The evolution of CSR life-history strategies in a plant model with explicit physiology and architecture

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ABSTRACT

This paper introduces a functional–structural plant model based on artificial life concepts and L-systems. This model takes into account realistic physiological rules, the architecture of the plants and their demography. An original benefit of this approach is that it allows the simulation of plant evolution at both functional and life-history levels implementing mutations to the L-systems and a set of genetic parameter values. The conducted experiments focus on the evolutionary emergence of different life history strategies in an environment with heterogeneous resource availability and disturbance frequency. It is found that, depending on the encountered conditions, the plants develop three major strategies classified as competitors, stress-tolerators and ruderals according to Grime's CSR theory. Most of the evolved characteristics comply with theoretical biology or field observations on natural plants. Besides these results, our modelling framework is highly flexible and many refinements can be readily implemented depending on the issues one intends to address. Moreover, the model can readily be used to address many questions at the interface between evolutionary ecology, plant functional and community ecologies and ecosystem ecology.

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1. Introduction

Ecological and evolutionary processes lead to complex and tangled interactions. Indeed, evolution is the result of natural selection that occurs at the ecological scale and is the result of interactions between environmental properties and the evolving organism traits. Conversely, the evolution of these traits changes the environment for two reasons: first, the traits of interacting individuals belong, in the broad sense, to the environment of these individuals. They, in fact, constitute their biotic environment. Second, most organisms modify in some way the properties of their physico-chemical environment, and species termed as ecosystem engineers have profound impacts on this environment (Jones et al., 1994). Evolutionary ecology traditionally studies the evolution of traits directly affecting fitness and population dynamics such as life-history traits (e.g. Stearns, 1992) or involved in predator–prey interaction (e.g. Geritz et al., 2007). The evolution of traits traditionally studied in functional and ecosystem ecology, such as traits allowing plants to capture resources, has been far less documented (but see for example Schieving and Poorter, 1999). In fact, ecology lacks studies and models linking ecosystem functioning and evolution (Fussmann et al., 2007), while such studies would be very useful to analyse how evolution has shaped present ecosystems.

A good place to start tackling such issues is to study plant evolution and the way it influences ecosystem properties since plants, as primary producers, have a direct and clear impact on ecosystem functioning. Some models have been developed in this spirit. There are many simple analytical models that study the evolution of a very limited number of traits (Kéfi et al., 2008; Loeuille and Leibold, 2008; Menge et al., 2008). These models give general theoretical results but lack realism and do not dwell on the details of the mechanisms of competition between plants, the way they capture resources such as light or mineral nutrients or the way they allocate their resources. Conversely, spatially explicit individual-based models describe in details the dynamics of plant communities (Pacala et al., 1996), primary production and water fluxes (Simioni et al., 2003) or the growth of plants taking into account their architecture and resource allocation strategy (Yan et al., 2004). However, such models are generally not designed to address evolutionary issues.

To meet all these needs, we present in the present article a new model bridging functional and evolutionary ecology and taking into account, in a spatially explicit context, plant architecture, resource capture and resource allocation. It allows simulating the evolution of life-history traits but also the evolution of plant architecture, and resource allocation strategy. To illustrate the model capabilities and

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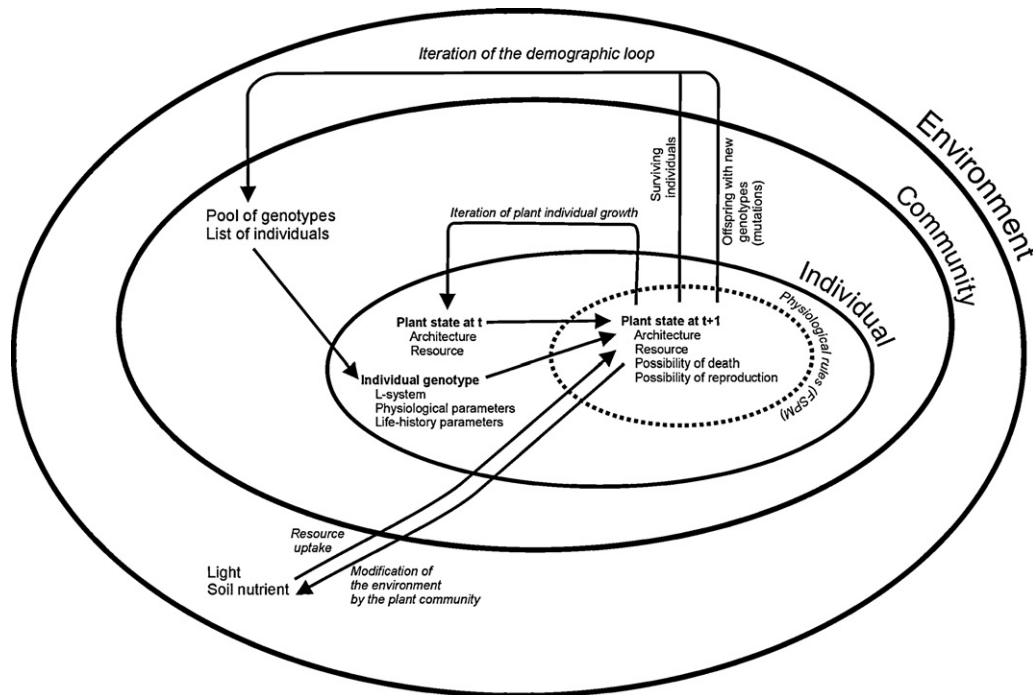 *E-mail address:* sb@eisti.fr (S. Bornhofen).

Fig. 1. Model general outline.

to test Grime's classification of plant strategies (Grime, 1977), we present simulations on the evolutionary outcomes of the combination of two gradients of constraints: a gradient of stress intensity (here soil richness in a limiting mineral nutrient) and a gradient of disturbance frequency.

