



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-Cothorn 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 $u(x, n) \geq 0$ ($\text{m}^2 \text{m}^{-3}$), 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-Cothorn 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 $\text{PAR}(n)$ ($\text{J m}^{-2} \text{y}^{-1}$) 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, $N(x, n) \in S_{\pm}^2$ 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-Cothorn 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-Cothorn 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

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

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 $B(x, n)$ 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,

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