by Bertalanffy for the modelling, interpolation, and derivation of the key information of the individual growth trajectories provided in Table 3. In summary the predominant and dominant trees of the von Guttenberg data showed amazingly late t_{culm} (mean 142–308 years) and high A_m values (mean 2.4–6.3 Mg) for mass growth. The respective stem diameters at the time of culmination were

$d_{culm} = 40.7 - 54.9\text{ cm}$ and asymptotic stem diameters $A_m = 68.9 - 93.1\text{ cm}$ on average (see Table 3).

The following derivation assumed $\eta = 2/3\text{ as}$ it refers to the original work by Bertalanffy von (1951) and it proved to result on average in smaller RMSE values when fitting the model $d_{mass}/dt = \eta mass^{2/3} - \kappa mass$ to the individual tree data from stem analyses, experimental plots, and increment core data.

2.4. Crown allometry and growing area

The relationship between stem diameter or stem volume and crown projection area, cpa, (Table 4) provides information for both tree allometry and translation of tree growth to tree productivity. As cpa is a substitute for tree growing area, the ratio between tree growth and cpa results in tree productivity, i. e., tree growth per occupied stand area. As crowns may overlap or stay in distance to each other due to crown shyness (Pretzsch et al., 2014) the real tree growing area may be lower or higher than the cpa. This may change the absolute level of the relationship between stem and crown size, but not the continuous increase of cpa with stem size.

When calculating tree growth/cpa for trees of progressing size, tree growth is divided by a continuously increasing cpa. This means that even for a tree with constant growth, productivity will decrease continuously with progressing stem size development. For the calculation of the stem volume productivity (iv/cpa) or tree mass productivity (mai/cpa) I used the mean allometric relationships between cpa and stem diameter shown in Fig. 2c for Norway spruce by example. The species-specific allometric relationship derived by Pretzsch (2019) and reflected by the species-specific coefficients in Table 4 were used for translation of tree growth to tree productivity in this study.

2.5. Effect of competition

The comparison between theory and reality of tree growth in the

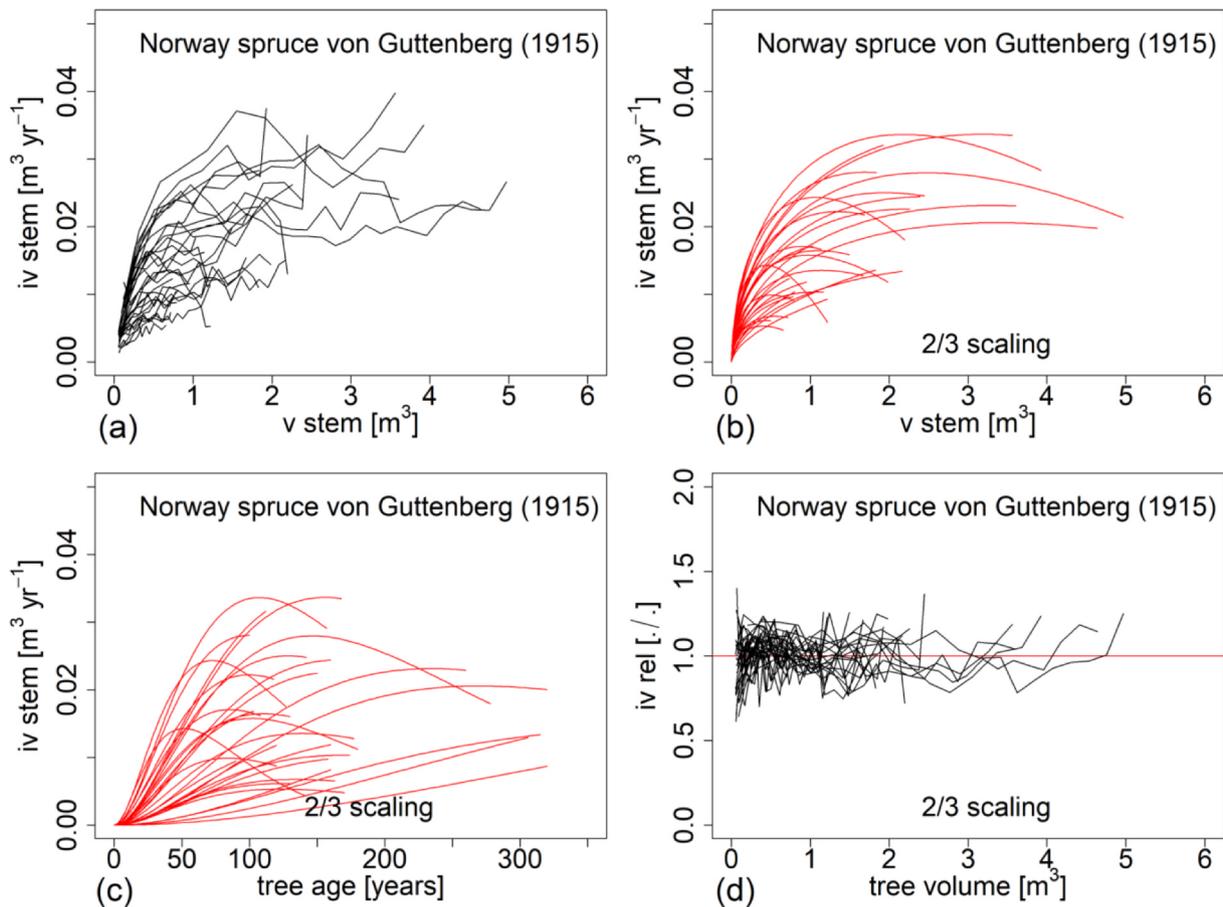


Fig. 5. Development of dominant Norway spruces according to stem analyses by von Guttenberg (1915). (a) annual stem volume growth plotted over stem volume at the beginning of the respective period. (b) The respective individual tree developments modelled by $iv = \eta v^{2/3} - \kappa v$ (Bertalanffy 1951). (c) the resulting development of stem volume growth over tree age. (d) observed volume growth versus volume growth predicted according to $iv = \eta v^{2/3} - \kappa v$ fitted by nonlinear regression (see Supplement Tables 1-2).

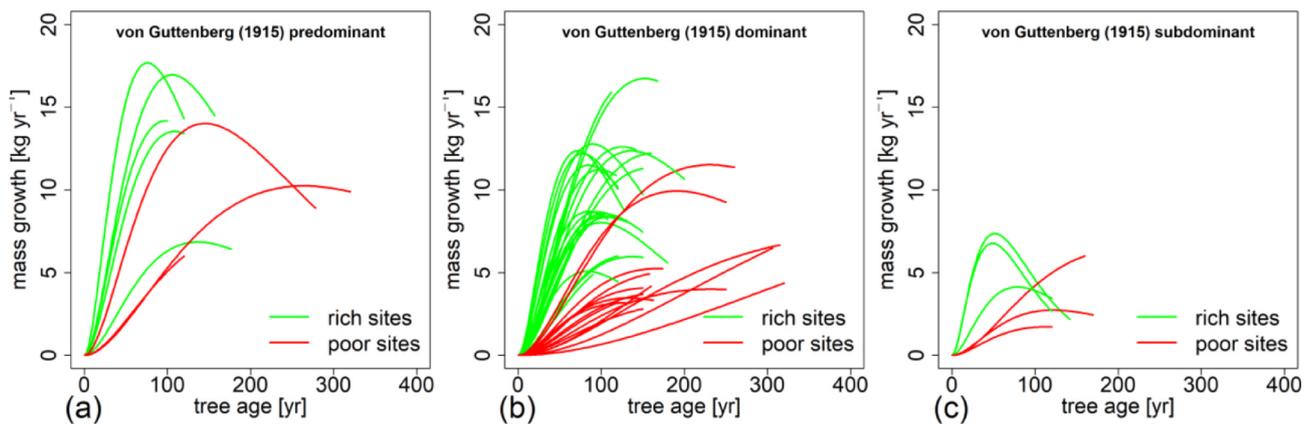


Fig. 6. Mass growth plotted over tree age of (a) predominant, (b) dominant, and (c) subdominant Norway spruces according to stem analyses by von Guttenberg (1915). The graph shows trees of different social classes growing on rich sites (green) versus poor sites (red). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

subsequent sections refers to predominant and dominant trees, as subdominant trees may represent not the potential but the growth under competition for resources. Sorted by social position and site conditions the Norway spruces analyzed by von Guttenberg (1915) showed the following basic tendencies regarding the behaviour of subdominant versus dominant and predominant trees (Fig. 6). On rich sites the trajectories of mass growth rose generally steeper in the first 5–10 decades and decreased earlier compared with poor sites (Fig. 6a). The culmination age of mass growth (mean ± SE) of predominant

(308 ± 23 years) and dominant trees (142 ± 16 years) was much later than of subdominant trees (86 ± 25) (Fig. 6, a and b, versus c). In order to avoid confounding competition and age or size effects on tree growth the analyses in the subsequent sections used only predominant and dominant trees.

