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Competition and evolution in virtual plant communities: a new modeling approach

Stefan Bornhofen · Claude Lattaud

Abstract This article presents studies on plants and their communities through experiments with a multi-agent platform of generic virtual plants. Based on Artificial Life concepts, the model has been designed for long-term simulations spanning a large number of generations while emphasizing the most important morphological and physiological aspects of a single plant. The virtual plants combine a physiological transport-resistance model with a morphological model using the L-system formalism and grow in a simplified 3D artificial ecosystem. Experiments at three different scales are carried out and compared to observations on real plant species. At the individual level, single virtual plants are grown in order to examine their responses to environmental constraints. A number of emerging characteristics concerning individual plant growth can be observed. Unifying field observation, mathematical theory and computer simulation, population level experiments on intraspecific and interspecific competition for resources are related to corresponding aggregate models of population dynamics. The latter provide a more general understanding of the experiments with respect to long-term trends and equilibrium conditions. Studies at the evolutionary level aim at morphogenesis and the influence of competition on plant morphology. Among other results, it is shown how the struggle for resources induces an arms race that leads to the evolution of elongated growth in contrast to rather ample forms at ground-level when the plants evolve in isolation.

Keywords Artificial evolution · Artificial life · Multi-agent system · Plant modeling · Population dynamics

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1 Introduction

In its classic definition, an ecosystem is a dynamic assemblage of organisms, interacting with each other and with the physical environment they live in. More precisely, Dansereau defines it as “a limited space where resource recycling on one or several trophic levels is performed by a lot of evolving agents, using simultaneously and successively mutually compatible processes that generate long or short-term usable products” (Dansereau 1992). Today, the study of the relations between these elements has become an important research field since it is more and more related to economic issues in agriculture and forestry as well as to the protection of the environment. Modeling is a fundamental tool for the comprehension of complex systems such as ecosystems. Models are simplified images of the reality, whose level of abstraction can considerably differ, depending on the objectives of the study. In the field of modeling plants, several basic approaches can be distinguished.

Aggregate models of population dynamics describe the overall behavior of plant communities. A system of equations denotes the development of significant mean values such as the overall biomass or average height of the population. These models constitute a compact description of the system, and additional mathematical analysis of the involved equations may lead to a deep understanding of its dynamics. However, since the plants are not explicitly represented, various potential differences between the individuals concerning morphological and physiological processes cannot be observed. Likewise, it is difficult to include environmental heterogeneity, such as an uneven repartition of resources. To overcome these problems, individual-based models consider the development of each single plant within a population. An individual may be divided into a fixed number of compartments that exchange various substances. By this means, many physiological processes inside the plant can be described, but its architectural structure is not modeled in detail so that important interrelations between morphology and physiology are not taken into account. For more than two decades, there has been a trend for models called “virtual plants” (Room et al. 1996). They explicitly describe the 3D spatial distribution of the plant organs as a collection of interconnected components and therefore draw a faithful picture of real plants by combining physiological and morphological aspects.

There already exists a variety of elaborate virtual plant models (e.g. Allen et al. 2005; Le Dizès et al. 1997; Perttunen et al. 1996; Rauscher et al. 1990; Weinstein et al. 1992), but few of them are intended for the study of population dynamics, let alone evolutionary dynamics in plant communities. They are most often accurately adapted to given plant species and do not consider evolutionary change. Moreover, their complexity involves a computational cost per individual plant which renders simulations of large communities difficult to realize for simple reasons of time. This paper presents a model of generic virtual plants for studies at individual, population and evolutionary levels.

In order to demonstrate the potentials of the model, three series of experiments are conducted. At individual level, single virtual plants are grown to examine their responses to different environmental constraints. Unifying field observation, mathematical theory and computer simulation, experiments at population level on competition for resources are conducted with the platform and subsequently compared to corresponding aggregate models. Studies at the evolutionary level investigate morphogenesis and the influence of competition on plant morphology. The results of all experiments are close to patterns observed in nature, so that the model can be considered as a sound basis for further studies of long-term dynamics within plant communities.

The next section gives an introduction to the modeling of plants. In Sect. 3 the virtual plant model is presented. The conducted experiments are described and discussed in Sect. 4. Section 5 concludes the paper with reflections about future works.

2 Background

The origins of the computer modeling and visualization of plants can be traced back to the 1960s, when Ulam simulated the development of branching patterns using cellular automata (Ulam 1962). About 10 years later, Honda was probably the first to introduce a computer model of tree structures (Honda 1971). Since then a huge amount of work has been devoted to this research field. Depending on the objectives, different approaches have been devised. This section is an introduction to the modeling of plants and presents the basic techniques of representing individual plants and plant communities as well as the state of the art of evolutionary models.

2.1 How to model a plant?

As the aims of study can differ from one computer model to another, the variety of individual plant representations is difficult to classify. Prusinkiewicz (1998) proposed to divide the existing models into empirical-descriptive and causal-mechanistic ones, whereas other authors like Godin (2000) suggested classifications according to the architecture of the plant model. For our purpose, it is sufficient to follow the traditional and straightforward classification recommended by Kurth (1994a), who proposed a distinction between physiological and morphological models.

2.1.1 Physiological models

These models, also called process-based models, reflect metabolic processes inside a plant. Their architectural description remains low detailed, as the individual plant is merely decomposed into a fixed number of compartments. They correspond to plant components like shoot and root, or to pools of organs like leaves and fruits, exchanging substances in terms of mass variables. The attention is primarily turned to carbon balance, due to its importance for plant growth, by modeling photosynthesis, carbon allocation and respiration. However other influential substances such as soil nutrients can equally be taken into account. The first physiological models were conceived by Thornley around 1970 (Thornley 1972a, b) and only contained a leaf and a root compartment whose dynamics were described by a system of differential equations. Since these constitutional works, physiological models have constantly been enhanced by adding new compartments, for instance a stem compartment (Deleuze and Houllier 1997), or by including additional substances such as water (Sperry et al. 1998). Concerning the exchange of substances between the compartments, two basic approaches can be distinguished: the growth rule-based approach and the mechanistic approach.

The growth rule-based approach uses a description of a priori relationships within the plant with a view to optimizing its growth. Carbon flow is considered more a consequence than a determinant of the growth pattern (Lacointe 2000). A fundamental concept of these models is allometry, i.e. implicit dependencies between different components of a plant. One typical relation is the principle of functional balance (Davidson 1969). It states that the carbon assimilation of the leaves and the nutrient assimilation of the roots tend to equilibrium with respect to their relative utilization. Lower light provokes a stronger growth of leaves in order to compensate the weak photosynthesis. In the same way, low supply of soil nutrients lead to a boosted root growth. The growth rule-based approach is based on suppositions that rely on field observations, but this does not mirror the underlying mechanisms of substance transport within a plant.

The mechanistic approach addresses this problem by assuming that resources move from producing compartments (sources) to consuming compartments (sinks). The flow can be regulated in various manners, for example by a hierarchical distribution (Grossman and DeJong 1994) or proportionally to the demands of different compartments in competition (Génard et al. 1998). The currently most mechanistic approach is the transport-resistance model (Thornley 1972): as the movement of resources inside a plant leads to a balance between the resource concentrations of the compartments, it is suggested that the substance transport proceeds according to the Muench theory of concentration gradients (Münch 1930). In its basic version, a plant is divided into two components: shoot and root. Both of them hold separate substrate pools for carbon and nitrogen. Photosynthesis charges the shoot carbon pool, and mineral assimilation supplies the root nitrogen pool. Growth occurs through the conversion of carbon and nitrogen into biomass, deducting a certain loss to litter. The exchange between the carbon and nitrogen pools is represented as a function of substrate concentration difference separated by a resistance (Fig. 1). These simple assumptions produce a variety of realistic allocation responses in plant development. Thornley suggested that all allocation models of plant development should start with this irreducible framework (Thornley 1998). The mechanistic approach is able to produce allometric relationships without explicitly formulating them. However, the parameters of these models are often delicate to measure so that assessing a set of values for quantitative adequacy can be difficult (Lacointe 2000; Sievanen et al. 2000).

Because of their manageable architecture and their small number of parameters, physiological models are convenient for modeling and interpreting the development of plants by an inner flow of substances at a rather coarse scale. They offer a framework to describe how these physiological processes interact under given environmental change (Landsberg and Gower 1997). For more detailed issues, like studying the branching structure of a tree crown, they turn out to be oversimplified, and more complex representations of the plant morphology have to be considered.

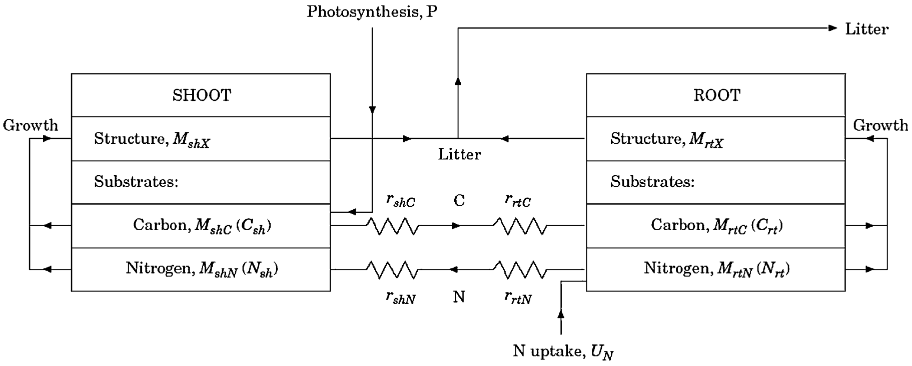


Fig. 1 The transport-resistance model (from Thornley 1998)

2.1.2 Morphological models

Morphological models do not primarily deal with resource flow but describe the architectural development of a plant by making use of its modular structure (Harper et al. 1986). They consider the plant as a composition of repeated modules or "elementary units" (Sievanen et al. 2000), such as the leaf, fruit and root organs which dynamically appear and disappear during the plant development according to a number of growth rules. Due to the particular morphological pattern of a plant, the modules are interconnected in a binary arborescent relation which gives rise to the notion of "tree graph" (Godin 2000) (Fig. 2).

Probably the most widely used representation of plant morphology is the L-system formalism. L-systems were initially designed in 1968 by Lindenmayer to model the development of simple multicellular organisms (Lindenmayer 1968), but their versatility makes them a powerful generic encoding scheme for the modeling of plant growth (Prusinkiewicz and Lindenmayer 1990) and many other natural phenomena. Among other applications, they have so far been used to model protein structure (Escuela et al. 2005), virtual creatures (Hornby and Pollack 2001) and the blood vessels of the eye (Kókai et al. 1999). L-systems are based on formal grammars, as introduced by Chomsky (1957), with the possibility of repeated applications in a parallel rewriting process. A grammar consists of a set of rules which are applied to elementary symbols of an alphabet. Plant components are represented by these symbols and arranged in a string that forms the whole the plant structure. A basic L-system can be described by the triplet $\{A, P, \omega\}$ where

- A is an alphabet, i.e. a finite set of symbols,
- P is a set of production rules specifying the possible transitions,
- ω is the initial string or "axiom" representing the primary structure.

A bracketed notation and a stack extend the linear string notation to tree-like structures. The symbol [means to push the current turtle state on the stack, and the symbol] indicates popping the state from the top of the stack and setting it as the current turtle state. As an example, let $\{(a,b), (P_1,P_2), a\}$ be an L-system with the production rules:

$$P_1 : a \rightarrow b[+a][-a]ba$$

$$P_2 : b \rightarrow bb$$

The special characters $+$ and $-$ denote fixed angle rotations in space. The translation of the produced string into a geometric structure is achieved by graphical interpretation using turtle geometry (Prusinkiewicz and Lindenmayer 1990). Figure 3 shows the resulting plant after several iterations.

