University of Göttingen
Faculty of Forest Sciences and Forest Ecology

Simulation of Fungal Growth and Structure

Current Research State and Development of an Extendable Basic Model of *Coprinopsis cinerea*

Master Thesis

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Contents

Abstract

The simulation and quantification of fungal growth is a topic of increasing relevance. Fungi produce metabolites beneficial for multiple purposes, for instance in medicine or environmental protection. Modeling can help analyzing influencing factors on the production of these metabolites and predict resulting yields.

This master thesis presents an overview of existing fungal growth models. Then, an extendable functional structural model of the fungus *Coprinopsis cinerea* AmutBmut using Lindenmayer systems is introduced. The model visualization is compared to experimentally observed fungal growth and shows good agreement with existing structures. Functional aspects can be implemented into the model to fulfill the user's individual aim.

Kurzfassung

Pilzwachstum zu simulieren und zu quantifizieren ist von steigender Bedeutung. Die von Pilzen hergestellten Stoffwechselprodukte sind vielfältig nutzbar, beispielsweise in der Medizin oder für den Umweltschutz. Bei der Analyse von Einflussfaktoren und der Quantifizierung der Metabolitproduktion kann Modellierung hilfreich sein.

Zuerst wird in dieser Masterarbeit ein Überblick über bereits existierende Modelle für Pilzwachstum gegeben. Danach wird ein erweiterbares Struktur- und Funktionsmodell für das Wachstum des Pilzes *Coprinopsis cinerea* AmutBmut vorgestellt, welches den Pilz mittels Lindenmayer-Systemen simuliert. Die Visualisierung des Modells wird mit tatsächlichem Pilzwachstum verglichen und zeigt gute Übereinstimmungen mit real existierenden Strukturen. Funktionale Aspekte können in das Modell implementiert werden, um individuelle Zielsetzungen des Nutzers zu erfüllen.

1 Introduction

Analyzing and understanding fungal growth is a highly relevant topic. Identifying ideal growth conditions is crucial for maximizing the yield of cultivated edible mushrooms and fungi producing metabolites of human interest. Ideal growth conditions thereby depend on the individual aim of growing fungi, since conditions favorable for mushroom formation may differ from conditions promoting metabolite production. For instance, the production of the enzyme laccase is induced by the addition of copper to the substrate, ultimately killing the fungus [Navarro González, 2008]. While growth of edible mushrooms like champignons (*Agaricus bisporus*) or shiitake (*Lentinula edodes*) has already been strongly optimized, there is need for the quantification of influencing factors on other processes.

Fungal metabolites can be used for different purposes. They are extracted for medical use as antibiotics, antimycotics or cancer treatment [Chua et al., 2005]. In the production of paper or textiles fungal metabolites may, among other uses, bleach cellulose pulps [Widsten and Kandelbauer, 2008] or decolourize dyes as a decentralized wastewater treatment technology for small textile or dyeing units [Kaushik and Malik, 2009]. With their ability to decompose environmental pollutants like petroleum, pesticides, toxic or electronic waste, fungi could contribute to a cleaner environment (e.g. [Gadd, 2001], [Pointing, 2001], [Adekunle and Oluyode, 2005], [Bumpus and Aust, 1987]). The kingdom of fungi is highly diverse and is estimated to comprise 1.5 million species, of which only 100,000 are yet described [Hawksworth, 2001]. This allows the assumption that further fungal products of human interest are still to be found and fungal research will be important in the future.

Coprinopsis cinerea, the fungus addressed in this thesis, is one of the two most commonly used model organisms for studying the developmental process of fruiting body formation in basidiomycetes [Kües, 2000]. At the faculty of forest sciences of the University of Göttingen *Coprinopsis cinerea* is researched because of its laccase enzyme. Laccase reacts with lignin inside wood and might substitute adhesives in the fabrication of wood-based products like fiberboards [Mai et al., 2004]. At maturation the cap autolyses, e.g. the tissue dissolves, drips to the ground and can be collected and used as ink [Buller, 1933]. Due to this process, the mushroom is of limited edible value but still cultivated as specialty in some countries, e.g. in Thailand it is called "Hed-Cone-Noy", meaning "Small Compost Fungus", harvested before maturation and eaten fresh or pickled in salt water [Kües et al., 2007]. Its antibacterial, antifungal and antiviral properties make it valuable for medicinal uses in form of preventive and curative mushroom-based biopharmaceuticals and food additives [Badalyan et al., 2005]. In conclusion, quantifying influences on *Coprinopsis cinerea* mycelial growth and fruiting body development provides benefits for numerous applications.

One way of quantifying changes and factors in structure and developmental processes is modeling. A model is a simplification with the aim to better understand, quantify or visualize complex systems like organisms which may help finding the best solution for a problem. The advantages of a model in comparison to experimental studies are high speed of simulation (e.g. simulating mushroom growth within seconds), infinite possibilities of varying parameters a laboratory might not be able to test and low costs.

During the author's "master project" the growth of *Coprinopsis cinerea* at different temperatures and nutrient concentrations was measured daily to investigate these factors' influence on the colonies' growth rate. The combination of such empirical studies with modeling may help quantifying the influence of growth factors.

In this work an overview of literature on fungal growth models is given. Then, a basic modeling framework for simulating growth of mycelium and fruiting bodies of *Coprinopsis cinerea* is presented, which allows input of empirical data for visualization and quantification of growth factors and optimization. The basic model is a functional structural model with an architectural part and a process part for analyzing interactions between function and structure.

2 Growth Models in Literature

The simulation of fungal growth and structure is a topic at the interface between two fields: Fungal morphogenesis on the one hand and computer simulation on the other. This review first gives a short overview of each field and then focuses on studies linking fungal morphogenesis and modeling. Thereby, a foundation for creating the model described in this master thesis is to be established. Since previous reviews on fungal growth models only cover the research up to 2012 ([Boswell and Davidson, 2012], [Davidson et al., 2011], [Rosling et al., 2009], [Davidson, 2007], [Meskauskas et al., 2004b], [Prosser, 1995b]), there is need for a review on recent developments in fungal colony modeling. The literature search for this review was made in March 2017 using the freely accessible search engine Google Scholar.

The ink cap mushroom, whose growth is to be simulated in this thesis, has been in focus of research for a long time [Pukkila, 2011]. Its life cycle and development have been thoroughly described ([Kües, 2000], [Navarro González, 2008], [Srivilai and Loutchanwo, 2009]). The mycologist David Moore dedicated his research career to this species and recently published an autobiography on 50 years of *Coprinopsis*-research containing not only information on mushroom morphology, development and genetics, but also a chapter on mathematical modeling [Moore, 2013]. Since *Coprinopsis cinerea* is a model fungus for genetic analyses with a completely decoded genome [Kües, 2000], most literature on this species relates to its evolution, mutation, genetic structure, proteins, enzymes and other metabolites as well as their extraction and isolation. Articles concerning molecular or genetic analyses were excluded from the literature search as this study deals with larger scales, i.e. the growth of fungal colonies. *Coprinopsis cinerea* was formerly known as *Coprinus cinereus*. The name was changed due to phylogeny analyses with molecular markers which overthrew the established classification of fungi that were formerly thought to form the family of *Coprini* [Redhead et al., 2001]. Both names were used as keywords for this review.

Fungal growth has been defined as an "orderly increase in cell components leading to an increase in biomass" [Prosser, 1995a]. The growth of *Coprinopsis cinerea* is affected by temperature, pH, moisture content and oxygen availability [Dix, 1995]. Though the mycelium can grow both in dark or in light, light intensity, spectrum and periods have an influence on the speed of its growth and on the formation of reproductive organs [Lu, 2000], [Kües et al., 1998]. Fungi consist of hyphae, cylindrical cells that increase in length by growth at one end. Fungal life starts when a spore germinates on a suitable substratum, either immediately after dispersal or after a phase of dormancy when conditions do not fit growth requirements. The germ tube emerging from the spore is called a hypha. It grows and branches and the branches in turn branch to form a radiating system of hyphae known as the mycelium. On the surface of a solid substratum in a Petri dish the mycelium

forms a circular colony, its diameter increasing at a constant rate and also growing down into the medium. In nature, where the mycelium also spreads on heterogeneous surfaces and penetrates the substratum, less uniform conditions cause a higher diversity of mycelial growth [Carlile, 1995]. The mycelium is built from different types of hyphae, leading and branch hyphae [Trinci, 1973]. Leading hyphae are wider and faster growing than their branches [Gow and Gooday, 1982]. The radius of mature fungal colonies on agar plates increases linearly [Trinci, 1971]. The young mycelium undergoes further developmental steps, namely lag, exponential and deceleration phase followed by a constant growth rate phase [Trinci, 1969]. While the colony's radius increases linearly its total mycelial length increases exponentially [Trinci, 1978], which is achieved by exponential branch production with individual branches extending at a linear rate after a short exponential growth phase [Zalokar, 1959], [Trinci, 1969]. Branching occurs when an organism intends to maximize its total area of contact with the environment that surrounds it [Davies, 2005]. In case of fungi, branching leads to improved nutrient assimilation and supports the exchange of nutrients and signals between different hyphae in the same colony [Harris, 2008]. Principles of fungal development biology have been stated, saying, for instance, that hyphae extend only at their apex and form cross walls called septa at right angles [Moore et al., 2005]. Fungal branching is considered the equivalent of cell division in animals or plants, since it is the only way in which the number of growing points can be increased. Two patterns of hyphal branching can be distinguished: apical (from the hyphal tip) and the more prevalent lateral branching (from the sides of the hypha) [Harris, 2008]. The development of *Coprinopsis cinerea* fruiting bodies was described and classified in a PhD-thesis including a picture catalogue showing the events that take place in fruiting body development, including fruiting body maturation and autolysis of the mushrooms [Navarro González, 2008] (Fig. 13, 14). The environmental factors regulating mushroom development are nutrient depletion, the C to N ratio, temperature, day/night rhythm, humidity, oxygen availability and CO2 concentration [Kües, 2000].

The second field of this review, computer modeling, brings many advantages for the understanding of ecological processes. A mathematical model can be defined as a "simplification and an idealisation" [Turing, 1952]. The aim of mathematical models is the reduction of a complex biological system to a simpler mathematical system which allows drawing conclusions on key properties of an organism [Davidson, 2007]. Models can be used to compress a time frame, since a simulation model run on a computer can be used to quickly investigate events that take place over a long time. A fungal life cycle may thus be simulated in a few seconds instead of having to observe real growth over days or weeks. Furthermore, complex systems can be studied that would otherwise be difficult to investigate due to high costs or insufficient laboratory equipment.

Mathematical modeling can be applied to the growth of filamentous fungi and thereby help to gain understanding on hyphal and colony behaviors in different environments [Lin et al., 2016]. Linking the fields of fungal biology and computer modeling can take place on highly different scales. Some scientists focus on the microscopic events taking place inside the hyphal tip [Bartnicki-Garcia et al., 1989] while others explore the extent of fungal colonies covering immense surface areas, e.g. a clone of *Armillaria gallica* having spread over 15 hectares of Canadian forest [Smith et al., 1992]. These extremes have been displayed in a review before [Davidson, 2007].

Models on macro scales focus on interactions of fungi with the environment. For instance, large-scale fungicide spray heterogeneity and the regional spread of resistant pathogen strains have been modeled on these scales [Parnell et al., 2006]. This model considers fungicide-resistant and sensitive strains of a fungal crop pathogen and is a spatially implicit metapopulation model to describe the dynamics of regional spread. Spatial variation in model variables has also been explicitly studied at large scales [Stacey et al., 2004]. Their approach to large scale modeling of fungal colony spread resembles that of [Parnell et al., 2006] but is spatially extended. The macro-scale growth has also been modeled with focus on the production of fungal biomass by consumption of substrates [Lamour, 2000] [Lamour, 2002].

