Proceedings of the 7th International Conference on Functional-Structural Plant Models, Saariselkä, Finland, 9 - 14 June 2013. Eds. Risto Sievänen, Eero Nikinmaa, Christophe Godin, Anna Lintunen & Pekka Nygren.
http://www.metla.fi/fspm2013/proceedings. ISBN 978-951-651-408-9.

Modelling Competition in Crop Populations via Reaction-Diffusion Foliage Dynamics. With an Outlook on Tree Modelling

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Highlights: Local leaf area index is considered as a spatially continuous variable, subject to dynamics of allocation, senescence and spatial propagation. This approach allows for inter-individual variability and competition while maintaining robustness – a key shortcoming of comparable models. Simulation results inspire a three-dimensional generalisation towards trees, alongside which an underlying dynamic branch system is devised, targeting finer morphological accuracy.

Keywords: leaf-area index, leaf area density, reaction-diffusion equations, optimisation

INTRODUCTION

Certain individual-based plant models applied in agronomy or forestry rely on a very precise geometric description of the plant, allowing for the radiative fluxes received by each plant organ to be computed by modelling the radiative exchanges in the whole canopy structure (Chelle et al. (2007) provide a review). Generally this geometry is difficult to obtain however and costly in terms of computation. Other approaches make use of competition indices, which are determined for each individual of a population according to the spatial configuration (Cournède et al., 2008; Pretzsch, 2002). Those in turn are usually restricted in terms of accuracy and extrapolation potential due to being based on empirical functions which are typically difficult to calibrate: They require heavy experimental data corresponding to detailed configurations and characteristics of all individual plants in various situations.

Aiming for a robust and adaptive technique to tackle scenarios of inter-individual competition for light, we explore a novel functional-structural approach leaving detailed geometry behind, while preserving macroscopic morphological properties. To this end, the spatiotemporal evolution of foliage is considered to be subject to certain partial differential equations, which stand out due to their inherent dynamic properties of self-organisation and spontaneous adaptation. First, this is done by considering the local leaf area index, LLAI, as the key variable. By contrast to the common LAI, it maps the non-constant course of the function that assigns to each position on the ground below a plant's foliage the number of layers of one-sided green leaf above this particular position. The thus derived model is afterwards tested on an experimental data set of sugar beet. The results motivate to consider in a similar way the LLAI's three-dimensional analogue, the local leaf area density, LLAD, which is embedded in a dynamical system modelling specifically tree growth.

MODEL FRAMEWORK

Let $L=L(x,y;t)$ denote a particular plant's LLAI at a ground position $(x,y)\in\mathbb{R}^2$ and time t. Following Beer-Lambert's law (Nilson 1971), its total biomass production at t reads

$$B(t)\propto PAR(t)\cdot\iint_{\mathbb{R}^2}1-e^{-\lambda\cdot L(x,y;t)}dxdy$$

with an extinction coefficient λ, and PAR denoting photosynthetically active radiation. This quantity is distributed among the plant organs. For the particular case of sugar beet, those are solely its root and its foliage. The respective time-dependent distribution ratios are readily determined empirically. The amount of produced biomass which is assigned to foliage, $B_{foliage}(t)$, is then spatially distributed: Here, this is done in the simple way that newly allocated leaf mass, $all=all(x,y;t)$, is proportional to the already existing amount of L in (x,y). Hence

$$all(t)\propto B_{foliage}(t)\cdot\frac{L(x,y;t)}{\iint_{\mathbb{R}^2}L(x,y;t)dxdy}$$

Leaf senescence, *sen*=*sen*($x,y;t$), is essentially chosen in a similar manner, deducting aged leaves from the set of photosynthetically active green leaves comprised in L.

Lastly and centrally, the spatial propagation of foliage, described by a dynamic flux term $\vec{\phi}$, is chosen according to a classical diffusion approach: It is said to follow foliage's negative gradient while being proportional to allocation. Hence

$$\vec{\phi}(x,y;t) \propto -\nabla L(x,y.t)\cdot all(t)$$

This reflects the morphogenetic idea that a plant tends to form new leaves in brighter rather than darker spots, i.e. those exhibiting lower rather than higher leaf-area surfacic density.

Combining allocation, senescence and this last spatial propagation term results in a two-dimensional partial differential equation, more precisely classifiable as reaction-diffusion equation. Minor adjustments suffice to take inter-individual competition for light, induced by overlapping foliage, into account. The generalisation for a population of plants can thus be derived, resulting in a coupled system of dynamic equations.

SIMULATION AND DATA COMPARISON

The complete model has been confronted to experimental data of three different spatial configurations of sugar beet populations, hence three distinct competition scenarios. Model parameters were partly chosen in accordance with Lemaire et al. (2009), additional ones were computationally estimated. The results are illustrated in Fig 1. The considerably different magnitudes of the production quantities, depending on field density are visibly well accounted for.

We emphasise that the set of model parameters is a single, global one – irrespective of field density. This is a desirable and not last a realistic feature, seeing that the simulated plant's response to a competitive situation is spontaneous, entirely handled by the adaptiveness of the dynamic model equations.

