Evolving CSR Strategies in Virtual Plant Communities

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Abstract

This paper introduces a functional-structural plant model based on Artificial Life concepts and reports studies on evolutionary dynamics in virtual plant communities. The characteristic of the present approach lies in plant evolution at both functional and structural levels. The conducted experiments focus on the 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.

Introduction

Life history theory seeks to understand the variation in traits such as growth rate, number and size of offsprings and life span observed in nature, and to explain them as evolutionary adaptations to environmental conditions (Stearns, 1992). 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, which prevail in the environment depending on the encountered levels of stress and disturbance:

- Competitors (C) live in fertile undisturbed habitats and are adapted for long-term occupation.

- Stress-tolerators (S) persist in low resource environments, or where survival depends on the allocation of resources to maintenance and defense.

- 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 studies using computer simulation 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.

In the area of plant modeling, there exists a variety of functional-structural plant models (FSPM) combining 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. The present paper intends to study CSR strategies through experiments with an evolutionary FSPM and addresses the question of if and to what extent recognizable growth patterns evolve, and which morphological characteristics emerge in addition to the physiological ones. Pertinent results would constitute a success in bringing Artificial Life concepts to bear in the science of plant modeling.

The experiments extend the studies on life history evolution described in (Bornhofen and Lattaud, 2006) by applying "implicit" selection in contrast to "explicit" selection. Explicit selection uses iterated generation steps and evaluates the whole population of every generation by an imposed fitness function. Implicit selection is not guided. It corresponds to the struggle for existence observed in natural systems, as originally proclaimed by Darwin (1859), and results in the emergence of characteristics that lead to high survival and reproduction in the encountered environment.

The next section gives an overview of the state of the art in evolutionary plant modeling. In Section 3 the used plant model is briefly presented. The conducted experiment is de-
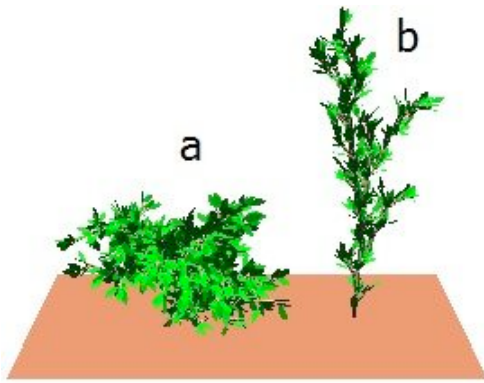
Figure 1: Evolved plants: isolation (a) and competition (b)

scribed and analyzed in Section 4. Section 5 concludes the paper and discusses the perspectives of the approach.

Plant modeling

FSPM 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). In order to accurately represent real plants, the model complexity most often involves a computational cost per individual which renders simulations of large communities difficult to realize for simple reasons of memory and time. Moreover, FSPM are typically customized by botanical data for individual or population level scenarios of specific natural species.

Aside from FSPM conceived within the scientific community of biologists, an amount of studies on plants have been carried out in the research field of Artificial Life. Their primary objective is the application and adaptation of ALife concepts and notably evolutionary algorithms (Holland, 1975) in the context of plant development. As the purpose of the conducted studies is different, priority is given to simplification. Plants are represented as structures based on a set of morphological growth rules, most often expressed by variants of the L-system formalism (Prusinkiewicz and Lindenmayer, 1990), with no or only minimal physiology and interactions with their environment.

Jacob (1994) published works concerning the evolution of context-free and context-sensitive L-systems representing simple artificial plants. He developed the "Genetic L-systems Programming" paradigm, a general framework for evolutionary creation of parallel rewriting systems. His approach was extended by Ochoa (1998) who evolved 2D plant structures and concluded that L-systems are an adequate genetic representation for studies which simulate natural morphological evolution.

With regard to more user interactivity, Mock (1998) mod-

eled artificial plants for a virtual world where the human observer chooses the most interesting-looking individuals for further reproduction and evolution. Likewise, some applications such as the Second Garden (Steinberg et al., 1999) or the Nerve Garden (Damer et al., 1998) appeared in the past years on the Internet, allowing users to grow and interact with artificial plant communities in online worlds.