Micro scale models of fungal growth, for instance of growth and shape of hyphal tips or growth and branching of single hyphae and mycelia have also been reviewed [Prosser, 1995b]. The influencing factor of tip growth models is the nutrient concentration inside the hypha and in the surrounding substratum, while the morphological representation of colonies or single hyphae is not in the focus of these models. Models of hyphal tip extension were the first models of fungal growth. For example an early model of tip growth and oriented elongation of the alga *Nitella* deriving expressions for the specific area growth rates at different locations on the tips of the alga's filaments ([Green and King, 1966], [Green, 1974]) was extended and generalized for fungi, assuming the shape of the hyphal tip to be elliptical and varying in eccentricity instead of being hemispherical [Trinci and Saunders, 1977]. The model was tested with three different types of data, including the data on wall extension in tips measured by microscopic observation of *Phycomyces blakesleeanus* [Castle, 1958], the incorporation of radiolabelled N-acetylglucosamine into the wall of several fungi [Gooday, 1971] and the influence of vesicle concentration on wall extension of *Neurospora crassa* [Collinge and Trinci, 1974]. The three different sets of data indicate that the model correctly assumes hyphal tips to have an elliptical shape [Trinci and Saunders, 1977]. Another model made the same predictions and linked tip shape, tip extension and wall extension [Ricci and Kendrick, 1972]. A different approach on modeling hyphal tips is called the Surface Stress Theory, saying that the shape of fungal hyphae results from internal turgor pressure on the wall of the extension zone and is influenced

by the wall elasticity and surface tension [Koch, 1983]. In opposition to this model stands the vesicle supply center model ([Bartnicki-Garcia et al., 1989], [Bartnicki-Garcia et al., 1990]). The mobile vesicle supply center coordinates the distribution of vesicles to the wall of the extension zone. When it moves from the center of a spore to the cell wall, it is said to cause a local bulging leading to germ tube formation (Fig. 1). The vesicle supply

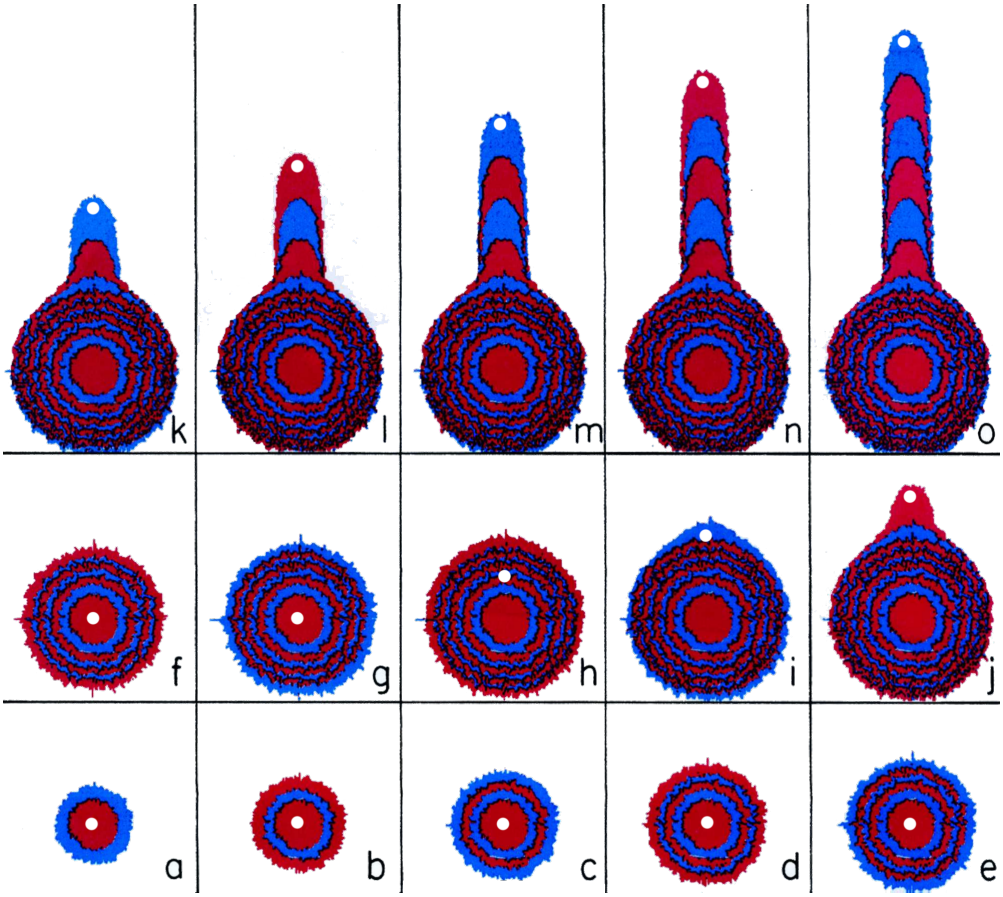

Figure 1: A computer simulation of spherical growth, germ tube formation and germ tube growth with the model of Bartnicki-Garcia *et al.* (1989, 1990). The white dot indicates the position of the vesicle supply center. (From Bartnicki-Garcia *et al.*, 1989)

center model was extended to include details of the transport of vesicles inside the hypha to the hyphal wall and the forming of new tissues [Tindemans et al., 2006]. In contrast to this theory of the vesicle supply center model stands the steady-state theory [Sietsma and Wessels, 1994]. It assumes that new wall material is continually deposited only at the hyphal apex. Processes of internal flow and network development inside hyphae have been simulated, stating that fungal thalli grow by extension at the hyphal tips and by the flow of cytoplasm and nuclei into the spaces created at the extending tips [Ramos-Garcia et al., 2009]. A newer model for growth of a single fungal hypha simulating nutrient and vesicle transport describes the intracellular transport of nutrients to a sub-apical zone where vesicles are formed and then transported to the tip for tip extension [Balmant et al., 2015]. Progress on small-scale models on growth of filamentous fungi in solid-state fermentation systems was reviewed by [Sugai-Guerios et al., 2015], linking the production of extracellular enzymes to morphological characteristics and basically stating that no suf-

ficiently complex model yet exists. On slightly larger scales than hyphal tip elongation, attempts on mathematical modeling of hyphal branching have been made to investigate the shape and conditions of branch formation ([Regalado et al., 1997], [Regalado, 1998], [Regalado and Sleeman, 1999]). Furthermore, the response of hyphae to heterogeneous environments has been modeled ([Davidson, 1998], [Boswell, 2003]).

At intermediate levels of scale several models have addressed fungal growth of hyphae, mycelia and single colonies [Boswell and Davidson, 2012]. The vesicular model aims to describe the early growth of mycelia on solid media and predicts changes in hyphal length and in the number and positions of branches and septa on the basis of changes in vesicle and nuclear concentration [Prosser and Trinci, 1979]. The predictions were in good agreement with experimentally observed data on growth of two different fungal mycelia. A stochastic model for mycelial growth of *Mucor hiemalis* [Hutchinson et al., 1980] aims to simulate morphologically realistic, symmetric colony growth from a single germ tube on agar medium. Branches usually arise closely behind the hyphal tip and only a small number emerge from older parts of the hyphae. The stochastic elements of this model reflect the natural variability of fungal growth. The hyphal population model is a mathematical model of mycelial growth, branching and death [Edelstein, 1982] [Edelstein and Segel, 1983]. It consists of partial differential equations for accumulation of hyphae by apical growth, uptake of nutrients and redistribution of a derived metabolite within the mycelium. The formation of concentric rings of colonies on solid media is explained. This model was extended to also include nutrient uptake [Liddell and Hansen, 1993]. The colony development model predicts four different types of biomass to quantify the amount of produced metabolites [Georgiou and Shuler, 1986]. The influence of environmental changes on fungal growth and differentiation is simulated. Experimentally measured growth parameters are converted into a model of 3D pellet formation of *Streptomyces tendae* [Yang et al., 1992b]. Stochastic elements varying the measured mean values were built in to create natural differences. This model was extended including a growth limiting nutrient to regulate tip extension [Yang et al., 1992a]. In the symmetric branching model, microscopic and macroscopic growth parameters are combined [Viniegra-Gonzalez et al., 1993]. The mycelial growth is approached by the growth of a symmetric tree. A model of nutrient depletion is combined with a two-dimensional reaction-diffusion model including external and internal factors influencing growth [Regalado et al., 1996]. The model is compared to experimental growth in spatially homogeneous and heterogeneous nutrient environments and reproduces the fractal nature of mycelia and the response of the structure to a spatially heterogeneous nutrient distribution. A growth model for the evolution of *Trichoderma reesei* from a single spore to a pellet was developed with random branching from parent hypha drawn from a frequency function which is proportional to the total hyphal length [Lejeune et al., 1995] [Lejeune and Baron, 1997]. Hyphal growth was curved through stochastically varied orientation. The simulated three-dimensional

structures had a fractal nature and were able to create realistic pictures of pellet growth, resulting in a constantly increasing radius of the pellet. A model of *Aspergillus oryzae* on solid media relates growth to age of nearest neighbor, nutrient supply and inhibiting effects by toxins [Lopez and Jensen, 2002]. Only the extension of the colony margin but no branching is simulated. Few models simulate the growth of fruiting bodies. As a mushroom consists of the same hyphae as the undifferentiated mycelium, the key to modeling fruiting bodies is to specify the position of cells [Money, 2004]. For instance, the Neighbor-Sensing model is able to simulate different species of mushrooms [Meskauskas et al., 2004b]. The Neighbour-Sensing model simulates growth of fungal mycelia of different species in three-dimensional space [Meskauskas et al., 2004b]. The mycelium is represented as a tree-like structure. The virtual hyphal tips can branch, grow and alter their growth direction in response to different tropisms determined by the user. Hyphae only grow and branch when there are less neighboring hyphal tips in their vicinity than a threshold determined by the user. The influence of gravitropism, i.e. the orientation in the gravity field to maintain a specific position, can be adjusted in the model (Fig. 2). Its parameters can be adjusted to represent different species growing in three-dimensional space and within a variety of nutrient distributions. The user-interactive model is free-to-use and can be accessed on the homepage of the British mycologist David Moore (http://www.davidmoore.org.uk/CyberWEB/). The recycling of biomass and the origin

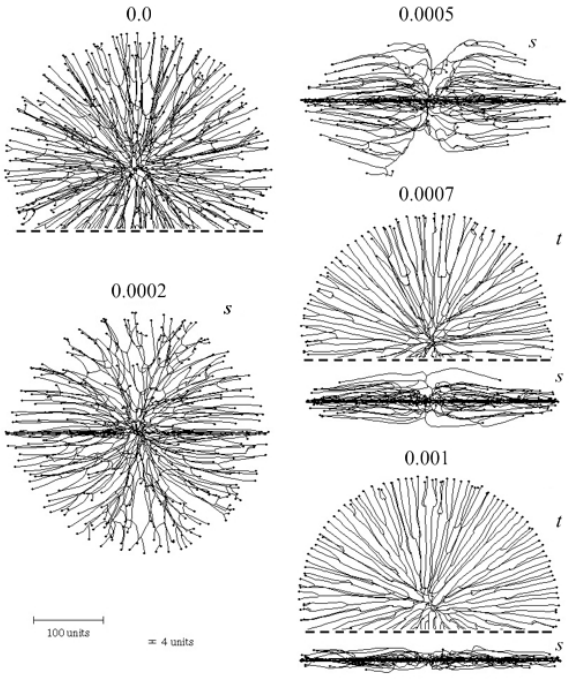

Figure 2: Colonies of virtual mycelium produced by the Neighbour-Sensing model by Meskauskas et al. (2004). The effect of horizontal plane tropism on the shape of the colony is displayed. The numbers above the images indicate the strength of the horizontal tropism. With an impact factor of zero the colony is spherical. For some of the symmetrical shapes only part of the view is shown, the dashed line indicating where the image has been cropped. Two viewing angles are shown, s = side view, t = top view. Taken from [Meskauskas et al., 2004b]

of phenotype in fungal mycelia was modeled [Falconer et al., 2005]. The model links the

fungal phenotype to its ability to recycle locally immobilized internal resources. These resources are recycled into a mobilized form capable of being directed to new internal sinks. Models simulating mycorrhiza, i.e. a symbiotic fungal-plant interaction, were designed, for instance, to investigate phosphate uptake and found that overall phosphate uptake was dominated by the fungus ([Schnepf and Roose, 2006] [Schnepf et al., 2008a] [Schnepf et al., 2008b]). On the development of fungal networks in complex environments a cellular automaton model of mycelial growth was created [Boswell et al., 2007]. It includes homogeneous and heterogeneous conditions with spatial and temporal nutritional heterogeneity as well as soil-like structures. The model reflects experimental observations of colony expansion rate and biomass distribution. Another mathematical model of mycelial growth explicitly incorporates the irregular branched and interconnected nature of the mycelium and simulates the flow of internally-located material ([Boswell and Carver, 2008], Fig. 3). The simulated hyphae realistically reflect existing mycelial structures and increasing the rate of nutrient translocation resulted in increasingly dense biomass structures.