Table 6

Growth curve characteristics and their dependency on site index shown for the long-term experiments of Norway spruce, Scots pine, European beech, and sessile oak in South Germany (see Supplement Table 4).

Data set 3	species	n	t_{culm}	$SE(t_{culm})$	m_{culm}	$SE(m_{culm})$	SI	$SE(SI)$	corr t_{culm} xSI	p	corr m_{culm} xSI	p
Experimental plots	all species	580	yrs 313	yrs 5.9	Mg 4.652	Mg 0.207	m 32.9	m 0.23	-0.47	0.000	0.001	0.987

t_{culm} , age of culmination of annual mass growth; m_{culm} , tree mass at the age of culmination of mass growth; SI, site index in terms of dominant height at age 100; corr, Pearson correlation coefficient; SE, one-fold standard error; p, tail probability.

3. Empirical evidence for the course of tree growth

3.1. Material and methods

3.1.1. Material

Reviewing the literature, one can find many theoretically oriented works about the assumed growth of trees and stands (Binkley et al. 2002, Coomes et al. 2011, Enquist et al. 1998, Valentine 1985, Zeide 1993), much information about tree and stand growth until usual rotation age of 50–150 years (Almeida et al., 2007, Bouillet, et al. 2013, Pretzsch 2020), but much less information about older trees and stands (Sillett et al. 2015, Stephenson et al. 2014). Thus I considered a lack of empirical evidence and compiled available measurements for further empirical analyses. In order to base this review on a broad dataset on tree growth in historic and at the present time, the following tree growth records were compiled.

As a first dataset (dataset 1) I used the already introduced 30 stem analyses by von Guttenberg (1915). For explanation of stem analysis see Pretzsch (2009, pp. 115–118). The dataset (Table 2) represents the growth of Norway spruce in Tyrol (at present Austria and Italy) in the period 1560–1882. The sampling occurred in 1879–1882 and the oldest trees are 320 years old. The time series of the d, h and v development are of special value as they should represent steady state environmental conditions of the 16th – 19th century at altitudes of about 800–1800 m a.s.l. The site quality ranges between good sites with a mean height of 33 m at age 100 and poor sites with a mean height of 13 m at this stand age (von Guttenberg, 1915, Table IX). The dataset comprises predominant, dominant, and suppressed trees from fully stocked to moderately opened stands.

A second dataset (dataset 2) comes from 165 stem analyses and increment boring of predominant and dominant trees on experimental plots of Norway spruce, Scots pine, European beech and sessile oak in Germany (Supplement Table 4). It includes trees up to 346 years old and 112 cm in stem diameter. Whereas the von Guttenberg dataset and the repeated measurements from the long-term experiments provide only mean periodical growth rates, the stem analyses and increment boring data covers annual growth records and reaches back to the middle of the 17th century.

A third dataset (dataset 3) comes from repeated tree measurements on long-term experimental plots of Norway spruce, Scots pine, European beech and sessile oak. This dataset was used for analyzing the effect of site quality in terms of site index, SI, on the course of mass growth (see Supplement Table 4). The site index was quantified according to the yield tables for Norway spruce, Scots pine, European beech, and sessile oak by Assmann and Franz (1963, 1965), Wiedemann (1943), Schober (1967, 1975) and Jüttner (1955) for moderate thinning.

Here, the measurements started in 1870 and the latest repeated measurements were in 2010. The maximum ages were 178 years, maximum stem diameters 54.8 m and tree heights 43.7 m.

The dominant height at age 100 varied between 20 and 42 m. Only those trees which were continuously dominant since the first survey were included.

A fourth dataset (dataset 4) for analyzing the combined effect of

fertilization and thinning compared with untreated reference comes from long-term experiments in Scots pine in Southern Germany (see Supplement Table 5). Here, I used 910 predominant and dominant trees, consisting of 90 control trees, 820 fertilized tree, from 10 long-term experiments and 92 plots, in Scots pine stands in Bavaria. Fertilizer of N (max. 1,200 kg ha⁻¹ in up to 5 applications) or NPKCaMg (max. 1,900 kg ha⁻¹ in up to 5 applications) were combined with different degrees of stand density reduction (unthinned, density reduction to mostly 80% or 50% of the control plots in terms of stand basal area). Scots pine was chosen for this analysis as it is a rather fast growing species that might show interesting behaviour of the course of growth already in relatively young early ages. Another reason was that it frequently occurs on poor sites and was in the focus of fertilization measures in the 1950–1970ies. The maximum tree ages are 129 years, maximum stem diameter and height 40.3 cm and 29.6 m (Supplement Table 5). For details about the fertilization, thinning, and growth and yield results see Foerster (1990).

A fifth dataset (dataset 5) was used for analyzing growth trends, i. e., for detecting changes of tree growth over tree age and calendar year (Supplement Table 6). This data set from increment boring of n = 591 trees was applied for analyzing the growth trends of European beech trees depending on tree age and calendar years. Part of this data was already used for analyzing growth trends in Europe (see Hilmers et al. 2019, Pretzsch et al. 2020, Pretzsch et al. submitted). Here, I used the data from the German plots involved in this study and added European beech stem analyses data by Rais et al. (2020a and b). In order to avoid any sampling bias by only using survivors (Martín-Benito et al. 2008; Nehrbass-Ahles et al., 2014) analogous analyses were repeated based on trees from long-term experiments of European beech (Supplement Table 4) with n = 160 trees from long term experiments of European beech and n = 580 trees from long-term experiments of Norway spruce, Scots pine, European beech, and sessile oak (Supplement Table 6).

For the estimation of the biomass production and carbon stock the general functions for above and below ground biomass by Forrester et al. (2017) were applied. They present the mean biomass-volume relationships for a broad number of tree species worldwide. The combination of the functions for above and below ground biomass allows the estimation of the total biomass. For the upsampling from the tree diameter of European beech to the stem and branch mass I used the function $\ln(mass_{branch,stem}) = -1.7843 + 2.3895 \times \ln(d_{1.3})$ and the correction factor $cf = 1.0921$ for retransformation ($mass_{branch,stem} = \exp(-1.7843) \times d_{1.3}^{2.3895} \times cf$) by Forrester et al. (2017). In order to derive estimations for the tree volume or the tree carbon content, the biomass may be multiplied by 2.0 or 0.5, respectively (Knigge and Schulz 1966, Pretzsch 2009, p. 66–71).

3.1.2. Statistical analyses and models

To analyse the relationship between tree growth and tree age, size, site index, calendar years etc. linear mixed effect models were applied with nested random effects on the experiment plot and tree level in order to account for spatial and temporal autocorrelation effects. The fixed effect parameters were a_0 – a_3 . The random effects b_i and b_j covered the levels of plot and tree. The indexes i, j, k in the following equations refer to the levels of experimental plot, tree within plot, and single

observation, respectively. The following numbers of the models refer to the results in the text (models 1 and 7) and in Table 4. The presentation of the results was restricted to the fixed effects.

The results of the extensive regressions analyses based on models 1a and 1b were summarized in Supplement Table 1 and 2; for all other models I showed the fixed effects in Table 4.

Model 1a

$$iv_k = a_0 \times v_k^{2/3} - a_1 \times v_k + \varepsilon_k$$

Model 1b

$$iv_k = a_0 \times v_k^{3/4} - a_1 \times v_k + \varepsilon_k$$

We used the equation by Bertalanffy von (1951) in case of model 1a with the exponent 2/3 for the anabolism term and 1.0 for the catabolism term and in case of model 1b with exponent 3/4 propose by Kleiber (1947) and later by Enquist et al. (1998) and West et al. (1997) as general exponent for metabolic scaling (nls function in the package stats, see Pinheiro et al. 2018).

Model 2

$$\ln(cpa_k) = a_0 + a_1 \times \ln(v_k) + \varepsilon_k$$

was fitted to crown measurement data from long-term experimental plots of Norway spruce, Scots pine, European beech, and sessile/common oak in Germany. Data has been described in Pretzsch (2019), the model parameters are given in Table 4 and the resulting formulas

were applied for calculating the trees stem volume growth per crown area in Figs. 1 and 7.

Model 3

$$\begin{aligned} \ln(\text{annualmassgrowth}_{ijk}) \\ = a_0 + a_1 \times \ln(\text{age}_{ijk}) + a_2 \times \ln(SI_{ijk}) + a_3 \times \ln(\text{age}_{ijk}) \\ \times \ln(SI_{ijk}) + b_i + b_{ij} + \varepsilon_{ijk} \end{aligned}$$

was fitted to mean annual mass growth rates of predominant and dominant trees on long-term experiments with known tree age and SI. As site index I used the dominant stand height at a standard age of 100 years as derived using the yield tables by Assmann and Franz (1963, 1965), Wiedemann (1943), Schober (1967, 1975) and Jüttner (1955) for moderate thinning.

