

Competition among plants: Concepts, individual-based modelling approaches, and a proposal for a future research strategy

Uta Berger^{a,*}, Cyril Piou^a, Katja Schiffers^b, Volker Grimm^c

^a*Institute of Forest Growth and Computer Science, Technical University Dresden, P.O. Box 1117, D-01735 Tharandt, Germany*

^b*Department of Plant Ecology and Nature Conservation, University of Potsdam, Maulbeerallee 2, 14469 Potsdam, Germany*

^c*Helmholtz Centre for Environmental Research—UFZ, Permoserstr. 15, D-04318 Leipzig, Germany*

Received 13 April 2007; received in revised form 2 November 2007; accepted 10 November 2007

Abstract

Competition is a key process in plant populations and communities. We thus need, if we are to predict the responses of ecological systems to environmental change, a comprehensive and mechanistic understanding of plant competition. Considering competition, however, only at the population level is not sufficient because plant individuals usually are different, interact locally, and can adapt their behaviour to the current state of themselves and of their biotic and abiotic environment. Therefore, simulation models that are individual-based and spatially explicit are increasingly used for studying competition in plant systems. Many different individual-based modelling approaches exist to represent competition, but it is not clear how good they are in reflecting essential aspects of plant competition. We therefore first summarize current concepts and theories addressing plant competition. Then, we review individual-based approaches for modelling competition among plants. We distinguish between approaches that are used for more than 10 years and more recent ones. We identify three major gaps that need to be addressed more in the future: the effects of plants on their local environment, adaptive behaviour, and below-ground competition. To fill these gaps, the representation of plants and their interactions have to be more mechanistic than most existing approaches. Developing such new approaches is a challenge because they are likely to be more complex and to require more detailed knowledge and data on individual-level processes underlying competition. We thus need a more integrated research strategy for the future, where empirical and theoretical ecologists as well as computer scientists work together on formulating, implementing, parameterization, testing, comparing, and selecting the new approaches.

© 2008 Rübél Foundation, ETH Zürich. Published by Elsevier GmbH. All rights reserved.

Keywords: Individual-based model; Grid-based model; Zone-of-influence; Ecological field; Tessellation; Field-of-neighbourhood

Introduction

Competition is a fundamental process in plant communities. Numerous models have developed as either a tool for understanding or prediction of plant

competitive processes. For many aspects of plant competition, however, population-level models that ignore individuals are of limited value. Plants interact locally, not globally, and competing plants can be very different regarding size and many other aspects, so that considering average individuals does not make very much sense. Moreover, plants, as any organisms, adapt their behaviour, for example growth and development, to changing environmental conditions. Such adaptive

*Corresponding author. Tel.: +49 35203 38 31892;
fax: +49 35203 38 31632.

E-mail address: uta.berger@forst.tu-dresden.de (U. Berger).

behaviour and phenotypic plasticity is hard to capture with population-level models.

Spatially explicit individual-based models are able to take into account local interactions, individual variability, adaptive behaviour, and heterogeneous distributions of resources and other environmental factors (Houston et al., 1988; DeAngelis and Gross, 1992; Grimm, 1999; Wyszomirski et al., 1999). Thus, they are being used in plant ecology for more than 10 years (in forest ecology for more than 30 years; Liu and Ashton, 1995), and several new approaches have been proposed over the last 10 years. It remains unclear, however, how good these approaches are in capturing essential aspects of plant competition. Most existing approaches only focus on the phenomenon of competition, e.g. the effect of local competition on growth, but not on the underlying mechanisms. We therefore are going to ask three questions: (1) What are the established concepts of competition among plants? (2) How well are these concepts taken into account in individual-based simulation models? (3) How should empirical studies, theoretical work, and simulation experiments be combined and developed in the future to improve our understanding of plant competition?

As a reference we use Czárán (1998), who described the state-of-the-art of modelling competition among plants 10 years ago. After summarizing his comprehensive overview, the main purpose of our paper is to review the progress over the last 10 years. Our review is based on a survey in ISI Web of Science from 1997 until February 2007. Although we are aware of the important role of other model types for studying plant competition (e.g., Cox et al., 2000; Law and Dieckmann, 2000; Shackleton, 2002), our review will exclusively deal with spatially explicit IBMs. The reason for this restriction is that, in our opinion, for gaining a mechanistic and comprehensive understanding of plant competition, spatially explicit IBMs will play the most important role.

We will focus on competition, but there is an increasing awareness of the ecological significance of positive interactions among plants, in particular facilitation (e.g., Callaway, 1995; Stoll and Weiner, 2000; Callaway and Pennings, 2000; Bruno, 2003; Brooker et al., 2008). We will not discuss approaches to modelling positive interactions separately, partly because so far only a few studies exist, and partly because most of the modelling approaches discussed in the following can be used for describing both negative and positive interactions.

Concepts and theories of competition among plants

At the level of populations or communities, the focus of studies on competition among plants has usually been

on population-level aspects: (1) density effects, i.e. how the mean size of plants decreases with increasing density; (2) changes in the size structure of the population or community, i.e. the emergence of size hierarchies, and (3) density-dependent mortality ('self-thinning'). Current thinking on plant competition has been based on the following axioms:

- (1) *Exploitation* – Competition implies exploitation of limiting resources in most cases. This is the basic definition of competition: plants compete for limited resources being essential for their life, i.e. light, water, and nutrients. Resource limitation is relatively easy to study for aquatic organisms (e.g., algae) or isolated plant individuals, but difficult for plants in their natural environments.
- (2) *Heterogeneity* – Resources are heterogeneously distributed. The fate of a plant thus depends to a large degree on its local environmental settings (e.g., Aerts, 1999).
- (3) *Modification* – Plants modify resource levels. They decrease for example light availability, may deplete nutrients or take up water from the soil. Thus, they actively change the environmental conditions of themselves and their neighbours (e.g., Stoll and Weiner, 2000). Some modifications can make it easier for other plant individuals to establish, grow, survive, and reproduce. These positive effects are referred to as facilitation (e.g., Callaway, 1995; Stoll and Weiner, 2000; Callaway and Pennings, 2000).
- (4) *Configuration* – Spatial configuration matters. Plant competition usually acts between neighbouring individuals. Thus, the distance between neighbours and their overall spatial configuration are important factors (e.g., Stoll and Weiner, 2000).
- (5) *Symmetry* – Although severe competition for specific limiting factors may occur between species (Mitchley, 1987), plant competition usually is size-specific rather than species-specific (MacArthur, 1972; Goldberg and Werner, 1983). Two modes of competition are distinguished: asymmetric and symmetric competition. Asymmetric competition means that larger individuals have a disproportionate advantage over smaller individuals leading to a growth depression of the latter (Weiner, 1990; Stoll and Weiner, 2000). With symmetric competition, plants share resources equally or proportionally to their size. It is usually assumed that light competition is size asymmetric whereas below-ground competition is size symmetric (Schwinning and Weiner, 1998). However, mechanisms, such as allometry and plasticity, which might modify the degree of asymmetric competition, are still not well understood (Schwinning and Weiner, 1998; Bauer et al., 2004).
- (6) *Below-ground competition* – Both above- and below-ground competition can affect aggregation and

repulsion patterns among plants (e.g., in semi-arid woodland trees [Martens et al., 1997](#)). Plant competition can, however, be different above- and below-ground. Studies on the relative importance of above-ground and below-ground competition trace back to [Donald \(1958\)](#). A meta-analysis of 23 studies revealed that competition is frequently stronger below-ground than above-ground ([Wilson 1988](#)).

- (7) *Adaptation* – Plants adapt to their environment. Here, we use the word ‘adapt’ to refer to developmental plasticity, not evolutionary change. In fertile environments, plants mainly compete for light. Several strategies might be successful: overtop neighbours, use light as effectively as possible, or change morphology. Traits supporting these strategies include the ability of vegetative ramification, high plasticity of crown shapes and physiology ([Schwinning and Weiner, 1998](#)), high turnover rates of leaves, and the production of relatively more leaf area in the top layers ([Aerts, 1999](#)). Some plants may be highly competitive in nutrient-rich habitats because they are able to optimize their allocation of above-ground biomass and/or increase nutrient uptake from the soil.

The role of plant competition in non-fertile environments is still debated. According to [Grime \(1988\)](#), traits for nutrient retention are much more important here than the ability for competitive nutrient uptake in nutrient poor environment. [Tilman \(1988\)](#) argues that competition is common in fertile as well as in unfertile environments, but the relative intensity of above-ground and below-ground competition changes along the gradient. Available data have not resolved this debate, but suggest that the rate of nutrient uptake is less important in non-fertile areas because nutrient supply is limited by the diffusion rate in the soil ([Aerts, 1999](#)). Plasticity in root morphology and adaptive root allocation are thus important traits for ‘searching for nutrients’ either by increasing root lengths or by increasing root biomass. These strategies, however, would only be successful in soils that include nutrient-rich spots.