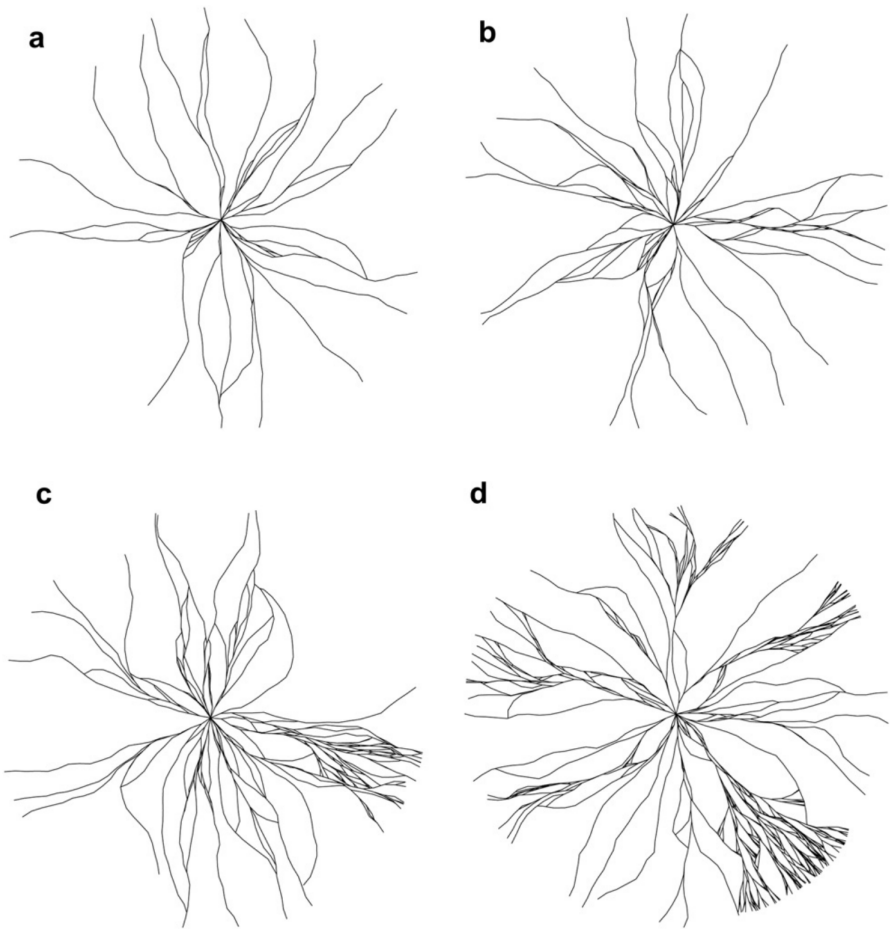

Figure 3: Mycelial growth simulated by Boswell and Carver. The fungal colony nourishes from an infinite source. The only difference between figures (a)-(d) is an increase in the diffusive translocation component. Taken from [Boswell and Davidson, 2012]

Models displaying the interactions in fungal colonies can be used to study systems of many interacting colonies. They create a platform upon which the links between

individual-scale behavior and community-scale function in complex environments can be built [Falconer et al., 2008]. Modelling the hyphal growth of the wood-decay fungus *Physisporinus vitreus* helps to understand how the complex system (fungus–wood) interacts under defined conditions [Fuhr et al., 2011]. The three-dimensional fungal growth model of the hyphal growth in the heartwood of Norway spruce considers hyphae and nutrients as discrete structures and links microscopic interactions between fungus and wood like degradation rate with macroscopic system properties including penetration depth of the fungus and biomass. A flexible mathematical model platform for studying branching networks of the fungus *Streptomyces coelicolor* is said to require few experimental values for parameterisation while delivering realistic simulations of fungal pellets [Nieminen et al., 2013]. Features predicted by the model are the density of hyphae, the number of growing tips and the location of antibiotic production within a pellet in response to pellet size and external nutrient supply. One of the most recent three-dimensional models on fungal growth in response to environmental stimuli is a spatially explicit model accounting for interactions between the fungus and different substrates and replicating in situ growth in a variety of growth environments [Vidal-Diez de Ulzurrun et al., 2017].

The model described in this thesis is a functional and structural model based on Functional-Structural Plant Modeling (FSPM). Structural elements of these models aim to accurately represent morphology while functional modeling focuses on metabolism and processes inside the organism. This type of model may lead to a better understanding of the development and functioning of complex organisms, for example in the testing of hypotheses concerning basic growth architecture. The structure of trees has been realistically simulated. For instance, spruce trees have been modeled in detail on the basis of measurements in a German spruce stand (Fig. 4) [Kurth, 1999] and a model of apple trees at several spatial and temporal scales helps investigating environmental influences and the dependence of growth on genetic variations [Bayol et al., 2016]. Simulations of growing roses allow conclusions on local light absorption and photosynthesis in a virtual greenhouse [Buck-Sorlin et al., 2011] and three-dimensional models can be created from a single two-dimensional digitized photo of tree architecture [Chi et al., 2016]. Ideas on making FSPM more efficient by reusing and enhancing existing models and standardizing design and communication were given which could simplify the utilization of models, lower costs and accordingly lead to an even broader acceptance of FSPM [Henke et al., 2015].

An effective way of creating functional structural plant models is using Lindenmayer systems. Lindenmayer systems, or L-systems, are string rewriting mechanisms developed in 1968 by the theoretical biologist and botanist Aristid Lindenmayer [Lindenmayer, 1968]. Each system consists of an *alphabet* of symbols. The start symbol, the beginning of a model, is called *axiom*. Rewriting rules or *productions* are applied in parallel to

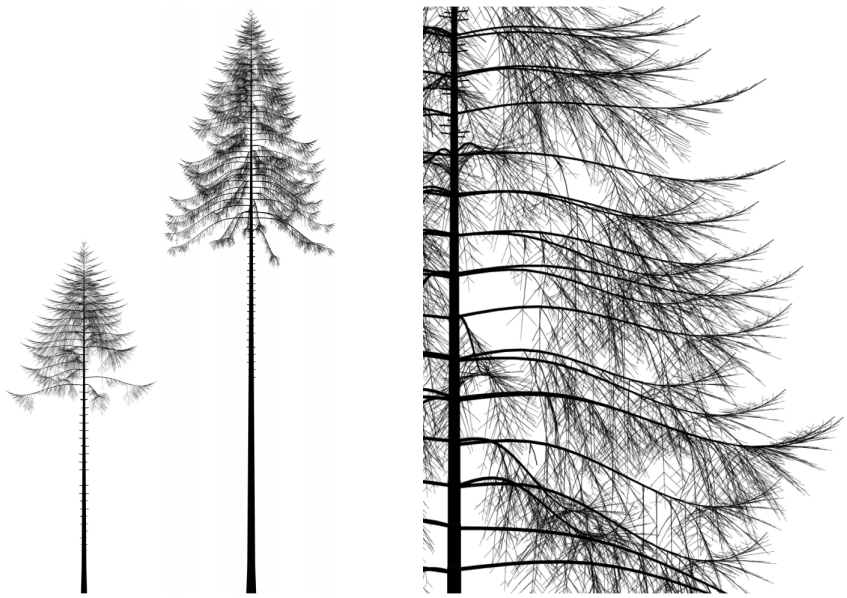

Figure 4: Spruce tree at the age of 71 and 113 years simulated with the model by [Kurth, 1999]. The figure on the right shows an extract for a more detailed view. Taken from [Kniemeyer, 2008]

all symbols of the axiom, rewriting the symbols. In the next step the new symbols are again rewritten and the growing of an organism is iteratively represented. The strings are interpreted as turtle graphics, a term in computer graphics using a relative cursor (the "turtle") upon a Cartesian plane, creating a both visually and structurally convincing simulation through the implementation of stochastic rules, each symbol having a different meaning. L-systems can be used to model realistic visualization of plant structures and growth processes of plant development [Prusinkiewicz and Lindenmayer, 1996]. A popular example of successively rewriting is the snowflake curve (Fig. 5) [Koch, 1906].

The following approaches on functional and structural modeling of fungi were made using Lindenmayer systems. To investigate how filamentous fungi may produce round colonies a model using deterministic, stochastic and parametric L-systems was developed and applied to different *Mucor*-species [Soddel et al., 1994]. The model simulates realistic two-dimensional circular fungal colonies on solid media. Results of the model show how a stochastic change of hyphal orientation leads to realistic images and the formation of circular colonies. A parametric L-system was used to create a model of *Aspergillus nidulans* [Tunbridge and Jones, 1995]. The flow of nutrients through the fungus to control growth was simulated. The production is thereby dependent on the levels of nutrients which are stored as parameters. The structural model is consistent with observations of the natural fungus. A three-dimensional L-System model for the growth of arbuscular mycorrhizal fungi within and outside of their host roots considers the growth of the roots and hyphae [Schnepf et al., 2016]. The relationship between the place of the inoculum and the speed of infection is observed.

No L-systems approach has yet been implemented on the modeling of *Coprinopsis*

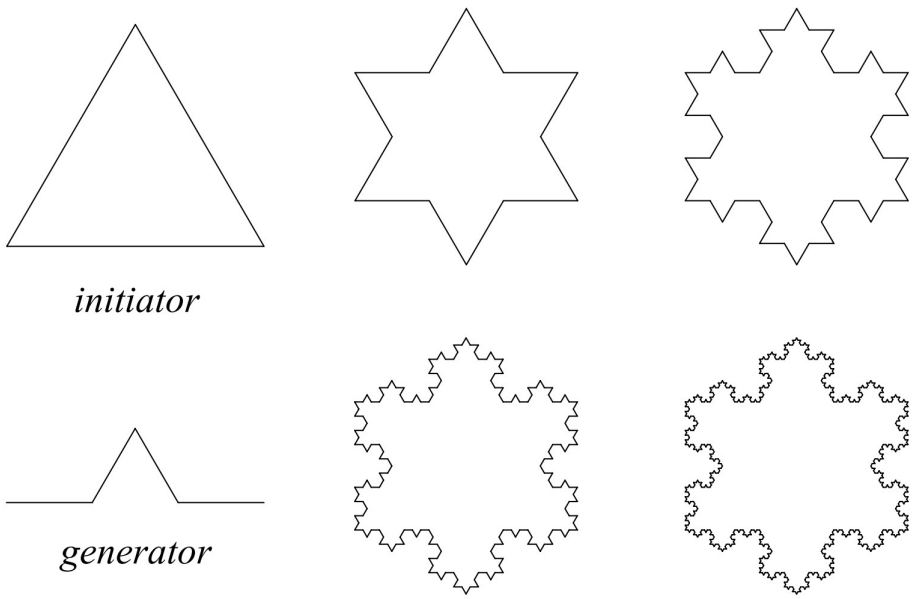

Figure 5: The snowflake curve being constructed in four iterations. The initial shape (*initiator*) of the Snowflake curve is an equilateral triangle. With every iteration, each line is replaced by the *generator*, i.e. an oriented broken line made up of 4 equal sides of length 1/3. Taken from [Prusinkiewicz and Lindenmayer, 1996]

cinerea, nor any other fungus of the class of basidiomycetes except in the context of mycorrhizal symbiosis, meaning there is no model on mushroom development, more precisely fruiting body development, using L-systems.

3 Model

3.1 Aims

The model created for this master thesis aims to realistically display the three-dimensional growth of a single colony of the mushroom *Coprinopsis cinerea* on solid medium. The simulated mycelium and the fruiting bodies are meant to closely resemble existing structures at laboratory conditions. Since modeling a complex organism requires large amounts of time and a master thesis only has a time frame of six months, the model is a simplification of the fungus focusing on branching and elongation of hyphae and development of early fruiting bodies. It is designed as an extendable basic model of mushroom colony development into which functions can easily be added to fulfill the user's specific purposes. While the focus is mainly on structural parts, the basis for implementing functional aspects is established.

3.2 Materials and Methods

The model was built using the Software GroIMP 1.5 (Growth grammar-related Interactive Modeling Platform, Copyright 2002-2008 Lehrstuhl Grafische Systeme BTU Cottbus, Copyright 2008-2016 GroIMP Developer Team). It was written in the programming language XL (for eXtended L-systems). XL is an extension of the Java programming language, combining the advantages of the rule-based paradigm with the strength of Java [Kniemeyer, 2008]. The language XL uses parallel graph-grammars that enable implementing L-systems.

3.3 Description of the Model

The simulated fungal colony consists of the modules *Hypha*, *Tip*, *Branch*, *FrubyCounter*, *Fruby*, *FrubyStem* and *FancyFruby*. The modules and procedures forming the fungal colony are displayed in a flow chart (Fig. 6). The module *Hypha* is a subclass of the forward movement, F, from which it inherits fields and methods like twigs in tree models (e.g. [Kurth, 1999]). It is drawn as a cylinder and forms the main tissue of the colony, the mycelium. Hyphae have two attributes, age and order. The order of a hypha increases by 1 with each branching. Young hyphae are white and gradually change towards a light cream color with increasing age. The module *Tip* reflects the hyphal tip and is responsible for apical growth and branching. Like *Hypha*, it extends the forward movement F and is drawn as a white cylinder. For lateral branching the module *Branch* is created. Comparable to a sleeping bud in tree models it starts growing with a certain branching probability and develops into a new hyphal tip. It is invisible and has the attribute order so the new hyphal tip can adopt this value for itself. The growth of fruiting bodies is induced by the module *FrubyCounter*. It has the attribute age and produces fruiting bodies with very low probability and at advanced age. The young fruiting body

(module *Fruby*) is displayed as a growing sphere sitting on an upwardly growing stem (module *FrubyStem*). The sphere's radius and the stem's length are identical, leading to the sphere sitting on top of the mycelia instead of growing into it. With increasing age the fruiting body is no longer well represented by a simple sphere and changes into the supershape object *FancyFruby*, which is a three-dimensional shape defined by 10 parameters. Supershapes are mathematically defined surfaces and the spherical product of two *superformulas* [Gielis, 2003].

