Life History Evolution of Virtual Plants: Trading off between Growth and Reproduction

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Abstract. This paper presents studies on the life history evolution of plants carried out by experimenting with a multi-agent platform of generic virtual plants. The conducted simulations address the trade-off between resource allocation to vegetative and reproductive structures. The trade-off is pointed out by evolutionary runs selecting for one of the two traits. It is further shown that the introduction of an age at maturity is an effective measure to enhance both life history traits. A third series of experiments highlights that competition in plant communities has an impact on the trade-off. Depending on the competitive pressure, plants evolve more investment of resources into growth than into reproduction. The results corroborate some hypotheses of life history theory.

1 Introduction

Life history is a term that refers to the pattern of survival, growth and reproduction exhibited by an organism [1]. One major challenge of life history theory is to study the variation in traits such as growth rate, age and size at maturity, reproductive effort, number and size of offspring and life span observed in nature, and to explain them as evolutionary adaptations to environmental conditions [20]. A fundamental component of the theory is the concept of trade-offs. Its framework is expressed in the "principle of allocation" which states that resources can only be allocated to one life history function and that investment in one activity is at the expense of the others [2]. As an example related to this paper, reproductive allocation reduces survival and growth rate and therefore is likely to decrease future reproduction. Understanding trade-offs is a key point in life history theory which, according to the evolutionary ecologists Stephen Stearns, like "no other field brings you closer to the underlying simplicities that unite and explain the diversity of living things and complexities of their life cycles." [20]. However, Stearns recently stated that "we have a lot of evidence that trade-offs exist; we have very little understanding of the mechanisms that cause them" [21].

Hypotheses relating to evolution are often difficult to verify due to its slow pace. This is why, for validation and analysis, mathematical models have been formulated [17]. Yet the computational power of modern computers offers the possibility to conceive individual based models and test evolutionary hypotheses

by simulating corresponding processes in silico [14]. For plants and their communities, there exists a large number of computer models, but they are most often specifically adapted to represent given plant species or plant community scenarios and not intended for evolutionary dynamics. This paper introduces a model of generic virtual plants designed for the study of plant evolution. The conducted experiments address the life history trade-off between resource allocation to vegetative and reproductive structures, and reveal age at maturity and competition to be two influential elements.

The next section gives an overview of the state of the art in the modeling of plants. In section three the virtual plant model and its simulation platform are presented. The conducted experiments are described and discussed in section four. Section five concludes the paper with reflections on the approach.

2 State of the art

The origins of the computer modeling of plants can be traced back to the 1960s, when Ulam simulated the development of branching patterns using cellular automata [24]. Since then a huge amount of work has been devoted to this research field. As study objectives can differ from one plant model to another, there exists a variety of approaches. According to the traditional classification suggested by Kurth [10], physiological and morphological models can be distinguished.

Physiological models, also called process-based models, reflect metabolic activities inside a plant. Their architectural structure remains low detailed, as the individual plant is merely decomposed into a fixed number of compartments such as root, stem and crown, 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. Because of their manageable architecture and their small number of parameters, physiological models are convenient for plant representations on a rather coarse scale [11].

Morphological models describe plant architecture by making use of its modular structure. They consider the plant as a composition of repeated modules like leaf, fruit or fine root which dynamically appear and disappear during the plant development according to a number of growth rules. Probably the most widely used representation of plant morphology is the L-system formalism [16]. L-systems are formal grammars with the possibility of recursive applications in a parallel rewriting process. Starting from an initial axiom ω, a set of rules P is iteratively applied in order to form a string of characters from an alphabet A. The string represents the plant, whereas each character represents an elementary module. Positional information of the modules can be integrated by using a bracketed notation. The translation of the string into a geometric structure is achieved by graphical interpretation using turtle geometry [16]. Figure 1 illustrates a sample L-system and the resulting plant after several iterations.
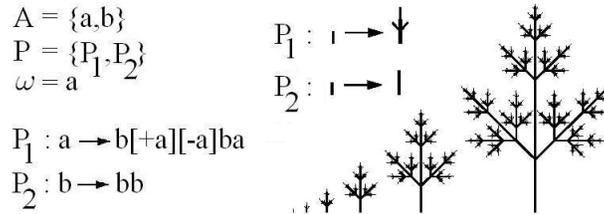
Fig. 1. Example of an L-system

Morphological and physiological processes of plant development are profoundly interwoven [12], and in the last decade many models emerged as the coupling of both aspects. They typically depict a 3D description of the plant where the organs interact with local environmental conditions and with one another according to the plant topology. Because of their complete picture of plant development, these models are also termed "virtual plants" [18]. Plant communities can be represented as a number of virtual plants which develop concurrently in a multi-agent approach [5]. Interaction results from the modifications that each individual contributes to the physical environment. In particular, the available resources become an object of competition between neighboring plants.