Model 4

$$\begin{aligned} \ln(\text{annualmassgrowth}_{ijk}) \\ = a_0 + a_1 \times \ln(\text{mass}_{ijk}) + a_2 \times \ln(SI_{ijk}) + a_3 \times \ln(\text{mass}_{ijk}) \\ \times \ln(SI_{ijk}) + b_i + b_{ij} + \varepsilon_{ijk} \end{aligned}$$

was analogous to model 3 using tree mass as independent variable instead of tree age.

Model 5

$$\ln(\text{xtculm}_k) = a_0 + \ln(SI_k) + \varepsilon_k$$

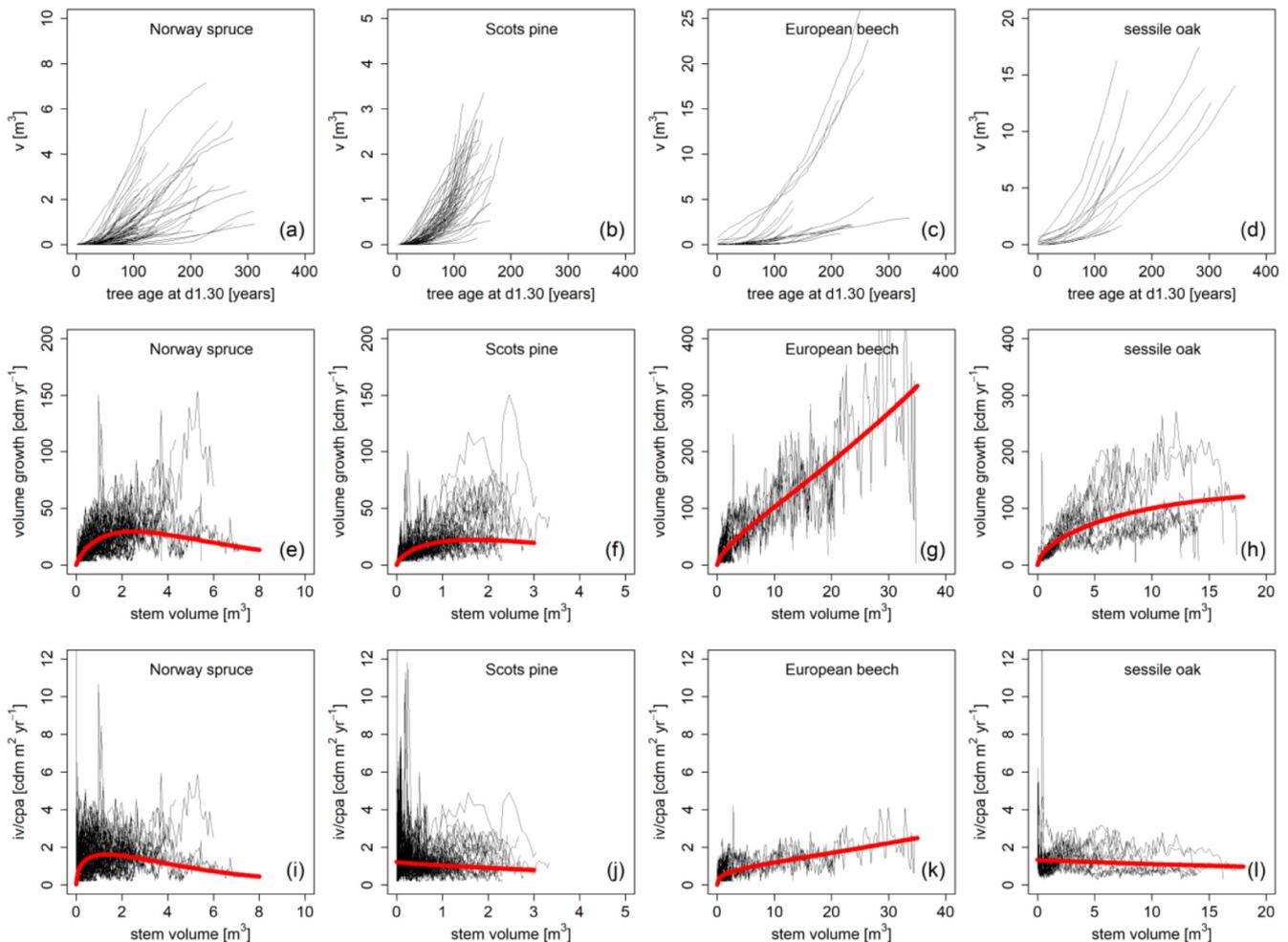


Fig. 7. Stem volume development (a-d), annual stem volume growth (e-h), and stem volume productivity (i-l) of dominant trees of Norway spruce, Scots pine, European beech, and sessile oak (from left to right). The courses are based on the dataset 2 of stem analyses and increment coring data as presented in Supplement Table 3. The red curves indicate the species-specific mean development of all included trees. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

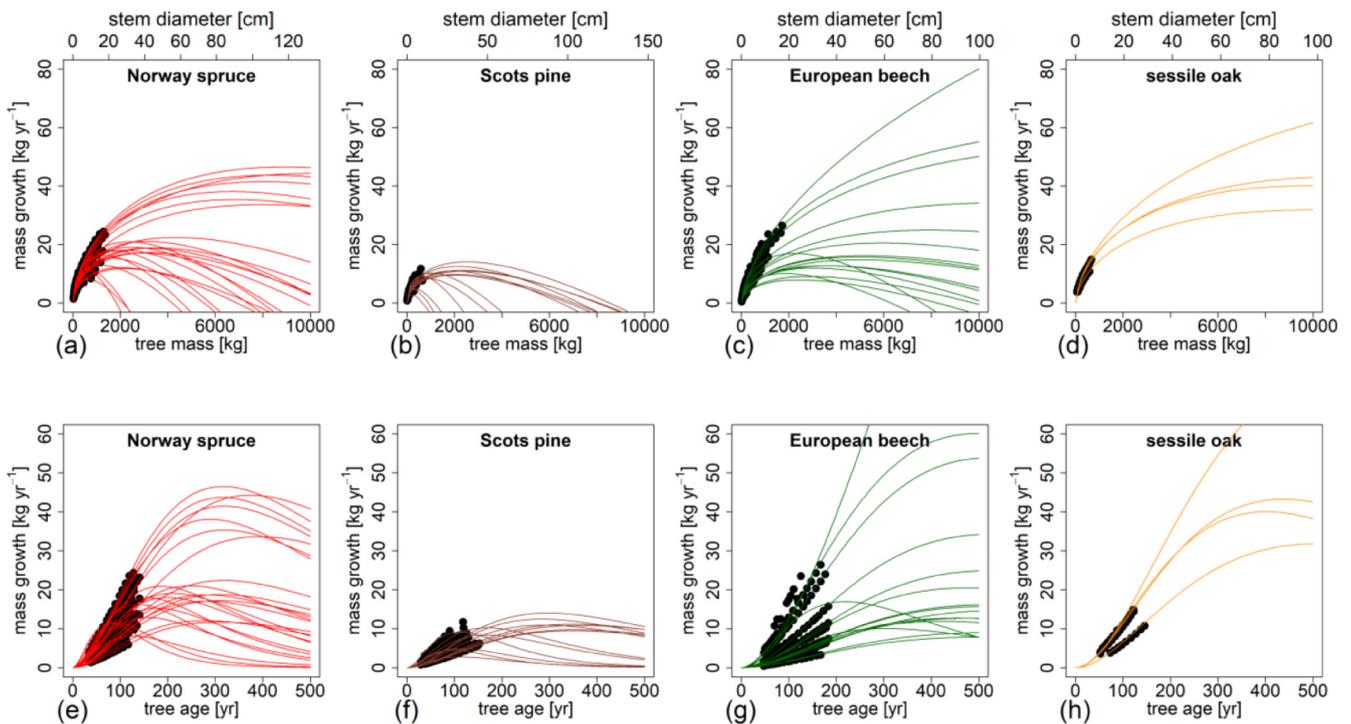


Fig. 8. Annual mass growth plotted and modelled over tree mass (a-d) and tree age (e-h) for dominant trees on long-term experiments of Norway spruce, Scots pine, European beech, and sessile oak. The black symbols indicate the observations on long-term experiments and the curves show the modelled course of individual tree growth based on (a-d).

In this model the dependent variable \times represents various tree attributes at the time of culmination of annual mass growth. Model 5 was applied to analyse any relationships between the time of mass growth culmination, $agetculm$, the tree mass at the age of mass growth culmination, $massculm$, and the stem diameter at the age of mass growth culmination, $dtculm$.

Model 6

$$\ln(annualmassgrowth_{ijk}) = a_0 + a_1 \times \ln(mass_{ijk}) + b_i + b_{ij} + \varepsilon_{ijk}$$

Was fitted to the data of predominant and dominant trees on long-term combined thinning and fertilization trials in order to analyze any differences between treatment versus reference trees regarding the tree mass growth-tree mass relationship.