In the realm of plant life, Grime (1977) identified two major environmental factors limiting growth. Stress is defined as "conditions that restrict production", e.g. shortages of resources or suboptimal temperatures. Disturbance is "the partial or total destruction of the plant biomass" and arises from the activities of herbivores or from abiotic phenomena such as wind damage or fire. Grime suggested the existence of three primary strategies, i.e. sets of life history traits, prevailing according to the local levels of stress and disturbance: (1) Competitors (C) live in fertile undisturbed habitats and are adapted for long-term occupation. (2) Stress-tolerators (S) persist in low resource environments, or where survival depends on the allocation of resources to maintenance and defence. (3) Ruderals (R) are found in frequently disturbed habitats and exhibit rapid development and reproduction. These types are extreme variants of the whole spectrum of plant life history strategies. The disturbance axis recalls the concept of the r-K selection continuum that depends on the predictability of the environment (MacArthur and Wilson, 1967; Pianka, 1970). Grime additionally assumed that plants cannot grow where disturbance and stress are both high. Although Grime's classification is central in plant life history theory, only few models have been published on the subject. Mustard et al. (2003) addressed the evolution of CSR strategies in a virtual environment by means of a mutable model of single plant growth based on a number of life history traits. They observed the emergence of a variety of physiological adaptations consistent with field and theoretical evidence. However, the model was restricted to a highly simplified morphology which could not evolve.

To go further in this direction we chose to build a functional–structural plant model (FSPM). Indeed, FSPM combines a 3D representation of the plant with the simulation of a number of physiological processes (Allen et al., 2005; Perttunen et al., 1998), but they are typically not designed for experiments at evolutionary scale. FSPMs are designed for the study of growth dynamics and

the impact of environmental factors on plant form development (Sievanen et al., 2000). Their detailed calculations of spatial architecture and resource flow draw a faithful picture of real plants in a virtual environment, giving rise to the notion of "virtual plants" (Room et al., 1996). To allow the architecture of the plants of our FSPM model to evolve we used the L-system approach. An L-system is a formal grammar, composed of symbols, rules and rewriting rules that have been developed to model the growth of organisms (Prusinkiewicz and Lindenmayer, 1990). Although L-systems were not initially conceived to be evolved (Stanley and Miikkulainen, 2003), their interest as a generative genetic encoding has been recognized by a number of authors. Jacob (1994) published works concerning the evolution of L-systems representing simple artificial plants. He developed the "Genetic L-systems Programming" paradigm, a general framework for evolutionary creation of parallel rewriting systems. Ochoa (1998) developed 2D plant structures and concluded that L-systems are an adequate genetic representation for the simulation of the evolution of morphologies. Here we have extended her approach by adding by adding a physiological component to the evolving virtual plants.

2. Methods

2.1. Model overview

The detailed description of the plant model and its parameters has been published in a computing journal (Bornhofen and Lattaud, 2009). We describe the model below using an ecologist-friendlier formulation. In a nutshell (see Fig. 1): (1) The model links in a spatially explicit way the dynamics of a plant community to the environmental state described by two resources (light, and a limiting mineral nutrient). (2) Individual growth and architecture is determined by their genotype (five real-valued parameters, and an L-system), physiological rules similar to the ones implemented in FSPMs (converting resources into biomass and allocating the biomass to organs) and the availability of resources. (3) Some biomass is also allocated to the production of seeds that can bear

mutations. Consequently, the model allows the evolution of plant architecture and life-history taking into account resource competition and the feedbacks between individuals, the community and the environment.

2.2. Environment

The artificial plants grow in a continuous 3D virtual environment which is composed of a soil and aboveground compartment, providing minerals and light respectively. Environmental heterogeneity is achieved by dividing both compartments into discrete cells called "voxels" that contain locally available resources.

The sky holds a vertical light source parameterized by its initial irradiance. If an object is situated in an aboveground voxel, it casts shadows such that the luminosity in all subjacent voxels decreases. In order to avoid time-consuming geometrical calculations, the shading factor of aboveground objects such as stems, leaves and flowers does not depend on the surface exposed to the light, but on their volume. Just as aboveground voxels contain a local light intensity, soil voxels contain a mineral resource that is considered to be limiting for plant growth. Only one mineral nutrient is considered as limiting in the present version of the model. Diffusion in three dimensions is modelled by Fick's first law (Fick, 1855) and leads to a flow from regions of high concentration to regions of low concentration (a coefficient of 0.01 was used). The limiting mineral nutrient goes through a simplified recycling loop: (1) the nutrient is assimilated by the plant along its life, (2) at the death of the plant the dead organic matter is deposited in the corresponding soil voxels (for the root) and at the soil surface in an infinitely thin layer of voxels (for the aboveground biomass), (3) the decomposition of dead organic matter is immediate.

2.3. Plant architecture

Plant architecture is described using the L-system formalism (Prusinkiewicz and Lindenmayer, 1990). L-systems were initially designed to model the development of simple multicellular organisms (Lindenmayer, 1968), but their versatility makes them a powerful generic encoding scheme for the modelling of plant growth and many other natural phenomena. L-systems are based on formal grammars (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. Plant components are represented by these symbols and arranged in a string that forms the whole 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 (denoting different plant organs).
- P is a set of production rules specifying the possible transitions (i.e. transformations the plant organs undergo when they grow).
- ω is the initial string or "axiom" representing the primary structure (describing the initial plant state).

For the purpose of plant growth, a bracketed notation extends the basic linear strings to nested expressions. Moreover, special characters like "+" and "−" are typically defined to denote fixed angle rotations in space. As an example, let $\{(a, b), (P_1, P_2), a\}$ be a 2D L-system, a and b denoting respectively apexes and stems, with the production rules:

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

$$P_2 : b \rightarrow bb$$

P_1 specifies that an apex is transformed into a stem segment, followed by two apices branching to the left and to the right, followed
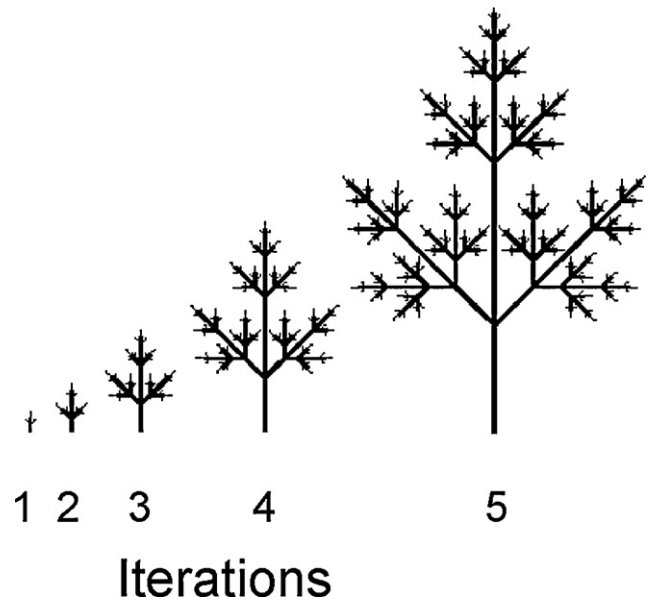