- (8) *Avoidance* – Plants species evolve strategies for avoiding competition. Strategies such as the use of different time niches, seed production adapted to environmental conditions, or long-range dispersal can decrease resource competition. These different temporal or spatial strategies might be the result of not only competition, but can also be due to other evolutionary factors ([Townsend Peterson, 2003](#)).
- (9) *Interference* – Plants do not only interact via resources – Recent empirical studies revealed that interference competition via, e.g., allelopathy is probably more common than originally thought (see e.g., [Stoll and Weiner, 2000](#) and references therein).

Classical individual-based modelling approaches

There are numerous ways to classify spatially explicit individual-based models describing plant competition. We choose [Czárán’s](#) classification ([Czárán, 1998](#)) where site-based neighbourhood models are distinguished from more complex individual-based models. The first class contains models that represent spatial relationships on regular (hexagonal or squared) lattices or grids, i.e., space is discretized. These models are often referred to as ‘cellular automata’ (CA), or more appropriately as ‘grid-based models’. The second class, individual-based neighbourhood models, contains tessellation models (TM) and distance models. The latter include fixed-radius-neighbourhood (FRN), zone-of-influence (ZOI), and ecological field (EF) models. They all have in common that they consider plant positions in continuous space.

We will now describe both the concepts underlying these modelling approaches and typical features of their implementation. For this, we include specific models as examples and explain their structures and outputs. Our aim is to show advantages and limitations of the approaches rather than to evaluate the models themselves.

Grid-based models

In grid-based models of plant populations, each grid cell might be empty or occupied by one or several plants ([Fig. 1](#), top). Some grid-based models also include the vertical dimension; for example different height classes of plants ([Rademacher et al., 2004](#)) or different soil layers characterized by different moistures ([Jeltsch et al., 1996](#)). A general feature of grid-based models is that within a grid cell space is uniform or averaged. A few grid-based models use more than one cell to represent one plant, usually to represent size differences among individuals (e.g., [Winkler and Stöcklin, 2002](#)), but this approach is not used very often because it loses one of the main advantages of grid-based models, its computational and conceptual simplicity.

Several reviews of grid-based models for modelling plant populations and communities exist ([Baltzer et al., 1998](#); [Caswell and Etter, 1999](#); [Jeltsch and Moloney, 2002](#); [Wang et al., 2003](#); [Molofsky and Bever, 2004](#); [Winkler, 2006](#)). Although often criticized for imposing a certain spatial resolution; the grid-based approach is still one of the most important modelling tools for analyzing plant interaction; pattern formation ([Dunkerley, 1999](#)), plant population dynamics ([Jeltsch et al., 1997a, b](#); [Jeltsch and Moloney, 2002](#)), and landscape dynamics (e.g., [Ostendorf et al., 2001](#); [Fall and Fall, 2001](#); [Perry and Enright, 2002a, b](#)).

[Czárán \(1998\)](#) gives further examples of successful applications of grid-based models in plant ecology.

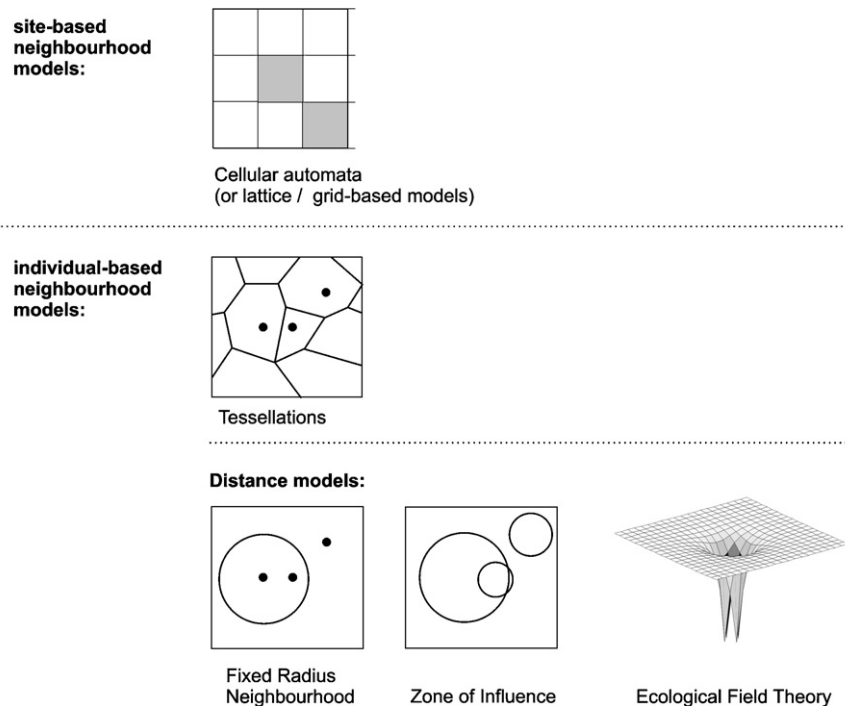


Fig. 1. Graphical representation of approaches to modelling competition among plants. The classification of the approaches follows Czárán (1998). The approaches are explained in the text.

However, he also demands the incorporation of plants' adaptation in response to spatio-temporal patterns in environmental conditions. In recent studies with grid-based models, we did find an increasing number of simulations focusing on the role of adaptation to environmental conditions for population dynamics. Most of these models are restricted to hypothetical species. For example, a simulation study investigating spatial competition between short- and long-distance dispersing plants shows that the outcome of this competition clearly depends on habitat heterogeneity and on the relative costs of the respective dispersal strategy (Hiebeler, 2004). Another study focuses on the joint effect of deforestation and disturbance regimes on plant diversity and community structure in a virtual forest where trees are able to adapt to previous disturbances in terms of variable mortality rates (Malanson et al., 2006). A modification of the classical *Daisyworld* model includes mutations affecting optimal growth temperature and albedo (Wood et al., 2006). In this model, plants can either adapt to changed environmental conditions or alter their environment resulting in a stronger and more regular oscillation of the system. There are also simulation experiments which focus on particular field plots. For example, the forest model TreeMig has been applied to simulate species adaptations to environmental conditions at the Swiss National Forest (Lischke et al., 2006).

In relationship to our above-mentioned concepts of plant competition, in grid-based models *configuration* is

taken into account. However, the consideration of the spatial configuration of neighbourhood plants is biased by the fixed spatial scale imposed by the grid. *Heterogeneity* of resources is ignored within a cell, but can be represented in different grid cells. *Size symmetry* of competition was ignored in early grid-based models. More recent grid-based models, however, make transition rules dependent on the plants' size (e.g., biomass) and can thus indirectly take into account different modes of competition. Grid-based models are flexible enough to include some *adaptations*, e.g., dispersal strategies and variable reproduction. So far, grid-based models rarely differentiate between above-ground and below-ground competition (*below-ground competition*). In general, most grid-based models of plant competition seem to be empirical in the sense that the outcome of the competition does not emerge from specific mechanisms but is more or less imposed by using empirical rules.

Tessellation models

If no sufficient empirical knowledge is available to formulate the empirical rules required for grid-based models, more mechanistic approaches are required. For example, TM (often also referred as Voronoi or Thiessen diagrams) assume that there is a direct linkage between plants' performance and the amount of (spatial) resources at the plants' disposal. For each plant, the smallest polygon is calculated around the

plant using perpendicular bisectors to the lines connecting the centre of the plant to the centres of its competitors (Fig. 1, middle). This polygon includes all points in the area that are closer to the focal plant than to any other. The polygons are mutually exclusive because each point of the plane is exactly assigned to one plant. Usually, the polygons are collectively exhaustive of the total area because the whole plane is subdivided among the plants. However, dynamic TMs also describe the establishment of plants at open areas. In such cases, plants do not cover the whole area initially, but only when they grow and reach each other (for details see Czárán, 1998).

Since TMs link species performance with resource availability, these models have potential for the description of the dynamics of plant systems. In 1998, Czárán concludes that this potential has not been exploited. He suggests the development of dynamic and multi-species TMs including life processes such as establishment, growth, and mortality.

Our literature survey reveals that Czárán's challenge has not yet been accepted. Until now, most studies have used Voronoi diagrams for mapping the distribution of plants as static spatial point patterns. Several papers evaluate plant biomass or growth rate as function of available resources depending on the 'area potentially available' (McInnis et al., 2004; Colombo and Or, 2006). Others investigate the influence of spatial uniformity and aggregation in plant distribution on grain yield or weed biomass (Hühn, 2000; Olsen et al., 2006). Voronoi diagrams have been used to plan root excavations in order to estimate the below-ground biomass of a Eucalyptus hybrid (Saint-André et al., 2005). Thiessen polygons have been used to calculate 'elevation triangles' determining the time a fire needs to spread between neighbouring locations in forests (Vakalis et al., 2004); or to calculate an indicator of asymmetric competition (Bauer et al., 2004). However, within these studies, the tessellation approach is 'only' another static application and cannot be considered as an improvement of TMs as demanded by Czárán.