In addition to the described modules, the following parameters are declared. The double-precision floating point number *fruitingProb* (short for fruiting probability) describes the probability of a fruiting body being created out of the module *FrubyCounter* at each time step. For apical elongation the parameter *eAngle* is needed to define the angle at which the hyphal tip elongates. The branching angle (double-precision floating point number *bAngle*) was set to 45 ° for *Coprinopsis cinerea* mycelia. For more realistic growth the standard deviation of the branching angle (*bStdw*) was also implemented. Since passed time is relevant for different modeling aspects (e.g. branching probability, snapshot naming), it is implemented as integer *t*. The branching probability (*bProb*) is dependent on time steps (integer t), aiming to simulate more frequent branching in the center of the colony. It is calculated by the formula: $bProb = 0.6 \cdot t^{-1,5}$. *HyphalDensity* is an important factor for biomass calculation. Since no data was available on the density of *Coprinopsis cinerea* mycelium, it was set to 1 as a placeholder for later implementation.

Table 1: Table of parameters. The branching angle is the mean of two published angles for hyphal branching of *Coprinopsis cinerea* ([Kües, 2000], [Polak et al., 2001]). The other parameters were estimated to create a realistic output.

Parameter	Description	Value
bAngle	branching angle mean	42.5
bProb	branching probability	$0.6 \cdot t^{-1,5}$
bStdw	branching angle standard deviation	5
eAngle	elongation angle mean	15
fruitingProb	fruiting probability	0.00004
hyphalDensity	density of mycelium	1
start	initial number of hyphal tips	150

The axiom initializing the model creates 150 hyphal tips with random two-dimensional orientation and sets the time counter to 1. It is inspired by Hemmerling's nerve model (2008, www.grogra.de).

The model procedures are included in the procedure *grow* which is displayed as a button in the modeling environment. It consists of the procedures *apicalGrowth*, *lateralBranching*, *fruiting*, *frubyGrowth*, *aging* and *snapshot*, followed by the increasing time calculator *time++*. Every procedure is followed by the method "derive()" forcing

it to completely run the rule applications in the right order and thereby preventing interference.

The procedure *apicalGrowth* is responsible for apical elongation and branching. In form of an if/else-function rules are applied to every Tip module. With branching probability, at first a new $Hypha$ module of the same order is created. Then, an apical branch is built either to the left or to the right of the hypha by the creation of a new hyphal tip with its order increased by 1. After placing new branches the parent branch builds a new hyphal tip to elongate at a random angle between $-eAngle$ and $eAngle$. The remaining hyphal tips, to which neither the first nor second condition applied ($100\% - 2 \cdot bProb$), form a hypha with the same order, then rotate in an orientation between $-eAngle$ and $eAngle$ and place a new module $Branch$ with its order increased by 1 for later lateral branching. Then, a module $FrubyCounter$ is created and followed by another hyphal tip.

Lateral branching is achieved by the procedure *lateralBranching*, building new hyphal tips to the left or to the right. Branches form at random angles between branching angle minus standard deviation and branching angle plus standard deviation. A tip is created of the same order as the branch module, because the order had already been incremented to create $Branch$. Remaining $Branch$ modules each form a new $Branch$ module for lateral branching in the following time steps.

The process of fruiting body development is described in the $fruiting$ procedure. Previously-placed, invisible modules for fruiting ($FrubyCounter$) develop into young fruiting bodies with a very small fruiting probability that is only called until a certain threshold age is exceeded. Making age a condition of fruiting leads to the formation of fruiting bodies rather in the center of the colony than at its edges. At first, young fruiting bodies are simulated as spheres sitting on stems growing upwards perpendicularly to the plane mycelium.

How fruiting bodies grow is described in the procedure $frubyGrowth$. The radius of the spherical module $Fruby$ and the length of the cylindrical module $FrubyStem$ grow linearly and are identical to guarantee the placing of the fruiting body above the colony without growing into the mycelia and the medium below. This reflects observations of fruiting body growth in reality. The procedure also includes the development of the $Fruby$ module into the supershape module $FancyFruby$.

Actualization rules are applied to hyphal age, color and *FrubyCounter* in the *aging* procedure. With every time step, hyphae and *FrubyCounter* age one step. The mycelium's color is supposed to shift from white to cream within four shades. Each lasts for 5 time steps and is implemented by an if/else function of hyphal age.

To automatically save a screenshot of the model visualization, the *snapshot* procedure which names pictures of the colony after each time step is applied. Therefore, the *DefaultView* is set as $View3D$, e.g. a $View$ which displays the graph created by the rule applications as a three-dimensional structure suitable for visualization. It takes the *DefaultView* from the workbench and is set as method *view*. *getViewComponent* gets the view component from *view* and applies the method *makeSnapshot* to it. *makeSnapshot* saves the image as a png-file in the selected folder and automatically names it according to the time step.

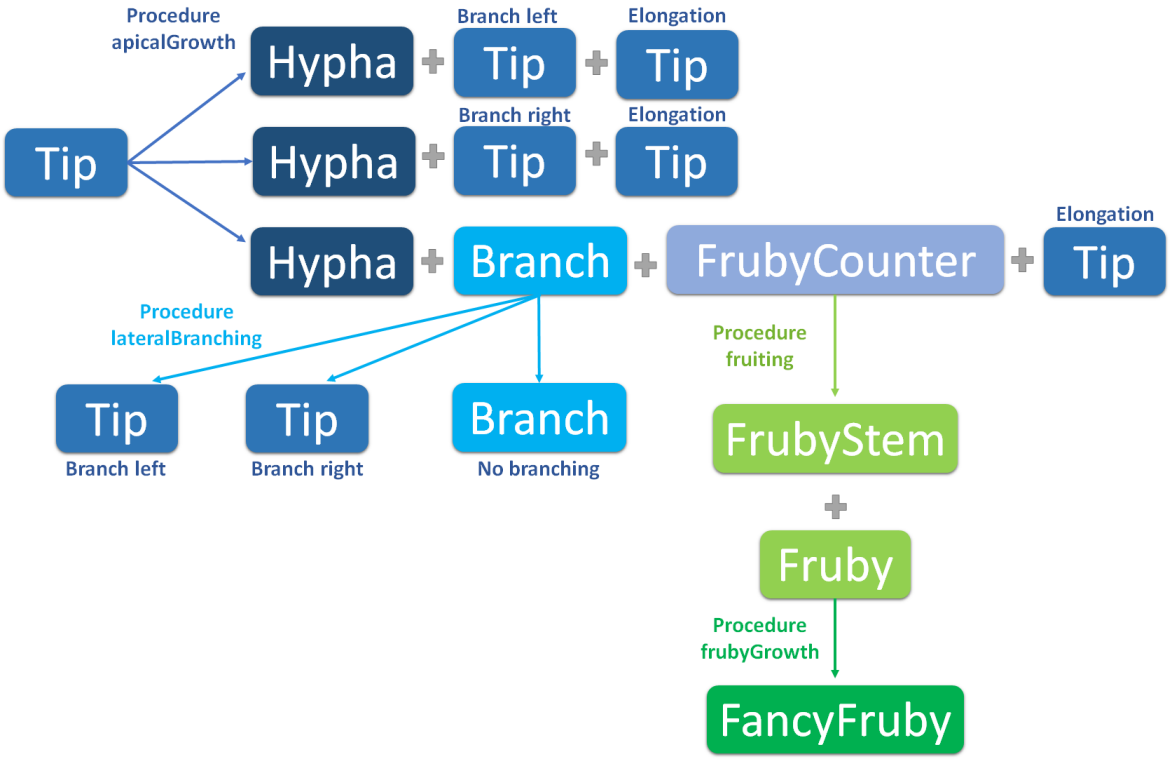

Figure 6: Flow chart displaying the modules (rectangles) and procedures (arrows) forming the simulated fungal colony. If multiple new modules are created in a procedure, they are sorted in order of their creation and linked by a +.

3.4 Results and Discussion

In 2016, colonies of *Coprinopsis cinerea* were grown at different temperatures and nutrient concentrations (Fig.7). The resulting images of daily colonial growth can be compared to the model visualization to validate the model results.

The axiom of the model (Fig. 8) resembles the newly formed colony one day after inoculation, i.e. the transfer of mycelium onto a new medium. In the following time steps, the model results for mycelial growth are in good agreement with observed structures (Fig. 9).

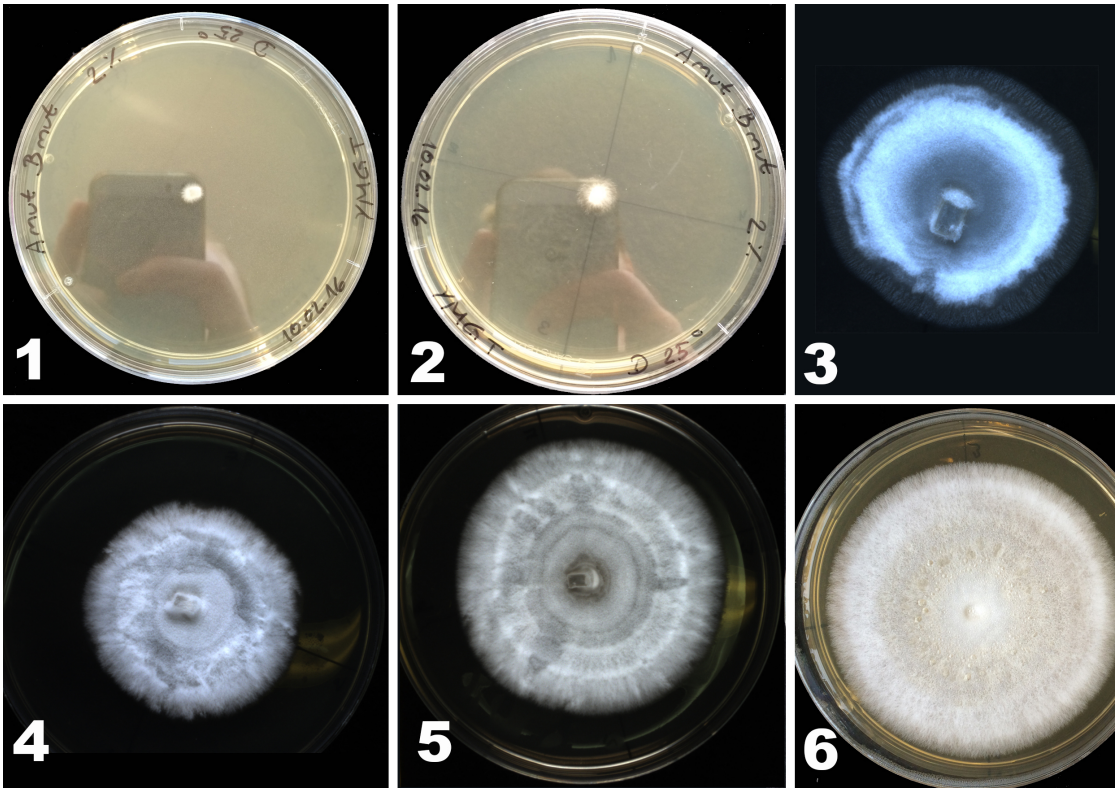

Figure 7: Colonial growth of *Coprinopsis cinerea* cultures on solid YMG/T medium (for yeast, malt, glucose and tryptophan) cultivated at 25 °C for own experiments in February 2016. The number indicates the days passed since inoculation. Image number 3 appears larger, because it was taken beneath the microscope to show hyphae.

Images of a fully grown colony show high similarities to existing structures (Fig. 10, Fig. 11). Also, the microscopic view of hyphae is in good agreement with the model's branching architecture (Fig. 12).

At early stages, fruiting bodies first resemble spheres and then elongate into egg-shaped objects (Fig. 13). The tissue surrounding the young fruiting body rips apart at a certain length of the fruiting body, the upper part forming the mushroom's cap and the lower part lingering on the stem (Fig. 14). The egg-shaped fruiting body is well represented by the supershape object *FancyFruby* (Fig. 15).