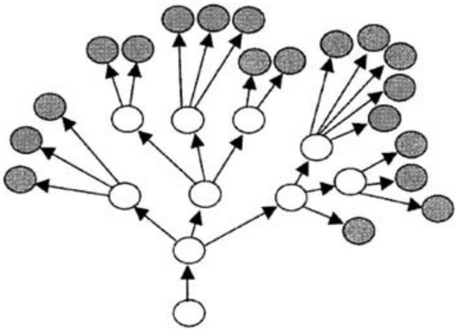
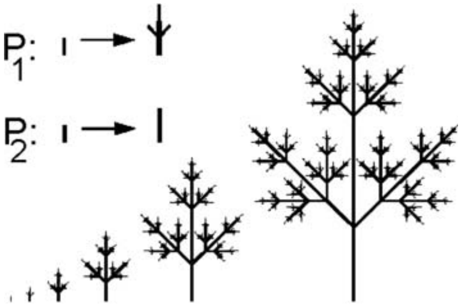


Fig. 2 Arborescent structure of a tree graph (from Godin 2000)

Fig. 3 Iterations of the L-system $\{(a,b),(P_1,P_2),a\}$ (from Prusinkiewicz et al. 1997)



The basic L-system formalism is not flexible enough to represent certain properties of plant development (Kurth 1994b). For this reason, many extensions have been proposed. In parametric L-systems (Prusinkiewicz and Lindenmayer 1990) the elementary units may hold variables containing additional information concerning physiological processes or their geometric aspect. Stochastic L-systems (Prusinkiewicz and Hanan 1989) associate each production rule with a triggering probability. By this means, different plants can be produced from the same set of production rules. In context-sensitive L-systems (Lindenmayer 1968) the activation of rules depends not only on the substituted symbols, but also on its neighbors. This extension allows modeling resource transport within a plant. Moreover, open L-systems (Mech and Prusinkiewicz 1996) include interactions between the plant and its environment.

The modeling group AMAP (AMAP website, http://amap.cirad.fr) aims at the design and evaluation of models for the architectural development of natural plant species. As an alternative to the L-system formalism, the plant representation is based on the ramification, latency and death of the plant meristems (De Reffye et al. 1988). Their behavior depends on probabilistic functions that are deduced from botanical studies on natural plants. For the analysis and simulation of plant growth at different time and space scales, a "multiscale model" of plant morphology was introduced (Godin and Carglio 1998). It features a layered data structure which acts at different levels of detail. Figure 4 illustrates how a plant can be represented at different scales: axis scale (a), growth unit scale (b) and

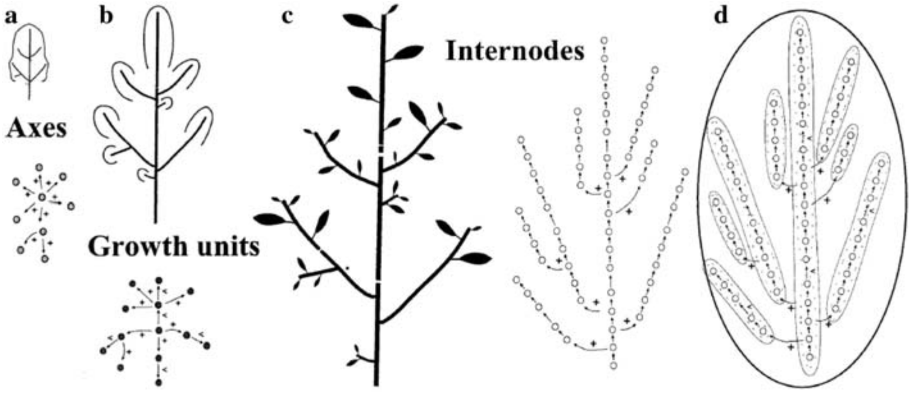


Fig. 4 Multiscale graph (adapted from Godin and Carglio 1998)

internode scale (c). The superposition of all three representations results in a multiscale graph (d).

The AMAP approach is particularly appropriate for the integration of field measures and botanical data into architectural plant models. It contains information at several levels of the plant morphology and allows representing plants at different growth stages in a high degree of realism. However the requirement of many botanical parameters and the computational complexity currently limit its use for large scale applications in plant modeling (Godin 2000).

2.1.3 Functional–structural models

In the previous sections, the models of morphological and of physiological processes have been distinguished. Yet these two aspects of plant development are profoundly interwoven. A complex plant architecture leads to local environments of the organs with differentiated access to resources. In turn, resource allocation to the organs has an impact on the plant architecture. This feedback loop is an important interaction between physiology (function) and morphology (structure) (Le Roux et al. 2001), and in the last decade so-called "functional–structural models" (Sievanen et al. 1997) emerged as the coupling of process-based models and detailed 3D representations of the plant architecture. The plant organs interact with one another, according to the plant topology, and with the local environmental conditions, characterized by global variables, like gravity, and local variables, like temperature or light (FSPM07 website, http://algorithmicbotany.org/FSPM07; Godin and Sinoquet 2005). Because of their complete picture of plant development, these models are also termed "virtual plants" (Room et al. 1996). Important examples are

- LIGNUM (Perttunen et al. 1998), especially designed for trees combining a physiological model with a morphological description of the tree crown. The model includes photosynthetic production depending on the local light climate as well as a detailed model of self-shading. It has been applied to several natural species such as the Scots pine (Perttunen et al. 1996), the Sugar maple (Perttunen et al. 2001) and the Jack pine (Lo et al. 2000).
- L-PEACH (Allen et al. 2005) using L-systems both to simulate the development of tree structure and to solve differential equations for carbohydrate flow and allocation.
- ECOPHYS (Rauscher et al. 1990) and SIMWAL (Le Dizès et al. 1997) which equally incorporate a process-based model into a 3D description of the plant structure and additionally feature elaborate submodels for the flow of assimilated substances.

Although some carbon transport and partitioning models of root systems exist (e.g. Bidel et al. 2000), root geometry is generally not, or only sparsely, taken into account in functional–structural models. Some of them indeed hold a simplified belowground representation like TREGRO (Weinstein et al. 1992) which associates root biomasses to soil layers, but individual roots are rarely modeled. This disproportionate representation constrains a balanced vision of the interrelations between the over and underground plant components (Pagès et al. 2000). One reason for the inconsistency could be the fact that most agriculturally significant processes like wood and fruit development are aboveground. Another factor is the difficulty of studying subsurface plant growth (Le Roux et al. 2001).

Due to their detailed description of the plant structure and the local environment of each plant organ, functional–structural models are computationally expensive, so that only a small number of individuals can be simulated at the same time. The next section introduces some alternative approaches to the modelling of large plant communities.

2.2 Plant communities

As agricultural and forest plants are widely exploited in our society, an important class of models deals with the development of plant communities. Two fundamental approaches can be distinguished. Models of population dynamics describe the evolution of variables representing aggregated data such as the number or density of the population. In contrast, in individual based models the plant community is composed of a number of individuals that develop concurrently in a multi-agent approach (Ferber 1995). Interaction does not occur directly but results from the modifications that every individual contributes to the physical environment. In particular, the available resources become an object of competition between neighboring plants.

2.2.1 Population dynamics

The concept of populations within ecological communities and the study of their growth, stability, and decline is of paramount importance in biology (Berryman 2002). Our working definition for a population is a group of individuals of the same species in a localized area (Ricklefs 1990).

Traditional aggregate models of population dynamics use dynamical systems (Katok and Hasselblatt 1995) to characterize and predict population growth. They are most often described by a system of autonomous ordinary differential equations, where significant parameters such as population density or inhabited area are modeled by one or more entries of the vector valued solution. One basic study of population dynamics concerns the development of a single population. It can be applied to the invasion process of a species in a new environment which is of particular interest due to its impact on the balance of an ecosystem. Resource limited growth has been mathematically described by Verhulst (1838) as the differential equation

$$\frac{\mathrm{d}N}{\mathrm{d}t} = rN\frac{K-N}{K}, \quad N(0) = N_0 \tag{1}$$

The positive constant r denotes the intrinsic rate of increase of the population N. K specifies the maximum possible number of individuals in the habitat called “carrying capacity”. In the literature, the equation is also known as the “Verhulst–Pearl logistic equation”, since Pearl used the curve to approximate human population growth in the United States (Pearl and Reed 1920).

Interspecific competition can be translated by coupling the logistic growth of two populations N_A and N_B, which results in the “Lotka–Volterra equations of interspecific competition” (Lotka 1924; Volterra 1926):

$$\frac{\mathrm{d}N_A}{\mathrm{d}t} = r_A N_A \frac{K_A - N_A - a_{AB}N_B}{K_A} \tag{2}$$

$$\frac{\mathrm{d}N_B}{\mathrm{d}t} = r_B N_B \frac{K_B - N_B - a_{BA}N_A}{K_B} \tag{3}$$

The competition coefficients $a_{XY} > 0$ denote the repressing influence of an individual of species Y on the growth rate of species X in proportion to an individual of species X.

To draw more general conclusions concerning the outcome of the competition between species A and B, phase space analysis (Edelstein-Keshet 1988) can be used. The phase space of autonomous ordinary differential equations is defined as a Euclidean space where every point is associated to a specific state of the system. In the Lotka–Volterra model, the growth of population N_A equals zero if $N_A = K_A - a_{AB}N_B$. This relation is termed “zero-isocline” of N_A and corresponds to a straight line in the phase plane. A state of the system above this line testifies to an abundance of resources, and the population N_A continues to increase. A state below the zero-isocline signifies too many individuals for the available resources, and N_A decreases. In the same way, the zero-isocline of N_B is described by $N_B = K_B - a_{BA}N_A$. The four graphs of Fig. 5 illustrate the possible outcomes of interspecific competition depending on where the two isoclines lie in relation to each other. In graphs 1 and 2, the system tends to the points (K_A, 0) and (0, K_B) which means that one species outcompetes the other. In graph 3, the surviving species depends on the starting point, i.e. the initial number of individuals. In contrast, there is stable equilibrium with coexistence of both species in graph 4.

2.2.2 *Crop yield models*

Crop yield models are designed to manage and predict the development of agriculturally used plant communities. In order to make it possible to make reliable predictions, they are most often based on empirical data and specifically customized for each investigated natural site. As early as the 19th century, the oldest types of crop yield models constituted graphical methods to represent the growth and production of forests (Peng 2000).

In one class of crop yield models, so-called “whole stand models”, a plant community is described by mathematical equations containing some aggregate mean values. In cases of homogeneous plantations, they prove useful for coarse approximations, but it is difficult to apply them to heterogeneous stands. Moreover, whole stand models provide no information on individual plants (Vanclay 1994).

Another class of more recent crop yield models simulates the development of a plant community on the basis of each individual plant before computing global results at a population level. For many practical oriented modeling issues it is not necessary to represent individual plants in a high degree of detail. Therefore, these models only concentrate on a limited set of relevant parameters in the plant community. An important representative of these individual-based models is the Forest Vegetation Simulator (FVS) (FVS website, http://www.fs.fed.us/fmsc/fvs; Van Dyck 2001). It is currently used as a prognosis tool for most forests of the United States and models each tree by means of its diameter, height and crown ratio. However, the FVS does not comprise location and precise morphology, so that many mechanisms of cooperation or competition between individual plants are not taken into account.