Model 7a

$$\ln(stemdiameter_{ijk})$$

$$= a_0 + a_1 \times \ln(age_{ijk}) + a_2 \times \ln(year_{ijk}) + a_3 \times \ln(age_{ijk}) \\ \times \ln(year_{ijk}) + b_i + b_{ij} + \varepsilon_{ijk}$$

Model 7b

$$\ln(treemass_{ijk})$$

$$= a_0 + a_1 \times \ln(age_{ijk}) + a_2 \times \ln(year_{ijk}) + a_3 \times \ln(age_{ijk}) \\ \times \ln(year_{ijk}) + b_i + b_{ij} + \varepsilon_{ijk}$$

These two models were applied for stem diameter and above ground mass development of various tree groups depending on tree age, calendar year, and interaction between both (see Table 4). Random effects on a_0 at the tree and plot level take into consideration any temporal (several successive surveys) autocorrelations and spatial correlation (several plots per experiment).

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

3.2. Species specific courses of growth and aging

Based on stem analysis and increment coring data (dataset 2, Supplement Table 3) Fig. 7 shows the species-specific courses of stem volume development (a-d), volume growth (e-h) and stem volume productivity (i-l) of Norway spruce, Scots pine, European beech, and sessile oak. Stem volume refers to the merchantable volume (> 7 cm diameter at the smaller end). The developments of v in dependence on age (a-d) represent the integration of the annual volume growth and therefore have a smooth course. The developments of iv (e-h) and iv/cpa (i-l) over age show a strong oscillation due to individual high- and low-growth years.

The courses of stem volume development (Fig. 7, a-d) are mainly S-shaped in case of Norway spruce and Scots pine, whereas they show mostly a continuously increasing exponential development in case of European beech and sessile oak.

The courses of the annual stem volume growth (e-h) of Norway spruces and Scots pines culminate between age 50 and 150 and significantly decrease afterwards in most cases. The corresponding courses of European beech and sessile oak culminate much later or not at all. Many trees show an increasing annual stem volume growth until the sampling cut and analyses at ages of 250–350 years.

The productivity (Fig. 7, i-l) of the two conifer species shows mostly a clear culmination and decreasing trend after age 25–50. In contrast, most of the two broadleaved species trees show a rather constant level of productivity until advanced ages. This means that Norway spruce and Scots pine may culminate in growth and productivity within the normal rotation turnus in forestry (75–125 years) whereas European beech and sessile oak keep a considerably high productivity even beyond the species-specific common rotation turnus of 150–250 years.

As the sample sizes were small for some tree species (Fig. 7), the species-specific growth pattern were furthermore analysed on the basis of repeated measurements of dominant trees on long-term experiments (see dataset 3, Supplement Table 4). Fig. 8 shows the observed and the fitted mass growth exemplarily for the dominant trees on the long-term

experiments. The black symbols indicate the observations on long term experiments; for the sake of clarity Fig. 8 shows just the development of the arithmetic mean development of all dominant trees for each plot. The shown courses of growth (Fig. 8, a-d) result from fitting von Bertalanffy's equation $d\text{mass}/dt = \eta \times \text{mass}^{2/3} - \kappa \times \text{mass}$ to the observations.

The modelled and extrapolated courses of growth shown in Fig. 8 indicated a long continuation of mass growth with increasing mass especially in case of European beech and sessile oak. The upper x-axis shows the species-specific tree diameters. It indicates that mass growth of Norway spruce culminates in a few cases when trees reach stem diameters of 20–40 cm, however, in most of the cases when stem diameters were 50–100 cm. Scots pines culminated when stem diameters were 10–40 cm. European beech and sessile oak hardly culminate before stem diameters of 50–100 cm were reached. The level of growth varies mainly depending on the site conditions of the underlying long-term experiments. As introduced in section 2.2 the individual-specific coefficients η and κ can be used for deriving $\text{mass} = A \times (1 - e^{-k \times \text{age}})^3$ and its first derivative $d\text{mass}/dt = A \times (1 - e^{-k \times \text{age}})^2 \times 3 \times k \times e^{-k \times \text{age}}$, that reflects the course of the mass growth over tree age (Fig. 8, e-h). The courses of mass growth over tree age visualize the rather late culmination at ages of 300–400 especially in case of the broadleaved tree species.

$d\text{mass}/dt = \eta \times \text{mass}^{2/3} - \kappa \times \text{mass}$ and (e-h) $d\text{mass}/dt = A \times (1 - e^{-k \times \text{age}})^2 \times 3 \times k \times e^{-k \times \text{age}}$. Latter is the first derivation of the growth function $\text{mass} = A \times (1 - e^{-k \times t})^3$.

Table 5 shows the mean growth curve characteristics for all tree of datasets 1–3, i. e., dominant trees from stem analyses, increment coring and long-term experiments. Mass growth of predominant and dominant Norway spruces, that is covered very well by the data, culminated on average at age 226, i. e., far beyond the usual rotation age of 60–120 years. Scots pine culminated on average earlier and at an age of 211 years. This explains the successful usual concept of hold-over trees harvested at the age of 150–250 years. European beech and sessile oak culminated amazingly late, at ages of 466 and 480 years, respectively. All these ages of culmination are far beyond those assumed for forest tree species in textbooks by among others Kramer (1988, p. 66), Bruce and Schumacher (1950, p. 377), Wenk et al. (1990, p. 74), Assmann (1961, p. 80), or Mitscherlich (1970, p. 83). Accordingly, the mean masses at the age of culmination of 1.575–26.629 Mg, the asymptotic final masses 5.320–89.962 Mg, stem diameters at culmination of mass growth 57.82–121.57 cm and asymptotic final stem diameters 98.90–197.33 cm are much higher than assumed in literature. In summary the mass growth of 735 dominant trees (Table 5) revealed mean culmination ages of age 211–480 with the ranking sessile oak > European beech > Norway spruce > Scots pine.

3.3. Effect of site conditions

To visualize the effect of site conditions on tree mass growth (Figs. 9

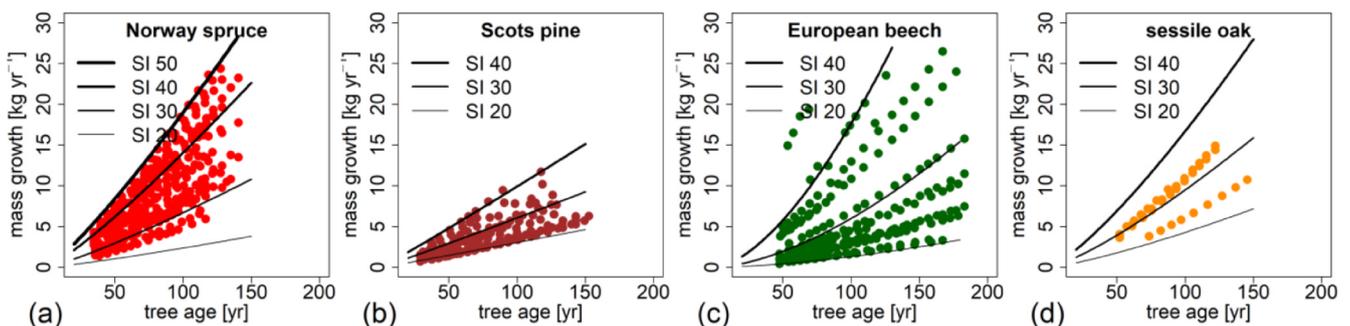


Fig. 9. Mass growth plotted over age for predominant and dominant trees on fully stocked long-term experiments of (a) Norway spruce, (b) Scots pine, (c) European beech, and (d) sessile oak growing under different site conditions in South Germany. The shown curves represent model 3 (see section 3.1.2 and Table 4) for the dependency of the mass growth on tree age and site index, SI, in terms of dominant height at stand age of 100 years.

and 10, Table 4) I first fitted the models 3 and 4 to the individual tree growth on long-term experimental plots (data set 3). This data has already been introduced in the last section (see Fig. 8); here, it was used for analyzing the effects of site quality in term of site index (dominant tree height at age 100). The repeated measurements of dominant trees on the long term experiments corroborated that mass growth of individual can increase until ages far beyond the normal rotation. The increases were steeper and lasted longer on rich compared with poor sites. Mass growth plotted over age increased exponentially and mass growth over mass progressed logarithmic (Figs. 9 and 10). Trees on rich sites grew 3–4-fold at the same age or mass compared to poor sites. Until the age of 150–180 years the observations and model curves showed no culmination of annual mass growth. There were no intersections between the curves for different sites conditions, so there was no earlier age- or mass-related decline of growth on the rich sites compared to the poor sites. The continuous and persisting age- and mass-related increase was evident for all four considered tree species with a ranking of European beech > sessile oak > Norway spruce > Scots pine. Notice, that for the sake of clarity Figs. 9 and 10 show only the development of the arithmetic mean development of all dominant trees for each plot.

For more detailed analyses the same data was fitted to the von Bertalanffy model $d\text{mass}/dt = \eta \times \text{mass}^{2/3} - \kappa \times \text{mass}$ in order to quantify the curve characteristic summarized in Table 6.