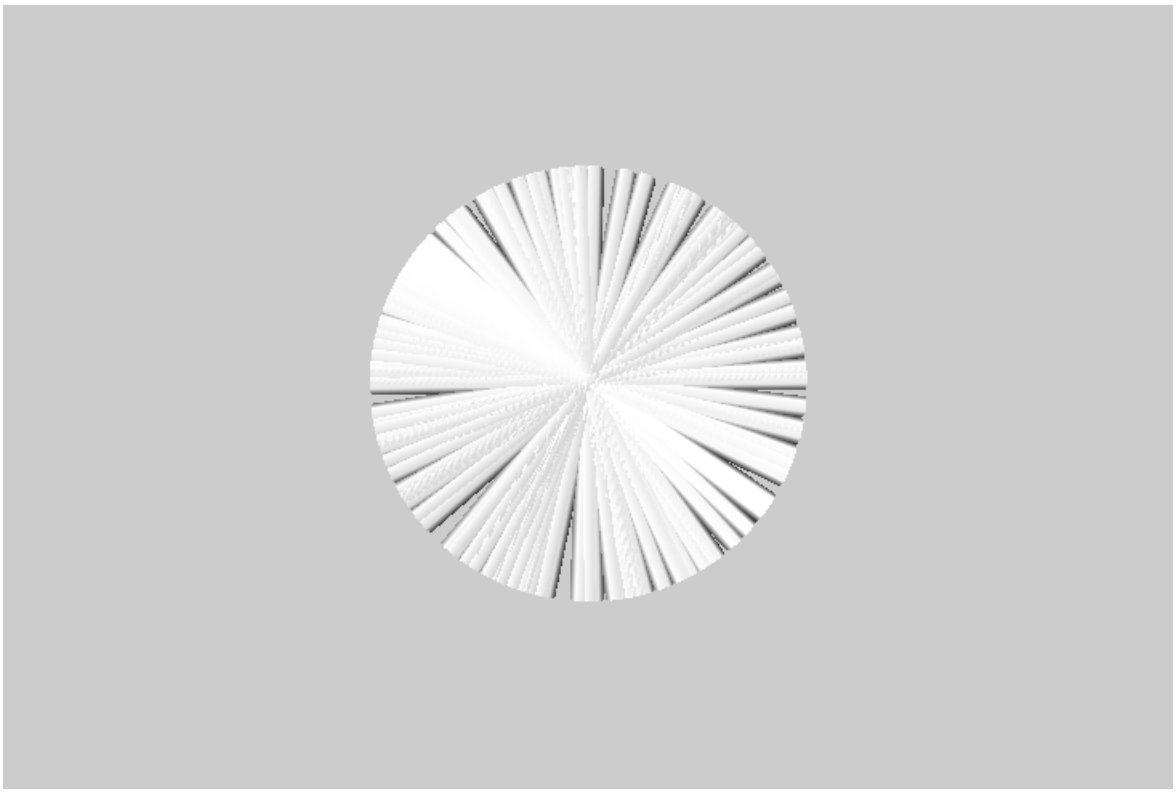

Figure 8: The axiom or initialization of the model. 150 hyphal tips with a random two-dimensional orientation are created at the center of the model.

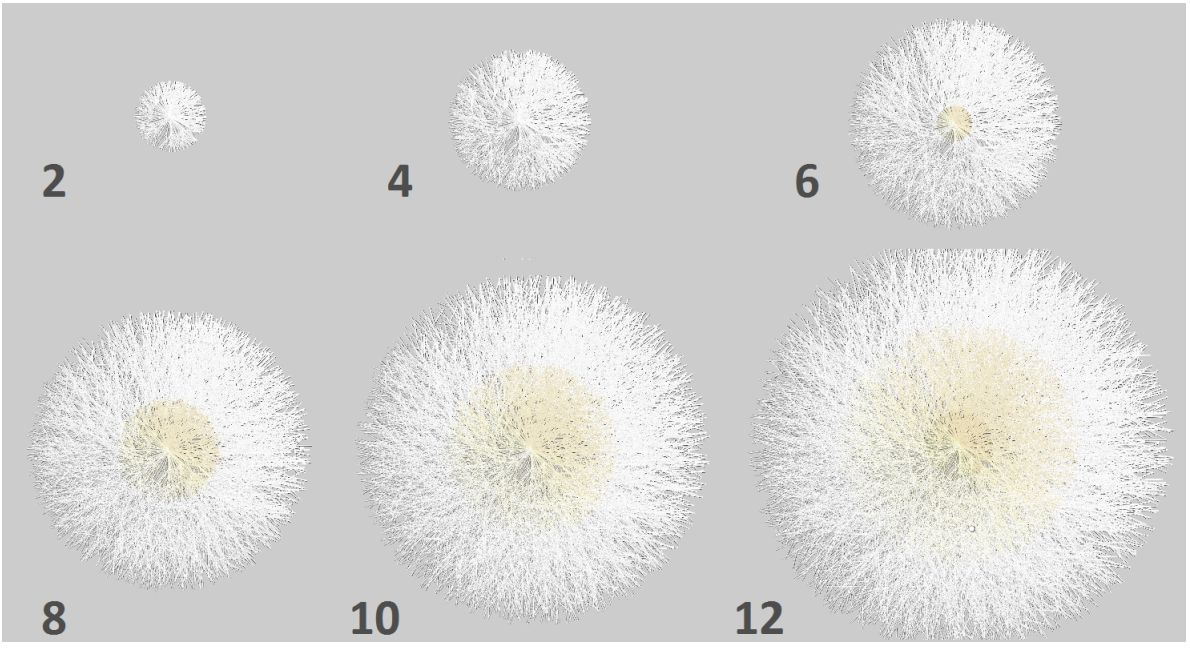

Figure 9: Model visualization after 2, 4, 6, 8, 10 and 12 time steps. Hyphal branching, elongation and increase in colony diameter can be seen, as well as age-related color-shifting from white to cream.

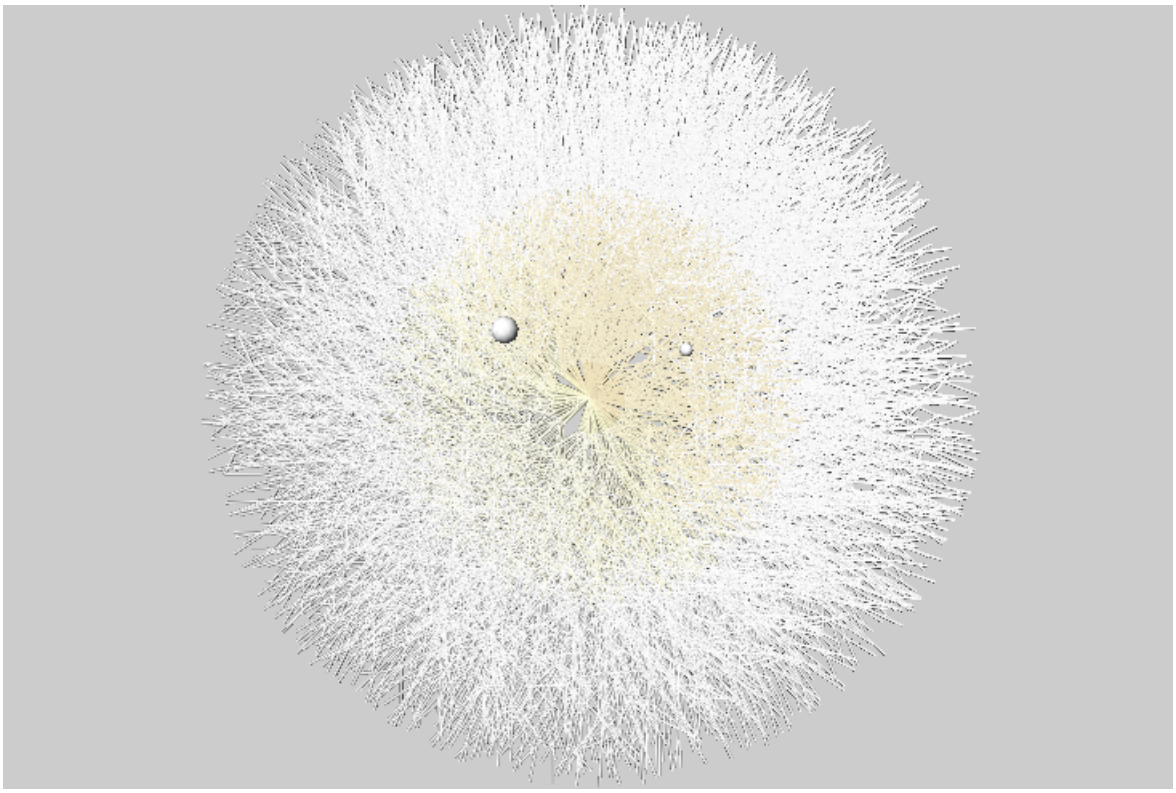

Figure 10: Top view on the simulated fungal colony after 11 timesteps.

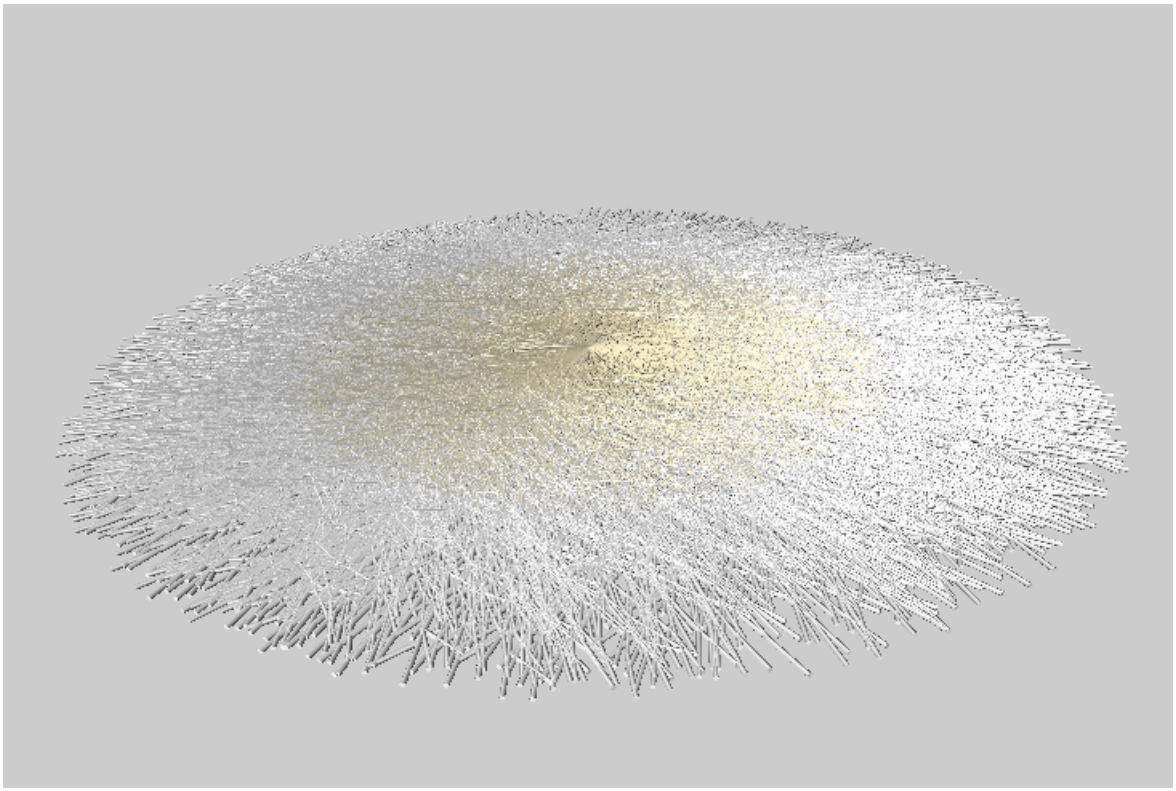

Figure 11: Side view on the simulated fungal colony after 13 timesteps.