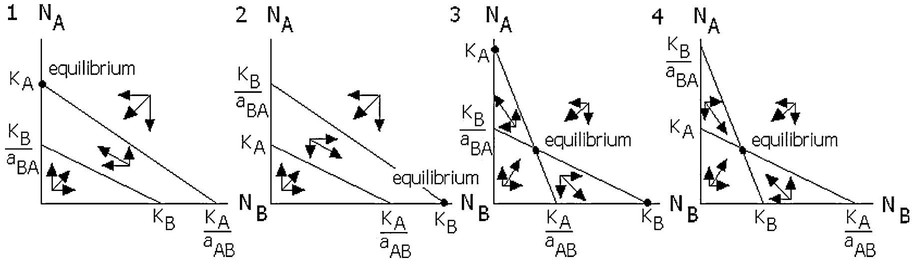


Fig. 5 Different outcomes of interspecific competition

2.2.3 Individual-based ecosystem models

These models address the simulation and visualization of large plant ecosystems by considering the impact of competition on the development of the individual plants. They generally apply a multi-level approach. A high-level model identifies the spatial distribution of the population using individual plant locations and a coarse description of the current plant conditions. After the simulation, lower-level models specify the plant shapes, and realistic visualizations may be obtained by substituting detailed plant models for the coarse ones.

The spatial distribution is typically determined using coarse representations of the individuals on a continuous 2D environment (Firbank and Watkinson 1985). Each plant is symbolized by a circle that corresponds to its size and specifies the neighborhood in which its development is affected. When two circles intersect, the plants are considered to enter competition, and the outcome of the interaction depends on a number of biologically motivated rules. In early models, the smaller plant simply dies and its corresponding circle is removed from the scene (Deussen et al. 1998). More elaborate competition models distinguish between symmetric and asymmetric plant competition (Alsweis and Deussen 2005) or below and aboveground competition (Alsweis and Deussen 2006). The definition of multi-set L-Systems, which are used to model groups of plants instead of single plants, allow extending the generation of spatial distribution with the patterns of clustering and succession (Lane and Prusinkiewicz 2002).

The neighborhood-based approach results in the emergence of some important phenomena for plant distribution such as self-thinning, i.e. the decrease in population density due to increasing space demands (Yoda et al. 1963) (Fig. 6). In order to visualize the simulation outcomes, photo-realistic 3D images are rendered by placing detailed lower-level plant models at the locations generated by the distribution model.

2.3 Artificial Life models

Aside from the previous models which are largely designed for practical issues, a small amount of works on plants have been carried out within the research field of Artificial Life.

Colasanti and Hunt devised a cellular automaton (CA) modeling 2D plants that acquire and allocate resources in their above- and belowground environments (Colasanti and Hunt 1997; Colasanti et al. 2001). In this model, a plant is considered as a self-assembling organism, such that whole-plant organization and behavior emerge from the interactions between its structural elements. These elements, called “modules”, are linked together in

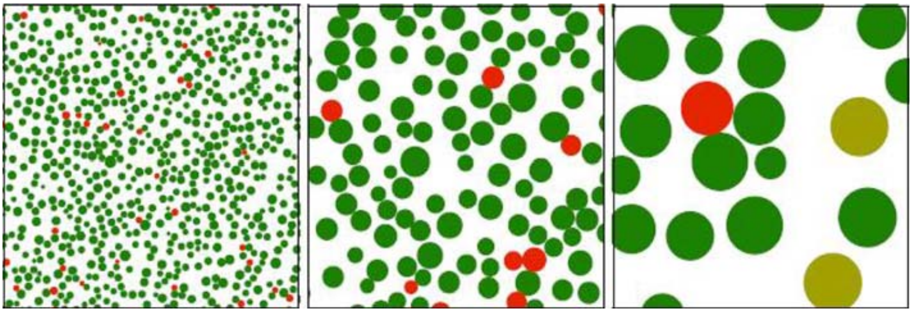


Fig. 6 Self-thinning in an ecosystem model (from Deussen et al. 1998)

two branched networks forming a root and a shoot system. The spatial area is represented as an array of cells that may or may not contain a single plant module as well as a number of resource units. The aboveground resource is modeled by “light units”, and the belowground resource by “mineral nutrient units”. Any plant module that occupies a cell is capable of capturing its resources that are subsequently transported through the plant network and used for the growth of new modules. The CA model reproduces a wide range of growth patterns observed on natural plants such as an S-shaped growth curve, plasticity in root-shoot allocation, and foraging behavior in heterogeneous resource environments. Concerning plant communities, the model complies with a number of population level dynamics such as the competitive exclusion principle that states that two species competing for the same resources cannot stably coexist (Gause 1934). Figure 7 illustrates the phenomenon of self-thinning in the model from a large population of initial seedlings to six remaining full grown individuals. All results emerge from a small set of rules defined at the level of the interacting plant modules.

A number of studies in Artificial Life address the application and adaptation of evolutionary algorithms (Holland 1975) in the context of plant development. In 1986, Niklas (1986) pioneered in this area by performing an adaptive walk through a virtual space of branching patterns, based on simple hypotheses concerning the factors that have the greatest effect on plant evolution. Sims (1991) and Mock (1998) evolved morphologies of artificial plants for virtual worlds by interactive selection where, similar to Dawkins’ Biomorphs (Dawkins 1986), a human observer chooses the most interesting-looking plants for further reproduction. However no ecological considerations have been integrated into their models.

Jacob (1994, 1996a, b) published a series of papers concerning the evolution of context-free and context-sensitive L-systems representing simple artificial plants. He introduced ecological aspects in his model by defining a fitness function which depends on the number of blossoms and leaves as well as the volume of the plant. His approach was extended by Ochoa (1998) who used a more elaborate fitness function to evolve 2D plant structures and concluded that L-systems are a suitable genetic representation for studies which simulate morphological evolution, due to their convenient distinction between genotype and phenotype as well as their creative power in generating novel and unexpected solutions.

Ebner (2002, 2003) developed a model which incorporates interaction between the plants and their environment. He defined a fitness function which evaluates the amount of captured virtual sunlight and showed that plants, evolved in competition, grow high compared to small bushy plants which develop when evolved independently. Additionally, some applications have appeared in the past years on the Internet such as the Second Garden (Steinberg et al. 1999) or the Nerve Garden Project (Damer et al. 1998), allowing users to build and interact with L-system based artificial plants and plant communities in virtual online worlds.

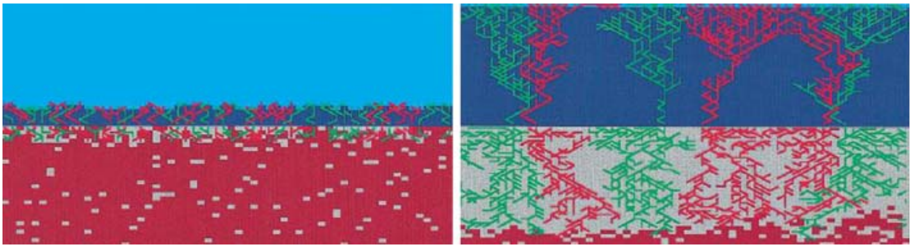


Fig. 7 Self-thinning in a CA based modular model (from Colasanti and Hunt 1997)

3 The virtual plant model

As seen in Sect. 2, there exists a variety of elaborate individual-based plant models, but to our knowledge no functional–structural model is specifically intended for the study of evolutionary phenomena within plant communities. On the other hand, the current evolutionary plant models developed in the context of Artificial Life incorporate no physiological processes and their environment possesses no or only minimal dynamics. Moreover, natural plants exhibit an important degree of adaptability, and as recently pointed out in (Grimm and Railsback 2005), so far virtually no individual-based plant model displayed this feature.

The following section describes the major characteristics of a plant model which is intended to fill this gap, i.e. to carry out long-term simulations at the population and evolutionary levels while emphasizing the most important morphological and physiological aspects of a single plant. The plants are based on ALife concepts, as they are emergent and adaptive structures with simple underlying rules, but at the same time they contain all the major elements of an FSPM, that is a 3D architecture combined with a framework of resource assimilation, flow and allocation.

3.1 The environment

The physical environment is a limited (bordered or toroidal) continuous 3D space which is composed of two components: the soil and the sky. The sky provides light which is captured by the leaves in order to produce carbon via photosynthesis. The soil contains minerals that are assimilated by the fine roots. These two resources are of prime importance for the growth of natural plants (Westoby et al. 2002). Other significant resources such as water and CO_2 are currently not modeled, which corresponds to the assumption that their supply is constant and sufficient. Most interactions between a real plant and its environment, in particular resource assimilation, depend on the spatial distribution of the plant organs (Godin and Sinoquet 2005). For this reason, the soil and the sky of the model are homogeneously divided into voxels that each contains local resources.

3.1.1 The sky

Light models approximate radiative fluxes received by the plant foliage for photosynthesis. The surface based approach uses the 3D geometry of a canopy and considers the size, position and orientation of each plant part to estimate the amount of light, however this method induces a high computational complexity when the canopy structure is described by a large set of elements (Chelle and Andrieu 2007). To accelerate the simulations, the presented model uses a simpler approach.

Virtual light is emitted by a number of light sources, parametrized by a variable representing the irradiance and a vector indicating the direction. The total irradiance in a voxel results from the sum of all light sources and is scaled to values between 0 and 1.

Each object of the simulation is located in a certain voxel. Since its geometry may not entirely be enclosed in one voxel, the central point is decisive. If it is situated in the aerial part, the object casts shadows. In such case, the irradiance in all voxels following the direction of light is decreased, that is, multiplied by a shading factor s between 0 and 1 (Fig. 8). To avoid time-consuming computation such as geometrical calculations or the use

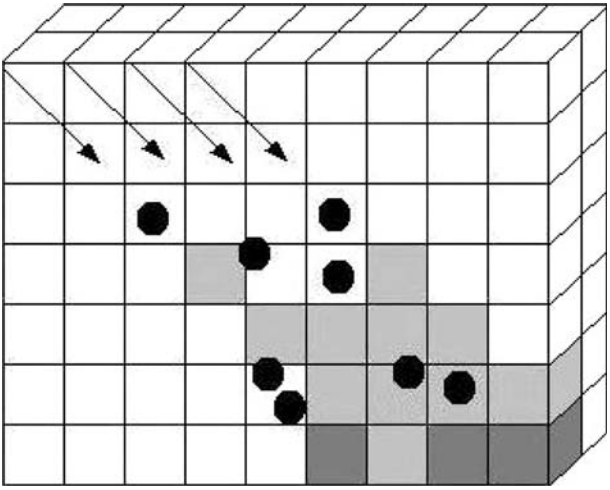


Fig. 8 Shadow casting in sky voxels

of computer graphics in order to determine how much light a plant receives with respect to each light source, the shading factor of an object A does not depend on the exposed surface of the object but on its volume $v(A)$ and is defined as

$$s = \max\left(1 - \frac{v(A)}{V}, 0\right) \tag{4}$$

where V is the volume of a single voxel.

3.1.2 The soil

Soil models allow the representation of a range of substances and their dynamics such as chemical equilibria, organic matter transformations and mineral weathering (e.g. Cosby et al. 1986; Gherini et al. 1985). However, as in the presented model priority is given to simplification, no such detailed description of soil chemistry is used.

Soil voxels contain an aggregate quantity of minerals, the second important resource for plant growth, which is equally scaled to values between 0 and 1. To estimate the flow of minerals between adjacent voxels, nutrient propagation is modeled by a simple diffusion equation based on Fick's first law (Fick 1855) (Fig. 9). Diffusion is a passive movement from regions of high concentration to regions of low concentration, and the resource flux between soil voxel i and its neighbors is:

$$\frac{\mathrm{d}N_i}{\mathrm{d}t} = D * \sum S_{i,j} \frac{N_j - N_i}{d_{i,j}} \tag{5}$$

where N_i represents the mineral concentration of voxel i, $S_{i,j}$ is the contact surface between the voxels i and j, $d_{i,j}$ the distance between the voxel centers and D the diffusion coefficient. The soil model respects a simplified mineral cycle. All the assimilated nutrients of a virtual plant are eventually redeposited in the soil so that their total amount within the environment is constant.