The above cited models focus on the morphological aspect of a plant and hold no or only minimal physiological and environmental dynamics, so that experimental results possess a limited significance with respect to natural plants. Recently, ALife plant models featuring more biological considerations have appeared. Most notably, Ebner et al. (2002) incorporated interactions between plant and environment by evaluating the individuals for their amount of captured virtual sunlight. As a major result, it was shown that under competition plants grow high whereas they grow small and bushy when developing independently (Figure 1).

Model Description

To take a further step on the path of evolutionary plant models, the following section introduces virtual plants that not only interact with the environment, but also combine morphology with physiological processes. 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. An artificial genome contains mutable information which describes numerous characteristics concerning morphological as well as physiological growth processes, 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. Previous papers (Bornhofen and Lattaud, 2006, 2007) already introduced the model and suggested its utility for studies on adaptations of morphology and life history parameters in comparison with natural plants. A detailed mathematical description of the model is given in (Bornhofen and Lattaud, 2008).

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
A...Z	apex, predecessor of a production rule
[ ]	indicates a ramification
+−<>$ &	represents a 3D rotation

Environment

The plants grow in a continuous 3D virtual environment which is composed of two components, the soil and the sky, providing light and minerals respectively. 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. Environmental heterogeneity is achieved by subdividing the soil and the sky into voxels that contain locally available resources.

The sky holds a vertical light source parameterized by its initial irradiance. If an object is situated in a sky voxel, it casts shadows such that the luminosity in all subjacent voxels is decreased. In order to avoid time-consuming computation such as geometrical calculations or the use of computer graphics, the shading factor does not depend on the exposed surface of the object but on its volume. Just as sky voxels contain a local light intensity, soil voxels contain minerals. A resource flow from regions of high concentration to regions of low concentration is modeled by Fick's first law of diffusion (Fick, 1855). All the assimilated nutrients of a virtual plant are eventually redeposited in the soil so that their total amount in the environment is constant within a simplified mineral cycle. The nutrients of dead roots are put in the corresponding voxels and those of the aerial compartment in a mold layer which gradually penetrates the upmost soil layer.

Plant phenotype

A virtual plant is divided into a shoot and a root component. The morphologies are expressed by two independent L-systems (Prusinkiewicz and Lindenmayer, 1990), whose alphabet is detailed in Table 1. The model allows for stochastic L-systems, but in the scope of this paper only deterministic context free L-systems are applied. This choice was made to disengage the evolutionary dynamics from contingencies at individual level.

The physiological processes of the plants are based on a two-substrate version of the transport-resistance model
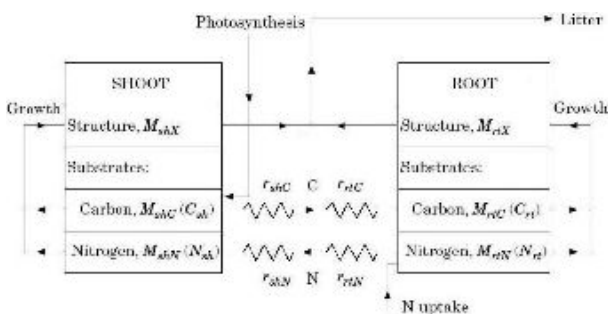

Figure 2: The transport-resistance model

(Thornley, 1998), where an aboveground and a belowground compartment assimilate, exchange and allocate the two resources carbon and minerals (Figure 2). However in the presented plant model, 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. 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 fine roots, that it serves.

Plant genotype

The development of the virtual plants is ruled by a set of "genetic information" recorded in a genotype. It contains the variables of the transport-resistance model such as growth and litter rates or resource assimilation and inhibition, as well as twelve additional real-valued physiological parameters like longevity, duration of bloom and seed biomass. Moreover, it specifies the parameters and production rules of the root and shoot L-systems.