3 The plant model

The following section presents a model for the study of evolutionary dynamics in plant communities. Based on a simple concept of generic virtual plants, it is able to carry out simulations of evolving plant communities while emphasizing the most important morphological and physiological aspects of a single plant. Thus individual responses to resource disposition and other environmental constraints can be observed.

3.1 The environment

The physical environment is a continuous 3D space composed of the soil and the sky, homogeneously divided into a number of voxels each of which holds local environmental information. Light and minerals are resources of prime importance for the growth of natural plants [25]. The sky voxels provide light which is captured by the leaves in order to produce carbon via photosynthesis. If an object is situated aboveground, it casts shadows. In such case, the light intensity of all sky voxels following the angle of incidence is decreased. Soil voxels contain minerals which are assimilated by the fine roots. Diffusion, a passive movement from regions of high concentration to regions of low concentration, leads to mineral balance between neighboring voxels. All the assimilated minerals of a virtual plant are eventually redeposited in the soil so that their total amount within the environment is constant. The minerals of dead roots are put in the corresponding

soil voxels and those of the aerial compartment in a mold layer which gradually penetrates the upmost soil layer.

3.2 The virtual plant

A virtual plant is divided into an aboveground and belowground component called shoot and root respectively. Their morphologies are each expressed by an L-system whose alphabet is detailed in figure 2. The geometric shape of the plant modules is based on sphyls (cylinders with spherical ends). In the scope of this paper, only deterministic context free L-systems, also called D0L-systems [16], are applied. The predecessor character of the first rule is A, of the second rule B and so on. The shoot and root morphologies of a virtual plant seedling both start with the single non-terminal character A. A small amount of initially available biomass allows the young plant to develop its first modules, but subsequently it has to rely on the acquisition of resources.

The physiological processes of a plant are based on a two-substrate version of the transport-resistance model [22]. Shoot and root hold separate substrate pools for carbon and minerals. Photosynthesis charges the shoot carbon pool, and root assimilation supplies the root mineral pool. Growth occurs through the conversion of carbon and minerals into biomass, deducting a certain loss to litter. The exchange between the carbon and mineral pools is represented as a function of substrate concentration difference divided by a resistance. Thornley suggested that all physiological models of plant development should start with this irreducible framework [23].

Produced biomass is distributed to the apexes and, in the shoot, reproductive modules according to a sink strength. Once an apex reaches the required cost for the production of a successor string, the appropriate production rule is applied. When a reproductive module attains a specified biomass, a seed is dispersed in the neighborhood of the plant. After a limited span of life the plant dies and its resources are restituted to the environment.

Character	Compartment	Geometry	Function
l	shoot	sphyl	captures virtual light to photosynthesize carbon
f	shoot	sphere	reproductive module producing seeds
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	represent predecessors of the production rules
[,]	shoot/root	none	indicate a ramification
+ - < > $ &	shoot/root	none	represent 3D rotations by fixed angles

Fig. 2. The L-system alphabet

Shoot chromosome
growth = 10.00
litter = 0.00
assimilation = 1.00
inhibition = 100.00
...
maxAge = 30.00
durationBloom = 0.00
biomassSeed = 1.00
...
rotateX = 0.3925
rotateY = 0.3925
rotateZ = 0.3925
lRule = (A,[>b[B]A]$$$$[>b[B]A]$$$$$[>b[B]A])
lRule = (B,>>l)

Transport-resistance parameters

Additional physiological parameters

L-system parameters and production rules

Root chromosome
growth = 10.00
litter = 0.00
assimilation = 1.00
inhibition = 100.00
...
maxAge = 30.00
...
rotateX = 0.3925
rotateY = 0.3925
rotateZ = 0.3925
lRule = (A,[<c[B]$$A][[B]$$A])
lRule = (B,>r)

Fig. 3. Sample shoot and root genotypes of a bush

3.3 The genotype

The development of the virtual plants is ruled by a set of "genetic informa-tion" 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 age limit, duration of bloom and seed biomass. Moreover, it specifies the parameters and production rules of the root and shoot L-systems. Figure 3 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. For the pur-pose of investigating the allocation to reproductive and vegetative structures, the evolving elements in the genotype are limited to the L-system production rules. Evolution may affect the trade-off between the two life history traits by insertion and deletion of reproductive (f) and vegetative modules $(l, b, A, B, ...)$ in the production rules of the shoot L-system. All other parameters are prede-fined and fixed in order not to obscure the results by too large a genetic search space. Mutations are introduced by several genetic operators each of which is associated with a probability. They are chosen such that any set of production rules can be constructed by evolution. The three operators