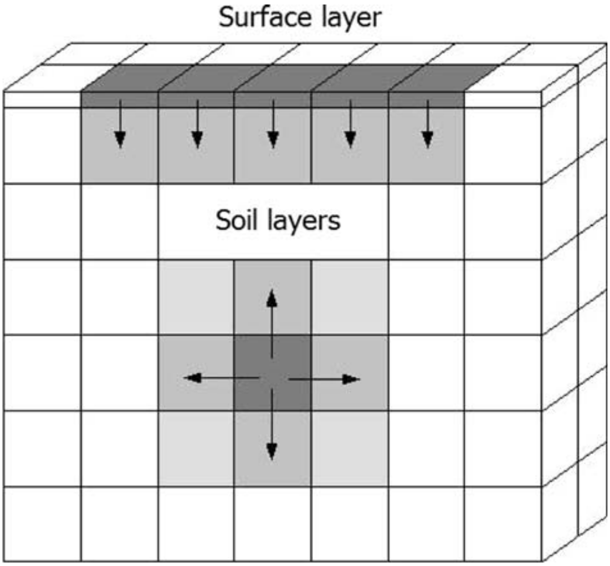


Fig. 9 Diffusion between surface and soil voxels

3.2 The plants

A virtual plant is divided into an aboveground and belowground component, called shoot and root, respectively. Both of them can be considered as independent agents whose morphology is described by an L-system. The shoot photosynthesizes carbon, whereas the root assimilates nutrients. The two components rely on each other by the fact that growth, i.e. the production of biomass, requires the presence of both resources. To perform evolutionary experiments, all parameters concerning the morphological and physiological aspects of plant growth are recorded in a mutable artificial genome, and evolutionary forces can act on these traits by favoring reproduction of those individuals which turn out to be adapted to a given selection process.

3.2.1 The morphological component

Shoot and root morphologies are each expressed by an L-system whose alphabet is detailed in Table 1. Uppercase characters are non-terminal symbols and represent the apices where the plant continues to grow. As an example, Fig. 10 shows the schematic representation of a small plant morphology. The L-systems are

- Parametric: Every module *i* is associated with a variable $M_{X(i)}$ representing its biomass. It increases when the module grows and affects the future behavior of the L-system. In particular for apices, i.e. non-terminal characters, the parameter $M_{X(i)}$ is a condition for the application of the production rule. The rule is not applied before $M_{X(i)}$ reaches the sum of the biomass costs for all plant modules that are produced.
- Stochastic: A non-terminal can be the predecessor of multiple production rules. In this case, the appropriate rule is randomly chosen by roulette wheel selection, i.e. proportionately to associated weights defined in the genotype.

Table 1 The L-system alphabet

Character	Compartment	Geometry	Function
l	Shoot	Sphyl	Captures virtual light to photosynthesize carbon
f	Shoot	Sphyl	Initiates florescence and produces a seed
b	Shoot	Sphyl	Creates a branching structure
r	Root	Sphyl	Assimilates nutrients in the soil
c	Root	Sphyl	Creates a branching structure
A…Z	Shoot/root	None	Represents an apex
[ ]	Shoot/root	None	Indicates a ramification
+ − / \ & ^	Shoot/root	None	Represents a rotation

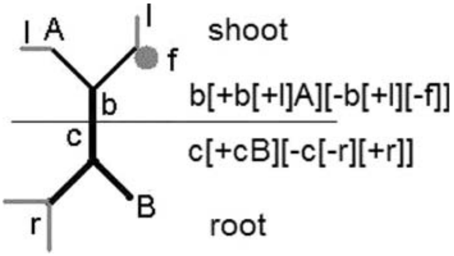


Fig. 10 Schematic representation of a plant morphology

- Context-sensitive: The left context of an apex can act as a condition for the production rules. In the presented model, there is no right context to consider because apices are always situated at the end of a branching. The context-sensitivity is not applied in the scope of this paper.
- Open: The access to resources, i.e. light intensity for the shoot and mineral concentration for the root, can act as a condition for the production rules. If so, the growth rule is only applied if a minimum quantity of resources *minResources* is available in the local environment.

The shape of the plant modules is based on sphyls. i.e. cylinders with spherical ends (Fig. 11). This geometry is particularly appropriate for rapid collisions detection. The exact form and size of the plant modules is genetically specified by their current biomass X as

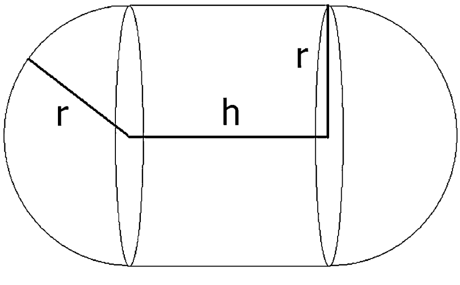


Fig. 11 Two parameters r and h specify the shape of a plant module

well as the genetic parameters density D and height-to-radius ratio R of the corresponding module type. The volume of a plant module is calculated by

$$V = \frac{X}{D}. \tag{6}$$

As the volume of a sphyl amounts to

$$V = \pi r^2 h + \frac{4}{3}\pi r^3 = \pi r^3 \left(R + \frac{4}{3}\right), \tag{7}$$

sphyl height h and radius r are

$$r = \sqrt{\frac{V}{\pi\left(R + \frac{4}{3}\right)}} \tag{8}$$

and

$$h = R * r. \tag{9}$$

3.2.2 The physiological component

The physiological processes are based on the transport-resistance model presented in Sect. 2.1.1 except that, on account of the simplifications of the virtual environment, nitrogen has been replaced by a generic notion of mineral nutrients. This choice is justified because nitrogen is quantitatively the most important mineral nutrient taken up from the soil by natural plants (Marschner 1995) and a major growth-limiting factor in ecosystems (Aerts and Chapin 2000). This section outlines the key equations of the transport-resistance model and their integration into the virtual plant physiology. For more details, see original papers such as Thornley (1998).

The leaves and fine roots of a plant assimilate carbon and minerals depending on the local presence of resources and store them in corresponding substrate pools M_{shC} and M_{rtN} according to the illustration in Fig. 1. For this purpose, the equations for the compartmental resource uptake of the transport-resistance model are broken down into the uptake of each individual captor module. The amount of fixed carbon by photosynthesis of leaf i is thus described by

$$P_i = \frac{k_C * I_{v(i)} * M_{X(i)}}{1 + \frac{C_{sh}}{J_C}} \tag{10}$$

where k_C is a fixed assimilation rate, $I_{v(i)}$ the irradiance in the voxel $v(i)$ where the leaf is located, and $M_{X(i)}$ the leaf biomass. According to Thornley (1998), the denominator slows photosynthesis down depending on the current carbon concentration $C_{sh} = M_{shC}/M_{shX}$ of the shoot compartment and an inhibition constant J_C. The mineral uptake of fine root j is modeled by an analogous equation:

$$U_i = \frac{k_N * N_{v(j)} * M_{X(j)}}{1 + \frac{N_{rt}}{J_N}} \tag{11}$$

where k_N represents the root assimilation rate, $N_{v(j)}$ the mineral concentration in the voxel $v(j)$ where the root is located, $M_{X(j)}$ the fine root biomass, $N_{rt} = M_{rtN}/M_{rtX}$ the mineral concentration of the root compartment and J_N an inhibition constant. It is important to understand that the original transport-resistance model features a third variable per compartment, the overall biomasses M_{shX} and M_{rtX}, whereas in the present model these values result from sum of biomasses of all modules the compartments are composed of.

The carbon and mineral transport between the shoot to the root compartments is determined by the resource concentrations, the compartment biomasses M_{shX} and M_{rtX} and given resistances ρ_C and ρ_{N}:

$$T_{C,sh\rightarrow rt} = \frac{C_{sh} - C_{rt}}{r_{shC} + r_{rtC}} = \frac{C_{sh} - C_{rt}}{\frac{\rho_C}{M_{shX}} + \frac{\rho_C}{M_{rtX}}} \tag{12}$$

$$T_{N,rt\rightarrow sh} = \frac{N_{rt} - N_{sh}}{r_{rtN} + r_{shN}} = \frac{N_{rt} - N_{sh}}{\frac{\rho_N}{M_{rtX}} + \frac{\rho_N}{M_{shX}}} \tag{13}$$

In both compartments, the amount of produced biomass is calculated depending on growth and litter rates. In the shoot compartment

$$\frac{\mathrm{d}M_{shX}}{\mathrm{d}t} = G_{sh} - L_{sh} \tag{14}$$

with the growth rate

$$G_{sh} = \frac{k_G * M_{shX} * C_{sh} * N_{sh}}{1 + \frac{M_{shX}}{K_G}} \tag{15}$$

depending on two fixed growth constants k_G and k_G (Note that the denominator containing k_G does not occur in the original formulation of the transport-resistance model, but has been added in order to control excessive plant growth), and the litter rate

$$L_{sh} = \frac{k_{lit} * M_{shX}}{1 + \frac{K_{lit}}{M_{shX}}} \tag{16}$$

with two parameters k_{lit} and K_{lit} The root compartment grows by analogous equations. The sink strength s_i of module i in the shoot is

$$s_i = w_i * \left(1 + \tau_{sh} * \left(I_{v(i)} - 1\right)\right) \tag{17}$$

and in the root

$$s_i = w_i * \left(1 + \tau_{rt} * \left(N_{v(i)} - 1\right)\right) \tag{18}$$

depending on the genetically defined weight w_i of the module type, the amount of resources (irradiation or minerals) in the respective voxel, as well as the plant's tendency to grow toward resources. "Phenotypic plasticity" means the capacity to develop different morphologies in response to the environment (Pigliucci 2001). The higher τ_{sh} and τ_{rt}, the more the biomass allocation is affected by resource heterogeneity in the environment.

The new biomass is distributed to the sinks, i.e. the apices and, in the shoot compartment, the growing flowers and seeds. Thus, for shoot module i, growth amounts to

$$\frac{dM_{X(i)}}{dt} = \frac{dM_{shX}}{dt} * \frac{s_i}{\sum s_j} \tag{19}$$

where the s_j represent the strength of all current resource sinks of the plant. An analogous growth equation holds for the growth of modules in the root compartment. Finally, the change of the amount of resources in the substrate pools is determined by assimilation, transport and growth:

$$\frac{\mathrm{d}M_{shC}}{\mathrm{d}t} = \sum P_i - f_C G_{sh} - T_{C,sh\rightarrow rt} \tag{20}$$

$$\frac{\mathrm{d}M_{rtC}}{\mathrm{d}t} = T_{C,sh\rightarrow rt} - f_C G_{rt} \tag{21}$$

$$\frac{\mathrm{d}M_{shN}}{\mathrm{d}t} = T_{N,rt\rightarrow sh} - f_N G_{sh} \tag{22}$$

$$\frac{\mathrm{d}M_{rtN}}{\mathrm{d}t} = \sum U_j - f_N G_{rt} - T_{N,rt\rightarrow sh}. \tag{23}$$

3.2.3 The plant life cycle

In the present model, the shoot and root L-system expressions of a plant seedling both start only with a single apex, i.e. the non-terminal character *A*. A small amount of initially available seed biomass reserve *XSeed* allows the young plant to develop its first modules, but subsequently it has to rely on the acquisition of resources.