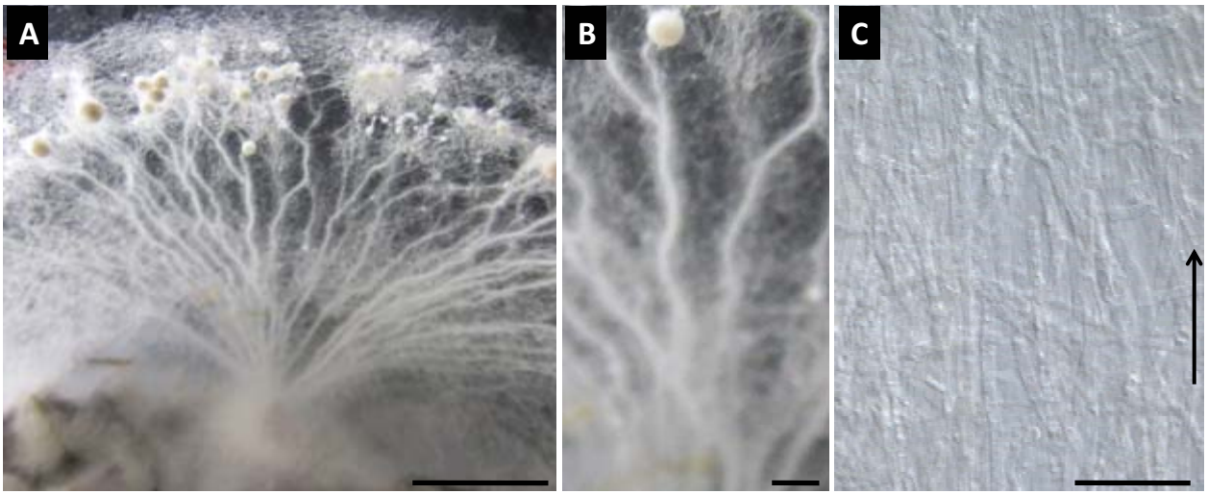

Figure 12: *Coprinopsis cinerea* AmutBmut hyphae grown on horse dung (A,B). C shows a microscopic view of hyphae growing parallel with perpendicularly interlacing hyphae for stabilization. Taken from [Badalyan et al., 2011]

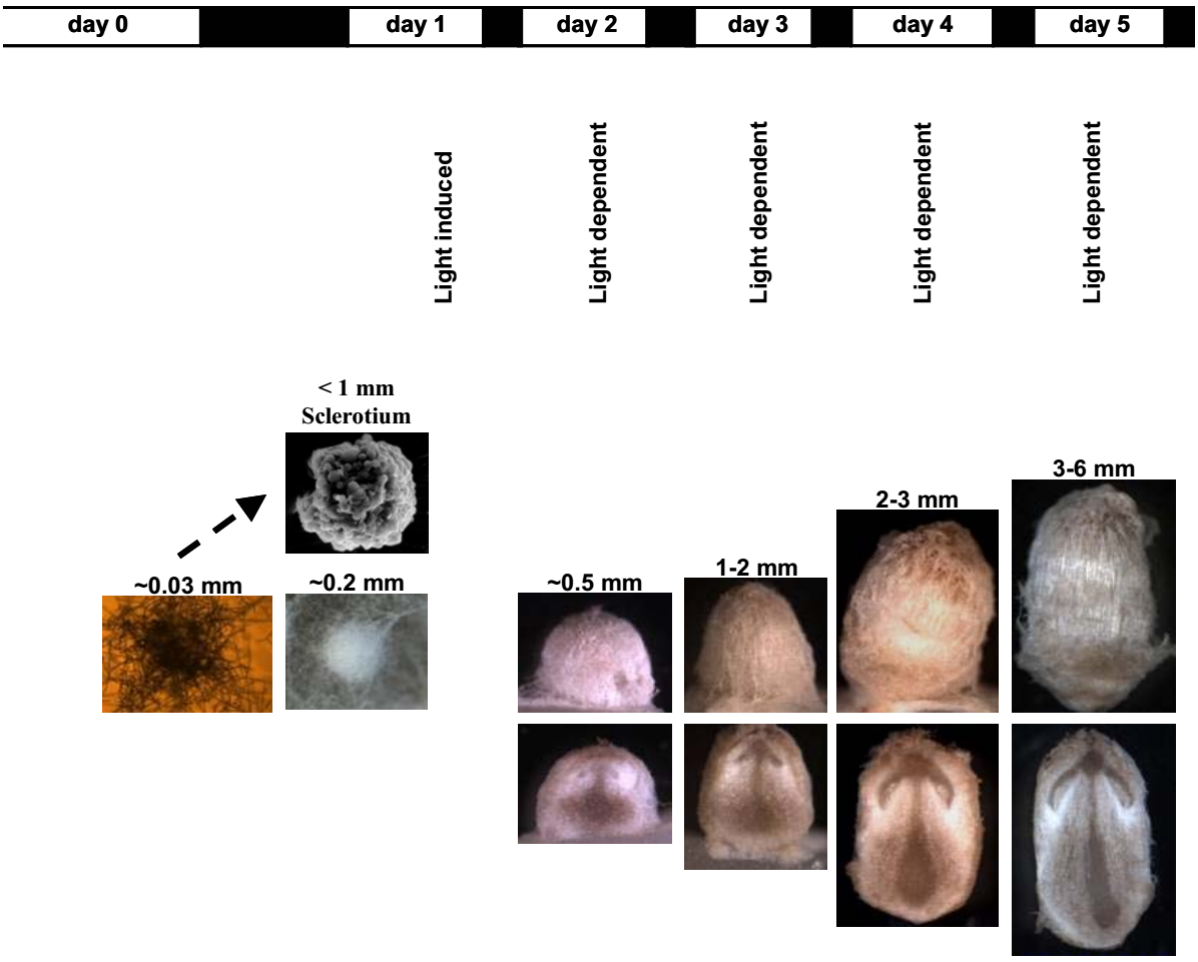

Figure 13: Microphotographs of early fruiting body development of *Coprinopsis cinerea* showing day 0 to 5 after storing the Petri dishes for 5 days at 37 °C in the dark. For fruiting, the colonies were taken to a climate chamber at a temperature of 26-28°C in a cycle of 12 h light/ 12 h dark. The black and white boxes indicate dark and light periods. Taken from [Navarro González, 2008]

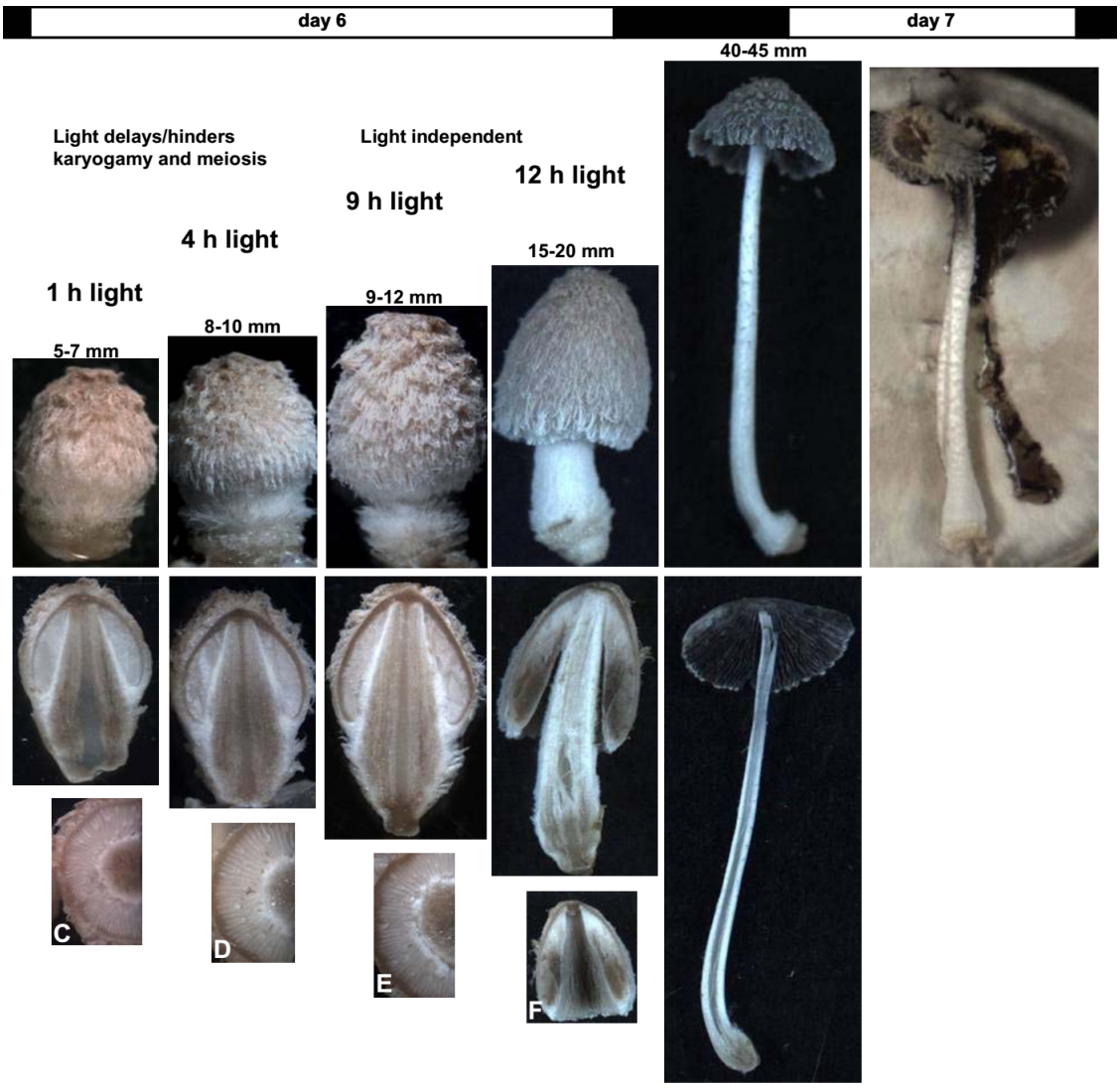

Figure 14: Microphotographs of fruiting body maturation and autolysis of *Coprinopsis cinerea*, showing day 6 and 7 of fruiting body development. The black and white boxes indicate dark and light periods. Taken from [Navarro González, 2008]

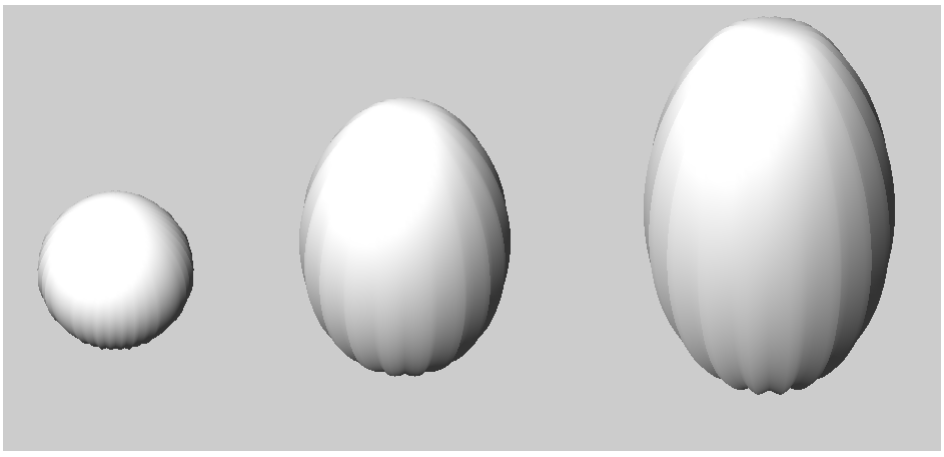

Figure 15: Supershape module *FancyFruby* for early fruiting body growth modeled with GroIMP (a=1, b=1, m1=40, n11=40, n12=5, n13=10, m2=2, n21=80, n22=35, n23=27)

For the simulation of mature fruiting bodies, the implementation of a second supershape object *FancyFruby2* creates a realistic mushroom shape (Fig. 16). This 12 parameter supershape can currently not be implemented in GroIMP, because supershape methods include either 6 or 10 parameters. A new method considering 12 parameters is currently being programmed and will soon provide the possibility to integrate realistic mushroom shapes into the model.

Figure 16: Supershape mushroom plotted with a superformula generator (http://mysterydate.github.io/superFormulaGenerator/). Parameters: a1=0.6, a2=0.1, b1=1, b2=0.1, m1=4, m2=6.1, n11=10, n21=10, n12=0, n22=6.1, n13=10, n23=-1.6

The parameters to implement the model were chosen carefully to visualize a fungal colony resembling *Coprinopsis cinerea*. Creating 150 hyphal tips in the axiom leads to dense early mycelia without causing runtime problems (Fig. 8).

Branching and elongation are usually oriented in a direction towards nutrients. Since the model assumes homogeneous conditions, elongation is varied at a random angle between -15 and 15° to shape a more realistic colony than with straight and unbent outwardly growing hyphae.

The branching angle of *Coprinopsis cinerea* mycelium differs between the monokaryon, i.e. a fungal mycelium in which each cell contains a single nucleus, and the dikaryon in which cells contain two nuclei after the fusion with another individual. *AmutBmut*, the strain to be modeled in this thesis, is a mutant homokaryon containing two identical nuclei. Its properties resemblme those of a dikaryon, for instance faster growth and the ability to form fruiting bodies. For the branching of dikariotic mycelia, different angles were measured, varying between an acute angle of 10-45° [Kües, 2000] and a broader angle of 65-75° [Polak et al., 2001]. For the model a branching angle of 42.5° was chosen, since it is the mean of the range from 10-75°. To induce a more realistic visualization, branching occurs at an angle randomly varied by a standard deviation of 5°.

Making the branching probability a time-dependent parameter causes dense, strongly branched mycelium in the center of the colony. The number of hyphal tips at the edges of the colony is increasing with each time step. Accordingly, fewer branching is required to cover the medium at advanced time steps. The function $bProb = 0.6 \cdot t^{-1,5}$ sets a branching probability of 0.6 for the first time step, causing 60 percent of the hyphal tips to branch. The probability then decreases rather rapidly with each time step, e.g. 21.2% at the second time step and 11.5% at the third.

The fruiting probability is set to such an extent that few fruiting bodies are produced when the colony reaches an advanced age. To set an example of how changing parameters or rules (e.g. fruiting probability, branching angle) affect the model result, a simulation with a very low fruiting probability (Fig. 17) and a simulation generating many fruiting bodies (Fig. 18) can be compared. A fruiting probability of 0.00004 normally creates between zero and two fruiting bodies in 22 time steps. In the same time, a fruiting probability of 0.5 leads to the formation of about 80 fruiting bodies.