Fig. 2. Example of plant resulting from a 2D L-system simple L-system: $\{(a, b), (P_1, P_2), a\}$, $P_1 : a \rightarrow b[+a][-a]ba$, $P_2 : b \rightarrow bb$, a = apex and b = stem.

by a stem segment and a final apex. P_2 specifies that a stem segment is transformed in two stem segments. The first three iterations of this L-system are:

- a
- $b[+a][-a]ba$
- $bb[+b[+a][-a]ba][-b[+a][-a]ba]bbb[+a][-a]ba$

The translation of the produced string into a geometric branching structure is achieved by an algorithm called "turtle geometry" (Prusinkiewicz and Lindenmayer, 1990). Fig. 2 shows the resulting "artificial plant" after several iterations.

In the presented model, a virtual plant is divided into two parts, namely a shoot and a root component. The shoot and root morphologies are each expressed by an L-system whose alphabet is detailed in Table 1. Lowercase characters represent plant modules such as leaves, stems or roots. Uppercase characters stand for apices where the plant continues to grow.

2.4. Plant physiology

The physiological processes of the plants are based on a two limiting resource, namely carbon and the limiting mineral nutrient, version of the transport-resistance model (Thornley, 1998). In this FSPM approach, an aboveground and a belowground compartment hold separate pools for carbon and mineral nutrient. Photosynthesis charges the shoot carbon pool, and nutrient uptake supplies the root mineral pool. Growth occurs through the conversion of carbon and nitrogen into biomass with a genetically fixed mean C:N ratio

Table 1
L-system alphabet of the used plant model.

Character	Function
l	Leaf, captures virtual light
f	Flower, represents a reproductive module
b	Branch, creates a supporting structure
r	Fine root, assimilates nutrients in the soil
c	Coarse root, creates a supporting structure for roots
$A \ldots Z$	Apex, predecessor of a production rule
[]	Indicates a ramification
+−<>\$ &	Represents a 3D rotation (in two possible directions, around three orthogonal axes)

per plant compartment. Exchanges of carbon and mineral nutrient between the two parts of the plant are represented as a function of the differences in resource concentration and resistances between these parts. These simple assumptions produce a variety of realistic allocation responses in plant development (Thornley, 1998).

Since the original transport-resistance model does not consider plant structure, the approach has been adapted to interface with the morphological part of our model: the leaves and roots of a plant assimilate carbon and minerals depending on the local presence of resources and store them in the corresponding resource pools. The transport-resistance model describes resource flow and the production of biomass. However, new biomass is not stored in a real valued aggregate variable, but distributed to the apices of the current plant morphology. An L-system rule is applied once the biomass of an apex reaches the required cost for the production of the corresponding successor string. This value is calculated from the genetically defined costs of all plant modules that will be produced (see below in Section 2.5). Growing apices also have to pay for the thickening of the supporting modules below them. This stipulation guarantees that the growth cost increases with the distance from the ground and refers to 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 roots, that it serves. The key equations modelling the described physiological dynamics are listed in an Appendix A of this paper. For more details, refer to Bornhofen and Lattaud (2009), as well as to Bornhofen (2008) concerning the values used for the physiological parameters.

2.5. Plant genotype

The development of the virtual plants is ruled by a set of "genetic information" recorded in a genotype. It contains all parameters of the transport-resistance equations, the L-system, i.e. rotation angles and production rules for both plant compartments; as well as five additional real parameters:

- *longevity*: an overall maximum lifetime. The plant dies when its age reaches the given value;
- *maturity*: an age of sexual maturity (defined as a fraction of the overall lifetime). Flower modules do not blossom before the shoot compartment attains a given age;
- *seedX*: the biomass of a full grown seed which will be dispersed;
- *seedD*: the maximum range of seed dispersal. A ripe seed is randomly placed within a circle of the specified radius around the mother plant;
- *kG*: the rate of conversion of resources into biomass.

2.6. Plant evolution

Just as in Mustard et al. (2003), real parameters are mutated by selecting a new random value within a range of 20% around the current value. L-system mutations occur via genetic operators, each of which being associated with a probability of 10% for each rule and each physiological parameter (see below). Such a high occurrence of mutations is not realistic and is higher than percentages usually used within the adaptive dynamics framework (Geritz et al., 1998). This percentage was however necessary to explore more quickly the genotypic space and its consequences on phenotypes simulating populations with relatively few individuals. The genetic operators are chosen such that any set of production rules can be constructed by evolution. The following three operators modify the number of rules: (1) a rule of the L-system is deleted; (2) an empty rule is added to the list of rules; (3) a rule is duplicated. Five other operators act on the successor strings of the production rules. Only minor changes, i.e. character by character, are possible between

successive generations. The applied operators are: (1) a character is deleted; (2) a character is inserted; (3) two characters are swapped; (4) a character is duplicated; (5) a character is replaced. In order not to obscure the results by too large a genetic search space, the evolving elements in the genotype have been limited for the purpose of this paper. Apart from the morphological growth rules, i.e. the L-system production rules, only five physiological parameters, are allowed to mutate (see above in Section 2.5).

