Leaf density-based modelling of phototropic crown dynamics and long-term predictive application to European beech

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ABSTRACT

The landscape of functional–structural tree growth models is divided into small-scale models with a topological architecture, and large-scale models based on a description of crown shape in terms of rigid structures such as empirical crown envelopes. Due to their computational heaviness, the former meet their limits in the simulation of old and large trees, whereas the latter are unable to allow for unrestricted spatial variability and plasticity. This article presents a mechanistic, spatially explicit tree growth model based on the characterisation of the spatial distribution of foliage in terms of the 3D leaf area density. This allows efficient and robust simulations while avoiding the complexity of branch topology and any a priori shape constraints. A key element of our model is the spatial expansion of the crown along the local light gradient or, in an equivalent teleonomic interpretation, in the optimal direction with respect to future biomass production. The calibrated model accurately predicts long-term growth dynamics for 16 stands of European beech (*Fagus sylvatica* L.), a species known to be particularly plastic. It generates complex properties in conjunction with crown shape, response to stand density, height dynamics and, in particular, the emergence of the allometric 3/4-rule. Simulation results motivate hypotheses on the weight of phototropism as one driver of the spatial growth of European beech in early and late stages as well as in and off competition.

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1. Introduction

Godin (2000) distinguished between global, spatial, geometric and topological representations in models of plant architecture. The first category refers to a crown being characterised in terms of an enveloping surface. Parameterisations range from simple forms such as spheres, cylinders or cones to more complex composite or asymmetric shapes (e.g. Cescatti, 1997; Pretzsch, 2009). A spatial representation is based on the partitioning of either space itself (Sonntag, 1996) or the tree envelope into cells, as in BALANCE (Grote and Pretzsch, 2002; Rötzer et al., 2010) and WHORL (Sorrensen-Cothern et al., 1993), in which vertically stacked disks form the crown. Due to their rigid structure, growth models based on both global and spatial representations are limited in their ability to allow for crown plasticity and spatial variability in response to local biotic and abiotic growth conditions. A geometric representation is fully local, but does not yet include the connections between organs. Godin (2000) mentioned the spatial density of roots and leaves as examples. Indeed, root density has received attention in root growth models (Reddy and Pachepsky, 2001; Dupuy et al., 2005, 2010). Leaf density has been introduced in a conceptually different and purely theoretical framework by Beyer et al. (2014), but never been applied in growth model practice. Lastly, topological representations additionally account for the interconnected network of plant organs, thus allowing explicit and mechanistic modelling of inner-plant transport processes. The rich detail of topological models is also their greatest challenge. It involves a large number of potentially sensitive parameters, as well as to computational heaviness. The latter can be controlled by artificially imposing limits on the maximum number of organs, which are presently below realistic values for large and old trees to such an extent that the simulatability of these is considered impossible in a topological framework Sievänen et al. (2000).

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Very different branch topologies do not seem to prevent old and large tree individuals of the same, plastic species growing in indistinguishable conditions from developing similar spatial distributions of foliage at a macroscopic scale. In light of the previous considerations, this motivates a different approach to representing plant architecture, which ignores topology, while at the same time not being constrained shapewise by predefined structure as in the case of global and spatial representations sensu Godin (2000). Here, we present a mechanistic growth model based on a geometric representation, characterizing trees in terms of 3D leaf density. Within this framework we aim to describe the spatial dynamics and variability of crowns on a large temporal scale. A key mechanism in our model is the local expansion of the crown in the direction of the greatest increase of light incidence, thus simulating phototropism under unconstrained plasticity. This aims to determine to which extent a teleonomic (or optimisation) approach like this can account for the tree's actual growth dynamics. Additional physiological mechanisms are simplified and the number of parameters kept small, aiming for as simple a model framework as possible, which is necessary to capture key features of tree growth dynamics over a long period of time – including, amongst others, the empirically well-documented allometric 3/4-rule.

Section 2 presents the individual tree model and a straightforward extension to populations. In Section 3, the calibrated model's predictive capacity is evaluated by testing simulations against long-term experimental data from 16 even-aged stands of European beech (*Fagus sylvatica* L.), a species particularly suitable to the approach in view of its strong crown plasticity. Section 4 discusses the simulation results and additional emergent phenomena, as well as potential insights into the crown dynamics of beech.

2. Model description

We consider the spatial leaf area density $u(x, n) \geq 0$ (m^2 m^{-3}), leaf density for short, for points $x \in \mathbb{R}^3$ and years $n \in \mathbb{N}$ (for rhythmically growing trees sensu Hallé and Martin, 1968). It allows us to describe arbitrary foliage distributions locally and without bias, without fundamentally increasing computational complexity as the number of leaves increases. Moreover, its smoothness with respect to the spatial variable opens up the possibility of capturing processes that are difficult to describe in individual-based models in a generic and compact way, for instance when spatial gradients are involved. These very features underlie the use of spatial population density-based models in theoretical ecology, often in conjunction with partial differential equations (e.g. Okubo and Levin, 2002; Cantrell and Cosner, 2003).