TM are appealing at least in their simple handling of *configuration*. Although the approach seems to have a large potential for describing the dynamics of plant populations and communities, currently available models are static. They still do not address the other concepts that we listed above, probably because of technical difficulties in making the approach dynamic (see Galitsky, 1990).

Distance models

Tessellation models make the assumption that plants use the area available to them exclusively, but space used by plants is not necessarily exclusive. Root systems

of neighbour plants are often not distinguishable from each other. The projections of neighbouring tree crowns also frequently overlap. In order to consider the effect of neighbouring plants on the area used by a focal plant, so called 'distance models' are more suitable (Czárán, 1998).

Fixed-radius-neighbourhood (FRN)

In fixed radius models, a circular area is assigned to each plant (e.g., Pacala and Silander, 1985). Plants whose centres are located within this area are counted as neighbours (Fig. 1, bottom). The radius of the area is arbitrarily chosen, but corresponds usually to the typical horizontal extension of the species' adult individuals. The focal plant is only affected by its neighbours. The survival and fecundity of the focal plant decrease with the density of neighbour plants. Germination probability is also often modelled as a function of neighbour density. Dispersal is mostly defined by probability functions describing a symmetric distribution of the seeds around the centre of the mother plant.

FRN models are easy to implement, but their main advantage is probably their relatively easy parameterization. It can be obtained by field experiments (measuring plant density and growth rates of plants) from a single generation. Czárán (1998) thus sees FRN models as a good link between field experiments and theory. He concludes "it would be interesting to see many data from such single-species and multi-species field experiments" to test the reliability of the predictive power of FRN. We therefore surveyed the literature for such studies published since 1998.

We found numerous empirical studies carried out in terrestrial forests where point-to-tree distance techniques (also known as k-tree or fixed count sampling) are established sampling methods for inventories and ecological surveys (e.g., Kleinn and Vilcko, 2006a,b). The FRN method has been used, for example, to estimate the effect of weed control and fertilization on the survival and growth of four pine species (Amishev and Fox, 2006), or to quantify competitive interactions in sub-boreal birch-spruce forests depending on topography (Green and Hawkins, 2005).

The FRN models consider local neighbourhood competition but only in terms of neighbourhood density neglecting the concrete *configuration* which is the specific locations of individuals within their neighbourhood. We did not find a model application dealing with the other concepts of plant competition mentioned above. Particularly *heterogeneity* of resource distributions is usually ignored because FRN models assume homogeneous abiotic environmental conditions and an isometry in dispersal mechanism and individual interactions. Moreover, the 'binary' nature of the neighbourhood definition seems to be too coarse in many situations: plants growing inside a fixed radius of a focal plant have a full

effect on the performance of this plant, whereas plants outside do not have any effect. In reality, however, the effect of neighbour plants usually decreases with distance. The so called ‘zone-of-influence’ models consider such effects plant by plant (e.g., Bonan, 1991).

Zone-of-influence models (ZOI)

Here, again a circular zone around the centre of each plant is assumed. In contrast to FRN models, however, the radius is not fixed but usually depends on the size (age or biomass) of the plant (Czárán and Bartha, 1989; Wyszomirski et al., 1999). It is assumed that a ZOI represents the area from which a plant exploits resources. Plants with overlapping ZOI are neighbours (Fig. 1, bottom). The size of the overlapping area defines the competition intensity between both plants, so that *configuration* is taken into account. In most models, the growth rate of a plant decreases with increasing ZOI overlap. So-called ‘collision rules’ define whether competition effects among multiple plants are simultaneously or sequentially considered (Czárán, 1998). Furthermore, ZOI models can consider *symmetric* or *asymmetric* competition. For example, it might be defined that the larger plant gets all resources within its zone which can lead to the death of all neighbours (asymmetric competition), or that all involved plants suffer equally from sharing resources (symmetric competition; see e.g., Benjamin, 1999; Weiner et al., 2001; Stoll and Bergius, 2005 for implementation details).

ZOI models have been successfully applied for investigating theoretical problems of plant ecology such as the coexistence of species with similar ecological demands. For example, Czárán and Bartha (1989) study the importance of local interactions and short-range dispersal on plant co-existence and periodical community pattern during the re-colonization of a coal mine in northern Hungary by weeds. Czárán (1998) consequently concludes that ZOI models can provide theoretical insights and indicators for ecological processes behind spatial distribution patterns of plants. However, he also mentions that ZOI models usually cannot provide a final proof whether their processes are really the ones that drive these patterns. He therefore calls for a systematic test of different hypotheses about the influence of other dynamic processes such as invasions.

We checked whether ZOI models were applied to such issues during the last decade and found several cases. For example, simulation experiments revealed the relative effects of competition modes among neighbour plants, the spatial distribution of plants, and plant density on the size variation in plant populations (Weiner et al., 2001). This study was a response to a previous similar work of Bonan (1991). Another simulation experiment focusing on local competition among *Arabidopsis thaliana* plants explains the forma-

tion of spatial patterns of plant distribution depending on different competition modes ranging from symmetric to asymmetric competition (Stoll and Bergius, 2005). This study includes a comparison of model predictions with the results obtained by field experiments. It shows that asymmetric competition drives density-dependent mortality and, subsequently, the formation of regular patterns during the development of *A. thaliana* populations. Benjamin (1999) incorporates three contrasting rules to quantify the partitioning of crop dry matter between individual plants in a ZOI model. These rules were based on different assumptions about competition modes (see e.g., Thomas and Weiner, 1989). The first rule mimics equal resource sharing and thus symmetric competition. The second rule assumes that dry matter is partitioned proportionally to the relative abundance of the plants representing relative-size symmetry of competition (Weiner, 1990). According to the third rule, shoot crowns increase in height in presence of neighbours (Weiner, 1990). In consequence, these plants attain more light. Simulation results were compared with growth experiments observed in carrots (*Daucus carota* L.). They support the hypothesis that plants are able to modify their growth through morphological adaptations in response to neighbour competition (concept *adaptation*).

The description of resource sharing among neighbouring plants is a specific strength of ZOI models. Using different layers for the description of plants and abiotic factors, such models can also consider the effect of gradients or heterogeneities, e.g., in nutrient availability or water supply (e.g., Wiegand et al., 2006).

Models applying ecological field (EF) theory

This approach takes another step forward. Plant competition is described via an EF that represents the effects of neighbouring plants on the resources available for a focal plant (Fig. 1, bottom; Wu et al., 1985). The EF is defined by one or a few equations (Czárán, 1998; Miina and Pukkala, 2002) that take into account the distances and the sizes of the involved plants. Applied around a focal plant, they result in an ‘influence region’ characterized by a relative availability of resources such as water, nutrient concentration, or light availability. Thus, this approach takes into account the concepts *configuration*, *heterogeneity*, and *modification*.

However, model parameterization is difficult because the influence of a single tree on resource availability at every point can hardly be measured where several plants affect a focal plant simultaneously. Thus, ordinary statistical methods are not suitable for estimating the parameters of the EF functions. This challenge has been a main difficulty of EF models. Czárán (1998) considers this, together with high computation times required and the importance of spatial stochasticity in real systems, as the main reason for the fact that EF models have been

restricted to small spatial scales (Wu et al., 1985). Therefore, we investigated the development of EF models over the last decade.

We found two promising studies. In the first one, Miina and Pukkala (2002) derive two competition indices from EF theory for predicting the diameter growth of Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*). The first index calculates the influence of each competitor on the location of the focal plant as a function of the competitor's stem diameter, height and distance, and the height of the focal tree. The resulting influence function decreases exponentially with the distance between the trees. The second index is the spatial integral of the first index, and predicts distance-dependent growth of both species with higher precision.

This study shows both at a species-specific and at a general level that EF models can be parameterized in principle. But the question remains whether such models can be used to simulate larger plant systems in a reasonable time frame. For this, Feagin et al. (2005) present an interesting solution in form of a hybrid model. They use a CA for analysing pattern formation of sand dune plant succession. The model describes plant species locations and environmental gradients at the resolution of the grid. Local neighbourhood interactions were related, however, to the ZOI concept, EF theory and the 'field-of-neighbourhood' (FON) approach.

