Spatio-Temporal Analysis of Vegetation Dynamics of Selected Successional Stages of Dry Acidic Grasslands

Experimental Studies and Model Simulations

Dissertation

zur Erlangung des akademischen Grades
Doktor der Naturwissenschaften (Dr. rer. nat.)

Fakultät für Biologie
Universität Bielefeld

vorgelegt von

Marcel Austenfeld

aus Bielefeld

Bielefeld, August 2009

Table of Contents

ACKNOWLEDGEMENTS - DANKSAGUNG

Bedanken möchte ich mich bei Prof. Dr. Wolfram Beyschlag, der mir die Möglichkeit gab, an diesem interessanten Thema zu arbeiten und der mir immer diskussionsbereit und helfend zur Seite stand.
Weiterhin möchte ich Juniorprof. Dr. Christiane Werner und Dr. Tom Steinlein danken für ihre Unterstützung und kritischen Anregungen während meiner Zeit am Lehrstuhl.

Elke Furlkröger und Barbara Teichner waren die helfenden Hände, wenn es darum ging die Theorie in Praxis umzusetzen und Praxis in Theorie. Dafür herzlichen Dank.

Ebenfalls danke ich Ursula Herlth für die guten Kaffeegespräche (mit Elke und Barbara) und die Unterstützung in allen organisatorischen Fragen und Angelika Mühlbrandt, die noch ein wenig in meiner Zeit mitorganisierte.

Was wäre eine Arbeit am Lehrstuhl ohne Kollegen, von denen ich einige kennen- und schätzen lernte:
Maik Bartelheimer und Ralf Peperkorn, die mir noch als Doktoranden in jeder Lebenslage halfen. Silke Friedrich und Stefan Böger die mir mit Rat und Tat in Nürnberg halfen. Vanessa Stahl, Nils Krämer und Stephan Unger für alle anregenden Diskussionen und Ratschläge.

Insgesamt dem ganzen Lehrstuhl für die nette und besondere Arbeitsatmosphäre.

Weiterhin möchte ich mich bei Ulrich Richhardt, Gerd Drexler und Nils Köhler bedanken für die elektrische und mechanische Unterstützung und bei Detlev Balten, Gebhard Sewing, Marcus Höpfner, und Uschi Büchner für die gärtnerische Hilfe und die netten Gespräche.

Und zum Schluss möchte ich mich bei meiner Freundin bedanken, für die Geduld meine Launen während der Arbeit zu ertragen und bei meinen Eltern für die Unterstützung und besonders dafür, nicht ständig nach dem Fortschritt der Arbeit zu fragen.

Summary

A generic modeling environment for the analysis and simulation of spatio-temporal phenomena in ecosystems was developed. This framework was built upon a Rich Client Platform (RCP) which uses new concepts of extensibility and software architecture for sustainable development and provides a solid basis for an Integrated Development Environment (IDE) for ecological models. The integration of various statistical tools, imaging routines and several specialized drawing panels, makes this environment particularly suitable for the analysis of the above mentioned spatio-temporal ecological processes.

Because of their comparatively low complexity, dry acidic grassland ecosystems have been repeatedly used for studying vegetation pattern formation and the underlying biotic interactions. In order to obtain an integrative view of the existing knowledge as well as to provide a possibility for further integrative analysis with the help of model simulations, the above described platform was used to develop an individual based Model structure for the investigation of long term effects of environmental changes on the stability of early successional stages such dry acidic grasslands which are typically dominated by the two pioneer species *Corynephorus canescens* and *Polytrichum piliferum.* The model was validated with experimental data and the spatio-temporal patterns created by the model were in good accordance with the measured natural patterns.

The model was then used to analyze the effect of changes in temperature, nutrient supply and disturbance rate on the long term behavior on this ecosystem. The results showed an overall high stability of this system under different temperature and nutrient scenarios as long as an intermediate disturbance frequency is assured.