Just as in (Mustard et al., 2003), real-valued parameters are mutated by selecting a new random value within a range of twenty percent around the current value. L-system mutations occur via genetic operators each of which is associated with a probability of ten percent. They are chosen such that any set of production rules can be constructed by evolution. The following three operators modify the number of rules:

- DeleteR (a rule of the L-system is deleted)
- InsertR (an empty rule is appended)
- DuplicateR (a rule is duplicated and appended)

Five other operators act on the successor strings. Only minor changes, i.e. character by character, are possible between successive generations. For example, if the production $A \rightarrow bl f A$ is selected to be mutated, some of the possible mutations are

- DeleteC (a character is deleted): $A \rightarrow bl f$
- InsertC (a character is inserted): $A \rightarrow b\&l f A$
- PermuteC (two characters are swapped): $A \rightarrow b f l A$
- DuplicateC (a character is duplicated): $A \rightarrow bl f f A$
- MutateC (a character is replaced): $A \rightarrow b+f A$

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 real-valued physiological parameters, controlling five major life history trade-offs, are allowed to mutate (Table 2). The significance of these parameters in the

Table 2: Genetic parameters and their trade-offs

Parameter	Trade-off
$0 < longevity$	Long life - early reproduction
$0 < maturity < 1$	Vegetative - reproductive allocation
$0 < k_G$	Rapid growth - resource conservation
$0 < seedX$	Seed size - seed number
$0 < seedD$	Seed propagation - seed survival

plant model is specified in the following subsection. Note that a number of other life history traits such as plant height or seed number are not encoded in the genotype but are emergent properties of the model.

Life cycle

The shoot and root morphologies of a seedling both start with the single non-terminal character A. 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 k_G of the transport-resistance model denotes the utilization rate of stored resources (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. Mutation is 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 pollinisation mechanisms have been implemented for implicit selection. During seed production, reproductive modules become a resource sink and compete with the apices for a share of newly produced biomass. When they attain the final seed biomass *seedX*, the seed is considered ripe and dispersed in the neighborhood of the plant at a maximum distance of *seedD*. After a limited span of life *longevity* the plant dies and its resources are restituted to the environment.

Experiments

The presented simulations focus on evolutionary adaptations in an environment with heterogeneous levels of disturbance and mineral stress. If recognizable CSR strategies emerged, the result would not only provide new theoretical support for Grime's theory by simulation in silico but also, more generally, point out how the scope of FSPM can be extended to the study of evolutionary dynamics in plant communities.

Setup

The environment is a bordered square terrain (extent: 40 length units) divided into 5x5 patches called A1 to E5 and
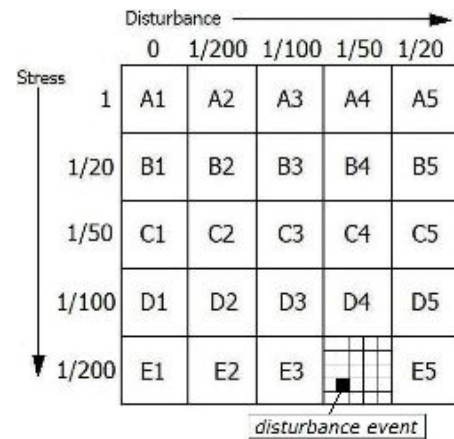

Figure 3: The different patches

featuring unequal levels of disturbance and stress. 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 5x5 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 downmost soil layer of each patch drain into a separate pool which is flushed back to the surface by random events. They correspond to rainfall which fertilizes the soil at irregular intervals, 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. Nutrient flow across the overall environment would blur the different levels of stress. Figure 3 schematically plots the environmental setup and indicates the applied probabilities of disturbance events and nutrient flushes per time step. The values along both dimensions are experimentally determined such that they allow the virtual plants to evolve different life history strategies under the extreme conditions of the patches A1, A5 and E1, whereas no population succeeds to settle in patch E5.

At the beginning of the simulation, one thousand 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
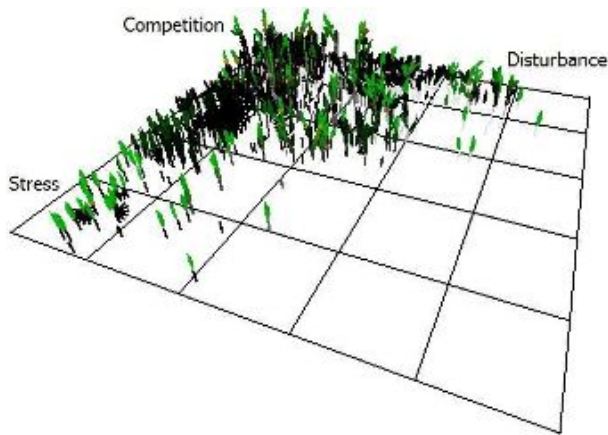
Figure 4: Sample view on the virtual environment

are randomly initialized within suitable limits which have been assessed experimentally by analyzing 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 $A \rightarrow r$ in the root compartment and $A \rightarrow lf$ 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.