2.1. Local light conditions

Foliage characterised in terms of leaf density has the properties of a continuous light-absorbing medium. Beer–Lambert's law describes the decrease of radiation passing through such and thus represents a generic way to compute inner-crown radiation transfer for a given u. It has also been applied in many spatial (Grote and Pretzsch, 2002; Sorrensen-Cothern et al., 1993; Sonntag, 1996) and topological models (Takenaka, 1994; Kellomäki and Strandman, 1995; Rauscher et al., 1990; Balandier et al., 2000). We compute the cumulative local light incidence $L(x, n)$ in the point x and in year n. For a cumulative photosynthetically active radiation PAR(n) (J m^{-2} y^{-1}) that reaches the tree from above in year n, it reads

$$L(x, n) = \text{PAR}(n) \cdot \lambda(x, n) \cdot \exp\left(-\int_{x_3}^{\infty} \lambda(\xi, n) \cdot u(\xi, n)\ d\xi_3\right), \quad (1)$$

where $\lambda(x, n) = \Lambda \cdot N(x, n)$ accounts for leaf transmittance $\Lambda \in [0, 1]$ (Monteith, 1969) and leaf inclination, $N(x, n) \in S_+^2$ denoting the

unit normal to the plane in which foliage in x lies (see Wang et al., 2007, for a review of readily incorporated leaf angle distribution models). The simplification of vertical light incidence is common to most large-scale tree growth models (Norby et al., 2001). Indeed, applying the altitude-dependent standard overcast sky model (Ross, 1981, used e.g. in the models by Takenaka, 1994 and Perttunen et al., 1998) accounted for negligible differences in our model, hence, like Sorrensen-Cothern et al. (1993), we pursue the vertical approach here. For the sake of convenience, we will assume the global value PAR to be approximately constant over the years.

2.2. Biomass production and transport

We assume cumulative local net biomass production $B(x, n)$ in x in year n to be proportional to local light incidence and leaf density via a radiation use efficiency RUE (g J^{-1}) according to the model by Monteith (1972):

$$B(x, n) = \text{RUE} \cdot L(x, n) \cdot u(x, n) \quad (2)$$

Relating local net biomass production to leaf area is common in many tree growth models (Le Roux et al., 2001), both at the scale of the whole tree (e.g. West, 1993; Bartelink et al., 1997) and, as done here, at the local shoot level (Sorrensen-Cothern et al., 1993; Takenaka, 1994; Kellomäki and Strandman, 1995). Medlyn (1998) provided an extensive discussion on the physiological basis of this linearity.

Strict local positive phototropism implies the transport and allocation of this produced biomass in the direction of the local light gradient, $\nabla_x L(x, n)$. In the model, the quantity $B(x, n)$ is thus transported and assigned to the point $x + k \cdot \nabla_x L(x, n)$, where $k > 0$ denotes a mobility constant. The locality of this mechanism is closely related to the concept of branch autonomy (Sprugel et al., 1991). For a given point $x \in \mathbb{R}^3$, the total biomass assigned to it for allocation thus equals

$$\mathcal{B}(x, n) = \sum_{\xi \in \mathbb{R}^3 : x = \xi + k \cdot \nabla_x L(\xi, n)} B(\xi, n). \quad (3)$$

According to (2), the light gradient $\nabla_x L(x, n)$ points in the same direction as the gradient of biomass productivity, $\nabla_x \frac{B(x,n)}{u(x,n)}$. In this way, local phototropism coincides with a spatial expansion that is, in a sense, optimal with regard to locally anticipated future biomass production. This mechanism falls into the line of teleonomic plant models, in which a certain goal-seeking behaviour, often in conjunction with biomass production, is presupposed (see Dewar et al., 2009, and references therein, Mäkelä et al., 2002, and reviews by Cannell and Dewar, 1994, and Mäkelä, 1990). In addition to these mostly compartment-based approaches, architectural models have been used to determine spatial structures that maximise light interception (reviewed by Fisher, 1992; Farnsworth and Niklas, 1995), which touch our approach as well.

In many spatially explicit growth models, the local light climate controls shoot growth (Sievänen et al., 2000). Beyond the punctual light incidence, primary growth in our model is determined by the local gradient of light incidence. Indeed, Sonntag (1996) argued this information to be available to the tree and to influence local growth.

2.3. Leaf-wood partitioning

The allocation of $\mathcal{B}(x, n)$ in x comprises its partitioning between foliage and sapwood. We apply the pipe model theory (Shinozaki et al., 1964), which has been widely used by tree growth models in this context (Le Roux et al., 2001). It states that every newly created leaf is mechanically and hydraulically supported by a sapwood pipe,

and that the pipe's mass is proportional to the leaf mass at its tip and to the root-to-leaf distance via a constant P (m^{-1}).