Finally, an experimental study on the effect of herbivory and competition on the *Corynephorus canescens* was conducted. In a controlled field experiment, the effects of the removal of various amounts of aboveground biomass on the above and belowground biomass allocation during the following regeneration phase was analyzed in the presence or absence of an intraspecific and interspecific competitor (*Hieracium pilosella*). The results show a rather high ability of *C.canescens* to compensate low to medium amounts foliage loss (reflecting the typical natural herbivory induced by grasshoppers and rabbits) without significant changes in its competitive ability. Belowground, no biomass effects of foliage removal and/or competition could be detected. Because of these negligible effects, herbivory was not implemented in the above described model.

Zusammenfassung

Eine allgemeine Entwicklungsumgebung wurde für die Analyse und Simulation von räumlich zeitlichen Phänomenen in ökologische Systemen entwickelt. Die gesamte Plattform basiert auf einer "Rich-Client-Platform" (RCP), die neue Konzepte der Modularisierung und allgemeinen Programmarchitektur mitbringt. Damit bietet sie die Grundlage, für eine nachhaltige Weiterentwicklung und ist somit eine solide Basis für eine integrierte Entwicklungsumgebung für ökologische Modelle. Die Integration verschiedener statistischer Werkzeuge, Methoden der Bildverarbeitung und spezielle Visualisierungen qualifizieren diese Umgebung besonders für die Analyse der oben genannten räumlich-zeitlichen Prozesse.

Aufgrund ihrer vergleichsweisen geringen Komplexität, wurden Sandlebensräume wiederholt für Studien von Vegetationsmustern und ihrer zugrunde liegenden biotischen Interaktionen genutzt. Für einen integrativen Überblick und weitere integrative Ansätze mit Hilfe von Simulationsmodellen wurde die oben genannte Plattform genutzt, um eine individuenbasierte Modellstruktur für die Analyse von Langzeiteffekten aufgrund von Umweltveränderungen auf die Stabilität von Sandlebensräumen zu entwickeln, die typischerweise von zwei Pionierarten, *Corynephorus canescens* und *Polytrichum piliferum* dominiert werden. Das Modell wurde mit experimentellen Daten verifiziert und die vom Modell erzeugten räumlich zeitlichen Muster zeigten eine hohe Übereinstimmung mit natürlich gemessenen Mustern.

Das Modell wurde dann genutzt, um Langzeiteffekte von Veränderungen der Temperatur, Nährstoffversorgung und Störungsraten in diesem System zu untersuchen. Die Ergebnisse zeigten eine generell hohe Stabilität des Systems unter veränderten Temperatur und Nährstoffbedingungen, wobei temporal wiederkehrende, kleinräumige Störungen als Grundlage notwendig waren.

Schließlich wurde noch eine Untersuchung über die Auswirkungen von Herbivorie und Konkurrenz auf *Corynephorus canescens* durchgeführt. In einem kontrollierten Freilandexperiment wurden die Auswirkungen von entfernter Biomasse von Blättern sowie die An- oder Abwesenheit eines intraspezifischen und interspezifischen Konkurrenten (*Hieracium pilosella*) auf die überirdische und unterirdische Allokation von Biomasse in der folgenden Regenerationsphase analysiert. Die Ergebnisse zeigten das *Corynephorus canescens* die Fähigkeit besitzt, leichte bis mittlere Blattverluste (die typische natürliche Herbivorie von Kaninchen und Paarhufern simulieren sollten) zu kompensieren ohne dabei an Konkurrenzstärke zu verlieren. Unterirdisch konnten keine Auswirkungen der simulierten Herbivorie bzw. Konkurrenz festgestellt werden. Aufgrund dieser zu vernachlässigen Effekte wurde Herbivorie nicht in dem Modell berücksichtigt.

1. Introduction

The complexity of vegetation patterns of plants is caused by biotic and abiotic factors which interact with each other in time and space. All these factors form an overwhelming complexity which makes it difficult for the scientist to understand the functioning of the system and to derive predictions of the development in the near future. Despite of the complexity of nature, scientists still believe that nature is to a certain amount predictable and that these predictions are valuable for management and conservation of ecological systems.