An L-system rule is applied once the biomass of a non-terminal reaches the required cost for the production of the successor string. This value is calculated from the genetically defined costs of all plant modules that will be produced. In addition to the new modules, growing apices have to pay for the thickening of the branching modules below them. This stipulation guarantees that the cost for apex growth increases with the distance from the ground and is based on the pipe model theory (Shinozaki et al. 1964) which states that any cross sectional area in a branching system, whether shoot or root, is proportional to the biomass of the captors, leaves or fine roots, that it serves.

The reproduction process has been modeled as follows. Blossoming is only possible after a period of juvenile stage, just as for many woody plants in nature (Stearns 1992). When a plant attains its age of sexual maturity *aBloss*, the flower modules initiate a period of bloom with a certain probability *pBloss*. In this case, the flower competes as a resource sink with the apices in Eq. 17 for a share of newly produced biomass. When the amount of biomass *XBloss* is attained, the flower is capable of producing a seed. Since no pollinating agents such as wind or insects have been modeled so far, pollination occurs with a probability *pSeed*. If so, the flower module is replaced by a seed module which is a new resource sink. Depending on the study, the seed contains either an exact or a mutated copy of the mother plant genotype. When the seed biomass *XSeed* is reached, the seed is ripe and randomly dispersed into the neighborhood of the mother plant with a maximum distance of *rSeed*.

After a limited span of life *longevity* the plant dies. Since no carbon cycle is modeled, this resource is considered to escape from dead plant parts. In contrast, the minerals are restored to appropriate soil voxels. The nutrients of dead roots are put in the corresponding voxels and those of the aerial compartment in a surface layer which gradually penetrates the upmost soil layer (see Sect. 3.1.2).

3.2.4 The genetic component

The development of the virtual plants is ruled by “genetic information” recorded in a genotype. It contains all parameters of the transport-resistance equations of Sect. 3.2.2, the L-system rotation angles and production rules as well as the following additional physiological real-valued parameters:

- $0 \leq$ *longevity*: an overall maximum lifetime. The plant dies when its age reaches the given value.
- $0 \leq$ *mobilization*: the mobilization rate of the initial seed reserves into biomass for growth.
- $0 \leq$ *minResources*: a minimum resource level needed for growth. An apex develops only if the specified quantity of resources is available in the local environment.
- $0 \leq$ *mutation* ≤ 1: the genetic mutation probability. To create a mutated genotype, a set of genetic operators is applied with the indicated probability.
- $0 \leq$ *aBloss*: an age of sexual maturity. Flower modules do not blossom before the shoot compartment attains the specified age.
- $0 \leq$ *pBloss* ≤ 1: the probability of flowering. When the shoot is mature, each flower module blossoms with the indicated probability (per time step).
- $0 \leq$ *XBloss*: the biomass of a full-grown flower. Pollination is possible only after the growth of the flower module is complete.
- $0 \leq$ *dBloss*: the maximum duration of bloom. If no pollination occurred so far, the flower is abandoned.
- $0 \leq$ *pSeed* ≤ 1: the probability of pollination. A flower module starts developing a seed with the indicated probability (per time step).
- $0 \leq$ *XSeed*: the biomass of a full-grown seed which will be dispersed.
- $0 \leq$ *rSeed*: the maximum range of seed dispersal. A ripe seed is randomly placed within a circle of the specified radius around the mother plant.

Furthermore, the genotype describe for each type of plant module (leaf, flower, fine root…):

- $0 \leq D$ and $0 \leq \mathrm{R}$: density and height-to-radius ratio specifying the shape of the module.
- $0 \leq X$: a primary biomass. This value allows calculating how much biomass an apex needs to accumulate in order to grow the implicated new modules.
- $0 \leq w$: a weight for the "resource sinks", i.e. the resource demanding modules, indicating their relative importance (apices, flowers and seeds only).

Figure 12 displays a portion of this genotype for a simple bush. Depending on the object of the study, some of its elements may be fixed and others subjected to evolution by a number of genetic operators which modify the data from one generation to another. Evolving real-valued parameters are mutated using a bell-curve around the current value. The genetic operators for the L-system production rules are applied with the probability *mutation*. They are chosen such that any set of rules can be constructed by evolution. The following three operators modify the number of rules:

- Delete rule (a rule of the L-system is deleted);
- Insert rule (an empty rule is added);
- Duplicate rule (a rule is duplicated and added).

Five other operators act on the successor strings and are applied to each L-system rule. Only minor changes, i.e. character by character, are possible between successive generations. In order to avoid improper nesting in the successor strings, the branching symbols [and] are not affected by the genetic operators. For example, if the production $A \rightarrow bl/A$ is selected to be mutated, some of the possible mutations are

- Delete character (a character is deleted): $A \rightarrow bl/$;

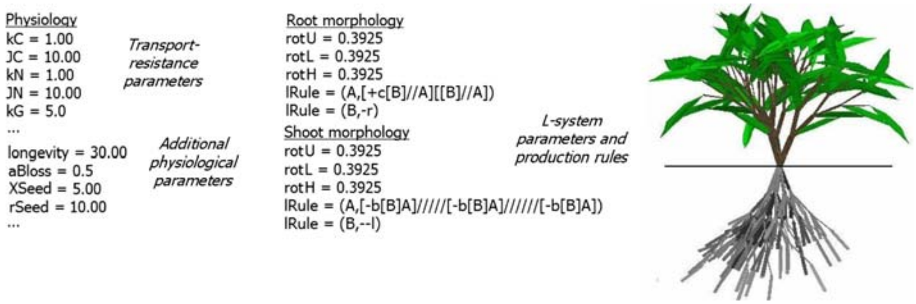


Fig. 12 Sample genotype of a bush

- Insert character (a character is inserted): $A \rightarrow b{\wedge}l/A$;
- Exchange character (two adjacent characters are switched): $A \rightarrow b/lA$;
- Duplicate character (a character is duplicated): $A \rightarrow bl//A$;
- Replace character (a character is replaced by a new one): $A \rightarrow b +/ A$.

4 Experiments

The model described in Sect. 3 has been implemented as a simulation platform. It was developed in C++ and uses the OGRE library (OGRE website, http://www.ogre3d.org) for graphical representations and the Open Dynamics Engine (ODE website, http://www.ode.org) for collision detection. This section presents a number of validating experiments conducted so far. They mainly aim at investigating if and to what extent simulations performed on different scales produce results that correspond to field observations. If so, it can be argued that the model constitutes a suitable starting point for future, more specific studies on plant communities.

4.1 Growth of a single virtual plant

The model is primarily intended for long-term simulations of plant communities. Therefore, the virtual plants had to be kept simple and concise. However in the absence of locomotion, natural plants adapt to their environment by a pronounced morphological and physiological plasticity (Hallé 1999). Therefore, particular importance was attached to the fact that the model exhibits a range of characteristic responses at the individual level to environmental modifications or constraints. The experiments highlight that a minimal plant model is sufficient to induce typical growth patterns of real plants.

4.1.1 Morphological responses

A sample virtual plant species has been designed which, under benchmark conditions, i.e. maximum vertical light and permanent maximum mineral supply, grows into a balanced and upright morphology. Moreover, its modules never decay, so that the observer can better retrace the phenotypic development at the end of a simulation. Figure 13 shows the morphology of four individuals grown under different environmental constraints. Such

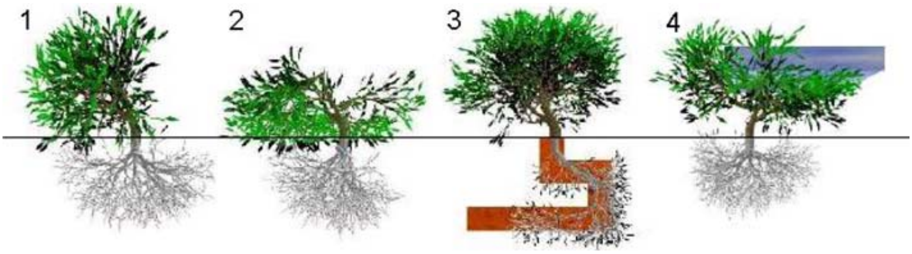


Fig. 13 Morphological differences due to environmental constraints

responses have also been observed in previous models (e.g. Colasanti and Hunt 1997; Mech and Prusinkiewicz 1996).

Plant 1 illustrates the property of phototrophism, i.e. the growth towards a light source (Firn 1994). Light was coming horizontally from the left, so that right-sided leaves and apices gradually found themselves in the shade. Since the biomass allocation and the activation of the shoot apices depends on the access to light, only left-sided apices continued to develop.

Likewise, the light for plant 2 was shining from the ground, directed vertically upwards. Although this environmental scenario is not realistic from a strict biological point of view, the plant adapted to the constraint by developing branches which are bent downwards. Root apices are often similarly sensitive to the access to nutrients (Filleur et al. 2005). This behavior is called chemotropism. Plant 3 was growing in a soil where minerals are available only in a small predefined corridor. It can be observed how the root growth followed this specified disposition of resources.

In order to simulate collisions, the growth of plant modules that conflict with already existing objects may be aborted. However, the involved geometric calculus increases the computational cost and is therefore disabled unless it is indispensable for the goals of the simulation. During the development of plant 4, the collision check was enabled for branches. The individual encountered a horizontal translucent plate which impeded its straight growth. The computation time for the growth of these virtual plants (without visualization) do not exceed a few seconds on a 2 GHz PC. Videos of all simulations can be downloaded from the LIAP5 Internet homepage (LIAP5 website, http://www.math-info.univ-paris5.fr/alife).

4.1.2 Physiological responses

In addition to morphological responses, real plants may also adapt to the environment by shifting resource flow and allocation. In the present virtual plant model, such behavior is engendered by the dynamics of the transport-resistance equations. In order to render the experiments of this subsection more intelligible, the simulations were parametrized such that the two resources are consumed in a symmetric way.