Without an explicit branch geometry at hand in this approach, we resort to the heuristic approximation $\|x\|_\Upsilon = x_3 + 2 \cdot \|(x_1, x_2)\|$ proposed by Sonntag (1996) for the distance $\|x\|_\Upsilon$ from a leaf in x to the root tip. More complex choices, e.g. incorporating empirically observed branching angles (Bayer et al., 2013) or alternative proxies for below-ground length (Valentine, 1985) have shown to not affect simulation results to an observable extent.

For one unit of biomass assigned to x, only a part $\gamma < 1$ of it will transform into new leaf mass, requiring $P \cdot \gamma \cdot \|x\|_\Upsilon$ for the appropriate pipe, for which the mass portion $1 - \gamma$ is available. From this balance condition, i.e. $P \cdot \gamma \cdot \|x\|_\Upsilon = 1 - \gamma$, we obtain $\gamma = \gamma(x) = (1 + P \cdot \|x\|_\Upsilon)^{-1}$.

2.4. Leaf density dynamics

Altogether, SLA $\cdot \gamma(x) \cdot \mathcal{B}(x, n)$, where SLA denotes the specific leaf area (m^2 g^{-1}), assumed constant, numbers the increment of leaf density in x in year $n+1$ as a result of the production in year n. Simultaneously the biomass $(1 - \gamma(x)) \cdot \mathcal{B}(x, n)$ forms the appropriate pipe.

Assuming the senescence and abscission of leaves to be a matter of time only, i.e. foliage that was created $n_{sen} > 0$ years ago falls, the leaf density of year $n+1$ in x is given by

$$u(x, n + 1) = u(x, n) + SLA \cdot \gamma(x) \cdot (\mathcal{B}(x, n) - \mathcal{B}(x, n - n_{sen})). \qquad (4)$$

For the particular case of deciduous trees where $n_{sen} = 1$, this simplifies to $u(x, n+1) = SLA \cdot \gamma(x) \cdot \mathcal{B}(x, n)$.

This discrete dynamical system is completed by an initial condition, which we describe to be Dirac in $x = (0, 0, 0)$, i.e. $u(x, 0) = u_0(x) = \delta(x)$ and where $\int_{\mathbb{R}^3} u_0(x)\,dx$ equals the surface area of the cotyledon.

2.5. Trunk diameter

Alongside the creation of foliage, new sapwood pipes are formed as described above. Pipes corresponding to dropped foliage persist, yet gradually become non-conductive and, over time, turn into heartwood (Shinozaki et al., 1964; Valentine, 1988). Thus, taking into account all pipes that have ever been formed, yields $\sum_{k=0}^{n} \int_{\mathbb{R}^3} \gamma(x) \cdot \mathcal{B}(x, k) \cdot P \cdot SWV\,dx$ for the cross-sectional area at the trunk base, $C(n)$, in year n, where SWV denotes specific wood volume (m^3 g^{-1}). As in the pipe model theory, swelling effects are not accounted for. We compute the diameter as $2\sqrt{C(n)/\pi}$.

2.6. Population of trees

The model extends straightforwardly to account for competition for light, which is considered to dominate competition for other resources (Sorrensen-Cothern et al., 1993). Light conditions are then determined by taking into account the foliage of all trees of a population. Let $u_1(\cdot, n), \ldots, u_m(\cdot, n)$ denote the leaf densities of m trees in year n, potentially shading each other and competing for light. The model remains essentially unchanged with the exception of (1) which changes to

$$L_i(x, n) = PAR(n) \cdot \lambda_i(x, n) \cdot \frac{\lambda_i(x, n) \cdot u_i(x, n)}{\sum_{j=1}^{m} \lambda_j(x, n) \cdot u_j(x, n)}$$

$$\cdot \exp\left(-\int_{x_3}^{\infty} \sum_{j=1}^{m} \lambda_j(\xi, n) \cdot u_j(\xi, n)d\xi_3\right) \qquad (1')$$

for each $i \in \{1, \ldots, m\}$. The fraction $\frac{\lambda_i(x,n) \cdot u_i(x,n)}{\sum_{j=1}^{m} \lambda_j(x,n) \cdot u_j(x,n)}$ is the part of the incoming radiation in x that is attributed to the foliage of tree i. In particular it reduces to 1 if tree crowns do not occupy common space.

Accordingly, (2)–(4) change to

$$B_i(x, n) = RUE \cdot L_i(x, n) \cdot u_i(x, n) \qquad (2')$$

$$\mathcal{B}_i(x, n) = \sum_{\xi \in \mathbb{R}^3 : x = \xi + k \cdot \nabla_x L_i(\xi, n)} B_i(\xi, n) \qquad (3')$$

$$u_i(x, n + 1) = u_i(x, n) + SLA \cdot \gamma(x) \cdot (\mathcal{B}_i(x, n) - \mathcal{B}_i(x, n - n_{sen})) \qquad (4')$$

respectively, for each individual $i \in \{1, \ldots, m\}$ of the population.