Because of their comparatively low complexity, dry acidic grassland ecosystems have been repeatedly used for studying vegetation pattern formation and the underlying biotic interactions. Less complex ecosystems are often considered as a good basis to identify driving forces behind patterns and to generate hypotheses on more complex vegetation patterns in order to better understand the key mechanisms behind biotic and abiotic interactions.

Figure 1: Dry acidic grasslands in Southern Germany

1.1 Objectives of this Thesis

This thesis consists of three parts:

The first part (chapter 2) contains a description of the development of an Integrated Development Environment (IDE) for ecological modeling. The reason for the development of this application was the need of a tool for the development of spatially explicit simulation models. Spatially explicit simulation models are theoretical tools which reduce spatial complexity by binning spatial relationships and complexity into a grid structure with arbitrary precise resolution. This saves calculation costs to simulate spatial relationships like plant communities without sacrificing the claim of reality. Such models are particularly popular in ecology because of their easy to understand rule-based formulation, which makes it easy to implement complex experimental data.

In the second part of this work (chapter 3) this framework is then used to develop and test an individual based model structure for the investigation of long term effects of environmental changes on the stability of early successional stages of dry acidic grasslands, which are typically dominated by the two pioneer species *Corynephorus canescens* and *Polytrichum piliferum*. The model is parametrized with experimental data and validated with independent experimental measurements. This part of the thesis also contains the results of the application of this model in order to analyze the effect of changes in temperature, nutrient supply and disturbance rate on the long term behavior on this ecosystem.

Part 3 (chapter 4) describes the results of a controlled field experiment on the effect of herbivory and competition on the *Corynephorus canescens* which was conducted to implement herbivory as a potential factor affecting the competitive strength of this species into the model.

1.2 Dry Acidic Grasslands

Dry acidic grasslands in Europe were formed during the last glacial period about 10000 years ago from melting glaciers transporting and sorting sediment and forming typical sandy landscape structures (ELLENBERG 1996, BURKART et al. 2004). The early successional stages of dry acidic grasslands exhibit rather extreme abiotic site conditions. The ecosystem is very nutrient poor and the sand has a low ability to store water which causes significant drought stress during the summer (JENTSCH & BEYSCHLAG 2003). Furthermore the sun can heat up the soil surface temperature up to 70 °C and another stress factor is the highly mobile substrate which leads to permanent erosions. (HOHENESTER 1960, BERGER-LANDEFELDT & SUKOPP 1965, RITESEMA & DECKER 1994, QUINGER & MEYER 1995).

The typical course of succession in dry acidic grasslands is depicted in Figure 2. The early successional stages which are the focus of the present work are colonized by highly adapted pioneer plant species which are able to grow under these extreme conditions (JENTSCH & BEYSCHLAG 2003) Naturally, these early stages are comparatively stable because frequently occurring small scale disturbances (e.g. by rabbits and ants) continuously recreate open sand areas and keep the succession from going on (JENTSCH 2001, JENTSCH et al. 2002, JENTSCH & BEYSCHLAG 2003, BÖGER 2007).