Figure 14 shows the responses of a virtual plant to variable resource access, illustrating the principle of functional balance described in Sect. 2. The individual grew in an environment that initially provided the benchmark conditions of Sect. 4.1.1. The beginning of the simulation led to a stabilization of the ratio between the shoot and root compartment, however the shoot developed more biomass than the root. The phenomenon is due to self-shading among the leaves, whereas there are no such dynamics in the soil. Self-shading leads to less resource uptake per unit biomass in the shoot than in the root, and as a

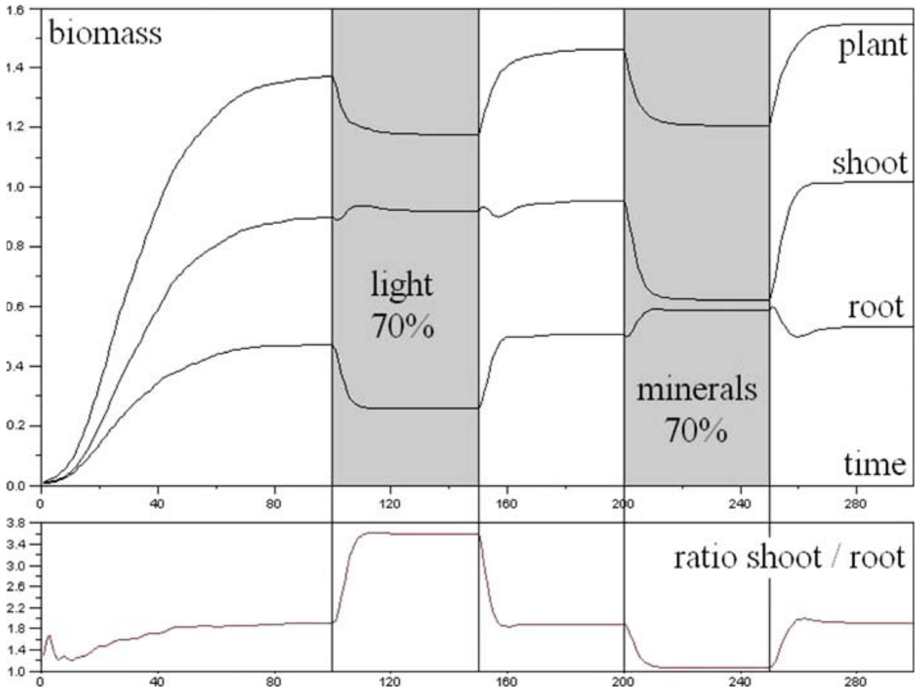


Fig. 14 Resource deficiency leads to shifts in biomass allocation

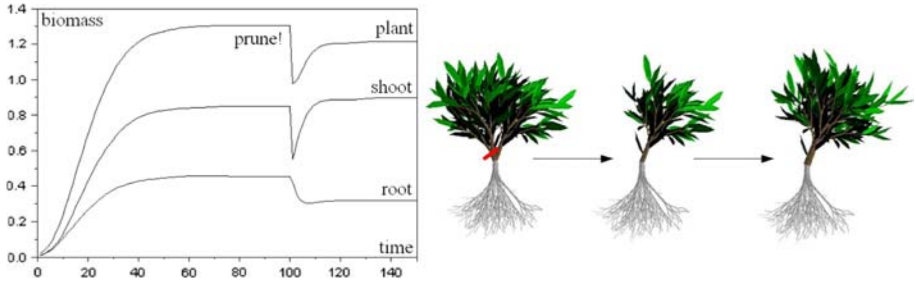


Fig. 15 Recovery after partial pruning

consequence of this disproportionality, resource allocation shifts in favour of the aboveground compartment.

Around time step 100 the plant reached full size, i.e. litter and newly produced biomass came into balance. When the light was lowered, the plant underwent a global loss of biomass accompanied by an increased resource allocation to the shoot compartment. After the light was restored, the plant recovered and the biomass ratio returned to its original value. In the same manner, the resource allocation shifted towards the root when the mineral concentration of the soil was reduced.

A major characteristic of the transport-resistance model is physiological recovery after a severe loss of biomass (Thornley 1998). Response to pruning in virtual plants was previously investigated in Prusinkiewicz et al. (1997). Figure 15 shows the physiological activity of a plant whose shoot compartment was partly truncated. It can be observed that the plant recovered but did not retrieve its original above and belowground biomass. A new balance between shoot and root was required because the differently regrown morphology of the shoot involved a change in the degree of self-shading and therefore in resource uptake.

4.2 Populations of virtual plants

The object of the following section is a series of experiments which serve as a validation at the level of plant communities. As a matter of fact, any individual-based model supposed to be pertinent should be able to reproduce major trends at population level. There exist a number of theoretically formulated plant population growth patterns which could allow benchmarking whether the present model is capable of reproducing dynamics observed in real plant communities. As an example, the self-thinning equation describes plant mortality due to competition in crowded even-aged stands (Yoda et al. 1963). Another example is the theory of Tilman (1984) which states that, in order for several species to coexist in an area, they must divide the resource for which they compete. Therefore, different plant species will be separated along resource gradients. The population level experiments conducted in the scope of this paper compare the population growth of virtual plants to theoretical predictions by the classical Verhulst (1838) and Lotka–Volterra equations (Lotka 1924; Volterra 1926) presented in Sect. 2.2.1.

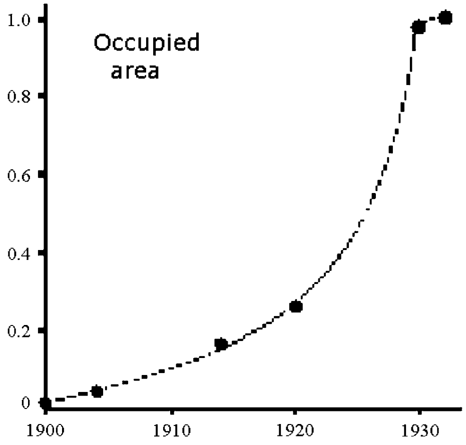
To represent populations of virtual plants on the platform, the reproduction process does not involve mutation, i.e. seeds contain the same genetic information as the mother plant. Since a large quantity of individuals has to be simulated simultaneously in a reasonable amount of time, morphological complexity in the population level experiments is reduced by adjusting the genetically defined growth parameters such that the individuals develop only few morphological units. This can be achieved in several ways, in particular by increasing the biomass cost of the modules. The relation to natural plants is maintained by interpreting growing modules such as root and leaf as clusters of their kind. Reducing the number of modules per virtual plant is an appropriate method to adapt the model to a desired level of abstraction.

4.2.1 Intraspecific competition

As stated in Sect. 2.1.1, the development of a single population corresponds to the invasion process of a species in a new environment. Ecologists divide invasion into three phases: Introduction, colonization and naturalization (Cousens and Mortimer 1995). After the introduction of a foreign species into a new region, its population may initially grow during an explosive colonization phase. However, as space and resources of natural environments are limited, intraspecific competition affects the development, fertility and survival of the individuals and ultimately stops the population growth. The species becomes naturalized in its new environment when it establishes a constant self-perpetuating population. Figure 16 plots data about the increase of area occupied by cheatgrass (*Bromus tectorum*) throughout the Great Basin of North America. Its population growth diminishes around 1930, when nearly the entire area is colonized (Radosevich et al. 1997).

In order to simulate the invasion of a plant species, one seed of a reproducing virtual plant species A was placed in a limited environment of the simulation platform. The density of the emanating population N_A was recorded during 1,000 time units which

Fig. 16 Invasion of *Bromus tectorum* (from Radosevich et al. 1997)



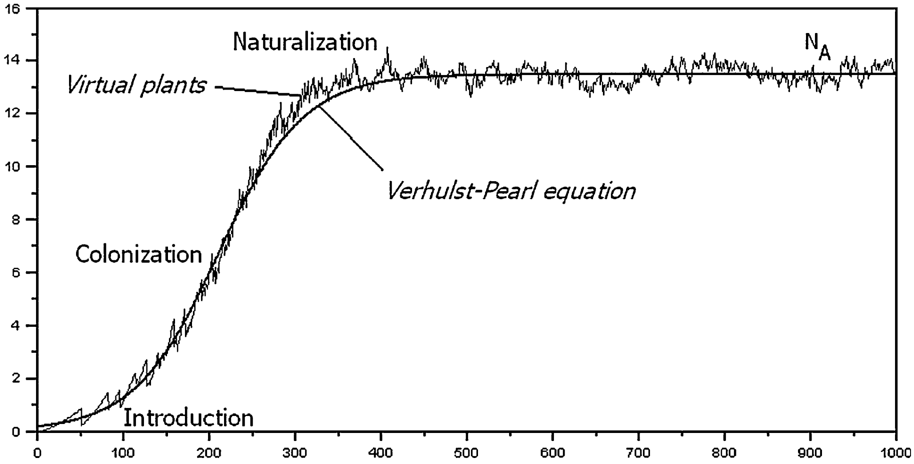


Fig. 17 Logistic growth on the simulation platform

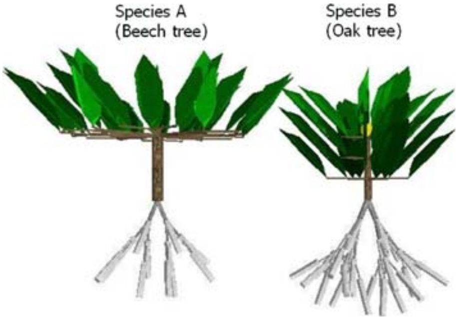
represent, considering the genetically defined maximum lifespan of 50 time units, about twenty to thirty generations. Longer simulations are not necessary because, due to the naturalization process, the system enters a stable state. Figure 17 shows the result of 10 independent runs that have been averaged. The parameters of the Verhulst–Pearl equation were identified in order to compare the experimental results of the individual-based model to the dynamical system. Such a close match can hardly be expected for natural populations. Their growth may considerably differ from the theoretical predictions due to various influential ecological parameters.

4.2.2 *Interspecific competition*

The presented experiment on competition for light between two plant populations is inspired from relations between the oak tree and the beech tree growing in the forest of Chaux in France, as described by Boullard (1999). In 1824 this forest, becoming a natural reservation, was mainly composed of oaks (90%) and only few beeches (10%). However in the middle of the last century, after 130 years of uncontrolled growth, the proportion had reversed. According to Boullard, this phenomenon can be largely explained by different traits in the competition for light. Beeches typically have high and expanded crowns in contrast to oaks, and their seedlings can sustain shading. Oaks grow poorly in the shade and consequently get eliminated over the years.

In addition to the virtual plant of the previous experiment, a species *B* featuring an different aboveground morphology was modeled. Species *A* with a high stem and broad crown represented the beech tree. Shade tolerance was considered by the fact that the initial biomass is sufficient for the seedlings to reach the forest canopy. Species *B*, representing the oak tree, featured a short stem and compact crown (Fig. 18). In reference to the forest of Chaux, one seed of species *A* was placed among nine seeds of species *B* in a limited environment. During 1,000 time units, the densities N_A and N_B of both populations were recorded. The averaged result of 10 independent runs is shown in Fig. 19. After a first rapid growth of the density N_B due to its initial numerical advantage, species *A* interfered with the growth of species *B* and drove it to extinction. This dominance was due to the advantages in the competition for light assigned to species *A*.

Fig. 18 Two competing virtual plant species



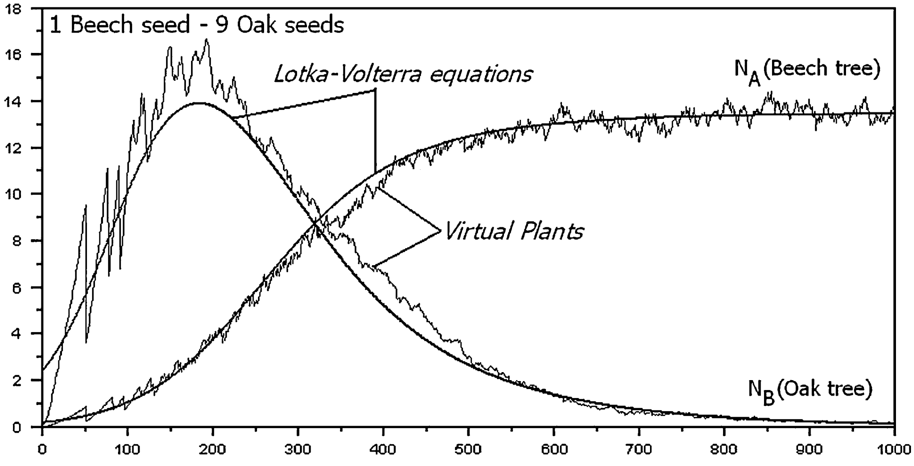


Fig. 19 Competition between two populations of virtual plants

In order to relate the dynamical system to the individual-based model, the free parameters of the Lotka–Volterra equations were determined to fit the result of the experiments. The obtained parameterization allows predicting the course of competition starting from any initial number of seeds. This proposition was validated by several control experiments with different starting values. Figures 20 and 21 oppose simulation results and mathematical solution for two other seed combinations. Phase space analysis allows predicting the outcome of competition between species A and B for any starting number of seeds. The parameterization of Fig. 19 yields

$$K_A > \frac{K_B}{a_{BA}} \quad \text{and} \quad K_B < \frac{K_A}{a_{AB}} \tag{24}$$