3. Results

3.1. Data description

European beech (*Fagus sylvatica* L.) is the most important deciduous tree species in the natural forests of Central Europe (Ellenberg, 1996). Without human interference, beech would probably currently cover more than two thirds of the Central European forest area (Bohn et al., 2000), and therefore can be considered as the most competitive Central European tree species (Leuschner et al., 2006). In reality, its current share in the forested lands has been reduced to less than one fifth by human interference (Bolte et al., 2007). However, the ongoing transition from monocultures to mixed-species stands will increase the portion of European beech in future. This process towards close-to-nature forest with high portions of beech is going on and is strongly promoted by policy in Europe (Bravo-Oviedo et al., 2014). Hence, models which appropriately prognosticate beech, its growth, structure, and wood quality were not too important in the past but will become highly relevant in future (Pretzsch and Rais, 2016). The overwhelming inner crown variability and crown plasticity, particularly in response to light, compared to other native trees species (Dieler and Pretzsch, 2013; Pretzsch, 2014) predestines it as a test case of our model.

As European beech is the naturally dominating species in Europe it attracted particular scientific effort since the beginning of systematic forest science. The longest surveys of experimental plots are available for beech and the empirical data base of tree and stand dynamics, including canopy structure and crown shape development, is better for European beech than for any other species (Kennel, 1972; Pretzsch, 2009; Assmann, 2013). We tested the model against long-term empirical tree height and trunk diameter data from 18 even-aged pure stands of European beech established in 1871 on six different sites throughout Southern Germany. Each site contains three separate experimental plots, differing in treatment variants ranging from the removal of only dead trees on plot A to intensive thinning on plot C, thus resulting in high, medium and low stand densities, respectively. Fig. 1 illustrates these for the experimental site "Fabrikschleichach 15"; the other sites' curves are qualitatively similar. Table 1 summarizes characteristic variables of the six sites. Further details can be found in Kennel (1972).

As the model does not cover harvesting and natural tree mortality, the number of trees per unit stand area over time for each plot (shown in Fig. 1 for "Fabrikschleichach 15") are required as input. In place of the entire stands, we simulated a single average tree for each stand, while accounting for competition by means of dynamic periodic boundary conditions along a cell in which the tree grows (as in Beyer et al., 2015), and whose surface area corresponds to the given density of the stand at the appropriate time. In other words, the horizontal space available for crown expansion of the simulated individual is equal to the area of the stand divided by the appropriate number of trees at all times. Investigating inter-individual
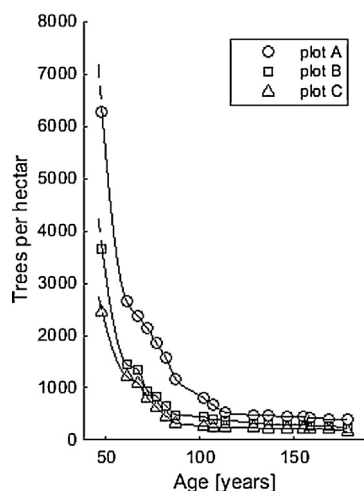
Fig. 1. Stand densities of plots A, B and C of the "Fabrikschleichach 15" site over time.

Table 1
Details of the experimental sites.

Experimental site	Latitude Mean annual temperature	Longitude Mean annual precipitation	Altitude
Kirchheimbolanden 11	7°93′07″ E 7.0 °C	49°63′21″ N 660 mm	610 m
Waldbrunn 14	9°80′27″ E 8.5 °C	49°72′23″ N 710 mm	360 m
Fabrikschleichach 15	10°57′12″ E 7.5 °C	49°91′86″ N 820 mm	470 m
Elmstein-Nord 20	7°91′86″ E 8.0 °C	49°39′08″ N 780 mm	400 m
Rothenburg 26	9°44′69″ E 7.0 °C	49°97′42″ N 1050 mm	475 m
Hain 27	9°33′47″ E 7.0 °C	49°99′25″ N 1080 mm	420 m

variability by simulating all trees of the stand individually would require data on highly local growth conditions, random effects as well as a mortality component in the model, all of which is beyond the scope of this approach.

3.2. Model validation

3.2.1. Long-term forest inventory data

Table 2 summarises the model parameters, three of which were calibrated using inverse estimation based only on the height and trunk diameter data of plot A and C of the "Fabrikschleichach 15" site (Fig. 2g and i). Beyond the accurate reproduction of the data from these two plots, the model accurately predicts height and trunk diameter data on the additional 16 plots from six sites (Fig. 2a–f, h, and j–s).