The age of culmination, t_{culm} , of mass growth was with on average 313 years for the four main tree species Norway spruce, Scots pine, European beech, and sessile oak far beyond normal rotation times and much higher than assumed in textbooks (Table 6). Trees on sites with high site index grew quicker, peaked and decreased earlier in annual growth; trees on poor sites culminated later in terms of age. Thus the t_{culm} decreases with site index, indicated by the negative correlation between t_{culm} and SI. There was no correlation between m_{culm} and SI (Table 6).

The courses of annual growth in dependence on tree mass ran more synchronous for trees growing under different site quality, they differed mainly in the level. On the long-term experiments was no correlation between m_{culm} and SI. The different courses and t_{culm} values for mass growth when plotted over age were not the result of age but the effect of different masses at the beginning of the respective periods. So, age is not the driving force, but tree mass as it represents the current state of the plant, the accumulated history and the preconditions for growth. Equivalent masses, however, are used with different efficiency on different sites, resulting in different levels but similar rhythm of growth over tree mass (Fig. 11 and Table 4).

In summary there was a clear tendency that mass growth culminated later on poor than on rich sites; t_{culm} was 400–600 years on poor and 100–300 years on rich sites. In contrast, the tree mass and tree stem diameter were rather similar on all sites when the mass growth culminated. It means that on poor sites trees grew simply slower than on rich sites and culminated later. They may also have a lower asymptote

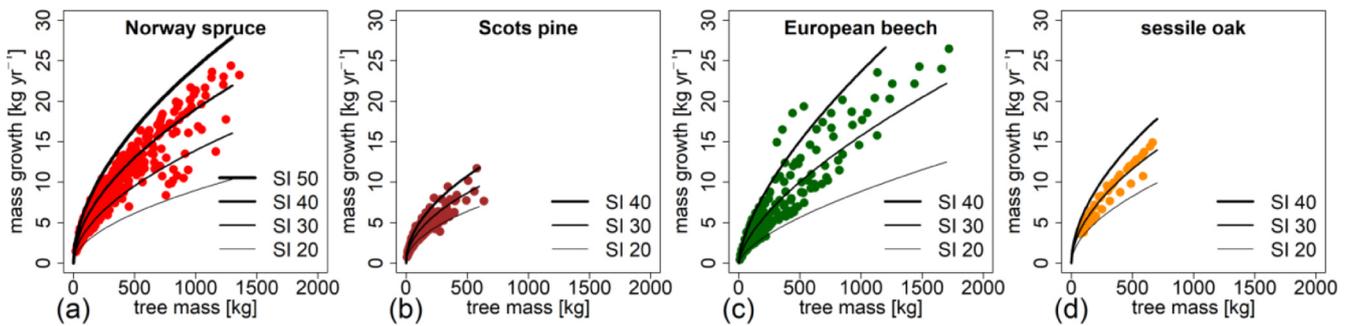


Fig. 10. Mass growth plotted over tree above ground tree mass at the beginning of the respective growth periods for predominant and dominant trees on fully stocked long-term experiments of (a) Norway spruce, (b) Scots pine, (d) European beech, and (d) sessile oak growing under different site conditions in South Germany. The shown curves represent model 4 (see section 3.1.2 and Table 3) for the dependency of the mass growth on tree mass and site index, SI, in terms of dominant height at stand age of 100 years.

and final mass, but the mass growth-mass allometry, the respective exponent and the trajectory varied much less over mass than over age. This suggested that the allometric exponent is inherent and less dependent on site conditions, whereas the allometric factor strongly depends on site quality.

3.4. Effect of combined fertilization and thinning

The question was whether the acceleration on size growth by fertilization causes an earlier decrease of annual growth or a long lasting increase of tree growth. Fig. 12 visualizes that the reference trees as well as the trees fertilized and promoted by thinning showed a steady upward trend of above ground mass development in the period with the fertilization (interval between the two vertical lines in Fig. 12) and still afterwards. For the sake of clarity Fig. 12 shows just the development of the arithmetic mean development of all dominant trees for each plot. The treated trees were higher in the level of growth and steeper in the upward trend. Most of the treated trees kept a superiority of above ground body mass up to 50% compared to the reference trees (Fig. 12b). Despite of the advanced mass development, the mass growth was not decreasing but similar to the growth trend of the untreated trees. With other words, the size development of treated trees was hurrying ahead of the untreated ones, however, at least until age 140 this did not result in a preponed decrease of growth of the fertilized trees due to advanced mass. The straight lines in Fig. 12c show that the mean upwards trend (allometric slope) is similar for untreated and treated trees, while the level (allometric factor) was higher for the latter ones. Test for differences of the two curves corroborated a significant difference in the intercept but a similarity of the slopes of both curves (see Table 4, model 6).

The fertilization effect on growth abated already some 5–7 years after the fertilizer applications (Fig. 12b) as large parts of the added nutrient may be stored in the system, especially in the additionally produced tree biomass and forest floor vegetation and may be no longer available for the seasonal annual turnover (Pettersson and Högbom 2004, Prietzel et al. 2008, Rehfuss 1981, p. 185). In summary the evaluation showed that at least within the measurement period so far (until age 140) there was no preponed size-related growth decrease of the treated trees. The presently ongoing eutrophication of forest sites in Europe via the atmospheric deposition, in contrast, is a continuous process over several decades (Prietzel et al. 2020, Skeffington and Wilson 1988) and may cause a permanent raise of the level of growth (Shen et al. 2001) comparable with a continuously repeated fertiliser application over longer time spans.

3.5. The effect of environmental changes. Comparison between historic and present courses with special focus on any age-related growth reduction

The third example in the introduction addressed that both diameter and mass development of European beech in the last decades might be significantly higher at defined tree ages than in historical times (< 1900). In this section, it will be analyzed to what extent the normal course of tree growth is superimposed by environmental changes.

European beech was selected for analyzing the effect of changing environmental conditions on the size-age development for two reasons. For European beech there firstly was a solid dataset available that reached backwards for about 400 years, and such long time spans are needed for indication of long-term effects on growth. Secondly, European beech is very relevant for forestry in Central Europe. Without its reduction by humans in the past (Mantel 1990) it would dominate

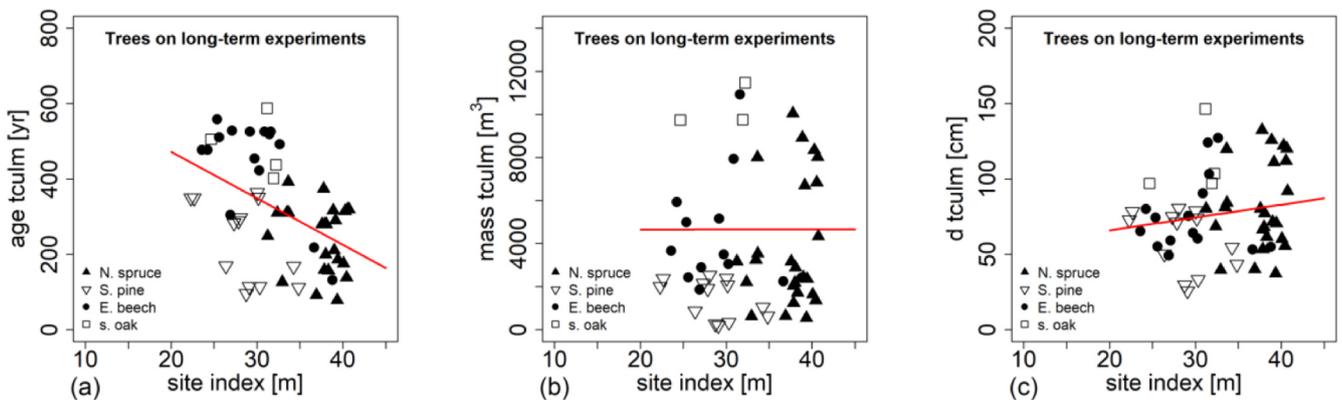


Fig. 11. Effect of site index, SI, on the (a) age of culmination of mass growth, (b) tree mass at age of culmination, and (c) stem diameter at age of culmination shown for dominant trees on long-term experiments of Norway spruce, Scots pine, European beech, and sessile oak (see Table 6). The species-specific symbols represent the observations and the straight lines the results of the overall regression analyses (Table 4) of age t_{culm} , mass t_{culm} , $d_{t_{culm}}$ depending on site index, SI.