Recent modelling approaches

Since 1998, three new modelling approaches have been developed to address concepts of plant competition that have been neglected or only roughly considered by the approaches described so far. These are models that

(i) emphasize the three-dimensional (3D) architecture of plants and their environment, (ii) use the so-called field-of-neighbourhood (FON) approach to go beyond ZOI models while avoiding the complexity of the EF approach and (iii) are based on the so-called particle-in-cell (PIC) approach.

Since the early presentation of the SORTIE forest model (Pacala et al., 1993), models that consider competition explicitly in three dimensions became increasingly important. Most of them are forest simulators, probably because of the specific importance of light competition among large-growing individuals such as trees. The majority of these models focuses on above-ground competition and ignore *below-ground competition*. We will discuss this issue below.

3D models

These models, which so far are all forest models and include the so-called process-models (Bossel, 1996), not only describe the tree's horizontal locations but also represent their 3D architecture, e.g., crown height, depth and radius (Fig. 2, left; e.g., West, 1993; Ditzer et al., 2000; Bartelink, 2000). The light regimes above forest canopies can be explicitly calculated based on daily and seasonal movements of the sun (e.g., Pacala et al., 1993; Deutschman et al., 1999; Chave, 1999). Such models do not describe light competition via competition indices but rather through local light availability beneath the crowns of the trees. They refer to the competition concepts *heterogeneity* and *modification*.

The FON approach

The FON approach was developed for forests (Berger and Hildenbrandt, 2000) and has also been applied to hypothetical plant populations (Bauer et al., 2002, 2004)

description of two competing trees:

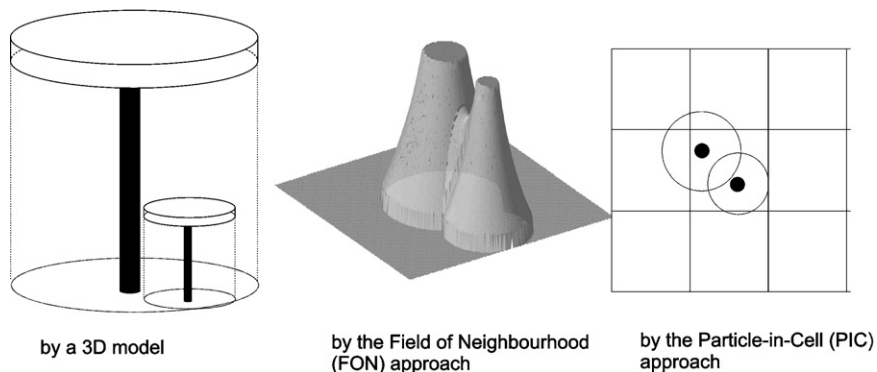


Fig. 2. Graphical representation of three new approaches to modelling competition among plants that were developed over the last 10 years. See text for explanations.

and even animal movement (Piou et al., 2007). The approach was first implemented in a simulator for mangrove forests (Berger and Hildenbrandt, 2000, 2003), which are generally characterized by scarce data on individual tree growth and annual tree response to local competition and environmental settings.

The FON approach is an extension of the ZOI approach. It describes the spatial location of each plant explicitly. A size-dependent circular zone around the plants' position marks the area within which a plant interacts with its neighbours. In contrast to a ZOI model, an FON is defined as a scalar field that decreases conically from its centre to its boundary (Fig. 2, middle). At each point on plants' ZOI, the FON describes the potential impact on a neighbouring plant. Thus, to calculate the influence of neighbours on a focal plant, the total FON of all neighbours on the ZOI of the focal plant is determined and then used to reduce the potential maximal growth rate of this plant by a factor representing neighbourhood competition.

Due to the shape of the scalar field, this approach not only allows the consideration of resource sharing among plants but also the influence of the concrete local constellation of the plants on their resource use (*configuration*). Berger and Hildenbrandt (2000) do not specify the meaning of the FON in terms of resources but describe it as a general decrease in competition pressure with increasing distance from the centre of the plant. But it is possible to relate the FON to specific resources: in a model addressing secondary succession of neotropical mangroves, Berger et al. (2006b) relate the FON directly to competition for light and nutrients. Moreover, Alsweis and Deussen (2005) use not only one FON to describe neighbour competition but two FONs and assign above-ground competition effects and below-ground competition effects to them (*below-ground competition*). Other applications, which do not necessarily focus on plant competition, show the high potential of this modelling approach. For example, Piou et al. (2007) use FON for the description of competition among mangrove crabs *Ucides cordatus* and investigate the relative importance of local crab interactions for recovery patterns after crab fishing.

The FON approach can – as any other approach that has to recalculate neighbourhood at every time step – be limited by run-time limitations because computation time increases exponentially with the number of plants. On current personal computers, several thousands of plants seem to be the upper bound, but there are algorithms for searching for neighbours in a certain radius that depend only logarithmically on the number of plants. For example, so-called Hilbert R-trees (Hildenbrandt, 2003) provide a very quick search of objects with dynamic data structures in overlapping and non-uniform-sized regions (Guttman, 1984; Arge et al.,

2004). A similar approach for searching for neighbours in databases is discussed by Bustos et al. (2006).

Although it has not been used in that context so far, FON has the potential to bridge between ZOI and EF models. In principle, FON provides the simultaneous calculation of changes in environmental conditions with plant growth using the spatial resolution of a plant (*modification*). It appears that not computer technology but empirical knowledge is the limiting factor here.

Despite the flexibility of the FON approach, its main limitation seems to be that both FON interactions and R-trees require quite complex implementations. Therefore, Bithell and Macmillan (2007) introduce an alternative and simpler approach to ecology, the so-called till-based or particle-in-cell approach.

The particle-in-cell (PIC) approach

This approach has been widely used for physical problems such as fluid modelling (Harlow, 1957, 1964; Munjiza, 2004) or hydrodynamics of particles (Koumoutsakos, 2005), but only recently has been proposed as a means to overcome certain limitations of grid-based models in ecology (Bithell and Macmillan, 2007). In grid-based models, imposing a basic spatial scale by choosing a certain cell size can be problematic if individuals are much smaller than cell size so that many individuals can be located in the same cell. The alternative to grid-based approaches – a continuous representation of space, as in the ZOI and FON approaches – is limited to representing only a few thousand individuals, because computation time for identifying neighbours increases quadratically with the total number of individuals. PIC provides a compromise between grid-based and continuous approaches. In the basic PIC approach, individuals within a cell have a continuous location and are maintained in a list (Fig. 2, right). In a modified version of PIC, no overall grid is maintained any more, but only a list of those grid cells that contain individuals. Grid cells can have irregular shapes similar to Voronoi diagrams or regular ones. The interaction distance can be larger than the PIC cells. Also interaction areas can have any shape (James et al., 2004). This modelling approach provides the advantage of a relatively simple implementation like CA models (see examples for JAVA code in Bithell and Macmillan, 2007). However, in contrast to grid-based models, they fully consider the spatial information coded in the location of plants (*configuration*). It seems that PIC is not an exclusive alternative to spatially continuous approaches like ZOI and FON, but an implementation method that tries to combine the computational effectiveness of grid-based models with the advantages of ZOI, FON, or any other distance model.

Discussion

The purpose of our review was to summarize the most important concepts dealing with competition among plants and to check how well these concepts are represented by the different individual-based modelling approaches. In the following, we first will summarize the most important gaps in the state-of-the-art that we identified. Then, we will discuss how these gaps can be filled.

State-of-the-art

Our comparison to the review provided 10 years ago by Czárán (1998) shows that during the last decade no individual-based approach for modelling competition among plants has appeared that can be considered to be substantially new. Rather, existing approaches have been refined or blended. Due to this development, almost all established concepts of plant competition can now be addressed by one or more of the different approaches albeit with different levels of detail (Table 1). The increasing technical potential of individual-based models now provides the power for simulation experiments to test different concepts and assumptions. However, whereas some of the concepts of plant competition are already well represented by various modelling approaches, others are only rather vaguely represented, in particular *modification*, *adaptation*, and *below-ground competition*.

Modification – To date, IBMs describe in detail the effect of abiotic conditions on the performance of individual plants that influences their competition strength. The opposite direction, namely the ecological impacts of plants on their abiotic environment, and in particular effects on local resource levels, usually is ignored. There still seems to be a large gap between the individual-based approaches considered in our review that are focused on organisms and their performance in the context of population dynamics and biogeochemistry that has its focus on physiology and the flow and storage of nutrients and other limiting resources. A further effect of modification, namely an improvement of the local environment for other individuals – i.e., facilitation – so far has also received only little attention in IBMs (Brooker et al., 2008).