Fig. 3a shows the cross-section of the crown corresponding to the simulations of plot A of the "Fabrikschleichach 15" site over the course of time. The shape is indeed similar to that of a typical beech crown in such growth conditions (Fig. 3b).

In contrast, Fig. 4a shows the simulated crown of a spatially isolated tree. The artificial absence of vegetal competition in the simulation only partially accounts for the unrestrained horizontal expansion that is not realistic during the early growth shown in the figure. We return to this aspect of the model in detail and discuss possible implications as to other growth determinants at early stages in Section 4. Irrespective of this, we note that in terms of shape, the simulated tree bears indeed some resemblance to a mature solitary beech tree (Fig. 4b).

Table 2
Model parameters. Unreferenced parameters were estimated (see text). As in Letort et al. (2008), PAR, assumed constant, and RUE were merged.

Parameter	Long name	Value	Reference
SWV (m³ g⁻¹)	Specific wood volume	0.0013	Bouriaud et al. (2004)
SLA (m² g⁻¹)	Specific leaf area	0.0232	Bouriaud et al. (2003)
$N(x, n)$ [1]	Normal to leaf surfaces	(0, 0, 1)	Monsi and Saeki (2005)
Λ [1]	Leaf transmittance parameter	1.0	Wang et al. (2004)
$\int u_0$ (m²)	Initial leaf area	$6.01 \cdot$ SLA	Coll et al. (2004)
RUE · PAR (g m⁻² y⁻¹)	Radiation use efficiency × photosynthetically active radiation	14.72	
k [1]	Mobility constant	0.0013	
P (m⁻¹)	Pipe model parameter	0.43	

3.2.2. Allometric relationships

Allometric scaling laws establish relations between different growth dimensions of an organism. For two such quantities x and y, an allometric equation is of the form $x \propto y^\beta$. Allometrically relating characteristic dimensions of trees has proven to be beneficial, and although in general the investigated allometric exponents β do vary, depending on specific conditions (Pretzsch and Dieler, 2012), that corridor is in fact rather narrow (Pretzsch, 2010). The 3/4-power law has received particular attention, which, in its broadest formulation states that an organism's metabolic rate Q scales to its body mass M as $Q \propto M^{\frac{3}{4}}$. The relationship has been observed in many particular cases across several length scales (see references in West et al., 1999). Pretzsch (2006) found empirical evidence from long-term experimental plots, including the ones presented in Section 3, that is supportive of the 3/4-power scaling.

West et al. (1997) initiated a series of models associated to the term of metabolic scaling theory, aiming to explain the relationship in an as general as possible theoretical framework. In the plant specific follow-up model by West et al. (1999), the law is derived from the optimization of different hydrodynamic and energetic properties of a space-filling, fractal-like network of root-to-petiole tubes. The assumption of constant tube radii throughout the tree in the original model is relaxed in follow-up work (West et al., 1999, see also Savage et al., 2010), in which conductive pipes, loosely embedded into non-conducting heartwood, are allowed to vary in diameter along their path. The theory has been heavily contested both conceptually and empirically. We refer to Petit and Anfodillo (2009) for an extensive list of references challenging logical and mathematical assertions, as well as a critical discussion of arguable anatomical and physiological assumptions and conclusions of the theory.

This criticism of the metabolic scaling theory, and at the same time the indisputable occurrence of the 3/4-rule in the flora, have motivated to put the development of plant models that can reproduce the rule in a more realistic, yet simple as possible framework on the agenda of the functional–structural plant modelling community. To date, this has not culminated in success.

Our model provides the total mass of the tree $M(n)$ and its metabolic rate $Q(n)$, given by the total net biomass production, in year n as