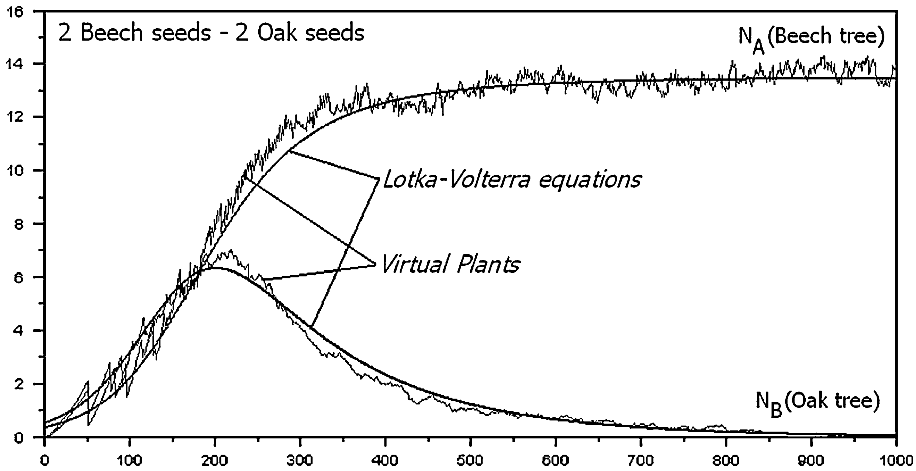


Fig. 20 Interspecific competition starting from 2 beech seeds—2 oak seeds

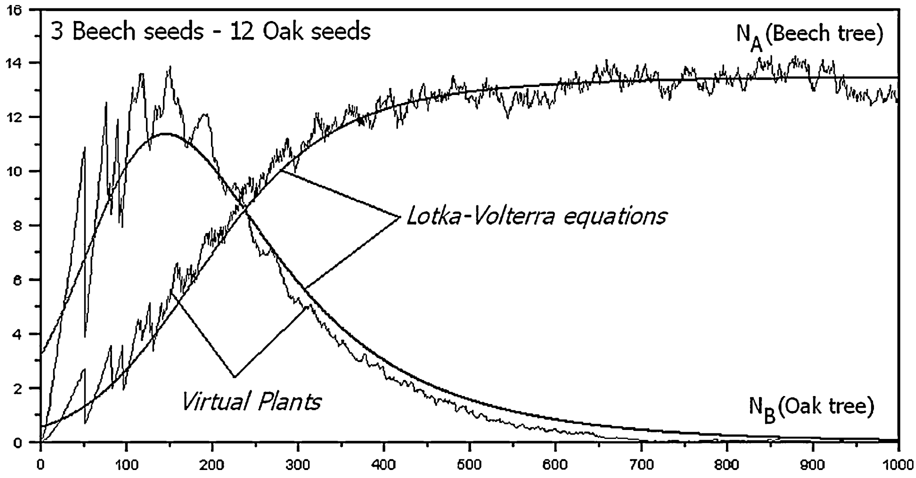


Fig. 21 Interspecific competition starting from 3 beech seeds – 12 oak seeds

so that species *B* goes extinct independently from the initial values. According to Gause's "competitive exclusion principle" (Gause 1934), the two virtual plant species do not seem to possess sufficient ecological differences to coexist.

The experiments of this section not only showed that the platform can produce known population growth patterns, but they also allowed unifying field observation, mathematical theory and computer simulation. On the one hand, differential equations allow a concise, yet comprehensive grasp of the system, but due to their high abstraction level the models suppose a certain homogeneity within the population. Individual differences as well as spatial distribution are omitted. On the other hand, individual-based modeling offers an alternative way of apprehending population dynamics by repeated simulations and statistical evaluation of selected data. The experimental way of reasoning with computer models has given rise to the notion of a "virtual laboratory" (Mercer et al. 1990). However the large amount of information available during a simulation may hamper the spotting and extraction of significant global phenomena and therefore obscure the results of the study. Moreover, an abundance of free parameters tends to call the accuracy of obtained conclusions into question.

In his critical review of ecological modeling, Grimm (1999) suggested a coupling between both levels of abstraction, aggregate and individual based models, because they are "not exclusive alternatives but rather complementary approaches which are mutually dependent". Individual-based models are able to provide more information than aggregate models, and they can be complexified more easily. In return, aggregate models can provide a validating theoretical framework for experiments with individual-based models. Moreover, theoretical considerations on the involved equations may allow generalizing the experimental results beyond the small number of conducted simulations.

4.3 Evolution of virtual plants

The third class of experiments addresses evolutionary phenomena. As numerous physiological and morphological traits of the virtual plants are encoded in a genotype, they may be adapted by variation and selection as originally proclaimed by Darwin (1859). The presented study focuses on the evolution of morphogenesis, i.e. the way to grow and form a phenotype depending on genetic rules, selection criteria and interactions with the environment. It shows how the virtual plants adapt to a given fitness function, that is the production of a maximum of biomass within a limited period of time. Other fitness functions and their impact on plant development are discussed in Bornhofen and Lattaud (2006a, b, 2007).

Only deterministic context free L-systems, also called D0L-systems (Prusinkiewicz and Lindenmayer 1990), are applied. The predecessor character of the first rule is *A*, of the second rule *B* and so on. The L-system is chosen to be deterministic in order to be able to observe and analyze evolutionary dynamics without the need to consider contingencies at individual level. Furthermore, the evolving elements within the genotype are limited to the L-system production rules. Mutations only affect the number of rules and the composition of their successor strings by applying the genetic operators presented in Sect. 3.2.1. All real-valued parameters described in the genotype are predefined and fixed. As this setup is close to that described by Ebner (2002) and Ebner (2003), it additionally offers a possibility of validation by comparing the simulation results. However, the experiments differ from his works in that the presented virtual plants possess a root compartment as well as a physiological component of resource assimilation and allocation.

4.3.1 Evolving morphologies in isolation

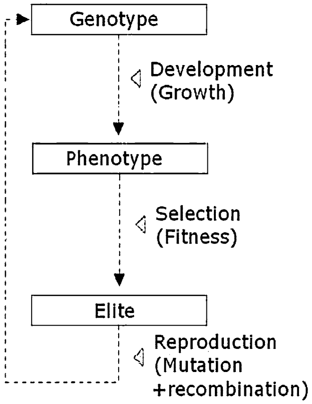
The plants are evolved by an evolutionary algorithm (Holland 1975). A run starts with an initial set of genotypes, also called "population" of genotypes. In the phase of development the genotypes are translated into a "population" of phenotypes. To do so, a seed of each genotype is placed in a sufficiently large environment and grown for a fixed amount of time. Selection then chooses a part of the population by measuring the phenotypes in terms of a predefined notion of fitness, that is, in this case, the total biomass acquired during the growth period. The selected individuals reproduce which leads to new genotypes and closes the evolutionary cycle (Fig. 22). Each succeeding population is thus composed of the selected individuals, commonly termed the "elite" (Goldberg 1989), as well as of newly created individuals. Elitism can increase the performance of evolutionary algorithms because it prevents losing the best found solutions of a generation.

As natural plant life features vegetative and sexual reproduction, the offsprings are half created asexually from a single parent genotype via mutation, and half from two parent genotypes in which case the L-systems are blended by a one-point-crossover. This means that all rules before a randomly selected one are inherited from the first plant, whereas all the following rules are inherited from the second plant. In the literature, there exist various selection methods for evolutionary algorithms. Tournament selection applied here is inspired by competition in nature and arranges "tournaments" to compare the fitness between a few randomly chosen individuals (Goldberg 1989). The best performing individual of every tournament is retained. This approach additionally offers the advantage to easily adjust selection pressure by changing the tournament size.

Just as in Ebner et al. (2002), the probability of each genetic operator is defined as 0.1. This value may be excessive compared to natural evolution, but has been chosen to accelerate the process. The populations are typically composed of 40 plants grown for 30 time units. Survival ratio, i.e. the share of surviving individuals per population, is set to 1/4 and tournament size to 10 individuals. This configuration has been determined experimentally and turned out to produce conclusive results in a reasonable amount of time. A run over 500 generations would take about two hours on a 2 GHz PC. 30 replicate runs were performed.

To grant evolution as much freedom as possible, the initial population only contains genotypes whose L-system holds the single empty production rule. Since there are no rules to apply, the plants of the first generation do not germinate, so that their fitness is zero.

Fig. 22 The evolutionary cycle



However, mutations may lead to the appearance of non-trivial rules. After a few generations, the first individuals that develop root and leaf modules obtaining the resources necessary for growth emerge, and evolution takes off.

Figure 23 plots the fitness values of the elite members during a typical evolutionary run. The graph shows that several plateaus where evolution is slow or even stagnating, are interrupted by phases during which fitness increases rapidly. Such leaps do not occur in every run, and their appearance varies in extent, i.e. duration and slope. The fitness graph additionally plots the average number of total production rules and the average number of used rules in the elite genotypes. The total number is increasing because the genetic operators “Insert” and “Duplicate” work against only one eliminating operator “Delete”. However it can be observed that only a part of the existing production rules in the genotypes is actually applied whereas others are not accessed because no non-terminal characters refer to them.

Such inactive rules are portions of the genetic encoding that do not play any role in determining the phenotype. Non-addressed rules are not submitted to selection pressure and accumulate genetic variation in the form of random mutations. Figure 23 illustrates two moments during the simulation where significant fitness leaps are accompanied by the increase of used rules (in either the shoot or root compartment). It can be concluded that evolutionary enhancements during a plateau phase concern minor modifications such as adding and deleting a plant module or a rotation command. In contrast, leaps seem to be initiated by fundamental structural changes in the network of active production rules. Such events profoundly affect the integrity of the genotype and mostly turn out to decrease fitness, so that the individual is eliminated by selection. However, in some cases, the mutation provides a selective advantage leading to its propagation through the entire population. After activation, the arising selective pressure on the integrated rule may introduce further enhancements within a few generations only, which results in the observed rapid but gradual fitness leaps. In particular, the study suggests that the mutations in non-addressed rules allow exploring new regions of the genotype space via neutral networks on the fitness landscape, which increases the chances for phenotypic innovation. A more detailed study on these neutral networks can be found in Bornhofen and Lattaud (2008).

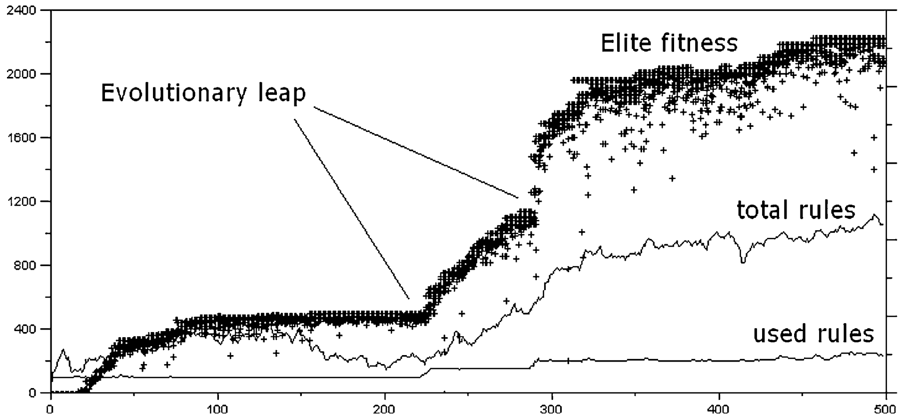


Fig. 23 Fitness values of the elite

Due to abounding space and resources, the virtual plants freely deployed leaves and roots so as to maximize their efficiency. The belowground compartment most often evolved into a dense cluster of roots which rapidly exploited the locally available minerals. The vertical light and the shading dynamics of the sky led to different architectures of the shoot compartment, as shown in Fig. 24. Most runs evolved into dense bushy or tree-like structures like plant 1. Another successful strategy, appearing less often but attaining the highest fitness values, is a star-shaped form spreading close to the ground, as adopted by plant 2. In some runs evolution did not discover branching and got stuck in a local maximum of the fitness landscape. Nevertheless, individuals like plant 3 optimized the photosynthesis by bending horizontally in order to catch as much light as possible. These three morphological classes have also been adopted by natural plant species (Fig. 25).