2.7. Life cycle

The shoot and root morphologies of a seedling both start with a single apex. A small amount of initial biomass *seedX* allows the young plant to develop its first modules, but subsequently it has to rely on the acquisition of resources and the production of biomass. In this process, the parameter *kG* of the transport-resistance model denotes the utilization rate of stored resources and therefore the growth rate (Thornley, 1998). Sexual maturity is determined by *maturity*, a fraction of the overall life span *longevity*. When a plant reaches the age of *maturity* × *longevity*, the reproductive modules initiate the development of a seed. Reproduction occurs asexually, i.e. seed genotypes are a mutated version of a copy of the mother plant genotype. Sexual reproduction tends to slow evolution down, and it has been shown that, at least in some cases, it does not produce considerable novelty compared to asexual reproduction (Kisdi and Geritz, 2000). Moreover, mutations are sufficient to explore the entire genotype space, and previous studies using explicit selection (Bornhofen and Lattaud, 2006, 2007) suggest a low efficiency of the applied crossover operators inspired by Ebner et al. (2002). Therefore, no pollination mechanisms have been implemented in the present version of the model. During seed production, reproductive modules become a resource sink and compete with the apices for a share of newly produced biomass. When a seed attains the final seed biomass *seedX*, it is considered ripe and dispersed in the neighbourhood of the plant at a maximum distance of *seedD*. After a limited span of life *longevity* the plant dies and its mineral resources are resituated to the environment.

Some trade-offs are directly described by the evolving five parameters. For example, due to resource allocation, the bigger the seeds are (*seedX*) the fewer they are. Or, the lower age at maturity is (*maturity*), the quicker the individual is to reproduce but this can threaten subsequent growth and resource capture. A number of other life history traits such as plant height or seed number are not directly encoded in the genotype but are emergent properties of the L-system and the physiological rules of the FSPM.

2.8. Simulations

The environment is a bordered square terrain (extent: 40 length units) divided into 5 × 5 patches called A1 to E5 and featuring unequal levels of disturbance and stress (Fig. 3). Along the horizontal dimension, "disturbance events" kill plants with a probability increasing from column 1 to 5. Such events are not applied to an entire patch, but they potentially occur in each cell of a 5 × 5 subgrid. The subdivision was chosen such that a single disturbance does not erase the whole population of a patch, but provides sufficiently large gaps for the establishment of new plants. Along the vertical stress dimension, an abiotic mineral cycle has been added to the environment. Starting from an initially homogeneous amount of nutrients, the resources of the down most soil layer of each patch drain into a separate pool which is flushed back to the surface by random events. This simulates soil capacity to retain nutrients, and mineral stress increases from row A to E with decreasing probabilities for these "nutrient flushes". In order to maintain the induced soil heterogeneity during simulation, diffusion only takes place between the voxels of the same patch.
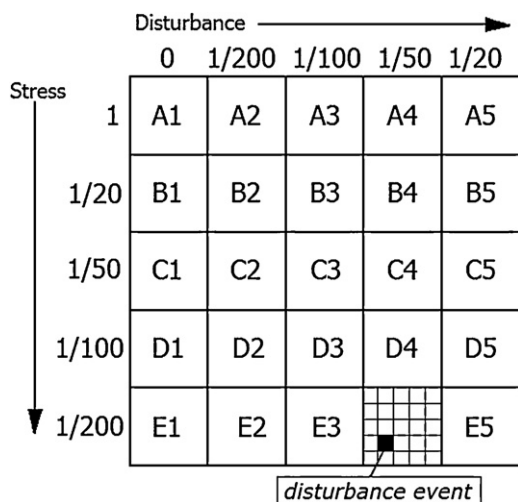
Fig. 3. Implementation of the gradients of disturbance and stress intensity.

Nutrient flow across the overall environment would blur the different levels of stress. Fig. 3 schematically plots the environmental setup and indicates the applied probabilities of disturbance events and nutrient flushes per time step.

At the beginning of the simulation, 1000 seeds are dispersed across the terrain. Their non-mutable genetic parameters are identical and have been adopted from previous simulations on life history evolution (Bornhofen and Lattaud, 2006). However, the L-system derivation depth of the plant morphology has been restricted to five productions. Higher values lead to an exponential increase of simulation complexity, and previous works attest that they do not induce evolutionary tendencies that are fundamentally different from those observed in this paper (Bornhofen and Lattaud, 2006, 2007). The mutable physiological parameters are randomly initialized within suitable limits which have been assessed experimentally by analysing the outcome of a series of evolutionary test runs in the same environment. To grant the morphological evolution as much freedom as possible, the initial seeds all start with the L-systems of a "minimal" reproducing virtual plant containing the single rule A → r in the root compartment and A → l in the shoot compartment. During the simulation, the plants grow, compete and reproduce freely via intrinsic selection, i.e. without imposed fitness criteria. Differences in life history dynamics emerge from mutations in every new seed genotype, and if a strategy turns out to ensure better survival and reproduction, it has a greater chance to increase its abundance in the population.

The size of the terrain and the number and length of model runs represent a trade-off between maximizing the amount of individuals and harnessing simulation time and allocated computer memory. In the scope of the presented study, 20 replicate runs were performed for a period of 10,000 time steps. These values were determined experimentally and turned out to produce quantitatively conclusive results in a reasonable amount of time. One run would take about 10 h and nearly use the full memory on a commodity PC – 3 GHz, 1 Go RAM. Throughout the simulations, the following measures are regularly recorded for each patch: the number of plants, the number of produced seeds, the total plant biomass, the averaged five mutable parameters. Next section presents the mean values over the 20 simulations.

3. Results

3.1. Propagation dynamics

The initial plants, dispersed throughout the entire environment, rapidly perish in most parts of the terrain and only persist in the

upper left corner, i.e. the neighbourhood of patch A1. All other regions turn out too hostile for plants with randomized characteristics. The remaining individuals start to reproduce and spread new seeds. As seed dispersal is not limited by the patch borders, the population steadily invades the terrain along the two dimensions toward the patches A5 and E1. Note that it is the gradual increase in difficulty that allows the plants to discover suitable survival strategies for these extreme environmental conditions. After only a few generations, the formation of the CSR triangle is recognizable. Fig. 4 shows a view on the virtual environment during a typical simulation. According to the experimental setup, the plants establishing in patch A1 will be called "competitors", those of patch E1 "stress-tolerators" and those of patch A5 "ruderals".

Fig. 5a plots the number of plants that grow in the three key patches throughout the simulations. Starting from the dispersed random seeds, the plants directly increase their population in the competitor corner A1. Stress-tolerators do not exist yet, and the initial plants of patch E1 disappear without offspring. Around time 1000, the population originating from A1 evolves a strategy to survive in this difficult environment and reinvades the patch. Similarly, the first plants of patch A5 are rapidly wiped out by disturbance before being able to reproduce, and it is not before time 2000 that a small population starts to persist.