Twenty replicate runs are performed for a period of 10000 time steps. The size of the terrain and the length of the simulations represent a trade-off between maximizing the number of simulated individuals and harnessing simulation time and allocated computer memory. One run would take about ten hours and nearly use the full memory on a PC - 3GHz, 1Go 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
   The results of the next section present mean values over the twenty simulations.

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 neighborhood of patch A1. All other regions turn out too hostile for random plants. 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 di-

mensions 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. Figure 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".

Figure 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's 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 plant increase per patch, a decrease is observed. This phenomenon is explained by the fact that from the initially defined minimal morphology, featuring one leave and one fine root, the plants evolve toward architectures consuming more resources per individual, which affects the carrying capacity of the patches. It is not the number of plants, but the amount of plant biomass per patch that is maximized by evolution (Figure 5b).

Physiological adaptations

Due to the five mutable real-valued parameters allowing the plants to physiologically adapt to the environmental conditions, each genotype maps to a vector in a five-dimensional space (however a one-to-one mapping is not given because the genotypes also contain the morphological L-system rules). In order to better apprehend the physiological component of the evolving strategies, the vectors of all the plants
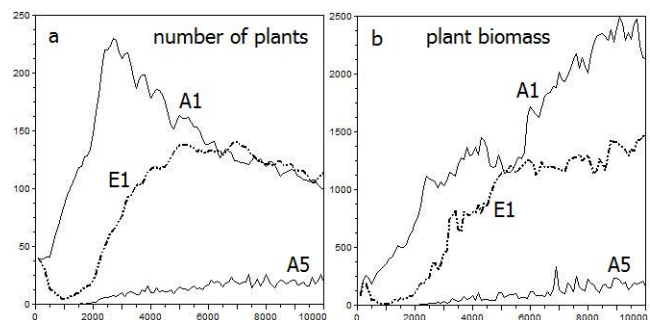

Figure 5: Number of plants and plant biomass per patch

in a patch are averaged. It is important to note that the resulting aggregated data is meaningful because the low numbers of plants per patch, i.e. not more than one hundred individuals occupying the same ecological niche, allow supposing that multiple strategies cannot coexist during one simulation. By evolution, these mean values move within the vector space toward positions which correspond to adapted strategies for a particular patch.

Just as in (Mustard et al., 2003), the resulting strategies at the simulation ends are analyzed using principal component analysis (PCA) (Jolliffe, 1986). The algorithm transforms a multi-dimensional data set to a new coordinate system such that maximum variability is visible. By considering lower-order principal components and ignoring higher-order ones, potential clusters in the cloud of data points may become recognizable. Figure 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 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 3.

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 (see Section 3). A low seed biomass *seedX* allows the production of many seeds in a short time. Ruderals also evolve a high growth rate k_G since this parameter is responsible for the amount of resources consumed per time step, and selection turns out to favor 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 few soil resources, growth and reproduction are slow. Therefore,
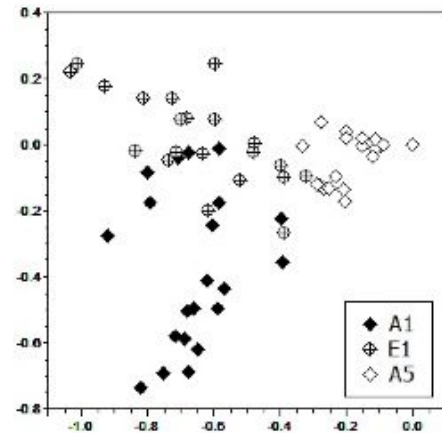