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

modify the number of rules. 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 $A \to bl f A$ is selected to be mutated, some of the possible mutations are

- Delete character (a character is deleted): $A \to bl f$
- Insert character (a character is inserted): $A \to b\& l f A$
- Permute character (two adjacent characters are switched): $A \to b f l A$

- Duplicate character (a character is duplicated): $A \rightarrow blffA$
- Mutate character (a character is replaced by a new one): $A \rightarrow b[A]fA$

4   Results

The model of section three has been implemented as a simulation platform. It is developed in C++ and uses the OGRE library [15] for graphical representations. This section presents the results of three different sets of experiments, aiming at the identification of evolutionary mechanisms in the life history trade-off between allocation to reproductive and vegetative structures.

4.1   Experimental setup

In every experiment, virtual plants are evolved by a typical evolutionary algorithm [9]. A run starts with an initial population of genotypes with the minimal production rules $A \rightarrow l$ and $A \rightarrow r$. 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 proportion of individuals by measuring the phenotypes in terms of a predefined notion of fitness. The selected individuals survive and give birth to the next generation of mutated genotypes. In the literature, there exist various selection methods for evolutionary algorithms. The tournament selection applied here is inspired by competition in nature and arranges "tournaments" to compare the fitness between a few randomly chosen individuals [6]. 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.

The probability of each genetic operator is defined as 0.1. This value may be overrated 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 is set to $\frac{1}{4}$ and tournament size to 10 individuals. This setup was 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 modern PC.

4.2   Revealing the trade-off

The first experiment is intended to point out the trade-off between allocation to reproductive and vegetative structures. A straightforward method to show an evolutionary trade-off is the comparison between breedings with selection for one of the two considered traits. Therefore, two series of evolutionary runs were conducted. In the first twenty runs, the virtual plants were selected for reproductive output, defined as the overall produced seed biomass during their lifetime [19]. In the second twenty runs, the individuals were bred for their amount of vegetative biomass at the end of the simulation.
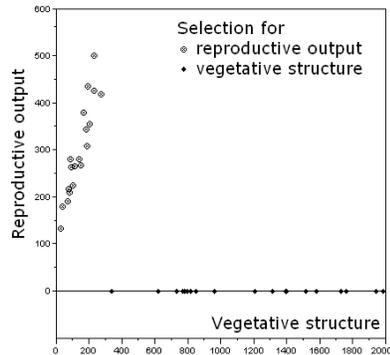
Fig. 4. Selection for reproductive and vegetative structure
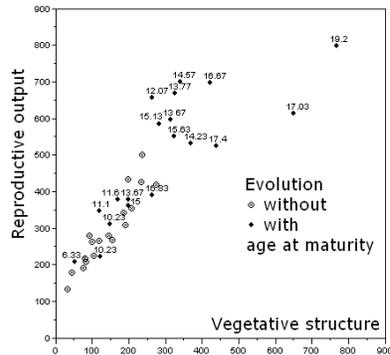
Fig. 5. Evolution with and without age at maturity (the indicated numbers correspond to the evolved parameter values)

The performance of the evolved plants with respect to both life history traits is shown in figure 4. Depending on the course of evolution, the runs result in different local fitness maxima. The plants selected for seed biomass only grow to a fraction of size of those selected for vegetative biomass. Reproduction is not completely exclusive of growth because fertility depends on resource acquisition, which is again correlated with plant size. In contrast, plants evolved for growth do not produce any reproductive output because seeds are disadvantageous resource sinks. Besides indicating the trade-off, the simulation notably highlights the advantage of computer models to accelerate evolutionary experiments which would simply take too long, if performed in nature.

4.3 Reproductive maturity

A closer look at the genotypes evolved for seed biomass reveals that the shoot L-system of well performing individuals is arranged in a particular way. Reproductive modules do not appear in all production rules, but develop only via the application of several preceding rules. By this means, the growing plant starts reproduction with a certain delay. Early investment into reproductive structure leads to the exhaustion of resources and incurs a cost in growth and therefore future fecundity. Therefore, natural plants most often possess a threshold size which has to be attained before reproduction is possible. Just as observed in the simulation, this can be due simply to the requirement to produce the necessary structures [4].