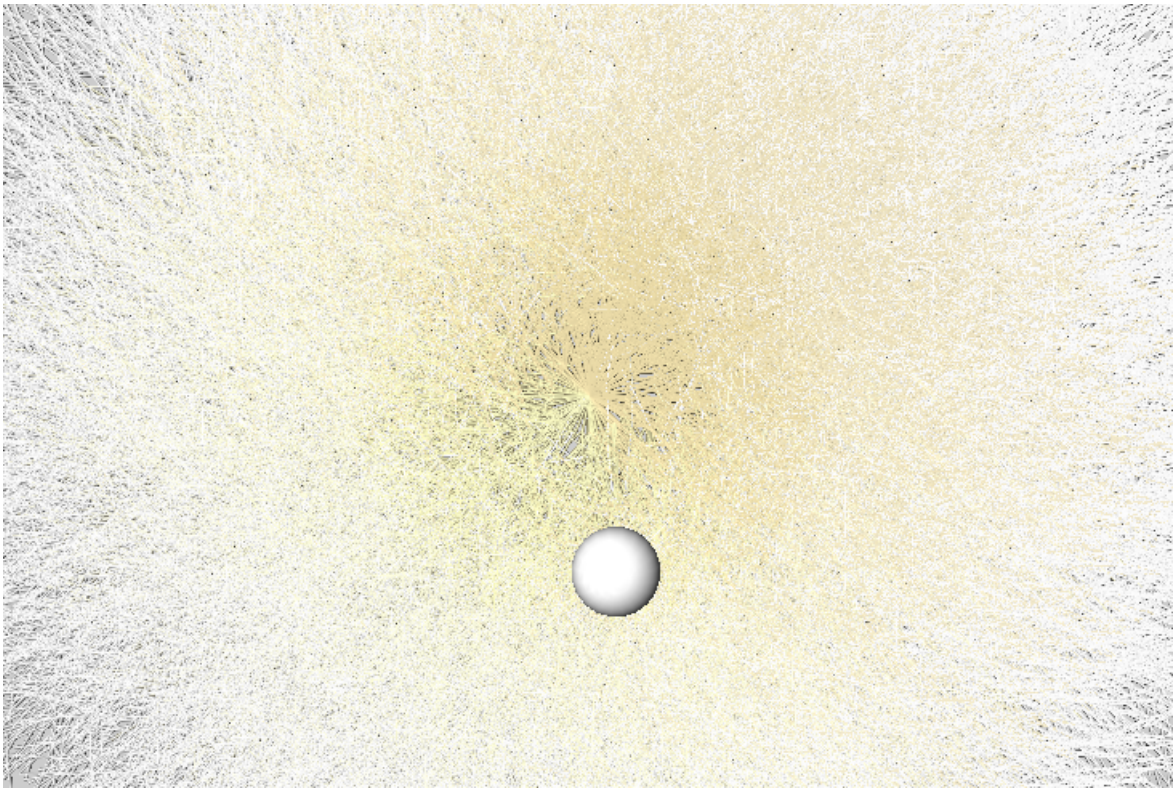

Figure 17: Simulated fungal colony after 22 time steps with fruiting probability set to 0.00004.

Some parameters are not particularly determined but simply their default values are used. For instance the attributes of the forward movement F, from which hyphae and hyphal tips extend, are unchanged. The length and diameter of these cylinders are default values and are not changed according to different age, temperature or nutrient concentration. If environmental influences were modeled, their varying impact on cell structure and growth rate could be implemented to cause more plausible results than default cell

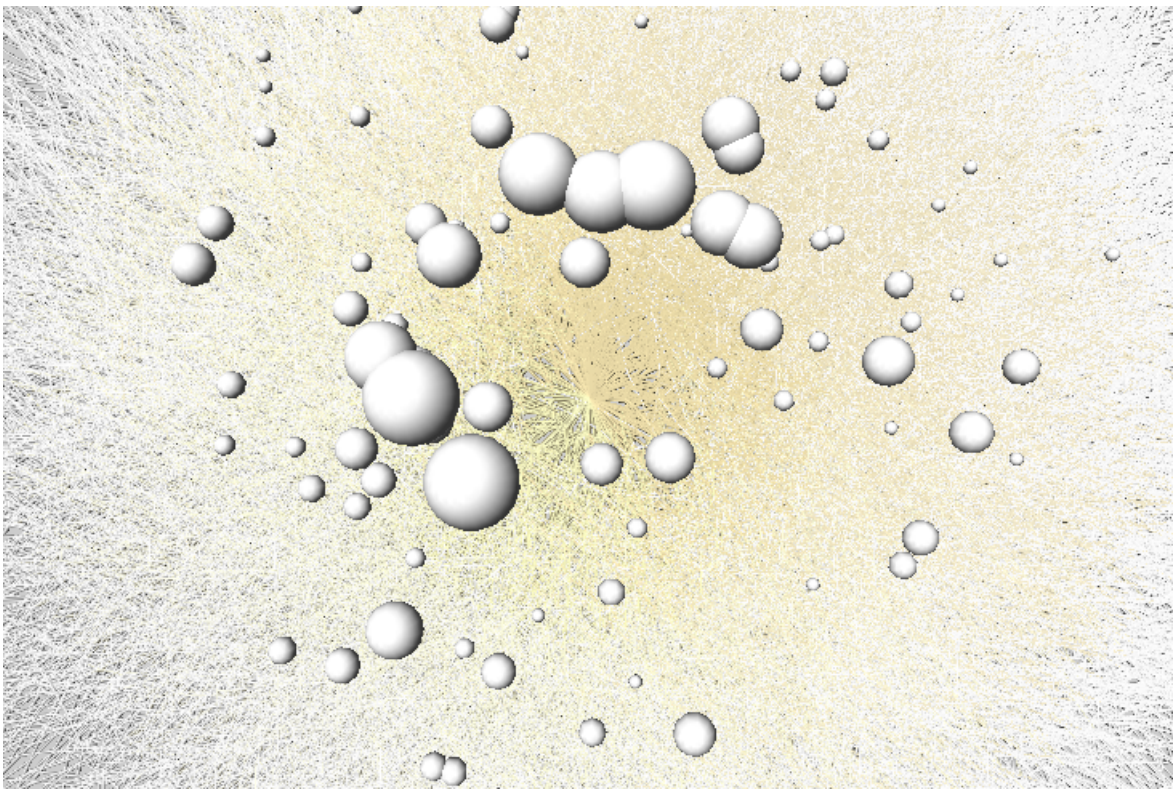

Figure 18: Simulated fungal colony after 22 time steps with fruiting probability set to 0.5

length and a constant growth rate.

The model fungus grows under strictly homogeneous conditions, displaying only laboratory conditions and growth on a homogeneous solid medium. The mycelial growth is currently unlimited and not confined by the margin of a Petri dish. Due to the two-dimensional orientation of the hyphal tips, the mycelium is entirely flat. In nature, the fungal colony is a thin tissue with aerial hyphae growing in three dimensions.

Fruiting bodies develop only under favorable conditions. The development depends on temperature, carbon/nitrogen relationship, day/night rhythm, humidity, oxygen and CO2 concentration [Kües, 2000]. In this thesis, simply assuming favorable conditions, none of these factors have been considered. The fruiting probability was estimated in order to result in a reasonable amount of fruiting bodies produced. Inside of the simulated colony, fruiting bodies are mostly placed neither at the outer and newer parts of the mycelium, since they are expressed only when the *FrubyCounter* reaches an age of 10 time steps, nor immediately at the center, because the central hyphae created in the axiom have no *FrubyCounter* module. This resembles the structure of real fungal colonies expressing fruiting bodies ([Navarro González, 2008]).

The hyphae in the model age. Their color shifts from white to cream just as in natural mycelia and their age attribute increases with each time step. Yet, age has no influence on hyphae apart from their changing color. They are not growing in width. Cell death of

hyphae or bigger parts of the mycelium are not modeled. An important process of programmed cell death is the autolysis of the mushroom cap which enables spore dispersal.

The model presently focuses on fungal structure and architecture. Functional aspects are not yet considered. For instance the analysis of produced biomass was not implemented due to lack of data on hyphal density. The developed basic model provides users with the possibility to implement further functions to fulfill their specific purposes.

The model contains rather few aspects specifically describing *Coprinopsis cinerea*. Only few parameters are specific for this species and typical characteristics like the autolysis of the cap are not yet included. Accordingly, the model is presently applicable for different species of fungi. By changing parameters to empirically measured values for different species, other mushrooms may thus be simulated with the model, broadening its field of application.

Modeling fungi with L-systems results in very realistic visualization [Meskauskas et al., 2004a]. However, the model currently does not consider rearranging and aggregation of hyphae. Hyphae frequently rearrange to change their position, e.g. to move towards nutrients or away from toxins, and aggregate to form mycelial cords or fruiting bodies. Rigid, non-parametric L-systems are therefore rather disadvantageous for simulating fungal morphogenesis [Meskauskas et al., 2004a]. The rearranging of hyphae, i.e. subsequently changing their position and orientation, could be modeled with parametric L-systems. For instance, providing rotation symbols with time-dependent or conditional parameters could enable subsequent rotation of a branch and every subordinate module. The length or diameter of existing hyphae could similarly be changed. Modeling hyphal aggregation, i.e. the accumulation and coalescing of hyphae to form mycelial cords or complex structures like fruiting bodies, is hardly possible with classical L-systems but could be feasible using relational growth grammars (RGGs) in GroIMP. Their advantage over L-systems which are designed specifically for the modeling of plant topology is the representation of general graphs and their dynamics via graph rewriting instead of string rewriting. Applicable for the simulation of aggregated fungal hyphae is, for instance, the model of a carrot field with rodents showing the potential of the true graph structure of RGGs [Kniemeyer et al., 2006]. In this model a water vole is digging a burrow system below a carrot field to feed on the roots. It cycles through the network of simulated tunnels and interconnections. Interactions with the environment like neighbor sensing could also be implemented with queries and sensitive rules in XL.

4 Outlook

On the basis of the extendable model framework, functions and empirically measured data can be added to investigate processes and quantify influences. Effects on growth and fruiting body development of environmental conditions, for instance the effect of temperature and nutrient concentration measured for the author's "master project", can be implemented. The cylindrical *Hypha*-module inherits the attribute length from the forward movement F. Linking faster growth to appropriate temperatures could be achieved by fitting a growth function to the length of hyphae. Temperature could be implemented with a regulator, so the user can adjust it manually before each simulation. The length could then be calculated by the growth function depending on temperature regulator.

Coprinopsis cinerea adapts to different light conditions [Corrochano, 2011]. Light/-dark cycles control its sexual reproduction [Lu, 2000] and the availability of blue light in the spectrum is important for all known differentiation processes [Kües et al., 1998]. Other factors to investigate in the model could thus be the comparison between growth at day/night cycles to growth in either only dark or light, the influence of different light intensities or spectra. The modeling platform GroIMP provides possibilities to simulate the influence of different light sources on the object modeled. In the way light absorption and photosynthesis are quantified in tree models, fungal light absorption could be simulated.

Furthermore, including effects of humidity, oxygen concentration or pH-value can lead to a more complex environment and, accordingly, more realistic growth conditions. Heterogeneous environments resulting, for instance, from a natural substrate like horse dung, could also be implemented to extend the model.

Age-, temperature- or nutrient-related growth rate has not been implemented in the model. Since there are more phases of mycelial growth than the constant growth rate phase, extending the model to link growth rate to age of individual hyphae as well as age of the whole colony could create more realistic images of growing fungal colonies. The mycelia presently grows unlimited. As the model displays fungal growth on solid medium at laboratory conditions, a barrier simulating the edge of a Petri dish could be implemented.

The specific requirements for fruiting body development could be built into the existing framework instead of simply assuming optimal conditions. The realistic shape of a mushroom using a supershape object with 12 parameters is still to be implemented (Fig. 16). Quantification of mushroom production would be interesting especially for edible mushrooms or to investigate metabolites stored inside the cap. Mushroom stems naturally elongate not straightly upwards, but with a bending function considering grav-

itropism which would lead to a more realistic visualization ([Moore et al., 1979], [Kher et al., 1992], [Zhang et al., 2014]).

When the mushroom cap reaches maturity, it starts dissolving to set free basidiospores. This process, called autolysis, could be implemented for more realistic visualization or in order to investigate spore dispersal or ink extraction. Autolysis is a form of programmed cell death, i.e. a process of controlled tissue removal. It is induced by calcium entering mitochondria. The cytoplasm then becomes hypertonic, causing water influx, swelling and lysis [Moore, 2013]. Autolysis and natural or toxin induced cell death can be implemented in form of a new procedure or added to the already existing *aging* procedure. In addition to natural and controlled death, the influence of toxin can be simulated. When a certain age is reached, dying modules could either be simply deleted or wilt and shrink depending on the aim of the simulation.