4.3.2 *Evolving morphologies under competition*

Thanks to their isolated growth, the evolved plants of the previous experiment did not encounter any influences from other individuals. Therefore, evolution optimized resource assimilation and growth without considerations of competitiveness. However, under natural conditions, individuals are far from being isolated, so that their environment is highly ruled by interactions with other organisms.

To study the influence of competition on the evolution of plant morphology, a second series of 30 replicate runs was conducted. In every generation, a population of 40 genotypes is developed into phenotypes for the same period of time as in the previous

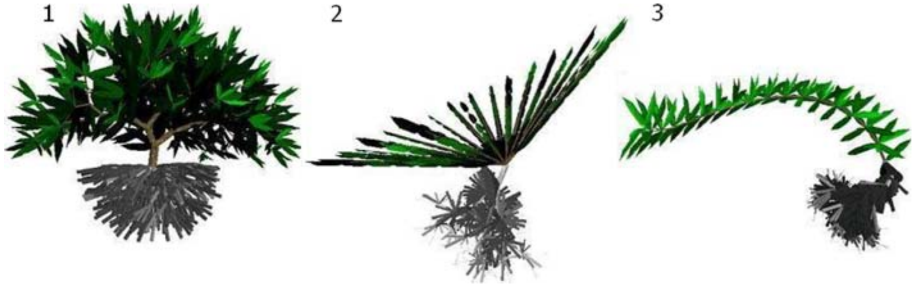


Fig. 24 Evolved morphologies in isolation

Fig. 25 Morphologies of natural plant species

Fig. 26 Competition between virtual plants in a limited environment

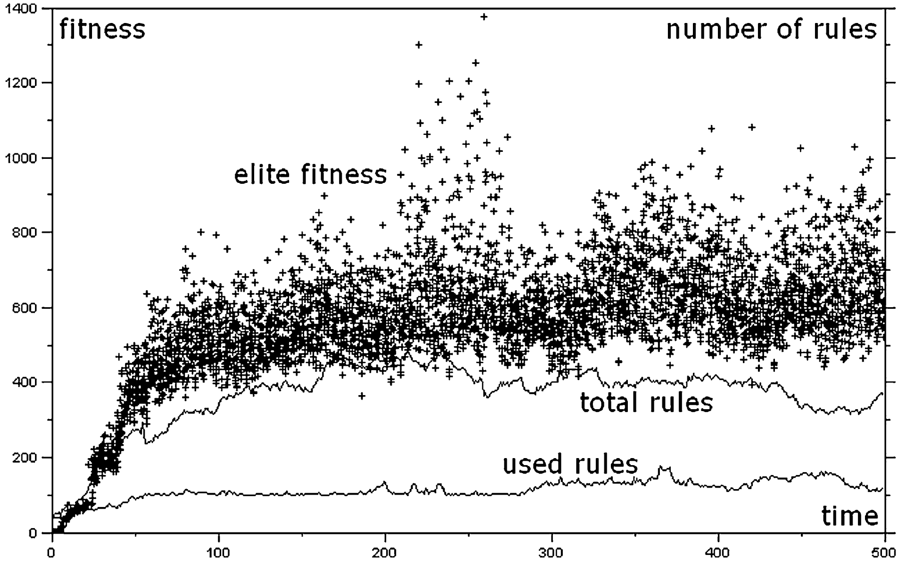


Fig. 27 Evolutionary run under competition

experiment. However, the plants are not grown individually but simultaneously and randomly placed in an environment with limited space and resources (Fig. 26). Afterwards, the fitness of all individuals is determined by measuring their biomass, and the 10 best performing ones are kept to produce a new population of genotypes.

The fitness of the elite members during a typical evolutionary run is plotted in Fig. 27. Fitness initially increases, but starting from generation 150, the average fitness does not improve any more. Looking at the varying average number of total and used L-system rules, it can be concluded that evolution is nevertheless progressing. Moreover, the best performance of each generation begins to oscillate, which means that the fitness landscape is not static. Fitness depends on the consequences of the interaction with neighboring plants. In particular, the elite members of one generation may attain poor fitness in the next generation because they find themselves impaired or even outgrown by nearby competitors.

In contrast to the morphologies evolved in isolation, which occupy large volumes, shoot and root adopt more elongated forms under competition in order to reach the resources. The minerals close to the ground are rapidly exploited by neighboring plants, so that they have to reach deeper in the soil. The aboveground morphologies assume high and tall shapes, stretching out to the sky in the effort to outcompete the other plants in the struggle for light.

Interestingly, the same basic architectures as in isolated breeding can be identified. They seem to constitute fundamental structures appropriate to plant growth (Fig. 28). Nature definitely offers more phenotypic diversification, but this has not been observed in the simulations. One major reason could be the limited genetic search space of the D0L-system which does not allow producing further variety.

The obtained results agree with the experiments conducted by Ebner who concluded that "during coevolution plants grow much higher compared to rather bushy plants when plants are evaluated independently" (Ebner et al. 2002). Such an evolutionary arms race occurs whenever individuals need to struggle for the continuity of their species (Dawkins and Krebs 1979). It is formulated in the "red queen principle" that states that for an evolutionary system, continuing development is needed in order to maintain its fitness relative to the systems it is co-evolving with Van Valen (1973).

To better compare the morphologies of both experiments, Fig. 29 compares the height and width of plants evolved in competition to plants evolved in isolation. The differences of the root compartments are not as significant as those of the shoot compartments. Moreover, there is a clear asymmetry between the elongation of shoot and root when evolved in competition, whereas the spatial proportions evolved in isolation are rather balanced.

These observations lead to the conclusion that, under competition, selection pressure towards elongated morphologies is higher in the shoot compartment than in the root compartment. In the conducted simulations, competition for light seems to be more severe than competition for mineral nutrients, due to the different dynamics of the two resources.

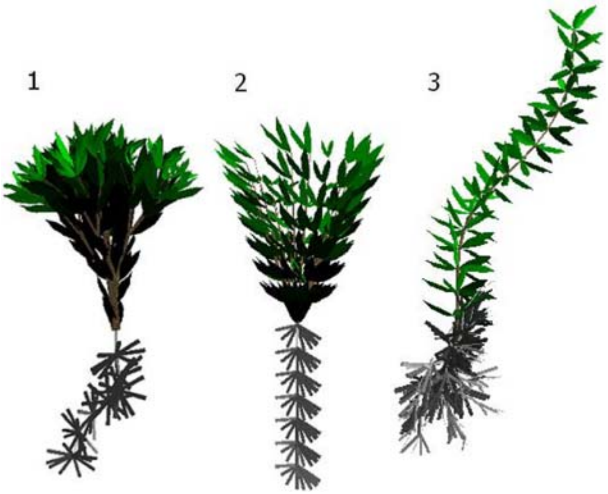


Fig. 28 Evolved morphologies under competition

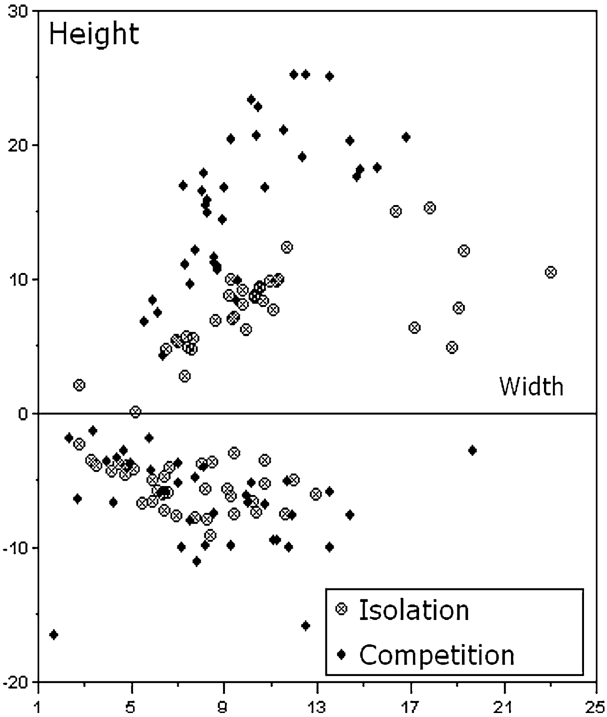


Fig. 29 Comparing the morphologies evolved in isolation and competition

In nature, ecologists refer to light as “size-asymmetric resource”, meaning that larger individuals obtain a disproportionate share of the contested resource, which intensifies the competition. In contrast, mineral nutrients are considered to be rather a “size-symmetric” resource, i.e. they are divided in proportion to the competitor sizes (Schwinning and Weiner 1998).

5 Conclusion and perspectives

Due to economic and ecological concerns, plant communities have become an important target of computer modeling. The concept of virtual plants, combining process-based models with structural models, allows representing plant development with respect to physiological as well as morphological aspects, and notably to embrace the relations between them. However, most existing functional–structural models are too complex to be appropriate for long-term simulations. To fill this gap, a plant model has been defined which especially aims at population level and evolutionary experiments. The virtual plants, growing in a 3D environment, are based upon the fusion between a two-substrate transport-resistance model and an L-system formalism. The model has been implemented as a simulation platform. In the scope of this article, three series of validating experiments on different scales were presented.

At individual level, characteristic morphological and physiological traits of single plants were observed. The simulations showed that a minimal model of virtual plants suffices to capture significant responses to environmental constraints. At population level, several simulations concerning intraspecific and interspecific competition were conducted.

Following the idea of coupling models at different abstraction levels (Grimm 1999), the obtained results provided a basis for the parametrization of corresponding aggregate equations of population dynamics. Phase space analysis contributed to the comprehension of the simulation and allowed drawing conclusions beyond the scope of experimental data. At evolutionary level, the influence of competition on the evolution of plant morphology was investigated. According to previous results on competition for light (Ebner et al. 2002; Ebner 2003), the shoot compartment evolved into elongated forms. Additionally, a similar competition for nutrients occurred between plant roots, and in both cases evolution initiated an arms race for the access to resources. However, aboveground competition seemed to be more severe than belowground competition due to the size-asymmetric character of light as a resource.

Although the simulations were not realistic from a strictly biological point of view, they are relevant in that they allowed to observe and analyze general evolutionary principles within plant communities. All the presented results find analogies in the natural world and therefore are encouraging for future developments of the model. The environment will be enriched with new abiotic parameters such as water and temperature. By this means, further experiments may address questions which need to consider more environmental factors influencing the evolution of plants. Another significant element is gravity which would confront the virtual plants with mechanical stress. Further evolutionary experiments may not only address morphology but also physiological processes, which leads to studies on the evolution of life history parameters such as the growth rate, age and size at maturity, reproductive effort, number and size of seeds or life span of a plant. Yet flora only constitutes a modest part of a complete ecosystem. Other agent types like fungi, parasites, herbivorous or pollinating insects could be modeled and allow producing cooperative and competitive dynamics in a system of different coevolving actors. In this respect, the current work may serve as the stepping stone for a biologically inspired virtual world.

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