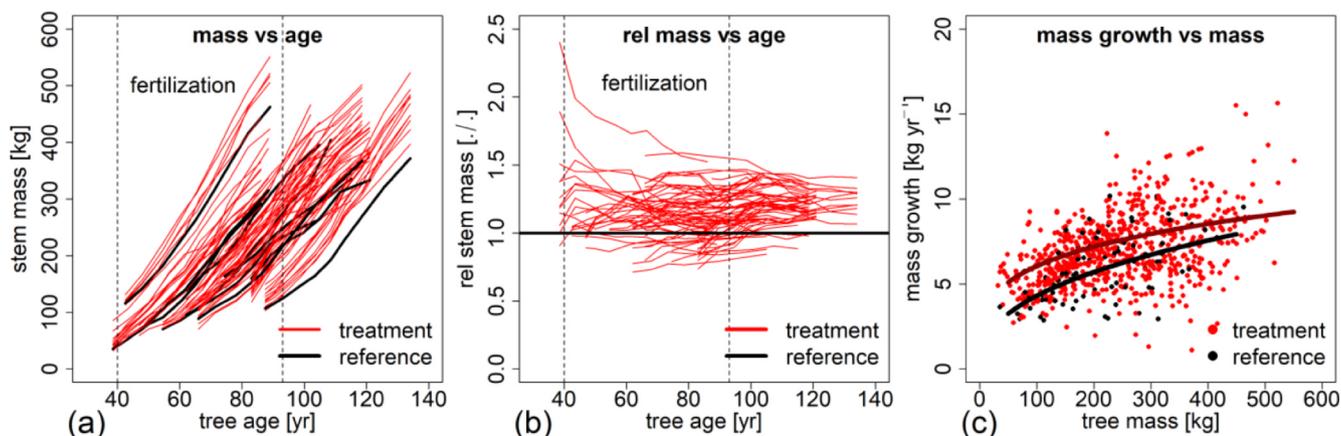


Fig. 12. Mass growth of dominant trees (red) with combined fertilization and thinning compared with untreated reference (black) based on 910 trees from 10 long-term experiments in Southern Germany. (a) Mean above ground mass development plotted over tree age. (b) ratio between mass development of treated and untreated trees. (c) annual mass growth plotted over mass for treated and untreated trees. The straight lines represent the mean development derived by double-logarithmic linear regression analyses (see Table 4, model 6). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Central European forests. Currently it is promoted by climate smart forestry (Bowditch et al. 2020), but its sensitivity to climate change is still under debate (Ammer et al. 2005, Bolte et al., 2016, Gefler et al. 2007, Rennenberg et al. 2004).

We scrutinized the effect of tree age, calendar year and interaction between both on stem diameter and above ground mass (stem and branch mass). The evaluation based on dataset 5 with $n = 591$ trees, with ages up to 469 years, diameter up to 81.4 cm, and mass up to 6.734 Mg. The increment coring covered calendar years back to 1546. All the trees were sampled in Germany and they represent sites indexes of 22–40 m at age 100 years Schober (1967, 1975).

Tree age was represented by age at dbh. The curves reveal the stem diameter or total mass trees achieved at various ages in 1850, 1900, 1950, and 2000.

Fig. 13 shows the logarithmic development of stem diameter (a) and the cubic shape of the mass growth (b) over age. From 1850 to 2000 this development was increasing in the slope; e.g., at age of 50 years, European beeches achieved a stem diameter of 14.20 cm in 1900 but 18.90 cm in 1950 and 24.97 cm in 2000 on average. The analogous values for tree mass in 1900, 1950 and 2000 were 0.104, 0.206 and 0.401 Mg, respectively. The acceleration slightly decreased with progressing calendar year; the increase of stem diameter growth was about 34% from 1850 to 1900 and decreased to 31% in the last 50 years. The acceleration of mass growth analogously was the highest 200–300 years

ago, is still on a high level but slightly decreasing. I restricted the curves and the discussion of the growth trends on the last 100–200 years that were very well covered by sample trees and increment cores by tree of various ages and sizes (see Supplementary Fig. 1).

We found a negative interaction between the effect of tree age and calendar year on size development (see model 7, a and b, Table 4). This means that the positive growth trend, i. e., the size growth acceleration slightly decreased over time. The age trend strongly accelerated till present, however, the acceleration slowed down as also found by Bosela et al. (2016) and Pretzsch et al. (2020). This concurrency of high growth level compared to the historic one and the ebbing away of the acceleration process may indicate an improvement of European beech growth as presented by Pretzsch et al. (2014a) and Spiecker (2000) but an exceedance of optimal conditions and change to suboptimal environmental conditions as discussed by Bosela et al. (2016), Dulamsuren et al. (2017), and Penuelas et al. (2007).

One of the limitations of the approach was that the tree ring data came only from trees that presently belonged to the predominant or dominant social classes. Although growth of dominant trees may provide good insight of European beech growth trends at different elevations and species mixtures, this sampling criteria may result in some bias when generalizing the results, and scaling up to the stand level (Forrester 2019). Bias can result because only some surviving trees may be sampled and currently dominant trees could have been suppressed in

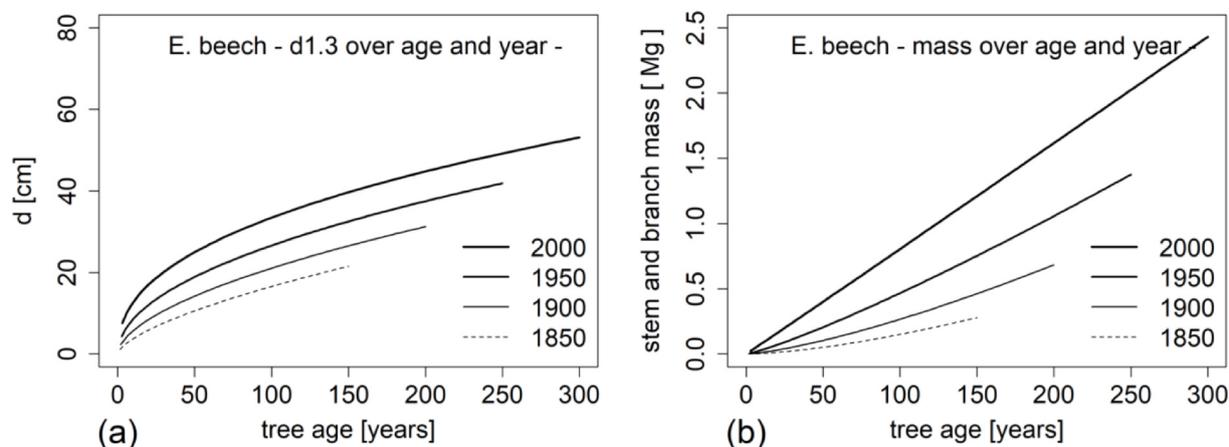


Fig. 13. Development of (a) stem diameter and (b) stem mass of European beech trees depending on tree age and calendar year. The analyses were based on $n = 591$ trees with 78,547 records of tree diameter measurements dating back to the middle of the 16th century (for data see Supplement Table 6 and for model see Table 4).

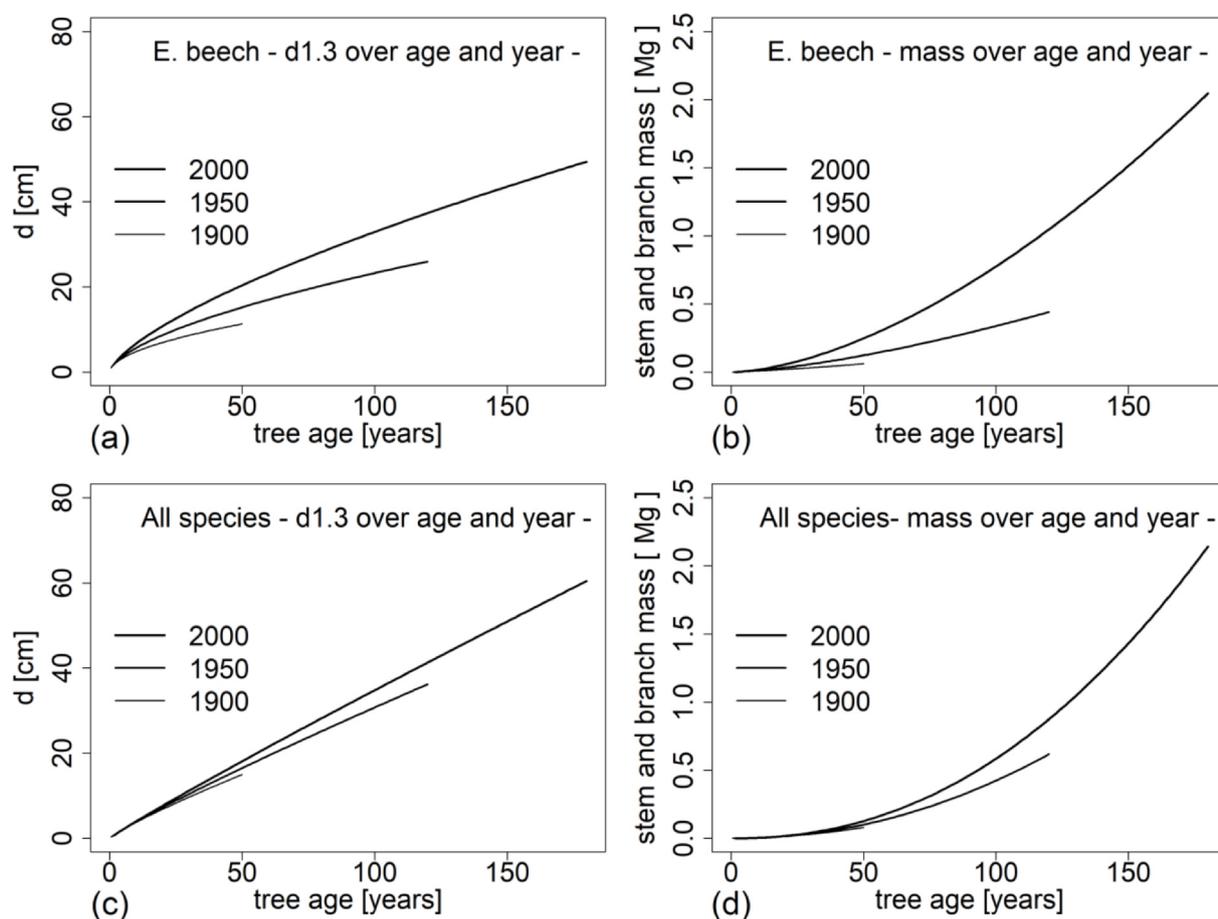


Fig. 14. Development of stem diameter and above ground mass depending on tree age and calendar year shown for dominant trees on long-term experimental plots in Germany. The growth trends are shown for (a and b) European beech and (c and d) for the main common tree species in South Germany Norway spruce, Scots pine, European beech and sessile oak on average.