$$M(n) = \underbrace{\sum_{i=0}^{n_{\text{sen}}-1} \int_{\mathbb{R}^3} \frac{u(x, n-i)}{\text{SLA}} \, dx}_{\text{total leaf mass}} + \underbrace{\sum_{i=0}^{n} \int_{\mathbb{R}^3} \frac{u(x, i)}{\text{SLA}} \cdot P \cdot \|x\|_\Upsilon \, dx}_{\text{total wood mass}}$$
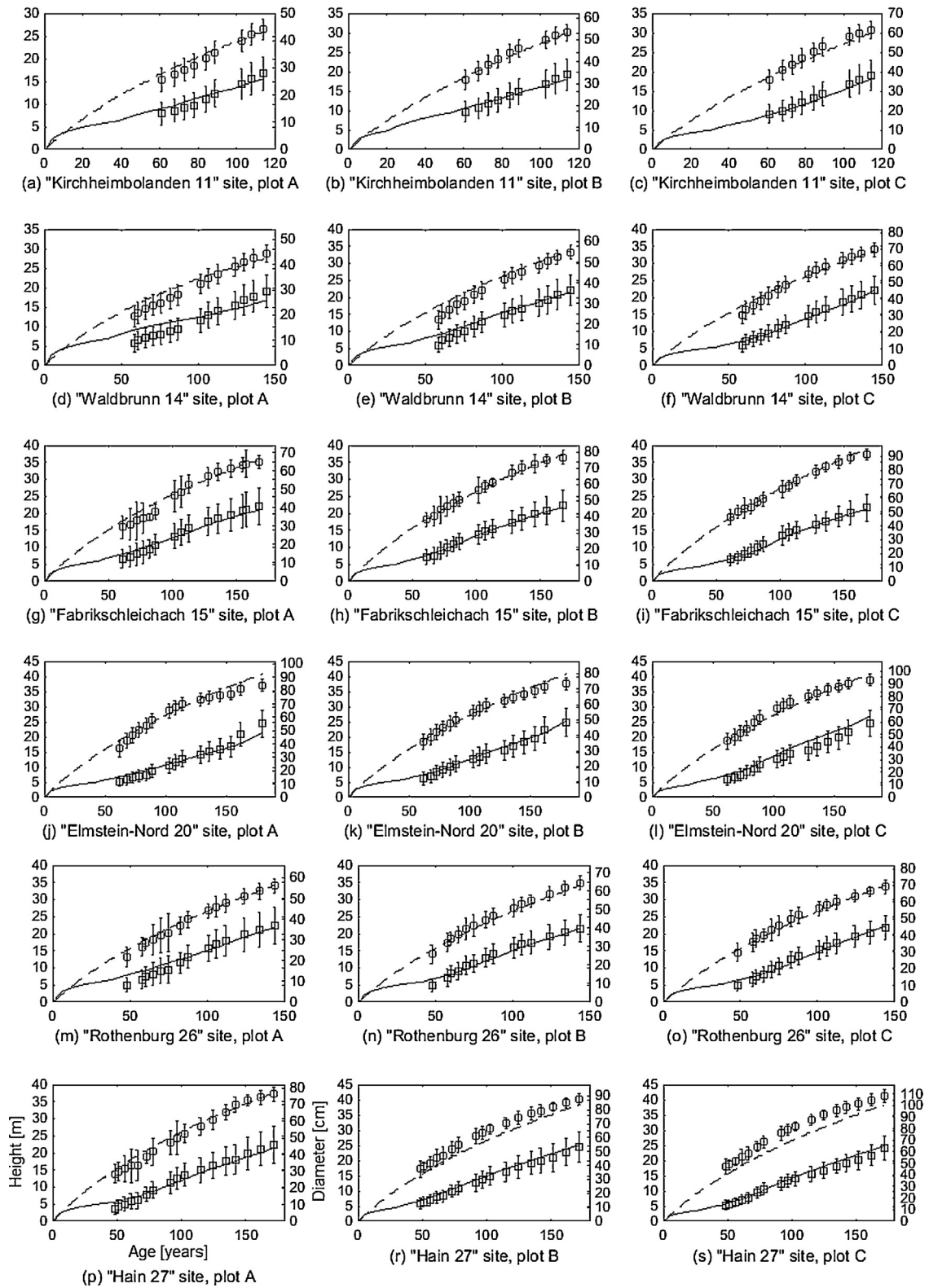
Fig. 2. Comparison of simulated (lines) to empirical (markers) stand average and standard deviation data of tree height (dashed lines and circles, respectively, left axis (m)) and trunk diameter at breast height (solid lines and squares, respectively, right axis (cm)) over time (years) for 18 plots, differing in stand density, on the six sites listed in Table 1.

and

$$Q(n) = \int_{\mathbb{R}^3} B(x, n)\, dx$$

respectively. Fig. 5 shows $\log(Q(n))$ against $\log(M(n))$ for the previous simulations corresponding to the three sub-plots of the "Fabrikschleichach 15" site (results are virtually identical for the other sites). The good linear regressions based on the last 173 (of
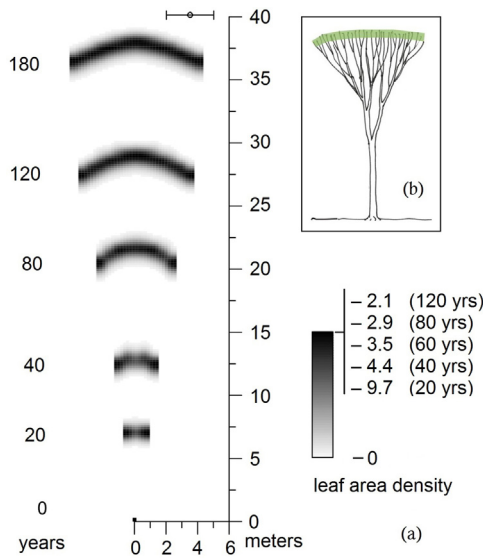
Fig. 3. (a) Vertical cross-section of a simulated crown over time, corresponding to plot C of "Fabrikschleichach 15", along with empirically observed crown radius (mean and standard deviation) available for this site and at 180 years. (b) Schematic representation of the crown structure of adult beech in even-aged pure stands, from Pretzsch (2014).