Adaptation – Phenotypic plasticity and adaptive behaviour should become increasingly considered in IBMs (Grimm and Railsback, 2005). Morphological plasticity, however, is seldom considered although it is a common response of plants, e.g., to heterogeneity in light availability. Models describing explicitly the growth of single trees have this feature but – for technical reasons – have been seldom applied to whole populations or communities (e.g., Hanan and Prusinkiewicz, 1996; Perttunen et al., 1996; Godin, 2000, also see Takenaka, 1994).

The ZOI and FON models use circular areas and do not switch to asymmetric shapes of the projection areas of the plants. Even 3D models, which calculate changes in crown extensions depending on the concrete shading situation by the neighbours, do usually not vary the symmetry of the crowns. However, Casper et al. (2003) have outlined an approach that allows for modelling how plants develop non-circular zones of influence, for example root systems or crowns, in response to neighbour plants and heterogeneities in abiotic conditions. Using recent advancements in computer technology (e.g., Prusinkiewicz et al., 2001; Alsheis and Deussen, 2005; Deussen and Lintermann, 2005), a consideration of these plant characteristic is possible and could improve our understanding how plant strategies for avoiding local competition influence, e.g., vegetation structure and species composition.

Below-ground competition – The majority of models describing local competition mechanistically focus on above-ground competition and particularly on light competition. Modelling approaches adapted to below-ground competition like FON describe this process either implicitly or phenomenologically. Due to the complicated methodology required, only a few empirical studies have been focusing on root competition in comparison to light competition. Nevertheless, this aspect has attracted more and more attention during the last years. A reflection of this development in IBMs can be expected but should not result in a separation of models focusing on above-ground or below-ground competition.

Filling the gaps: a research strategy for the future

Why are the three concepts *modification*, *adaptation*, and *below-ground competition* less well represented in individual-based modelling approaches than the other concepts dealing with competition? Do they reflect a limitation only in ecological modelling, or a more general limitation? We believe that these limitations reflect a general lack of knowledge, data and understanding that can only be overcome by a research strategy that integrates field studies, experiments, and modelling.

In order to set up a future research strategy, the general needs and research aims in population and community ecology have to be specified and formulated. We think that there are two main tasks for researchers (which cannot be considered separately however): the further development of ecological theory, on the one hand and promoting a predictive understanding of population and community dynamics on more applied fields of research, on the other hand. In the context of theory building, IBMs are specifically useful for investigating the role of inter-individual variability in

Table 1. Overview about the concepts about plant competition explained and whether they were addressed by studies using modelling approaches discussed in this paper

S. no.	Concept	CA	TM	FRN	ZOI	EF	3D	FON
1	Exploitation	Yes	Implicit	Implicit	Implicit	Yes	Yes	Implicit
2	Heterogeneity	Roughly with grid resolution	No	Possible	Not frequent but possible	Yes	Yes	Yes
3	Modification.	Sometimes	No	No	No	Yes	Yes	Yes
4	Configuration	Forced by grid neighbourhood	Yes	No, only plant density	Yes	Yes	Yes	Yes
5	Symmetry	Defined by transition rules	No	No	Yes	Yes	Yes	Yes
6	Below-ground competition	Sometimes	Possible	Possible	Implicit	Yes	Mostly above-ground	Yes
7	Adaptation	Yes	No	No	Yes	No	Possible	Possible
8	Avoidance	Yes	No	Possible	Yes	Possible	Yes	Yes
9	Interference	Possible	No	Possible	Possible	Possible	Not addressed	Possible

CA – cellular automaton, TM – tessellation model, FRN – fixed-radius-neighbourhood, ZOI – zone-of-influence, EF – ecological field, 3D – models describing spatial complexity three-dimensional, FON – field-of-neighbourhood. The point-in-cell (PIC) approach is not listed because we consider it as a search algorithm improving modelling performance rather than as a modelling approach by itself.

all aspects like size, life-history traits, location in space, or genotypic and phenotypic characteristics for population and community dynamics. The aim we formulate for more applied research is to develop a framework for more mechanistic, individual-based models that can easily be parameterized with field data and that can be used as a module for predictions under a changing environment. Some useful approaches already exist (as seen above), but still can be improved and have to be promoted for a wider use.

In the following, we list the four most important issues that need to be addressed for developing a more comprehensive and predictive framework for individual-based modelling of plant competition:

(1) *Incorporating additional processes that might be important for population and community dynamics* – As shown in State-of-the-art some processes of competition that have been shown to affect population dynamics in empirical research have not been comprehensively considered in individual-based modelling approaches so far, i.e. *modification*, *adaptation* and *below-ground competition*. Micro-evolution and genetic differences and dynamics might be further issues. With the existing modelling approaches and fast computers it is technically possible to include these processes and explore their ecological significance. It should be kept in mind, however, that it has to be tested whether the higher complexity of the resulting models is needed for reliable results (see paragraph on model selection

below). A further direction for modelling plant interactions is to also consider positive interactions, such as facilitation. Understanding positive interactions might be critical in many plant communities. However, modelling facilitation does not necessarily require inventing completely new approaches. Some of the existing approaches can equally well be used for negative and positive interactions, in particular grid-based, FON and PIC approaches.

(2) *Model parameterization with field data* – Parameterization is a key to the success of individual-based models. The original individual-based JABOWA forest model (Botkin et al., 1972; Shugart, 1984; Liu and Ashton, 1995) was rather unrealistic in many aspects, but it is not only conceptually very simple but also relatively easy to parameterize (A. Huth, personal communication) because the necessary data are easily accessible. This aspect is still important. While numerous studies exist that provide easily accessible data (e.g., the number of seeds or the survival rate of seedlings), empirical studies that provide data to parameterize more mechanistic models (e.g., for parameterizing the shape of the zones of influence) are sparse. There are, however, some approaches that indirectly estimate plants' zones of influence by evaluating the effects of neighbours on the fitness of the target individuals (e.g., Damgaard et al., 2002; Purves and Law, 2002 and Schneider et al., 2006). Also, studies exist that focus directly on soil–plant interactions. For example, the nutrient amounts taken up by a plant at

different distances can be determined by injecting nutrient tracers at different distances from a target plant into the soil. Such studies provide a quantitative estimation of the shape of the influence kernel in terms of resource uptake (Casper et al., 2003). Data like these are highly useful for modelling plant interactions and – being available for a whole range of species – would certainly improve the development of powerful IBMs. However, it would be desirable to detect more easily accessible variables of the plants that may work as surrogates for the size and shape of interaction kernels for different species or plant functional types.

Besides the availability of data the parameterization itself can also be improved. New approaches for connecting models with data – e.g., Bayesian modelling (Schneider et al., 2006), should be considered when opting for method of parameterization. Also the different methods for inverse modelling may be especially useful for parameterizing interaction kernels, for example by fitting IBMs to entire sets of patterns that were observed on different spatial, temporal, and hierarchical scales. Pattern-oriented parameterization as employed by Wiegand et al. (2003, 2004), which can also be referred to as Monte-Carlo filtering, has been shown to be powerful for parameterizing grid- and individual-based models of plant and animal population dynamics. The idea of this method is that information about, e.g., the interaction kernel is reflected in different patterns, such as spatial distributions, size distributions, or the response to disturbances. By trying to find combinations of submodels and parameter sets that allow a model to reproduce all these patterns simultaneously, uncertainty about parameters and the most appropriate representation of certain processes can be greatly reduced.

- (3) *Model validation* – Also in this field empirical data are highly needed. An optimal strategy would be to combine the collection of process data (e.g. nutrient uptake of an individual plant) with an independent measure of individuals' responses (e.g. fitness) to their local conditions such as the size or location of their neighbours. Process data are essential for the description and parameterization of the ecological processes in the model. Data on the 'outcome' of these processes at the level of individuals provides a means for validating whether the model catches the processes adequately.
- (4) *Model selection* – The 3D, FON, and PIC models are examples of a more general trend in plant ecology towards a higher complexity of the models. Focusing on applied aspects and particularly on a forecast of ecosystems' responses to environmental changes, this development of simulation models seems to be reasonable. However, a higher complexity of models

has its price. It is connected with difficulties in parameterization and evaluation of model function. In this context, pattern-oriented modelling (POM) is a promising strategy to optimize overall model complexity while maintaining structural realism. The POM approach is based on systematic and repeated analyses of spatial and temporal patterns observed in nature and in simulation experiments. A model structure is chosen that in principle allows the same set of patterns to emerge in the model that has been observed in real systems. Then, to identify the most appropriate set of submodels describing key processes, statistical methods can be used for comparing real and predicted patterns (Grimm et al., 2005; Grimm and Railsback, 2005).

An important element of a future research strategy for individual-based modelling of plant competition would also be to develop methods that are analogous to model selection in statistics or for very simple ecological models (Schneider et al., 2006). This would help in making simulation modelling more rigorous and in finding the most parsimonious models.