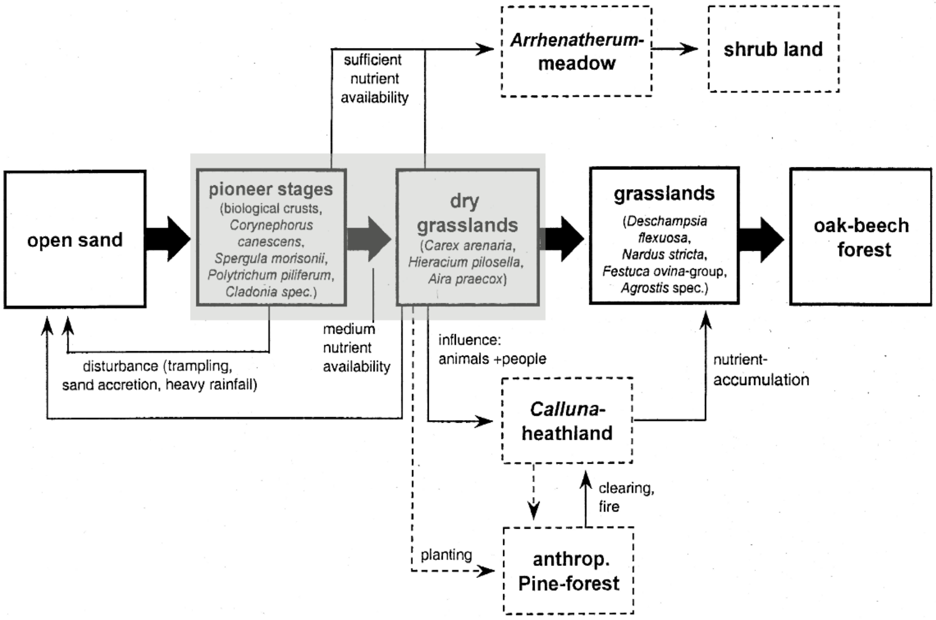


Figure 2: Succesional pathway on inland dunes (Weigelt 2001).Grey marked: successional stages important for this thesis.

Dry acidic grasslands are rather valuable ecosystems because they harbor a large number of rare and endangered plant and animal species but they become increasingly endangered by habitat fragmentation and anthropogenic nutrient deposition from the atmosphere which leads to quick ruderalisation (see Figure 2) and loss of the typical species (HEIL & BRUGGINK 1987, BERENDSE & ELBERSE 1990, AERTS et al. 1991, QUINGER & MEYER 1995, BOBBINK et al. 1998, JENTSCH 2001, FROMM et al. 2002, JENTSCH et al. 2002b, RUSSEL 2002).

1.3 Selected Plant Species of the Early Successional Stages

The three dominating plant species of the early successional stages of dry acidic grasslands (Spergulo morisonii-Corynephoretum canescentis) are the bunchgrass *Corynephorus canescens* (Grey Hair Grass), the clonal rosette plant *Hieracium pilosella* (Mouse-ear Hawkweed) and the moss *Polytrichum piliferum* (Awned Hair Cap). Two of them, *Corynephorus canescens* and *Polytrichum piliferum* play an important role in fixing and stabilizing the open sand (they both tolerate burial of sand) as well as in accumulating nutrients and offering safe sites for other less well adapted species. Thus they open the pathway of succession towards higher diverse and more complex plant communities. The model simulations of part two of the present work deal with a variety of the Spergulo morisonii-Corynephoretum canescentis where only two species (*C. canescens* and *P. piliferum*) dominate.

Figure 3: *C. canescens*, *P. piliferum*(dark-grey areas) and *H. pilosella* on early stages of dry acidic grasslands