4. Discussion

4.1. Emergent properties

Based on the concept of leaf area density, we have developed a mechanistic model of tree growth whose spatial dynamics are solely determined by the local growth towards light or, equivalently, biomass productivity. In this simple framework, the model reproduced data used for calibration (Fig. 2g and i) and accurately predicted (Fig. 2a–f, h, and j–s) the growth of European beech over a wide range of even-aged pure stand conditions. In addition, we observed a realistic crown shape emerging in model simulations (Fig. 3). Simulated tree crowns spontaneously self-organise, depending on the competitive situations present in the different plots. This demonstrates the model's adaptability.

For a common set of parameters, the differences in the simulated quantities in Fig. 2 depending on stand density arise from the light gradient principle: The fact that produced biomass is transported locally towards the light will limit the formation of new foliage in regions already shaded by a competitor (as induced by periodic boundary conditions). A reduced horizontal expansion, in turn, brings about an increased self-shading and thus in the medium and long term a reduced biomass production compared to that of a tree under less competition.

The property of the experimental data set that tree height appears to vary only little between the different densities (Fig. 2) has been observed for a reasonable range of stand densities (Lanner, 1985). It is also an emergent phenomenon of the model.

The same applies for the decreasing slope of the tree height curve. With increasing height, increasingly longer soil-to-leaf pathways require more biomass for the formation of the appropriate sapwood pipes according to the pipe model theory – biomass that is not available for foliage. This leads to relatively lower local leaf densities which, in turn, result in a smaller light gradient and thus
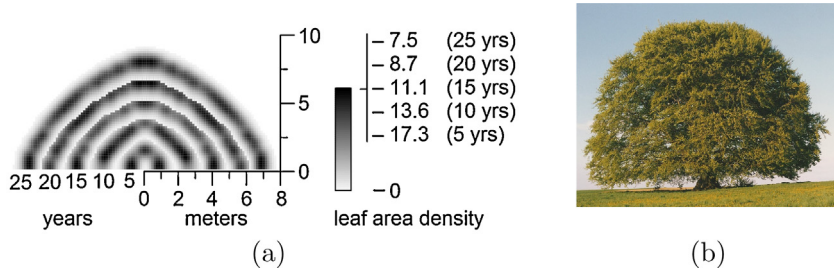
total 180) simulated years yield allometric exponents 0.765, 0.762, 0.773 for the three sub-plot conditions (i.e. high, medium and low stand density), respectively. Including the first 7 growth years in the regression yields slightly deviant exponents 0.787, 0.785, 0.794 respectively. We address the arguable applicability of the model in very early growth stages in Section 4. Altogether, our model simulations are in very good agreement with the desired value of 0.75, especially across different stand density scenarios.

Fig. 4. (a) Vertical cross-section of a simulated singular tree over 20 years. Note the self-similarity of the shapes, which extends to older crowns in equal measure (not shown). (b) *Bavaria-Buche* (Nature Park Altmühltal, Germany, estimated age: 500–800 years).
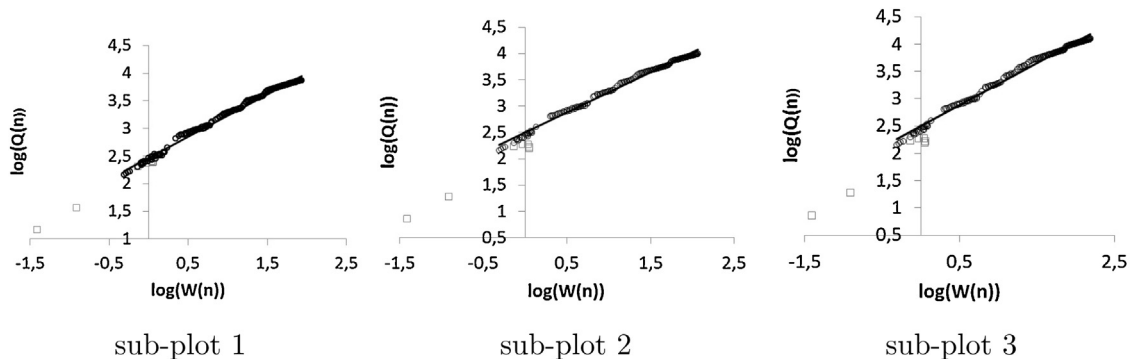

sub-plot 1   sub-plot 2   sub-plot 3

Fig. 5. Logarithms of metabolic rate $Q(n)$ against total mass $M(n)$ for years $n = 1, \ldots, 7$ (□) and $n = 8, \ldots, 180$ (○), the latter with linear regression lines with slopes 0.765, 0.762, 0.773, respectively. In all cases $R^2 > 0.95$. These lines are indistinguishable from suitable ones with slope 0.75.

a decelerated height growth, in terms of our model. In a theoretical analysis, Mäkelä (1986) already linked the pipe model theory to the slowdown of height growth.