After an initial peak, the number of competitors diminishes and nearly comes into balance at the simulation end. Although one might expect evolutionary adaptation to lead to a continuous increase in plant number per patch, a decrease is observed. This phenomenon is explained by the fact that from the initially defined minimal morphology, featuring one leaf and one fine root, the plants evolve toward architectures consuming more resources per individual, which affects the carrying capacity of the patches in terms of density of individuals. Here, it is not the number of plants, but the amount of plant biomass per patch that increases along the evolution (Fig. 5b).

3.2. Evolution of the mutable traits

Just as in Mustard et al. (2003), the resulting strategies at the simulation ends are analysed using principal component analysis (PCA) (Jolliffe, 1986) for the five traits that can directly mutate (as opposed to morphological features that result from the evolution of the L-systems). By considering lower order principal components and ignoring higher-order ones, potential clusters in the cloud of data points may become recognizable. Fig. 6 plots the first two components of the PCA applied to the set of evolved strategies in the key patches A1, E1, A5 during all replicate simulations. It can be
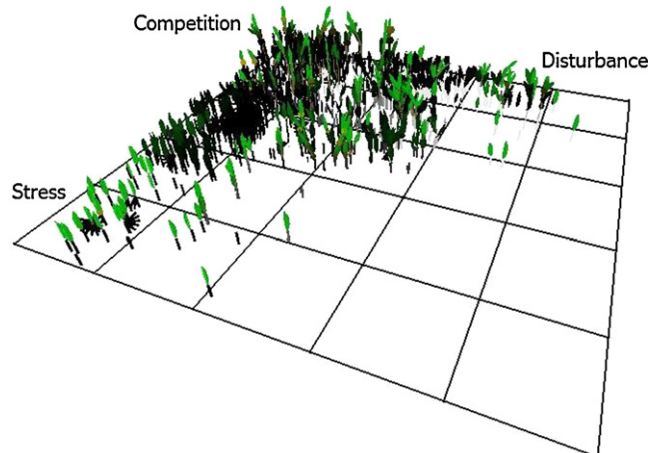

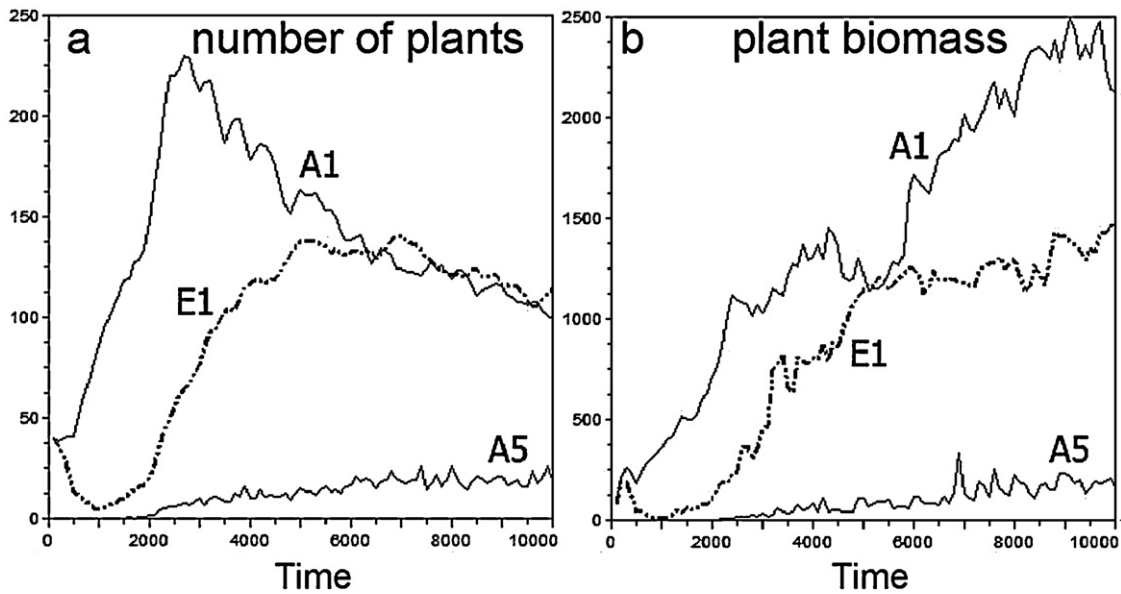**Fig. 4.** Sample view on the virtual environment.

Fig. 5. Number of plants and total plant biomass per patch in the three extreme patch types (E1, A1, A5). .

observed that the results associated to each patch tend to cluster. The pattern attests that the environmental factors disturbance and stress lead to the emergence of contrasting strategies in the virtual plant model. As a next step, it is studied if these physiological adaptations match the predictions of Grime's CSR theory or show other similarities to natural plants found in analogous environments. The evolved mean values of the mutable parameters are summarized in Table 2 for the three contrasting patches (A1, E1 and A5).

Ruderals possess a low maturity, i.e. only a minimum share of lifetime is devoted to individual growth before investing biomass into seeds. Frequent catastrophes force them to spawn as early as possible, so that there is selection pressure toward small values. For the same reason, selective forces lead to the evolution of low longevity, as the threshold of sexual maturity scales linearly with life span in the model. A low seed biomass *seedX* allows the pro-

duction of many seeds in a short time. Ruderals also evolve a high growth rate *kG* since this parameter is responsible for the amount of resources consumed per time step, and selection turns out to favour high resource utilization in order to accelerate the life cycle. This suite of traits matches the life history strategy of r-selected plants in unpredictable environments (Pianka, 1970).

Competitors feature a significantly higher maturity than ruderals. They need a distinctive period of vegetative growth in order to gain height and get access to light. Moreover, as no disturbance events occur in their patch, longevity tends to evolve high values in order to obtain more time for reproduction. Due to strong competition in the patch, these plants develop a high seed biomass *seedX* in order to increase seed survival. Again, the observed values comply with the theory of K-selected plants in constant environments (Pianka, 1970).