The result of the first experiment suggests that a preliminary growth period without any allocation to seed biomass may enhance the final reproductive output. Age and size at maturity are considered as key parameters in the life history of most organisms [20]. The second series of experiments goes further and investigates if and to what extent a physiologically controlled age at maturity can influence the trade-off. To model this life history trait, an additional, real-valued
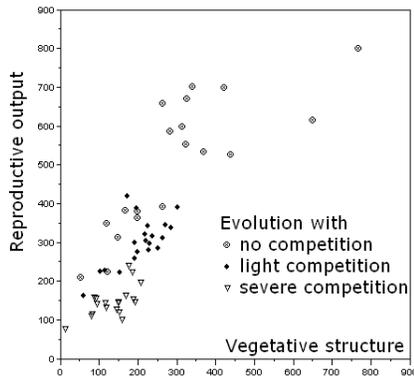
Fig. 6. Competitive pressure influencing the trade-off

Fig. 7. Evolved morphologies of isolated and competing plants

genetic parameter has been introduced into the genotype and subjected to evolution. With this parameter, the allocation of biomass into reproductive modules is only activated when the plant attains the indicated age. A new series of twenty runs selecting for reproductive output was conducted. Figure 5 compares the performance of the previous plants to those featuring an age at maturity. It can be observed that the new parameter allows to evolve significantly better values with respect to both life history traits. Moreover, well growing plants defer their age at maturity in order to make the most out of the exponential character of their juvenile growth period. It can be concluded that the introduction of an age at maturity is an effective measure to enhance both considered traits. Many natural plants indeed start reproduction only after a period of juvenile stage [3].

4.4 Competition

Thanks to their isolated breeding, the plants of the previous experiments did not encounter any interference from neighboring individuals. Consequently, evolution optimized resource allocation without considerations of competitiveness. However, except for some colonizing species, natural plants rarely encounter such open environments but grow in crowded communities where resources are more limiting. A third series of experiments therefore addressed the impact of competition on the studied allocation trade-off. This time, the plants of a population were not grown individually but simultaneously, randomly placed in an environment with limited space and resources. Afterwards, the reproductive output of all individuals was determined and the ten best performing plants were kept to produce a new population of genotypes.

Figure 6 compares the isolated breeding with evolutionary runs at two degrees of competition. Light competition occurs in an environment which confronts the plants with few interferences from neighbors. Severe competition is induced by quartering the size of the terrain. Due to the limitation of resources, the

competing plants generally develop less vegetative and reproductive structures. Moreover, they decrease their reproductive effort, defined as the proportion of the total resource budget devoted to reproductive processes [8]. Depending on the competitive pressure, the plants need to invest more resources into growth. Figure 7 illustrates this conclusion by opposing the best performing specimen evolved in isolation to a group of competing individuals. Light becomes a particularly limiting factor, so that the plants need to adopt high and tall shapes stretching out to the sky in the effort to outcompete their neighbors. This result agrees with Harper's hypothesis that, as individual success is based on the capture of resources, competing plants need to sacrifice fecundity in order to develop competitive ability [7].

5 Conclusion

Trade-offs play a central role in life history theory [20]. To contribute to the understanding of the evolutionary mechanisms involved, three series of experiments have been presented in this paper. They addressed the trade-off in plants between resource allocation to reproductive and vegetative structures, conducted with a multi-agent platform of generic virtual plants. The plants, growing in a 3D environment, are based upon the fusion between a two-substrate transport-resistance model and an L-system formalism.

The trade-off was pointed out by evolutionary runs selecting for one of the two life history traits. The introduction of a physiological parameter representing an age at maturity was shown to be an effective measure to enhance both traits. A third series of experiments highlighted that competition in plant communities has an impact on the trade-off. Depending on the competitive pressure, plants evolved more allocation into growth than into reproduction, sacrificing fecundity in order to gain access to the available resources. These simulations showed that age at maturity and competition are two influential elements in the life history evolution of plants and revealed some of their implications.

Combining process-based with structural models, virtual plants allow to represent plant development with respect to physiological as well as morphological aspects and notably to embrace the interrelations between them. This may yield new insights on the evolution of life history traits which are intrinsically tied to both aspects. Moreover, virtual plants complement the mathematical approaches with the possibility of producing a number of results for the same general type of computation, by adding a stochastic component, which may be relevant for inherently statistical hypotheses of evolutionary biology. Even if biological hypotheses cannot be actually proved by computer modeling, they can be partially confirmed or, in the opposite case, suggested to be modified or rejected [14].

As a major extension, the model will be enriched with abiotic parameters such as water, temperature and gravity. By this means, further experiments may address questions which need to consider more environmental factors influencing the evolution of plants.

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