In general, the diversity of IBM provides an excellent environment for comparing model structures and their implications. Like Odysseus trying to avoid both monsters, Scylla and Charabydis, modellers always have to compromise between 'Ockham's Razor' on the one hand (Bugman et al., 2001; Busing and Maily, 2004; Reynolds and Ford, 2005), which says we should always go for the most parsimonious explanation, and the algorithm of theory development proposed in 1321 by Walter of Chatton: "If three things are not enough to verify an affirmative proposition about things, a fourth must be added, and so on." (cited after C. Topping, personal communication).

The future research strategy should be based on a comprehensive list of all processes that are potential candidates for explaining a certain pattern at the population level. The 'theory development cycle' described by Grimm and Railsback (2005), could then, in combination with new methods of model selection, be used to identify those submodels or theories of how plants interact that outcompete other theories in reproducing multiple patterns observed in real plant populations and communities. It should be noted, however, that model selection will usually have to focus on different submodels, for example different representations of the ZOI or FON. Comparing entirely different models, for example grid-based and FON, is less productive, because the underlying assumptions, and the questions addressed, are usually too different for a direct comparison (also see Hendry et al., 1996). In any case, a common framework for describing individual-based models of plant systems would be a prerequisite for the successful implementation of our

future research strategy. Such a framework for model documentations already exists: the so-called ODD protocol (overview, design concepts, details; Grimm et al., 2006).

Conclusions

Of course it is always easy to conclude that more complex models are needed to overcome the current lack of understanding and knowledge in a certain field of research. But we are not arguing for more complexity per se – predictive IBMs of plant competition of the future might in fact be rather simple – but for a more comprehensive and systematic development, parameterization, and analysis of IBMs that try different representations of the most important aspects of competition among plants. This research strategy would have at least two benefits: it would make modelling and model testing more rigorous and less *ad hoc*, and it would force us to combine the skills from different disciplines. Due to increasing model complexity, the technical and scientific requirements increase so that there is an urgent need for a stronger co-operation of empirical and theoretical ecologists, computer scientists, statisticians, and specialists in computer graphics. Moreover, ecologists and modellers that focus on different plant systems need to collaborate more closely and exchange their ideas. For example, the improvement of forest simulators developed for terrestrial forests could stimulate a more detailed consideration of light competition in mangrove forests (Courbaud, 2000; Ditzer et al., 2000; Bartelink, 2000). Vice versa, mangrove forest models are well designed for considering gradients in abiotic factors and different dispersal strategies of plants (Chen and Twilley, 1998, 1999; Twilley et al., 1999; Berger and Hildenbrandt, 2000; Berger et al., 2006a), which are often ignored in terrestrial systems.

It should be noted that our review is about individual-based modelling approaches, because we believe that for a mechanistic understanding and for the ability to predict the response of plant systems to environmental changes, these types of models is indispensable. This does not, however, deny the important role of other types of models. Simple, analytically formulated models will continue being important for developing new ideas and concepts, and for demonstrating the significance of key factors.

Acknowledgements

We would like to thank Dirk Lohmann for providing important references and two anonymous referees for very useful comments and suggestions. Detailed sugges-

tions by Kirk A. Moloney improved the manuscript. K.S. acknowledges support from the German Science Foundation (JE 207/3-2).

References

- Aerts, R., 1999. Interspecific competition in natural plant communities: mechanisms, trade-offs and plant–soil feedbacks. *J. Exp. Bot.* 50, 29–37.
- Alsweis, M., Deussen, O., 2005. Modeling and visualization of symmetric and asymmetric plant competition. In: Galin, E., Poulin, P. (Eds.), *Eurographics Workshop on Natural Phenomena*. The Eurographics Association, pp. 1–7.
- Amishev, D.Y., Fox, T.R., 2006. The effect of weed control and fertilization on survival and growth of four pine species in the Virginia Piedmont. *Forest Ecol. Manag.* 236, 93–101.
- Arge, L., deBerg, M., Haverkort, H.J., Yi, K., 2004. The priority R-tree: a practically efficient and worst case optimal R-tree. In: *Proceedings of 2004 ACM SIGMOD International Conference on Management of Data*, ACM Press, New York, pp. 347–358.
- Baltzer, H., Braun, W.P., Kohler, W., 1998. Cellular automata models for vegetation dynamics. *Ecol. Model.* 107, 113–125.
- Bartelink, H.H., 2000. Effects of stand composition and thinning in mixed-species forests: a modeling approach applied to Douglas-fir and beech. *Tree Physiol.* 20, 399–406.
- Bauer, S., Berger, U., Hildenbrandt, H., Grimm, V., 2002. Cyclic dynamics in simulated plant populations. *Proc. R. Soc. B—Biol. Sci.* 269, 2443–2450.
- Bauer, S., Wyszomirski, T., Berger, U., Hildenbrandt, H., Grimm, V., 2004. Asymmetric competition as natural outcome of neighbour interactions among plants: results from the field-of-neighbourhood modelling approach. *Plant Ecol.* 170, 135–145.
- Benjamin, L.R., 1999. A comparison of different rules of partitioning of crop growth between individual plants. *Ecol. Model.* 115, 111–118.
- Berger, U., Hildenbrandt, H., 2000. A new approach to spatially explicit modelling of forest dynamics: spacing, ageing and neighbourhood competition of mangrove trees. *Ecol. Model.* 132, 287–302.
- Berger, U., Hildenbrandt, H., 2003. The strength of competition among individual trees and the biomass-density trajectories of the cohort. *Plant Ecol.* 167, 89–96.
- Berger, U., Adams, M., Grimm, V., Hildenbrandt, H., 2006a. Modeling secondary succession of neotropical mangroves: causes and consequences of growth reduction in pioneer species. *Perspect. Plant Ecol., Evol. Syst.* 7, 243–252.
- Berger, U., Adams, M., Grimm, V., Hildenbrandt, H., 2006b. Modeling secondary succession of neotropical mangroves: causes and consequences of growth reduction in pioneer species. *Perspect. Plant Ecol., Evol. Syst.* 7, 243–252.
- Bithell, M., Macmillan, W.D., 2007. Escape from the cell: spatially explicit modelling with and without grids. *Ecol. Model.* 200, 59–78.
- Bonan, G.B., 1991. Density effects on the size structure of annual plant populations: an indication of neighbourhood competition. *Ann. Bot.* 68, 341–347.