Stress-tolerators evolve the longest life span. Due to a low availability of mineral nutrient, growth and reproduction are slow. Therefore, only high values of longevity may grant enough time to run through a complete life cycle. Natural stress-tolerators typically feature an inherently slow biomass production in order not to overconsume the available resources (Chapin et al., 1993). In the simulations, their virtual counterparts likewise develop low *kG*, but the difference to competitors is not significant. The environmental nutrient flushes in patch E1 might not be rare enough to induce a more distinct result.

Interestingly, in contrast to the other physiological values, the evolution of *seedX* does not exhibit a monotonically increasing or decreasing curve. Fig. 7a indicates that, starting from the initial random values, *seedX* first rapidly drops in all patches before it starts to rise again around time 2500. This phenomenon is caused by the fact that the pioneering plants do not encounter severe compe-
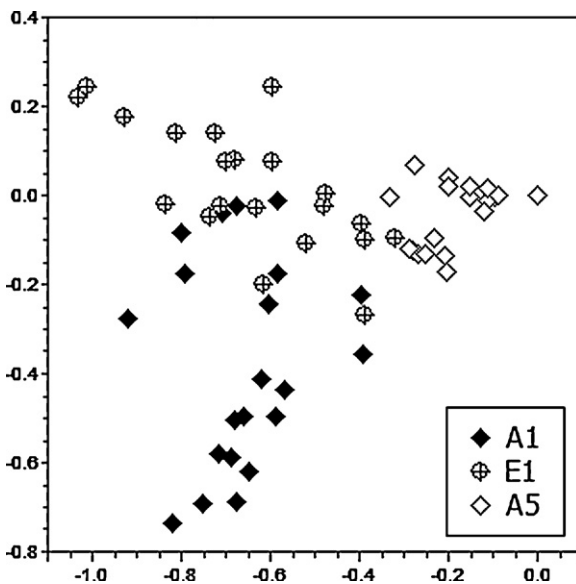

Fig. 6. Plots of the first two components of the PCA applied to the set of evolved strategies in the extreme patches A1, E1, A5 during all replicate simulations. Variables are the five numerical traits that can directly mutate. Each observation corresponds to values averaged over all individual of a patch at the end of a simulation.

Table 2
The averaged five mutable parameters in the three extreme patches (A1, E1, A5) after the evolutionary simulations.

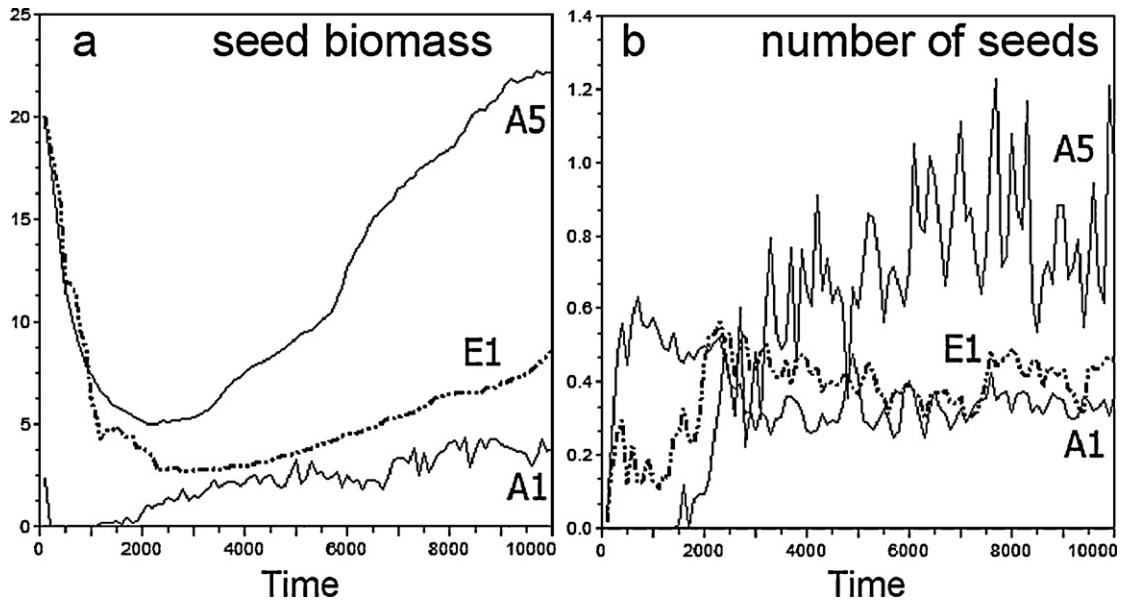|	A1 competitors	E1 stress-tolerators	A5 ruderals
Longevity	627.58	801.47	196.33
Maturity	0.09	0.12	0.03
kG	0.95	1.09	3.62
seedX	22.16	8.65	3.85
seedD	6.25	7.40	6.25

Fig. 7. Mean seed biomass (*seedX*) and seed number per patch (E1, A1, A5).

tition so that, in the short term, there is selection for small and numerous seeds. However, when the plant population densifies and morphological evolution increases the size of each plant individual, seedlings require a higher initial biomass to survive and acquire resources and thus a higher seed mass. The simulations attest that this constraint is particularly crucial for competitors. Just as in nature, large seed size facilitates the establishment in shady stable plant communities (Foster and Janson, 1985). Conversely, ruderals are selected for a higher number of offspring than competitors (Fig. 7b).

The evolution of the distance of seed dispersal, *seedD*, involves a trade-off between the capacity of colonization and individual survival. Too small values impair the spread of genetic information, and moreover seedlings may suffer resource deficiency from the proximity to each other and their mother plant. With high *seedD*, on the other hand, offspring potentially end up in regions they are not adapted to. The simulations yield no significantly contrasting results for this parameter. The evolved values in all three key patches correspond to slightly less than the dimensions of these patches (8×8 length units). An explanation can be found in the experimental setup. In the corners of the virtual terrain most of the adjacent areas are lethal, so that strong selection pressure exists toward spawning offspring inside the same patch, and no further differences depending on disturbance and stress can be observed. Although *seedD* does not yield differentiated results as regards the CSR strategies, the values demonstrate an evolutionary adaptation to the risks of long distance seed dispersal. As an example in nature, it has been observed that plants which colonized islands started to evolve reduced dispersal distances presumably because selection favoured individuals whose seeds do not get lost in the surrounding ocean waters (Cody and Overton, 1996). The evolution of long distance dispersal in ruderals has not been observed, probably because an environment promoting ruderals only exists in one corner of the simulated terrain. Simulation runs with perturbations occurring frequently enough on the whole landscape are likely to provoke such an evolution, just as observed in nature.