The mycelium presently grows and branches in only two dimensions. In nature, fungal tissue forms a thin film on top of the medium. Three-dimensional, aerial hyphae could, for instance, be implemented with tropisms as in the neighbor sensing model (Fig. 2) [Meskauskas et al., 2004a]. The model using L-systems seems to be suitable and applicable for simulating fungal colony architecture.

Functional aspects are not yet included in the model, but can easily be added into the extendable basic model framework. For instance, with only information on hyphal density and a method calling up the volume of the colony, biomass can be calculated. When researching the production of enzymes, the influencing factors can be built in quickly and the amount of enzymes produced be set as a target variable. In this way, metabolite production can be investigated and quantified, leading to a better understanding of fungal growth and possibly providing benefits for numerous applications including medicinal purposes and protection of the environment.

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Anhang

Model Code with German comments

```
/* Dieses Modell ist Teil der Masterarbeit von Sandra Kelleter

3D-Wachstumsmodell des Pilzes Coprinopsis cinerea auf Hyphenbasis

Hinweis: Zur Nutzung der Snapshot-Funktion Dateipfad anpassen.
*/

////////////////////////////
/////// MODULE /////////////
////////////////////////////

// Die simulierte Pilzkolonie setzt sich aus folgenden Modulen zusammen:

// Das Modul Hypha ist (wie die Zweige bei Baummodellen) ein Erbe der
// Vorwärtsbewegung F, bei der ein Zylinder gezeichnet wird.
// Es bildet den Hauptbestandteil des Myzels.
// Hyphen haben die Attribute Alter und Ordnung. Ornung wird mit jeder
// Verzweigung um 1 inkrementiert. Die jungen Hyphen sind weiß.


module Hypha(int age, int order) extends F()
{{ setShader(WHITE);}}

// Das Modul Tip entspricht der Hyphenspitze, ist ebenfalls ein Erbe von F und
// wird als Zylinder gezeichnet. Es ist als Zentrum des Wachstums für apikale
// Verlängerung und Verzweigung zuständig.

module Tip(int order) extends F()
{{ setShader(WHITE);}}

// Das Modul Branch wird für die laterale Verzweigung benötigt.
// Es ist zu vergleichen mit einer schlafenden Knospe, die mit einer
// festgelegten Wahrscheinlichkeit sprießt.
// Das Modul hat das Attribut Ordnung und ist unsichtbar.
// Aus diesem Modul entspringen auch mit geringer Wahrscheinlichkeit
   Fruchtkörper.

module Branch(int order);
```

```
38
39 // Der Fruchtkörper (fruiting body, Modul Fruby) wird zunächst als wachsende
40 // Kugel simuliert, die an einem senkrecht nach oben wachsenden Stamm sitzt.
41 // Das zuvor erzeugte Modul FrubyCounter ist unsichtbar und eine schlafende
42 // Knospe wie Branch. Sie wächst bei bestimmtem Alter zum Modul Fruby heran.
43
44 module FrubyCounter(int age);
45
46 // Kugel sitz an Stamm FrubyStem (Erbe von F), damit sie über dem
47 // Myzel sitzt und nicht ins Medium hineinwächst.
48 module FrubyStem() extends F(0.1)
49 {{ setShader(WHITE);}}
50 module Fruby() extends Sphere(0.1)
51 {{ setShader(WHITE);}}
52
53 // Mit zunehmendem Alter ähneln die Fruchtkörper nicht mehr simplen Kugeln.
54 // Dazu wird das Modul FancyFruby als Supershape-Objekt (mathematisch
55 // definierte Oberfläche, das sphärische Produkt zweier Superformeln
56 // nach Gielis) eingeführt.
57 // Bisher wird ein Methode mit nur 10 Parametern verwendet.
58 // Eine neue Methode mit 12 Parametern für realistischeres Wachstum wird
59 // aktuell implementiert.
60
61 module FancyFruby()
62 extends Supershape(1, 1, 40, 40, 5, 10, 2, 80, 35, 27)
63 {{ setShader(WHITE);}}
64
65 ////////////////////////////////
66 ///////// PARAMETER ////////////
67 ////////////////////////////////
68
69 // Initiale Hypehnanzahl
70 // 150, damit Myzel im ersten Schritt bereits dicht ist,
71 // bevor Verzweigungen möglich sind, jedoch keine Laufzeitprobleme auftreten
72 const int start =150;
73
74 // Fruchtkörperbildungswahrscheinlichkeit aus FrubyCounter
75 // Creates realistic image, not too many FBs
76 const double fruiting_prob = 0.00004;
77
78 // Verlängerungswinkel, Elongation
79 const double e_angle = 15;
80
```

```
81 // Mittelwert aus KUES 2000 und POLAK et al. 2000
82 const double b_angle = 42.5;
83 // Standardabweichung für natürlicheres Aussehen
84 const double b_stdw = 5;
85
86 // Verzweigungswahrscheinlichkeit
87 // Wahrscheinlichkeit von Zeitschritt abhängig,
88 // dadurch in der Mitte stärker verzweigt
89
90 public float b_prob(int time)
91    {
92    return (0.6*Math.pow(time, -1.5));
93    }
94
95 // alternativ als Konstante: const double b_prob = 0.15;
96
97
98 // Integer time zählt Zeitschritte, z.B. für automatische Bildbenennung der
99 // Snapshot-Funktion und für zeitabhängige Verzweigungswahrscheinlichkeit
100 int time = 1;
101
102
103 // Berechnung der Biomasse (bisher nicht implementiert)
104 // Keine Angaben zur Hyphendichte in der Literatur
105 const float hyphalDensity = 1;
106
107
108 ////////////////////////
109 /////// AXIOM /////////
110 ////////////////////////
111
112 // Startblock mit dem Startwort (Axiom) erzeugt initiale Nummer Hyphenspitzen
113 // mit zufälliger 2D-Orientierung
114
115 // Axiom inspiriert vom Nervenmodell von Reinhard Hemmerling (2008, Grogra HP)
116
117 protected void init()
118 [
119    {
120      time = 1;           /* Zeitzähler initialisiert */
121    }
122    Axiom ==>
123       for((1:start))
```

```
124         ([RU(random(0,360)) Tip(1)]);
125
126 ]
127
128 ////////////////////////////////
129 ///////MODELL-PROCEDURES//////////
130 ////////////////////////////////
131
132 // öffentlicher Block (erscheint im Menü als Button) public void grow()
133 // "derive()", damit sich die (parallel angewandten) Regeln aus den einzelnen
134 // Blöcken nicht "ins Gehege kommen", erzwingt die vollständige Abarbeitung
135 // der aktuellen Regelanwendungs-Warteschlange
136
137 public void grow()
138 {
139    apical_growth(); derive();
140    lateral_branching(); derive();
141    fruiting(); derive();
142    fruby_growth(); derive();
143    ageing(); derive();
144    snapshot(); /* Auskommentieren wenn nicht verwendet, Dateipfad (unten)! */
145    time++;
146 }
147
148 // Verlängerung an der Spitze und apikale Verzweigung mittels if/else Funktion
149 // Mit jeweils der Verzweigungswahrscheinlichkeit bildet das Modul Tip zunächst
150 // eine Hyphe derselben Ordnung wie Tip aus. Daraufhin folgt entweder die
151 // apikale Verzweigung nach rechts oder links durch Bildung einer Hyphenspitze
152 // in entsprechendem Winkel mit Ordnung +1. Der Hauptast bildet eine neue
153 // Spitze in einem zufälligen Winkel.
154 // Die übrigen Hyphenspitzen (100%-2*branching probability) bilden zunächt eine
155 // Hyphe derselben Ordnung wie Tip. Dann erfolgt die Orientierung in einem
156 // zufälligen Winkel zwischen e_angle und -e_angle und die Platzierung der
157 // Module Branch mit Ordnung +1 für spätere Verzweigung, FrubyCounter und einer
158 // neuen Spitze derselben Ordnung.
159 // Das Modul Branch für laterale Verzweigung wird platziert.
160
161 protected void apical_growth()
162 [
163    Tip (order) ==> if(probability(b_prob(time)))
164           (Hypha(0, order)[RU(random(b_angle-b_stdw, b_angle+b_stdw))
165           Tip(order+1)] RU(random(-e_angle, e_angle)) Tip(order))
166         else
```

```
167             (if(probability(b_prob(time)))
168             (Hypha(0, order)[RU(random(-b_angle-b_stdw, -b_angle+b_stdw))
169             Tip(order+1)] RU(random(-e_angle, e_angle)) Tip(order))
170             else
171                (Hypha(0, order) RU(random(-e_angle, e_angle))
172                [Branch(order+1)] [FrubyCounter(0)] Tip(order)));
173 ]
174
175 // Laterale (seitliche) Verzweigung aus dem Modul Branch
176 // Das Modul verzweigt sich jeweils mit Verweigungswahrscheinlichkeit im
177 // definierten Verzweigungswinkel und bildet eine Spitze. Die übrigen
178 // Branch Module bleiben Branch Module und bilden evtl. im nächsten Zeit-
179 // schritt Äste aus.
180
181 protected void lateral_branching()
182 [
183    Branch(order) ==>
184    if(probability(b_prob(time)))
185       (
186          RU(random(b_angle-b_stdw, b_angle+b_stdw)) Tip(order)
187       )
188       else
189       (
190          if(probability(b_prob(time)))
191          (
192             RU(random(-b_angle-b_stdw, -b_angle+b_stdw)) Tip(order)
193          )
194          else (Branch(order))
195       );
196 ]
197
198 // Prozess der Fruchtkörperbildung
199 // Zuvor platzierte unsichtbare Fruiting-Module (FrubyCounter) wachsen mit
200 // sehr geringer Wahrscheinlichkeit und erst in fortgeschrittenem Alter los.
201 // Dadurch keine Fruchkörper am Rand der Kolonie.
202 // Fruchtkörper in jungem Stadium als Kugel dargestellt. (vgl. Bilder Navarro-
203 // Gonzalez). Kugel sitz an Stamm FrubyStem (Erbe von F), damit sie über dem
204 // Myzel sitzt und nicht ins Medium hineinwächst.
205 // Der Stamm wächst senkrecht nach oben.
206
207 protected void fruiting()
208 [
209 FrubyCounter(age), (probability(fruiting_prob) && (age >= 5) && (age <= 10))
```

```
    ==>
RL(90) FrubyStem() Fruby();
]

// Der Fruchkörper wächst.
// Radius von Fruby und Länge von FrubyStem wachsen linear und sind identisch.
// Die Umwandlung in das Modul FancyFruby ist momentan auskommentiert, da auf
// das Modul mit der neuen 12 Parameter Methode gewartet wird.

protected void fruby_growth()
[
   fb:Fruby ::>
   {
   fb[radius] +=0.1;
   }

   fs:FrubyStem ::>
   {
   fs[length] +=0.1;
   }

   /*
   Fruby(age), (age>=10) ==>
      (FancyFruby());

   grow:FancyFruby ::>
    {
    grow[a]+=0.2;
    grow[b]+=0.2;
    }
   */

]

// Alterung. Aktualisierung des Hyphenalters und des FrubyCounters.
// Die Farbe der Hyphen soll sich mit zunehmendem Alter von weiß zu creme
// verändern.

protected void ageing()
[
    hyp:Hypha ::>
      {
      hyp[age]++;
```

```
252       }
253
254     col:Hypha ::>
255      {
256      if(col[age]<5)
257      col.setColor(0xFFFFFF);
258      else if(col[age]<10)
259         col.setColor(0xF5ECCE);
260          else if(col[age]<15)
261             col.setColor(0xF2E6C0);
262                else if(col[age]<20)
263                   col.setColor(0xEEDEAA);
264      }
265
266
267
268     fbc:FrubyCounter ::>
269       {
270       fbc[age]++;
271       }
272
273 ]
274
275 // Speicherung eines Schnappschusses für jeden Zeitschritt im angegebenen
276 // Ordner mit automatischer Bennenung nach Zeitschritt
277 protected void snapshot()
278 [
279    {
280    de.grogra.imp3d.View3D view = de.grogra.imp3d.View3D.getDefaultView
281    (workbench());
282    view.getViewComponent().makeSnapshot(
283    new ObjectConsumer() {
284       public void consume(Object image) {
285          de.grogra.imp.IMP.writeImage((java.awt.Image)image,
286          new java.io.File(String.format("C:/Users/Sandra
                Kelleter/Documents/Masterarbeit/Modell/bilder/snapshot%03d.png",
                time)));
287          }
288       });
289    }
290 ]
```

Hiermit versichere ich gemäß §7 Abs. 5 der Master-Prüfungsordnung vom 23.09.2010, dass ich die vorliegende Arbeit selbständig verfasst und keine anderen als die angegebenen Quellen und Hilfsmittel benutzt habe.

Datum, Unterschrift