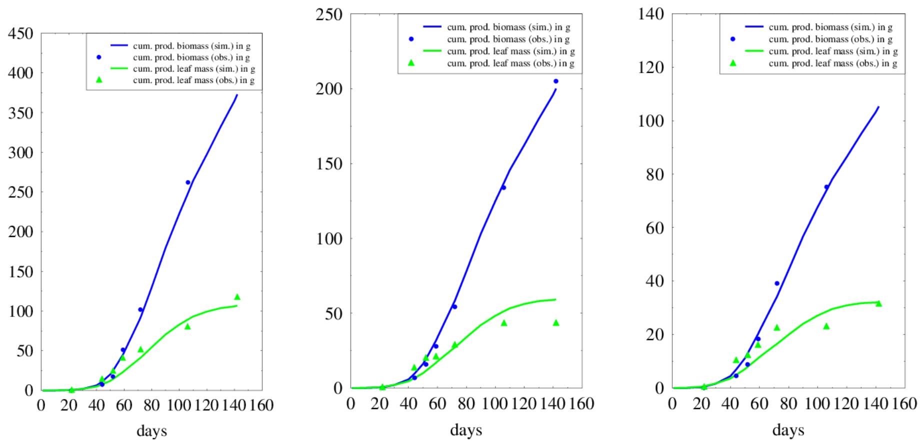

Fig. 1. Model simulation results for densities of arrangements of (from left to right) 5.4, 10.9, 16.4 plants per m^2 field. Shown quantities are per plant.

OUTLOOK: THREE-DIMENSIONAL EXTENSION

The purpose of tackling three-dimensional structure initiates the subsequent exploration of a model extension, developed specifically with a view to trees. The LLAI's three-dimensional counterpart is the local leaf area density LLAD, $L^*=L^*(x,y,z;t)$, defined as the total one-sided surface of green leaves in a ball centred in (x,y,z), at time t, divided by the ball's volume. (Formally, the ball's radius is infinitesimal; while in the context of numerical implementation as well as real data acquisition, cubes are used to prevent overlapping.) Hence $\int_0^\infty L^*(x,y,z;t)dz$ is nothing else but the LLAI in (x,y). Now, L^* can be assumed to be virtually continuous in x,y,z, making it possible to approach it with a similar reaction-diffusion technique as before.

The computation of biomass production is again carried out using Beer-Lambert's law. Yet, while the simplification of vertical light incidence was acceptable for sugar beet, it is not so for trees. Instead, for any given point ($x,y,0$) on the ground and any time t we can now integrate L^* along the line connecting ($x,y,0$) to the sun’s position, and thus compute the intercepted radiation. In this context, the effects of both self shading and of shading by a competitor, placed between the sun and the tree in question, come dynamically into play.

As for the spatial propagation, merely a straightforward transfer of the above diffusion flux is not productive. Instead, an additional element of structural heterogeneity is included to contribute to morphological realism: the tree's branch system. The basic principle, reflected in the respective differential equations, is to retain foliage's tendency to move from darker towards brighter regions – likewise in situations of inter-individual competition –, yet to impose a drift in order for it to remain close to the branch it corresponds to.

Having ticked off foliage dynamics, the dynamics of the branch system are addressed, namely in terms of the questions of the branches' own spatiotemporal propagation and growth, as well as ramification processes.

The former can be approached in terms of a mathematical optimisation problem: We assume that, at any point in time, the (infinitesimal) forward elongation of a branch is chosen to quantitatively optimise the tree's biomass production in the subsequent time step: Since LLAD dynamics are closely coupled to the growth of the branches, any change in the branch structure immediately affects foliage configuration, and thus biomass production. More specifically, the optimisation problem is formulated in the way that the *gain* of a potential elongation, in terms of an increment in future productivity, is weighted against its *cost*. This latter is chosen to be a function of the (infinitesimal) length and of the curvature of the elongation in question, notably taking into account hydraulic constraints.

As for the ramification processes we resort to a concept originally developed in botanical phyllotaxis, which is readily adapted in the present context and conceptually consistent with the further model framework. Brought forward by Snow & Snow (1952), it provides a principle to determine time and location of the formation of a bud at the apex, following the hypothesis that a new bud will only appear along the apical ring when and where there is enough space for it – the notion of 'enough' being related to a dynamic parameter. The principle is readily adapted to the ramification processes of a tree, for which the species-specific parameter evolution in the course of tree growth can be reconstructed by statistical means.

Once produced biomass is determined, as before, it needs to be distributed among foliage and wood. As for local foliage allocation, we assume that the increase of L^* in a position (x,y,z) is proportional to how much foliage at this position contributes to the overall biomass production. Meanwhile, biomass allocation to wood is provided by applying the (simplified) pipe model theory formulated by Shinozaki et al. (1964): For each additional unit of L allocated in (x,y,z), a “wooden” pipe is thought of to be installed, leading from (x,y,z) to the trunk base and below ground. Satisfying this principle determines the ratio of biomass partitioning among foliage and wood uniquely.

CONCLUSION

The two-dimensional LLAI model proved to be suitable for modelling production rates, handling arbitrary competition scenarios self-adaptively – a trait provided by the reaction-diffusion equations approach. The morphogenetic concept of spatial foliage formation, underlying the original model dynamics, has subsequently been utilized in a more complex model framework. This extension, tackling functional and structural properties at equal value for the case of a tree, was sketched and is subject to further exploration.

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