- Bossel, H., 1996. TREEDYN forest simulation model. *Ecol. Model.* 90 (3), 187–227.
- Botkin, D.B., Janak, J.F., Wallis, J.R., 1972. Some ecological consequences of a computer model of forest growth. *J. Ecol.* 60, 849–872.
- Brooker, R.W., Maestre, F.T., Callaway, R.M., Lortie, C.L., Cavieres, L.A., Kunstler, G., Liancourt, P., Tielbörger, K., Travis, J.M.J., Anthelme, F., Armas, C., Coll, L., Corcket, E., Delzon, S., Forey, E., Kikvidze, Z., Olofsson, J., Pugnaire, F., Quiroz, C.L., Saccone, P., Schiffrers, K., Seifan, M., Touzard, B., Michalet, R., 2008. Facilitation in plant communities: the past, the present, and the future. *J. Ecol.* 96 (1), 18–34.
- Bruno, J.F., Stachowicz, J.J., Bertness, M.D., 2003. Inclusion of facilitation into ecological theory. *TREE* 18, 119–125.
- Bugman, H.K.M., Wullschlegel, S.D., Price, D.T., Ogle, K., Clark, D.F., Solomon, A.M., 2001. Comparing the performance of forest gap models in North America. *Climatic Change* 51, 349–388.
- Busing, R.T., Maily, D., 2004. Advances in spatial, individual-based modelling of forest dynamics. *J. Vegetation Sci.* 15, 831–842.
- Bustos, B., Keim, D., Saupe, D., Schreck, T., Vranic, D., 2006. An experimental effectiveness comparison of methods for 3D similarity search. *Int. J. Digit. Libr.* 6 (1), 39–54.
- Callaway, R.M., 1995. Positive interactions among plants. *Bot. Rev.* 61, 306–349.
- Callaway, R.M., Pennings, S.C., 2000. Facilitation may buffer competitive effects: indirect and diffuse interactions among salt marsh plants. *Am. Nat.* 156, 416–424.
- Casper, B.B., Schenk, H.J., Jackson, R.R.B., 2003. Defining a plant's belowground zone of influence. *Ecology* 84, 2313–2321.
- Caswell, H., Etter, R., 1999. Cellular automaton models for competition in patchy environments: facilitation, inhibition, and tolerance. *Bull. Math. Biol.* 61, 625–649.
- Chave, J., 1999. Study of structural, successional and spatial patterns in tropical rain forests using TROLL, a spatially explicit forest model. *Ecol. Model.* 124, 233–254.
- Chen, R., Twilley, R.R., 1998. A gap dynamic model of mangrove forest development along gradients of soil salinity and nutrient resources. *J. Ecol.* 86, 37–51.
- Chen, R., Twilley, R.R., 1999. A simulation model of organic matter and nutrient accumulation in mangrove wetland soils. *Biogeochemistry* 44, 93–118.
- Colombo, A., Or, D., 2006. Plant water accessibility function: a design and management tool for trickle irrigation. *Agric. Water Manag.* 82, 45–62.
- Courbaud, B., 2000. Comparing light interception with stand basal area for predicting tree growth. *Tree Physiol.* 20, 407–414.
- Cox, D.R., Isham, V., Northrop, P., 2000. Statistical modeling and analysis of spatial patterns. In: Dieckmann, U., Law, R., Metz, J.A.J. (Eds.), *The Geometry of Ecological Interactions*. Cambridge University Press, Cambridge, pp. 65–88.
- Czárán, T., 1998. *Spatiotemporal Models of Population and Community Dynamics*. Chapman & Hall, London, Weinheim, New York, Tokyo, Melbourne, Madras.
- Czárán, T., Bartha, S., 1989. The effect of spatial pattern on community dynamics: a comparison of simulated and field data. *Vegetation* 83, 229–239.
- Damgaard, C., Weiner, J., Nagashima, H., 2002. Modelling individual growth and competition in plant populations: growth curves of *Chenopodium album* at two densities. *J. Ecol.* 90 (4), 666–671.
- DeAngelis, D.L., Gross, L.J., 1992. *Individual-Based Models and Approaches in Ecology*. Chapman & Hall, New York.
- Deussen, O., Lintermann, B., 2005. *Digital Design of Nature—Computer Generated Plants and Organics*. Springer.
- Deutschman, D.H., Levin, S.A., Pacala, S.W., 1999. Error propagation in a forest succession model: the role of fine-scale heterogeneity in light. *Ecology* 80, 1927–1943.
- Ditzer, T., Glauner, R., Forster, M., Kohler, P., Huth, A., 2000. The process-based stand growth model Formix 3-Q applied in a GIS environment for growth and yield analysis in a tropical rain forest. *Tree Physiol.* 20, 367–381.
- Donald, C.M., 1958. The interaction of competition for light and nutrients. *Aust. J. Agric. Res.* 9, 421–435.
- Dunkerley, D.L., 1999. Banded chenopod shrublands of arid Australia: modelling responses to interannual rainfall variability with cellular automata. *Ecol. Model.* 121, 127–138.
- Fall, A., Fall, J., 2001. A domain-specific language for models of landscape dynamics. *Ecol. Model.* 141, 1–18.
- Feagin, R.A., Wu, X.B., Smeins, F.E., Whisenant, S.G., Grant, W.E., 2005. Individual versus community level processes and pattern formation in a model of sand dune plant succession. *Ecol. Model.* 183, 435–449.
- Galitsky, V.V., 1990. Dynamic 2D model of plant communities. *Ecol. Model.* 50, 95–105.
- Godin, C., 2000. Representing and encoding plant architecture: a review. *Annu. Forest Sci.* 57, 413–438.
- Goldberg, D.E., Werner, P.A., 1983. Equivalence of competitors in plant communities: a null hypothesis and a field experimental approach. *Am. J. Bot.* 70, 1098–1104.
- Green, D.S., Hawkins, C.D.B., 2005. Competitive interactions in sub-boreal birch-spruce forests differ on opposing slope aspects. *Forest Ecol. Manag.* 214, 1–10.
- Grime, J.P., 1988. *Comparative Plant Ecology: A Functional Approach to Common British Species*. Unwin Hyman, London, UK.
- Grimm, V., 1999. Ten years of individual-based modelling in ecology: what have we learned and what could we learn in the future? *Ecol. Model.* 115, 129–148.
- Grimm, V., Railsback, S.F., 2005. *Individual-Based Modelling and Ecology*. Princeton University Press, Princeton, NJ.
- Grimm, V., Revilla, E., Berger, U., Jeltsch, F.L., Mooij, W.M., Railsback, S.F., Thulke, H.-H., Weiner, J., Wiegand, Th., DeAngelis, D.L., 2005. Pattern-oriented modeling of agent-based complex systems: lessons from ecology. *Science* 310, 987–991.
- Grimm, V., Berger, L., Bastiansen, F., Eliassen, S., Ginot, V., Giske, J., Goss-Custard, J., Grand, T., K. Heinz, S., Huse, G., Huth, A., Jepsen, J.U., Jørgensen, Chr., Mooij, W.M., Müller, B., Peer, G., Piou, C., Railsback, S.F., Robbins, A.M., Robbins, M.M., Rossmanith, E., Ruger, N., Strand, E., Souissi, S., Stillman, R.A., Vabog, R., Visser, U.,

- DeAngelis, D.L., 2006. A standard protocol for describing individual-based and agent-based models. *Ecol. Model.* 198, 115–126.
- Guttman, A., 1984. R-trees: a dynamic index structure for spatial searching. In: Proceedings of 1984 ACM SIGMOD International Conference on Management of Data, ACM Press, New York, pp. 47–57.
- Hanan, J., Prusinkiewicz, P., 1996. Virtual plants: new perspectives for ecologists and agricultural scientists. *Trends Plant Sci.*, 33–38.
- Harlow, F.H., 1957. Hydrodynamic problems involving large fluid distortions. *J. Assoc. Comput. Mach.* 4, 137–142.
- Harlow, F.H., 1964. Particle-in-cell computing method for fluid dynamics. *J. Comput. Phys.* 3, 319–343.
- Hendry, R.J., McGlade, J.M., Weiner, J., 1996. A coupled map lattice model of the growth of plant monocultures. *Ecol. Model.* 84 (1–3), 81–90.
- Hiebeler, D., 2004. Competition between near and far dispersers in spatially structured habitats. *Theoret. Pop. Biol.* 66 (3), 205–218.
- Hildenbrandt, H., 2003. Simulationsmodelle zur Untersuchung der Dynamik von Mangrovenwäldern. Ph.D. Thesis, University of Bremen.
- Houston, A., Clark, J.C., McNamara, J., Mangel, M., 1988. Dynamic models in behavioral and evolutionary ecology. *Nature* 332, 29–34.
- Hühn, M., 2000. Note on the effect of non-regular spatial patterns of plants on yield per area based on a logarithmic relationship between single plant yield and individual area. *J. Agronomy Crop Sci.* 184, 133–136.
- James, R., Bennett, P.G., Krause, J., 2004. Geometry for mutualistic and selfish herds: the limited domain of danger. *J. Theor. Biol.* 228, 107–113.
- Jeltsch, F., Milton, S.J., Dean, W.R.J., Rooyen, N.V., 1996. Tree spacing and coexistence in semiarid savannas. *J. Ecol.* 84, 2414–2427.
- Jeltsch, F., Milton, S.J., Dean, W.R.J., Van Rooyen, N., 1997a. Analysing shrub encroachment in the southern Kalahari: a grid-based modelling approach. *J. Appl. Ecol.* 34, 1497–1508.
- Jeltsch, F., Milton, S.J., Dean, W.R.J., Van Rooyen, N., 1997b. Simulated pattern formation around artificial waterholes in the semi-arid Kalahari. *J. Vegetation Sci.* 8, 177–188.
- Jeltsch, F., Moloney, K.A., 2002. Spatially-explicit vegetation models: what have we learned? *Prog. Bot.* 63, 326–343.
- Kleinn, C., Vilcko, F., 2006a. A new empirical approach for estimation in k-tree sampling. *Forest Ecol. Manag.* 237, 522–533.
- Kleinn, C., Vilcko, F., 2006b. Design-unbiased estimation for point-to-tree distance sampling. *Can. J. Forest Res.* 36, 1407–1414.
- Koumoutsakos, P., 2005. Multiscale flow simulations using particles. *Annu. Rev. Fluid Mech.* 37, 457–487.
- Law, R., Dieckmann, U., 2000. Moment approximation of individual-based models. In: Dieckmann, U., Law, R., Metz, J.A.J. (Eds.), *The Geometry of Ecological Interactions*. Cambridge University Press, Cambridge, pp. 252–270.
- Lischke, H., Zimmermann, N.E., Bolliger, J., Rickebusch, S., Löffler, T.J., 2006. TreeMig: a forest-landscape model for simulating spatio-temporal patterns from stand to landscape scale. *Ecol. Model.* 199, 409–420.
- Liu, J., Ashton, P.S., 1995. Individual-based simulation models for forest succession and management. *For. Ecol. Manage.* 73, 157–175.
- MacArthur, R.H., 1972. *Geographical Ecology*. Princeton University Press, Princeton, NJ.
- Malanson, G.P., Zeng, Y., Walsh, St.J., 2006. Landscape frontiers, geography frontiers: lessons to be learned. *Prof. Geogr.* 58, 383–396.
- Martens, S.N., Breshears, D.D., Meyer, C.W., Barnes, F.J., 1997. Scales of above-ground and below-ground competition in a semi-arid woodland detected from spatial pattern. *J. Vegetation Sci.* 8, 655–664.
- McInnis, L.M., Oswald, B.P., Williams, H.M., Farrish, K.W., Unger, D.R., 2004. Growth response of *Pinus taeda* L. to herbicide, prescribed fire, and fertilizer. *Forest Ecol. Manag.* 199, 231–242.
- Miina, J., Pukkala, T., 2002. Application of ecological field theory in distance-dependent growth modelling. *Forest Ecol. Manag.* 161, 101–107.
- Mitchley, J., 1987. Diffuse competition in plant communities. *Trends Ecol. Evol.*, 104–106.
- Molofsky, J., Bever, J.D., 2004. A new kind of ecology? *BioScience* 54, 440–446.
- Munjiza, A., 2004. *The Combined Finite–Discrete Element Method*. Wiley, Chichester.
- Olsen, J., Kristensen, L., Weiner, J., 2006. Influence of sowing density and spatial pattern of spring wheat (*Triticum aestivum*) on the suppression of different weed species. *Weed Biol. Manag.* 6, 165–173.
- Ostendorf, B., Hilbert, D.W., Hopkins, M.S., 2001. The effect of climate change on tropical rainforest vegetation pattern. *Ecol. Model.* 145, 211–224.
- Pacala, S., Silander, J., 1985. Neighborhood models of plant population dynamics, error analysis, and dynamics. *Am. Nat.* 125, 385–411.
- Pacala, S., Canham, C.D., Silander, J., 1993. Forest models defined by field measurements: I. The design of a north-eastern forest simulator. *Can. J. Forest Res.* 23, 1980–1988.
- Perry, G.L.W., Enright, N.J., 2002a. Humans, fire and landscape pattern: understanding a maquis–forest complex, Mont Do, New Caledonia, using a spatial ‘state-and-transition’ model. *J. Biogeogr.* 29, 1143–1158.
- Perry, G.L.W., Enright, N.J., 2002b. Spatial modelling of landscape composition and pattern in a maquis–forest complex, Mont Do, New Caledonia. *Ecol. Model.* 152, 279–302.
- Perttunen, J., Sievänen, R., Nikinmaa, E., Salminen, H., Saarenmaa, H., Väkevä, J., 1996. LIGNUM: a tree model based on simple structural units. *Ann. Bot.* 77, 87–98.
- Piou, P., Berger, U., Hildenbrandt, H., Grimm, V., Diele, K., D’Lima, C., 2007. Simulating cryptic movements of a mangrove crab: recovery phenomena after small scale fishery. *Ecol. Model.* 205, 110–122.
- Prusinkiewicz, P., Mündermann, L., Karwowski, R., Lane, B., 2001. *The Use of Positional Information in the Modeling of Plants*. ACM Press, New York, NY, pp. 289–300.