3.3. Morphological adaptations

The virtual plants evolve in their environment not only by changes in physiology. The mutating shoot and root L-systems additionally lead to the emergence of distinct adapted above- and belowground architectures. A look at the plant forms growing in the key patches at the end of the runs reveals that the three life history strategies are associated with recognizable morphological characteristics. Fig. 8 illustrates some typical plant architectures which evolved during the simulations. In all the runs, competitors develop a high stem without branches in order to rapidly reach the light in their crowded environment. Small plants are penalized as they do not photosynthesize enough carbon for reproduction. As mineral nutrients are abundant, competitors do not invest much biomass into roots.

Note that, since no mechanical constraints such as gravity or wind are modelled, high and slim shoot structures do not require deep roots to provide physical support. Ruderals have the most simple, condensed morphologies. They do not struggle for minerals, and biomass needs to be invested into the rapid production of seeds, so that the root structure remains elementary. Moreover, catastrophes constantly remove plants and create clear gaps in the patches. Enough light attains the surface and it is sufficient for photosynthesis to deploy a small number of leaves near the ground.

Stress-tolerators feature the greatest variety of shoot morphologies without distinct evolutionary tendencies. Some runs lead to competitor-like stems, others to only a tuft of low growing leaves. However, due to the phenomenon of "functional balance", plants in low resource patches typically possess a decreased shoot-to-root
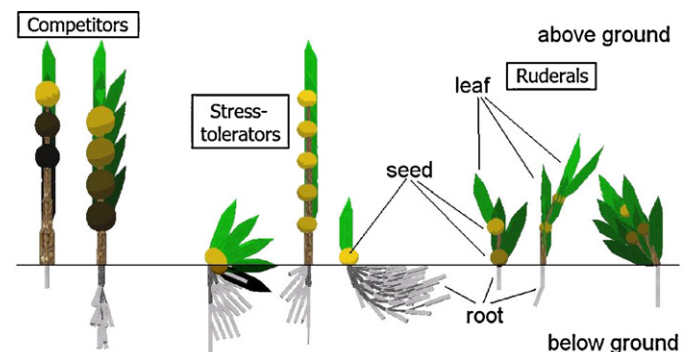

Fig. 8. Examples of evolved morphologies in the three patches (E1, A1, A5).

ratio. This principle states that the resource assimilation of shoot and root tends to an equilibrium with respect to their relative utilization. Lower light provokes a stronger growth of leaves, and a lower availability in soil nutrients increases root growth (Davidson, 1969). Thus, the stress-tolerators tend to invest an important share of their biomass into root structure which results in the evolution of differentiated belowground architectures.

4. Discussion

We have conducted an experiment on the emergence of life history strategies with a simulation platform of virtual plants. The plants, growing in a 3D environment, are based upon the fusion between a two-substrate transport-resistance model as functional component, and an L-system formalism as structural component. Evolution occurs at both functional and structural levels. Depending on the degree of encountered disturbance and stress, plants develop three major strategies which can be termed competitors, stress-tolerators and ruderals according to Grime's CSR theory (Grime, 1977). Most of the evolved characteristics correspond to theoretical hypotheses on the evolution of plant life history and strategy to face environmental constraints or field observations on natural plants. The emergence of the CSR triangle corroborates the conjectured impact of disturbance and stress on plant evolution and illustrates that plant strategies depend on the intensity of both types of environmental factor. The fact that the three main strategy types postulated by Grime evolve in our model and that no other strategy types have evolved suggests that, indeed, these three strategies constitute a very general ecological pattern. Hence, our model supports Mustard et al.'s own modelling results (Mustard et al., 2003). In addition to their results, and thanks to the L-system approach, our model also predicts the evolution of plant architecture and these predictions are in accordance with Grime's theory. Extending the current simulations, the impact of crucial parameters in the experimental setup such as patch size and disposition needs to be studied more closely. Here, environmental gradients have been implemented, which suggests that the CSR strategies could evolve at the landscape scale and when environmental constraints vary gradually. Thinner scale heterogeneity could also be implemented to determine whether intra-ecosystem heterogeneity could also allow the evolution of the CSR strategies. The virtual environment could also feature patches with a lower light availability as a second kind of stress, which might lead to other morphological and physiological adaptations for the stress-tolerating plants. Finally, we could relax the constraint that limits the complexity of plant morphology (by allowing a higher L-system derivation depth than five productions). This could allow for the emergence of more realistic plant structures.

Besides, our modelling framework is highly flexible and many refinements can be readily implemented depending on the issues one intends to address. Nutrient cycling could for example be described in a more realistic way, taking into account one or several organic matter compartments, inputs and outputs of nutrient to and from the ecosystem (see for example Barot et al., 2007; Boudsocq et al., 2009), more than one limiting nutrient (Daufresne and Hedin, 2005), or downwards mineral nutrient movement due to water circulation. Some aspects of plant growth and resource allocation could also be refined. For example, slight changes in the model would allow for different carbon-to-nutrient ratios used for the growth of plant organs. Leaf physiology is typically more expensive in terms of nitrogen consumption than other above-ground plant components (Gurevitch et al., 2006). Therefore, differential C:N ratios would add more realism and might yield interesting insights into the dynamics of plant resource allocation. Moreover, the death of plant organs (leaves, stem and roots) according to

their age could be taken into account. This would increase the cost of maintaining a large photosynthetic surface or root system and could subsequently allow the life-history of the plants to emerge from the resource allocation strategy: for example, this could constrain plant survival in such a way that all plants would die before reaching their maximum longevity. Taken together this would allow all life-history characteristics and trade-off to emerge and evolve in relation with the L-system, the physiological rules and the resource allocation strategy. In the same vein, allowing for the death of plant organs would allow taking into account herbivores and their ecological and evolutionary effect on plant growth, resource allocation and life-history (Crawley, 1996).