the past (Cherubini et al. 1998), although I tried to mitigate this effect by removing trees showing periods of growth suppression in the past. On the other hand, dominant and suppressed trees can show distinct growth trends and responses to climate (Martín-Benito et al. 2008; Nehrbass-Ahles et al., 2014). For shade tolerant species like European beech, dominant trees were found to be more sensitive to climate than suppressed trees (Mérián and Lebourgeois 2011), so that lower temporal changes could be expected at the stand compared with the tree level. However, under more stressful conditions, growth partitioning among trees in beech stands may be more symmetric (Pretzsch et al. 2018), which suggests the suitability of dominant tree behaviour as an indicator of response to climate change.

To avoid the above discussed survivor bias and to further scrutinize any long-term growth trends I completed a similar analysis based on long-term experiments. In this way any sampling bias could be avoided by including only those trees in the evaluation that were always dominant or predominant since the first survey. For data and model characteristics see Supplement Table 6 and Table 4. In this case the data reached back just to 1870, so that I restricted the visualization of the growth trends on 1900–2000 (Fig. 14). European beech showed an accelerated development of stem diameter and mass growth (Fig. 14, a and b), similar to the overarching analyses based on increment cores. The increase from 1950 to 2000 was 38% for diameter growth (31% in case of the overarching analysis based on increment cores) and 99% for mass growth of trees at age 50. The minor differences to the overarching evaluation (Fig. 13) may result from the mentioned sampling bias (Nehrbass-Ahles et al., 2014) and the fact that the overarching analyses encompassed a broader set of plots including those in mountain areas where trends at the edge of the distribution range of

European beech may be stronger (Dulamsuren et al. 2017).

An analogous analysis of the stem and mass growth trend of all four main tree species, Norway spruce, Scots pine, European beech and sessile oak together (with tree species as an additional random factor in the model, see Table 4) revealed a growth acceleration with a slightly lower slope (Fig. 14, c and d). Interestingly, the curves for the stem diameter showed a nearly proportional and the curves for mass a cubic development till advanced tree ages. The acceleration triggers a faster increase but so far no earlier decrease of growth. The increase from 1900 to 2000 was 10% and 26% for stem diameter and mass growth, respectively, of trees at an age of 50 years.

The length of the curves represents the coverage of the model by data. For the data base and model characteristics see Supplement Table 6 and Table 4.

The evaluation of the von Guttenberg (1915) data in section 2 showed that even under steady state environmental conditions the growth of big trees continues longer and on higher level as predicted by theory. This section revealed that on top of this the growth is accelerated and prolonged by environmental changes. They may cause steeper courses of growth of young trees and an even longer continuation of growth of old trees. Figs. 13 and 14 suggest that in the early past growth was generally lower and flatter, compared with the recent past. The growth curves of middle aged or old trees that started low and flat are probably kept on a higher and increasing level by growth-accelerating environmental changes.

4. Discussion, conclusions and future research

4.1. The course of tree growth. Theory and reality

Empirical examples for the long-term course of mass growth of individual trees are rare. So, the principles and courses are mostly explained for height growth, that develops quicker (Fig. 4). However, mass growth is certainly a better indicator for the tree's life cycle. Our historical as well as current data showed for dominant trees a culmination of the annual tree volume and mass growth far beyond the common rotation age of 100–200 years.

The historic stem analyses of Norway spruce by von Guttenberg (1915) indicated a culmination at an average age of 308 years for predominant trees and 142 years for dominant trees (Table 3).

The mass growth of 735 dominant trees mainly analyzed by stem analyses and increment coring revealed mean culmination ages of age 211–480 with the ranking sessile oak > European beech > Norway spruce > Scots pine (Table 5). In order to avoid survivor sampling bias (Martín-Benito et al. 2008; Nehrbass-Ahles et al. 2014) I also analyzed trees of the same species from experimental plots with known history and always dominant or predominant position. This yielded estimated culmination ages of 364–1135 (Figs. 9 and 10) and corroborated culmination ages and continuing growth far beyond textbook assumptions.

Trees on sites with high site index grew quicker, peaked, and decreased earlier in annual growth, whereas trees on poor sites culminated later in terms of age. The courses of annual growth in dependence on tree mass ran more synchronous on different sites, and they differed rather in the level than in the rhythm of growth.

In total 910 Scots pines on combined thinned and fertilized compared with control plots revealed for both groups a continuous increase of growth and no preponed size-related growth decrease of the treated trees until high ages. With other words, the size development of treated trees is hurrying ahead of the untreated ones, however, at least until age 140 this does not result in a preponed decrease of growth (Fig. 12).

For analyzing any modification of the course of growth by environmental changes I used a dataset of 591 cored E. beeches and for corroboration 580 permanently surveyed trees from long-term experiments of the above mentioned main species. On top of their long-lasting growth, all tree species together showed a strong acceleration of annual growth; the acceleration was the highest in 1850 to 1900, less in the last 50 years, and did not trigger any preponed age- or size related decrease (Figs. 13 and 14).

Many textbooks assume an age- or size-dependent decrease of volume or mass growth by the increasingly detrimental ratio between assimilating surface area of a tree and respiring volume or mass. However, the ages of culmination found in this study were mostly far beyond those assumed for forest tree species by among others Kramer (1988, p. 66), Bruce and Schumacher (1950, p. 377), Wenk et al. (1990, p. 74), Assmann (1961, p. 80), or Mitscherlich (1970, p. 83). Accordingly, the mean observed and predicted final masses and diameters were also much higher than assumed in literature.

We hypothesize that trees lose considerable parts of their crown when developing, and that this is not directly physiologically driven by assimilation or respiration, but by abandonment of organs mechanically or by losses due to wind and storm damage of the crown and mechanical abrasion.

Von Bertalanffy (1915) developed and tested Eq. (1) for animals and microorganisms which have mainly living and respiring tissue inside similarly to herbaceous plants. But this characteristic should not be transferred and applied for trees. With increasing age latter may no longer maintain the inner parts but use the stable heart wood cores as non-respiring low-cost scaffolding. CT scanning of whole stems substantiated that considerable parts of the stem represent dead non-respiring tissue, relevant as scaffolding for the tree but hardly lowering the assimilation to respiration ratio (Pretzsch 2005a). Despite of these differences, the von Bertalanffy function was flexible enough for trees as

its allometric factor κ (Eq. (1)) can consider only low respiration compared with other organisms.

We come to the conclusion that any growth decrease by the ratio between assimilating surface area of a tree and respiring volume or mass may happen, but probably far beyond tree ages or tree size assumed so far. The asymptotic course of height growth, especially on water limited sites, is mainly caused by hydraulic restrictions (Koch et al. 2004, Ryan and Yoder 1997) and results among others in the well known correlation between stand height and site quality (used for site indexing). The limited height growth means also a reduced crown length (Pretzsch 2019) and may cause disadvantageous photosynthesis to respiration ratios. The limited vertical crown expansion (i.e., restricted assimilating surface) combined with a continuing extension of crown volume and stem growth (i.e., proceeding expansion of respirating volume and mass) means a decline of the assimilation to respiration ratio. The contribution of the photosynthesis to respiration ratio to the growth decrease with increasing size (and age) may differ between tree species (Hunt, 1999, Law et al. 1999, Ryan and Waring 1992) and site conditions (Ryan 1990, 1995). However, the shown courses of tree growth suggest that the ratio may determine age and mass related growth decrease, but much later and more moderately.