- Purves, D.W., Law, R., 2002. Fine-scale spatial structure in a grassland community: quantifying the plant's-eye view. *J. Ecol.* 90 (1), 121–129.
- Rademacher, C., Neuert, C., Grundmann, V., Wissel, C., Grimm, V., 2004. Reconstructing spatiotemporal dynamics of Central European natural beech forests: the rule-based forest model BEFORE. *Forest Ecol. Manag.* 194, 349–368.
- Reynolds, J.H., Ford, E.D., 2005. Improving competition representation in theoretical models of self-thinning: a critical review. *J. Ecol.* 93, 362–372.
- Saint-André, L., M'Bou, A.T., Mabilia, A., Mouvondy, W., Jourdan, C., Rouspard, O., Deleporte, P., Hamel, O., Nouvellon, Y., 2005. Age-related equations for above- and below-ground biomass of a *Eucalyptus* hybrid in Congo. *Forest Ecol. Manag.* 205, 199–214.
- Schneider, M.K., Law, R., Illian, J.B., 2006. Quantification of neighbourhood-dependent plant growth by Bayesian hierarchical modelling. *J. Ecol.* 94, 310–321.
- Schwinning, S., Weiner, J., 1998. Mechanisms determining the degree of size asymmetry in competition among plants. *Oecologia* 113, 447–455.
- Shackleton, C., 2002. Nearest-neighbour analysis and the prevalence of woody plant competition in South African savannas. *Plant Ecol.* 158, 65–76.
- Shugart, H.H., 1984. *A Theory of Forest Dynamics: the Ecological Implications of Forest Succession Models*. Springer, New York.
- Stoll, P., Bergius, E., 2005. Pattern and process: competition causes regular spacing of individuals within plant populations. *J. Ecol.* 93, 395–403.
- Stoll, P., Weiner, J., 2000. Neighbourhood view of interactions among individual plants. In: Dieckmann, U., Law, R., Metz, J.A.J. (Eds.), *The Geometry of Ecological Interactions*. Cambridge University Press, Cambridge, pp. 11–27.
- Takenaka, A., 1994. A simulation model of tree architecture development based on growth response to local light environment. *J. Plant Res.* 107, 321–330.
- Thomas, S.C., Weiner, J., 1989. Growth, death and size distribution change in an *Impatiens pallida* population. *J. Ecol.* 77, 524–536.
- Tilman, D., 1988. *Plant Strategies and the Dynamics and Structure of Plant Communities*. Princeton University Press, Princeton, NJ.
- Townsend Peterson, A., 2003. Predicting the geography of species' invasions via ecological niche modeling. *Q. Rev. Biol.* 78, 419–433.
- Twilley, R.R., Rivera-Monroy, V.H., Chen, R., Botero, L., 1999. Adapting an ecological mangrove model to simulate trajectories in restoration ecology. *Mar. Pollut. Bull.* 37, 404–419.
- Vakalis, D., Sarimveis, H., Kiranoudis, C., Alexandridis, A., Bafas, G., 2004. A GIS based operational system for wildland fire crisis management I. Mathematical modelling and simulation. *Appl. Math. Model.* 28, 389–410.
- Wang, J.H., Kropff, M.J., Lammert, B., Christensen, S., Hansen, P.K., 2003. Using CA model to obtain insight into mechanism of plant population spread in a controllable system: annual weeds as an example. *Ecol. Model.* 166, 277–286.
- Weiner, J., 1990. Asymmetric competition in plant populations. *Trends Ecol. Evol.* 5, 360–364.
- Weiner, J., Stoll, P., Muller-Landau, H., Jasentuliyana, A., 2001. The effects of density, spatial pattern, and competitive symmetry on size variation in simulated plant populations. *Am. Nat.* 158, 438–450.
- West, P.W., 1993. Model of above-ground assimilate partitioning and growth of individual trees in even-aged forest monoculture. *J. Theor. Biol.* 161, 369–394.
- Wiegand, T., Jeltsch, F., Hanski, I., Grimm, V., 2003. Using pattern-oriented modeling for revealing hidden information: a key for reconciling ecological theory and application. *OIKOS* 100 (2), 209–222.
- Wiegand, T., Revilla, E., Knauer, F., 2004. Dealing with uncertainty in spatially explicit population models. *Biodivers. Conserv.* 13 (1), 53–78.
- Wiegand, T., Camarero, J.J., Rüger, N., Gutiérrez, E., 2006. Abrupt population changes in treeline ecotones along smooth gradients. *J. Ecol.* 94, 880–892.
- Wilson, J.B., 1988. Shoot competition and root competition. *J. Appl. Ecol.* 25, 279–296.
- Winkler, E., 2006. Recent trends in plant-ecological modelling: species dynamics in grassland systems. *Prog. Bot.* 67, 420–440.
- Winkler, E., Stöcklin, J., 2002. Sexual and vegetative reproduction of *Hieracium pilosella* L. under competition and disturbance: a grid-based simulation model. *Ann. Bot.* 89, 525–536.
- Wood, A.J., Ackland, G.L., Lenton, T.M., 2006. Mutation of albedo and growth response produces oscillations in a spatial Daisyworld. *J. Theor. Biol.* 242, 188–198.
- Wu, H., Sharp, P.J., Walker, J., Penridge, L.K., 1985. Ecological field theory: a spatial analysis of resource interference among plants. *Ecol. Model.* 29, 215–243.
- Wyszomirski, T., Wyszomirska, I., Jarzyna, I., 1999. Simple mechanisms of size distribution dynamics in crowded and uncrowded virtual monocultures. *Ecol. Model.* 115, 253–273.