More generally, beyond the interest of describing the evolutionary foundation of Grime's theory on plant strategies, our results reveal the potential of the model to readily address many questions at the interface between evolutionary ecology, plant functional and community ecologies and ecosystem ecology. Many appealing issues could thus be tackled. By tracking the diversity of genotypes, and corresponding phenotypes along evolutionary simulations, our modelling approach will allow studying directional evolution and evolutionary branching (i.e. speciation) as in the models developed within the adaptive dynamics approach (Dieckmann, 1997; Geritz and Gyllenberg, 2005). Within this approach, phenotypic quantitative traits are assumed to be determined by a high number of genes and mutations are simulated directly by small changes in the quantitative traits while, in our case, with the L-systems, there is a clear distinction between the genotype and the phenotype. It would be relevant to study how this unique characteristic of our model influences evolutionary dynamics.

In the same vein, a crucial issue in modern ecology consists in determining the links between biodiversity in plant species and ecosystem functioning. While many studies have documented positive effects of plant species richness on primary productivity (Loreau et al., 2001), the underlying mechanisms allowing plant species to be complementary in the way they use resources, environmental heterogeneity and variability remains poorly understood (but see Fornara and Tilman, 2009). Our modelling platform can be readily used to reproduce biodiversity experiments (see for example Hector et al., 1999) using random assemblages of plant species defined by randomized plant genotypes. This could give some hints on the possible mechanisms, in terms of architecture and resource allocation, allowing for complementarity between plant species. Subsequently, instead of using randomized genotypes, plant species could be allowed to coevolve in the same ecosystem before being used in our in silico biodiversity experiments. This would allow studying the interplay between evolution, biodiversity and ecosystem properties which is a crucial issue (Fussmann et al., 2007) and testing the influence of evolution on the effect of biodiversity on ecosystem functioning.

One limitation of the presented approach is the fact that most of its simulations ask for computing and memory resources that are considerable for today's commodity computers. In the presented study, patch number, patch size as well as plant structure had to be kept low in order to control the model complexity in terms of memory space and computation time. A larger environment would have allowed a better exploration of intermediate strategies and coexistence of competitors, ruderals and/or stress-tolerators. More complexity in plant architecture is not only likely to yield more morphological variety, but it would also allow addressing the question of how sensitive the obtained results are to initial plant structures. Such a "complexity barrier" has been observed in many artificial life models featuring morphological evolution (Taylor, 2000). Modern infrastructures designed for parallel computing, such as clusters and grids, might be an interesting option to overcome this issue. In a nutshell, we have presented here a modelling approach combining (1) L-systems and simple physiological

rules to define the growth of plants, (2) the possibility of feedback between plant growth and the environmental state, at least through resource use and (3) mutations in the L-systems. We have shown that this allows simulating complex behaviours resulting from the interplay between ecological and evolutionary dynamics such as the evolutionary emergence of the CSR strategies. However, this is only one example of the issues that our modelling approach allows tackling. While the study of the interplay between evolution and ecosystem functioning is pretty much in its infancy, the use of the L-systems and FSPM to define plant growth and the implementation of mutations of the L-systems allows modelling the evolution of plant strategies in a more realistic and refine way than currently published models (see for example Kéfi et al., 2008; Menge et al., 2008) that remains rather theoretical. This should in turn help linking theories on the effect of plant evolution on ecosystem functioning with empirical data.

Appendix A.

The physiological processes are based on the transport-resistance model (Thornley, 1998) except that, on account of the simplifications of the virtual environment, nitrogen has been replaced by a generic notion of mineral nutrients. The plant is divided into a shoot and a root compartment, each of which holds two substrate pools for carbon and minerals, called M_{shC}, M_{shN} and M_{rtC}, M_{rtN} respectively.

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}. The amount of fixed carbon by photosynthesis of leaf i is described by

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

where k_C is a fixed assimilation rate, $I_{v(i)}$ is the irradiance in the voxel $v(i)$ where the leaf is located, and $M_{X(i)}$ is the biomass of leaf i. 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 modelled by an analogous equation:

$$U_j = \frac{k_N \times N_{v(j)} \times M_{X(j)}}{1 + (N_{rt}/J_N)}$$

where k_N represents the root assimilation rate, $N_{v(j)}$ represents the mineral concentration in the voxel $v(j)$ where the root is located, $M_{X(j)}$ represents the biomass of fine root j, $N_{rt} = M_{rtN}/M_{rtX}$ the mineral concentration of the root compartment and J_N an inhibition constant.

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:

$$T_{C,sh \to rt} = \frac{C_{sh} - C_{rt}}{(\rho_C/M_{shX}) + (\rho_C/M_{rtX})}$$

$$T_{N,rt \to sh} = \frac{N_{rt} - N_{sh}}{(\rho_N/M_{rtX}) + (\rho_N/M_{shX})}$$

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

$$\frac{dM_{shX}}{dt} = G_{sh} - L_{sh}$$

with the growth rate

$$G_{sh} = \frac{k_G \times M_{shX} \times C_{sh} \times N_{sh}}{1 + (M_{shX}/K_G)}$$

depending on two fixed growth constants k_G and K_G, and the litter rate

$$L_{sh} = \frac{k_{lit} \times M_{shX}}{1 + (K_{lit}/M_{shX})}$$

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

$$s_i = w_i \times (1 + \tau_{sh} \times (I_{v(i)} - 1))$$

and in the root

$$s_i = w_i \times (1 + \tau_{rt} \times (N_{v(i)} - 1))$$

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. The higher τ_{sh} and τ_{rt}, the more the plant exhibits phenotypic plasticity because the biomass allocation is affected by resource heterogeneity in the environment. Note that $I_{v(i)}$ and $N_{v(i)}$ are normalized values between 0 and 1.

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

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

where the s_j represents 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:

$$\frac{dM_{shC}}{dt} = \sum P_i - f_C G_{sh} - T_{C,sh \to rt}$$

$$\frac{dM_{rtC}}{dt} = T_{C,sh \to rt} - f_C G_{rt}$$

$$\frac{dM_{shN}}{dt} = T_{N,rt \to sh} - f_N G_{sh}$$

$$\frac{dM_{rtN}}{dt} = \sum U_j - f_N G_{rt} - T_{N,rt \to sh}$$

The parameters f_C and f_N specify respectively the proportion of carbon and minerals in the plant biomass.

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