Figure 6: PCA of the final plant strategies

only high values of *longevity* may grant enough time to run through a complete life cycle. The delayed *maturity* suggests that there exists significant competition between the individuals so that they have to ensure survival before producing offspring. Natural stress-tolerators typically feature an inherently slow biomass production in order not to over-consume the available resources (Chapin et al., 1993). In the simulations, their virtual counterparts likewise develop low k_G, 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. Figure 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 competition so that, in the short term, there is selection for small and frequently produced seeds. However, when the plant population densifies and morphological evolution decreases the carrying capacity of the patches, seedlings require more biomass to survive and grow toward resources. The simulations attest that this constraint is particularly crucial for competitors. Just as in nature, there is a relationship between large seed size and establishment in shady stable plant associations (Foster and Janson, 1985). Figure 7b shows that the number of produced seeds is opposite to seed biomass. In particular, ruderals are selected for a high number of offsprings.

The evolution of *seedD* involves a trade-off between propagation speed 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 ends up in regions they are not adapted to, or even outside the virtual environment. The simulations yield no significantly contrasting
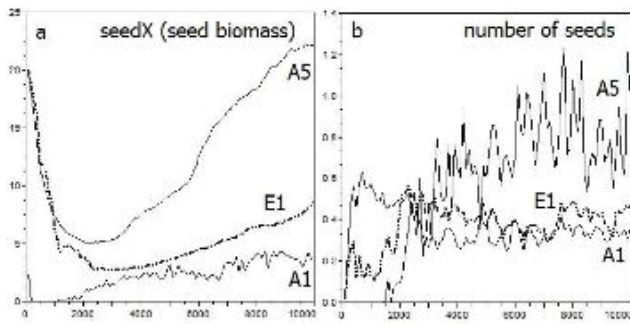
Figure 7: Mean seed biomass and number per patch

Figure 8: Evolved morphologies

results for this parameter. The evolved values in all three key patches correspond to slightly less than their extent (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 favored individuals whose seeds do not get lost in the surrounding ocean waters (Cody and Overton, 1996).

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. Figure 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

Table 3: The resulting averaged mutable parameters

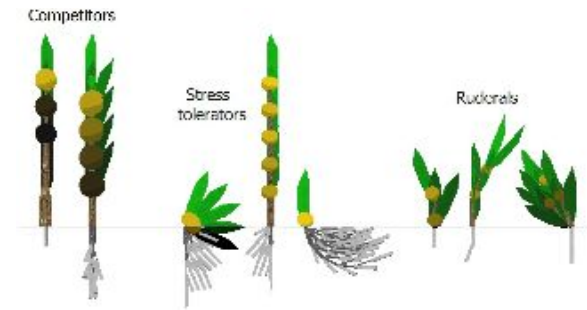|	A1(comp.)	E1(stress)	A5(rud.)
longevity	627.58	801.47	196.33
maturity	0.09	0.12	0.03
k_G	0.95	1.09	3.62
seedX	22.16	8.65	3.85
seedD	6.25	7.40	6.25

mechanical constraints such as gravity or wind are modeled, 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 ratio. This principle states that the resource assimilation of shoot and root tend to an equilibrium with respect to their relative utilization. Lower light provokes a stronger growth of leaves, and few soil nutrients lead to a boosted 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 belowgound architectures.

Conclusion

An experiment on the emergence of life history strategies has been conducted 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. It was observed that, depending on the degree of encountered disturbance and stress, the plants develop three major strategies which can be termed competitors, stress-tolerators and ruderals according to Grime's CSR theory. Most of the evolved characteristics correspond to hypotheses in life history theory 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 environmental factors.

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. In particular, a toroidal environment can be used to avoid edge effects. The virtual environment could also feature low light as a second kind of stress, which might lead to other morphological and physiological adaptations of the stress-tolerating plants.

The presented results do not only support plant strategy theory by simulations in silico. More generally, they suggest that the scope of FSPM is not restricted to population level experiments, but they also allow for studies on plants at evolutionary scale by integrating adaptive algorithms based on Artificial Life concepts. Due to their inherent contingencies and the qualitative character of emergent phenomena, such models might offer reduced accuracy from a strict biological point of view, but in return they yield insight into the selective forces and constraints which rule adaptation in natural plant life.

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