One of the most striking features of the model is the emergence of the 3/4-rule, especially across different competitive conditions. We believe our model to be based on less controversial assumptions than the 'WBE models' while at the same time not being less concise. Although we have not been able to derive this property rigorously, we believe that our approach represents a major step in the quest for functional–structural plant models to generate the rule.

4.2. Conclusions

Under the given additional model assumptions, the crown shapes in (Fig. 3a) and off (Fig. 4a) competition – as a matter of fact qualitatively virtually independent of the parameter values – could be regarded as the morphology of a tree whose spatial expansion is solely determined by positive phototropism. This may give a qualitative impression of the extent to which a species' growth follows this principle or, inversely, for which other determinants and architectural constraints are more influential. In particular, it suggests the crown shape of European beech to be strongly determined by the imperative of local growth towards light.

Our model would predict the shape of an at all times perfectly isolated beech tree to be similar to Fig. 4a even in early growth stages – which is not the case. Instead, at early ages, vertical growth dominates horizontal expansion (Krahl-Urban, 1962; Roloff, 2001), pointing out a limitation of the model and indicating that in this phase other growth strategies prevail. The vertical escape from herbivores and even more importantly, other competitors such as grasses and shrubs which are not considered in our model, suggests itself as an explanation (King, 1990; Peters, 1997). Curiously, we observed the same increased allocation of biomass more towards vertical than horizontal growth in our competition simulations (Fig. 3a). This could suggest that this very behaviour is genetically imprinted to such an extent, that, in juvenile stages, it applies whether the tree grows in isolation or not, before eventually, in later stages (seen in Fig. 4), the plasticity in terms of almost unconstrained local phototropism prevails (King, 1990). It could explain the peculiarity of beech to start with rather slim crowns followed by a wider and wider extension as the evolutionary outcome of coping with the selective pressure. We hypothesize that beech, as a late-successional species which has to establish and grow in the deep shade, invests into height growth on the expense of lateral expansion in the early stage. This enables surviving in or even growing out of the understory phase. This strategy of coping with crowding changes completely in favor of lateral extension as soon as beech arrives in the overstory. At this point, its efficient space occupation by lateral extension outcompetes neighbours (Pretzsch, 2006, 2010).

Lastly, the applicability of the model in young stages may be arguable in light of the factual strong impact of topology during very early growth. Spatial foliage distribution at this point could be considered too irregular and sparse for leaf area density to be reasonably applied.

4.3. Perspectives

Our results refer to rather moist sites in the Central European highlands where tree growth is mainly limited by light and the length of the growing season except in the extremely dry years (Pretzsch et al., 2014). In such an environment, a model as ours, with only light as driving factor, may be adequate. However, on dry sites and in drought years especially the tall trees in a stand get limited by water, loose their advantage to pre-empt the light and the understory trees can benefit in relation to their tall neighbours (Wichmann, 2002). Such changes in growth distribution within the population caused by water limitation occur in pure stands as well as mixed stands (del Río et al., 2014) and their simulation requires the integration of water as a driving factor (Roetzer and Pretzsch, 2013). Additional possible sophistications include the refinement of the global light model used here, the radiation use efficiency concept (cf. Demetriades-Shah et al., 1992, but also Arkebauer et al., 1994) and the pipe model, given that the parameter P, which relates leaf mass to sapwood pipe mass, has been argued to, in general, be dependent on tree height and age (Mokany et al., 2003), site quality, stand vigour and density, water availability and average vapor pressure deficit (White et al., 1998). These aspects have been deliberately kept simple in this model version to highlight the effects and range of the key mechanisms.

We focused on European beech for the parameterisation and application of our model because of its particular ecological and economic importance, the uniquely extensive data available for model validation, as well as the empirically shown exceptional phototropic plasticity which complies particularly well with our model assumptions. However, since our general approach is generic, it could be used, after an appropriate parameter re-estimation, to test to which extent the assumption of phototropism being the predominant driver of spatial crown expansion is appropriate for other species as well. While a comparative analysis was beyond the scope of this paper, we hypothesise this to generally be the case for other broadleaved species, whose crowns tend to be similarly rounded, more than for conifers, featuring conic crown shapes. Other growth factors constraining phototropic plasticity, e.g. in relation to the transport system, leaf features (Hallé et al., 1978), reproductive success or mechanical stability (Niklas, 1994), as well as space occupation being influenced by mechanical abrasion in addition to competition for light (Hajek et al., 2015), would have to be added to the existing framework, in order to account for deviations from our current assumptions.

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