It is more likely that healthy predominant or dominant trees keep on growing until damaged by mechanical disturbances or pathogens instead of continuously decreasing in growth due to prevalence of respiration. Any increasing respiration may certainly slow down the size growth at higher ages and sizes, however, it is not the prevailing cause of death in old ages. It rather seems that trees can continue growing much longer as assumed so far until extrinsic forces cause their death (Sillett et al. 2015a; b). The revealed long continuation of growth also contradicts common explanations that growth decrease within common rotation periods are inevitable if trees are strongly thinned. The results rather suggest an amazing rate and continuity of growth until advanced ages and sizes for trees when released by competitors by thinning (Pretzsch 2005b).

4.2. Consequences for stand ecology and management

Many papers and textbooks assume a rather early culmination of the annual mass growth of individual trees as show schematically in Fig. 15a, course 1. In the past there was a lack of empirical facts and a tendency to adapt findings from organisms with lower longevity, such as herbaceous plant and animals (von Bertalanffy, 1951), to forest trees (Pretzsch 2010). However, already von Guttenberg (1915) and later other (Sillett et al. 2015b; Stephenson et al. 2014) showed that the slope of the volume growth trajectory can be steeper than expected and the culmination can be far beyond the common rotation time (Fig. 15a, course 2). Climate change may have additionally accelerated the annual mass growth (Fig. 15a, course 3) in a way that it increases nearly exponentially or at least linearly until the stand rotation age (Pretzsch et al., 2017, 2020).

The velocity of individual tree size growth drives the growing area occupation, self-thinning, mortality, and productivity at the stand level. The acceleration of the individual tree size growth may cause an earlier reach of the self-thinning line of young stands after planting and a faster development along this line with accelerated mortality frequently reported by empirical works (Pretzsch et al. 2014a) and model studies (Lei et al. 2016). The faster the size extension of the individual trees, the faster space and resource become limited, individual tree number reduced and the earlier growing area efficiency and productivity culminate and subside (see Fig. 15b). The remaining trees may arrive earlier at a less efficient use of growing area. Thus, the current annual stand increment, CAI, and mean annual increment, MAI, may be higher but culminate earlier (Fig. 15b, CAI 3 vs. 1; MAI 3 vs. 1). Latter may suggest a shortening of any MAI based rotation time in mono-specific age class stands. Thinning may be scheduled more frequently and final harvest earlier than in the past (del Río et al. 2008, Pretzsch et al.

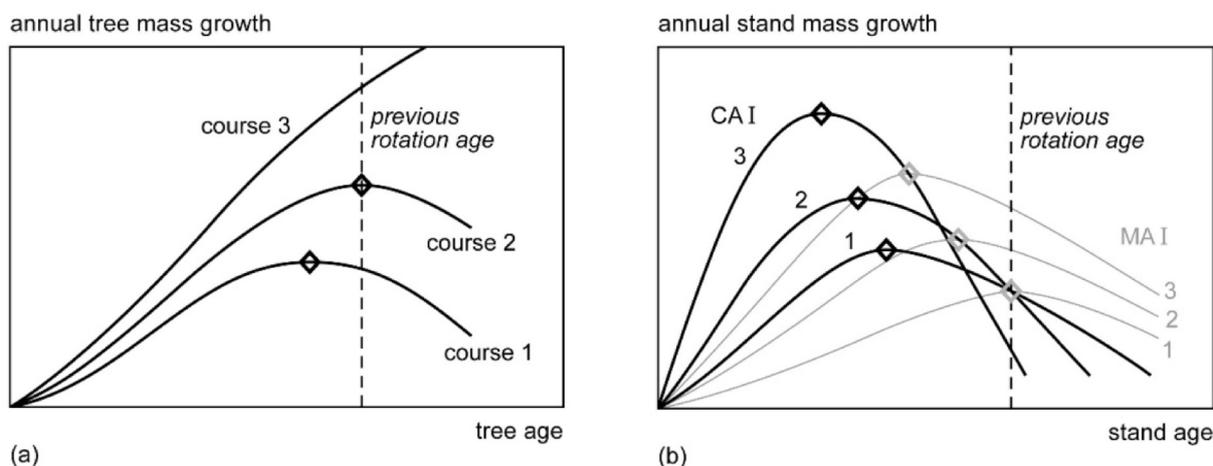


Fig. 15. Courses 1–3 of mean annual mass growth at the individual trees level (a) and the effects on the current (CAI) and mean annual increment (MAI) at the stand level (b). (a) The slope and continuity of the annual mass growth of individual trees may be higher than assumed in the past (see course 3 versus course 1). (b) Faster individual tree growth may result in an accelerated stand growth, earlier culmination of current and mean annual increment (CAI 3 versus CAI 1; MAI 3 versus MAI 1) and suggest a shortening of any MAI based rotation time in even-aged forest stands.

2014a).

The faster and longer continuation of size growth improves the potential for production of high dimension and quality timber (e.g., in European beech and sessile oak stands) in more reasonable time than in the past. For European beech and sessile oak could be shown (Figs. 7 and 8) that mass growth increases till ages of 200–300. Even if mass productivity (growth/growing area) may decrease, the increase of value may continue in case of high-grade timber production until higher stand ages (Schmid et al. 2015). This may apply for both tree and stand level.

For our analysis of the growth trends (Figs. 13–14) mainly fully stocked and just unthinned or slightly thinned stands were used. The revealed positive growth trends are presently very obvious in many Central European forests, because of eutrophication, temperature raise, and extension of the growing season (Pretzsch et al. 2014a, 2018, Spiecker 2000). Similar trends were even found for urban trees (Pretzsch et al., 2017). High growth levels, even after strong thinnings, partly result from this positive growth trend and should not be ascribed to thinning. Unthinned stands on similar sites nearby may also display enhanced growth due to environmental changes; in this way unthinned plots reflect that this is a general trend of increasing growth and stand density. The growth acceleration should not be misinterpreted as a particularly favourable growth reaction on thinning. In forest practice, where unthinned plots are not available, modern rigorous density reduction might be promoted as practitioners do not realize that the growth after thinning simply represents a short-term effect and are so high partially because growing conditions are generally improving due to environmental changes. Thus, under changing growing conditions, the unthinned reference plots are becoming increasingly relevant in order to avoid misinterpretation of thinning responses.

The long lasting growth of dominant individual trees creates a high silvicultural flexibility. It means that the growth of released crop trees by thinning from above does not decrease precociously as considered by Assmann (1961, p. 307). It also means that big old trees may proceed growing on high level in the transition phase while smaller and younger trees are already highly efficient in the understorey (Sterba 1999, 2019, Reininger 1987, Vuokila 1977). Big trees, suppose they are mechanical stable and healthy, may be highly productive in the extended phases of forest conversion (Schütz 2002). This is an additional benefit beyond their important regulation function for natural regeneration and structure (Dieler et al. 2017, Koskela et al. 2007).

As it extends the flexibility of suitable ages or size for tree harvest and removal, the longer lasting growth may be of special relevance for

multi-aged silviculture concepts (O'Hara 2014) such as selection forest systems, as well as for the transitioning from monospecific to continuous cover forestry (Pommerening and Murphy 2004). On top of their function for structure and habitat improvement, the remaining old trees may grow more in mass and value than assumed so far. Thus big trees may provide higher contribution to stand growth and carbon sequestration as expected so far when keeping them classically as hold-over (Baader 1939, Faltl and Breit 2012) or variable retention trees (Beese et al. 2003, Mitchell and Beese 2002) for regeneration and biodiversity purposes (Dieler et al. 2017).

4.3. Consequences for further research

Our findings of long continuation of tree growth until ages of several hundred years suggest that senescence and death are hardly determined by prevalence of respiration versus assimilation but more likely by biotic (parasites, pathogens) or abiotic (windbreakage, embolies) damages. Further clarification of the main causes and their dependency on tree history and structure may contribute to better understanding and silvicultural steering of tree growth dynamics. Future research may address for a broader set of species the growth-mass relationship, the assimilation to respiration ratios and the causes for mortality. Further research may also better trace the effects of the accelerated growth to the stand level, schematically represented in Fig. 15. Of special interest are any growth acceleration effects on mortality and maximum stand density. The effects may be species-specific and their clarification is important for derivation and updating of silvicultural prescriptions.

Classical growth theory explains and models the tree mass growth depending on the current mass and resource supply. However, the internal structure (e.g., tree ring structure, past low growth periods, sapwood/hardwood ratio, embolies), and external allometry and morphology (e.g., crown size, root size, stem shape) may in addition strongly determine the growth rate beyond the sole total mass. Thus any changes in age- or mass-related growth may also be caused by modified silvicultural treatment in the past, modified allometry and structure and respective growth behaviour. Knowledge of the dependencies between internal stem structure, crown morphology and growth pattern is highly relevant under the paradigm of adaptive forest management (Bolte et al. 2009, Messier et al. 2015). It may enable the identification of those trees with a special potential of long and prospering size growth and deserve special silvicultural promotion.

The database of this study came mainly from forests in Central

Europe; though the reported results and drawn consequences should be validated for environmental conditions and species different from Europe.

Declaration of Competing Interest

The authors declared that there is no conflict of interest.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.foreco.2020.118508>.

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