1.3.1 *Corynephorus canescens*

Figure 4: *Corynephorus canescens*

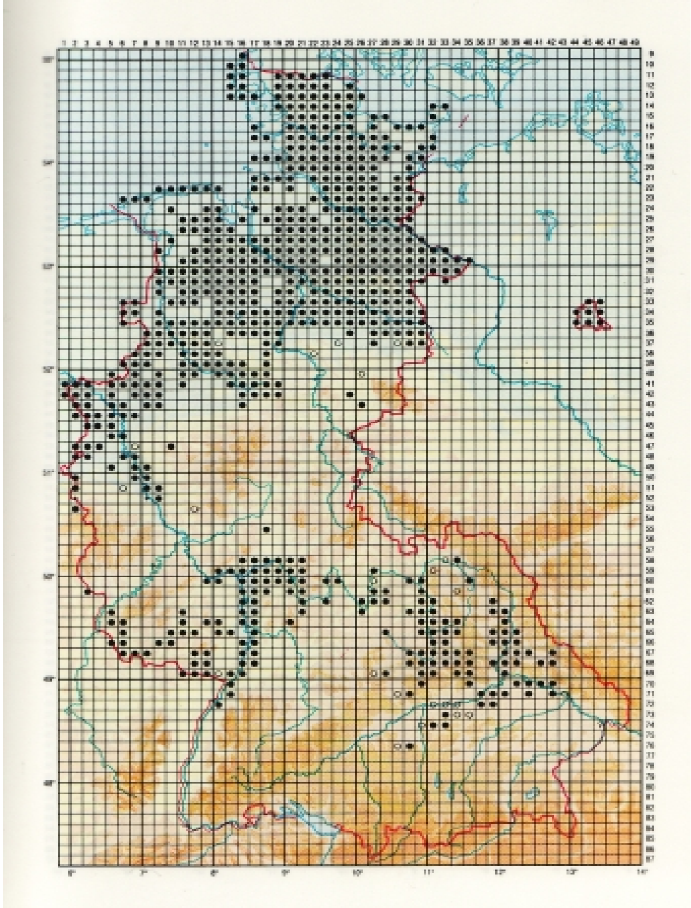


Figure 5: Distribution of *C. canescens* in Germany (Haeupler et al. 1989)

Corynephorus canescens (L.) Palisot Beauvais (P.B.), the grey hair grass is a perennial Pocaceae which is highly adapted to the early stages of dry acidic grasslands. The grass itself is growing as a bunch grass very well on mobile sand systems (TÜXEN 1967, SYMONIDES 1985). The flowering of *C.canescens* occurs typically in June, July and sometimes in August. The extensive root system of *Corynephorus canescens* can reach a depth of 15-50 cm (OBERDORFER 1994, ELLENBERG 1996) and attaches the plants securely to the ground which is necessary for survival on the mobile substrate of the early successional stages on sandy ecosystems. *C.canescens* can effectively reduce the transpirational area of its leaves by rolling or folding them. The grass occurs all over Europe, in North Africa, North and South America. In several parts of Germany *C.canescens* is endangered for example in Bavaria and North Rhine-Westphalia (category 3 source: BFN) .

Ellenberg Numbers: Light: 8 Temperature: 6 Kontinental: 5 F: 2 Reaction: 3 N: 2

1.3.2 *Polytrichum piliferum*

Figure 6: *Polytrichum piliferum*

Polytrichum piliferum, the Awned Hair-Cap Moss belongs to the Polytrichaceae family of the Bryopsida (FRAHM 1992, FRAHM 2001, STRASBURGER 2002). It grows in colonies which are often circular and well adapted for dry sandy conditions. The stems of the moos can be 2-5 cm long and bear lanceolate phylloids, 4-6 mm long with long white Glashairs and the end of the leaf. During drought the phylloids become in-curved exhibit their dark brown colored backside which together with reflective glass hairs at the phylloid tips protects the photosynthetic pigments against excessive radiation and also has glass hairs to reflect sunlight (SHAW & GOFFINET 2000). Thus, the color of the moos is green if growing under well watered conditions but appears brownish under dry low water conditions. *P.piliferum* produces up to guessed 50 million spores in its capsules on top of a 1-4 cm long Seta enclosed by the Calyptra which is mostly light brown which arises from the middle of the stem. Alhough it produces so many spores most of the colonies seem to arise vegetatively from gametophyte fragments or small clumps of shoots (MEUSSEL 1935, HOBBS & GIMINGHAM 1984, HOBBS & PRITCHARD 1987, FREY & HENSEN 1995). *P.piliferum* is a widely spread moss which grows mostly on sandy, dry, acidic and sunny spots.

Ellenberg Numbers: Light: 9 Temperature: 2 Kontinental: 5 F: 2 Reaction: 2 N: -

1.3.3 *Hieracium pilosella*

Figure 7: *Hieracium pilosella*

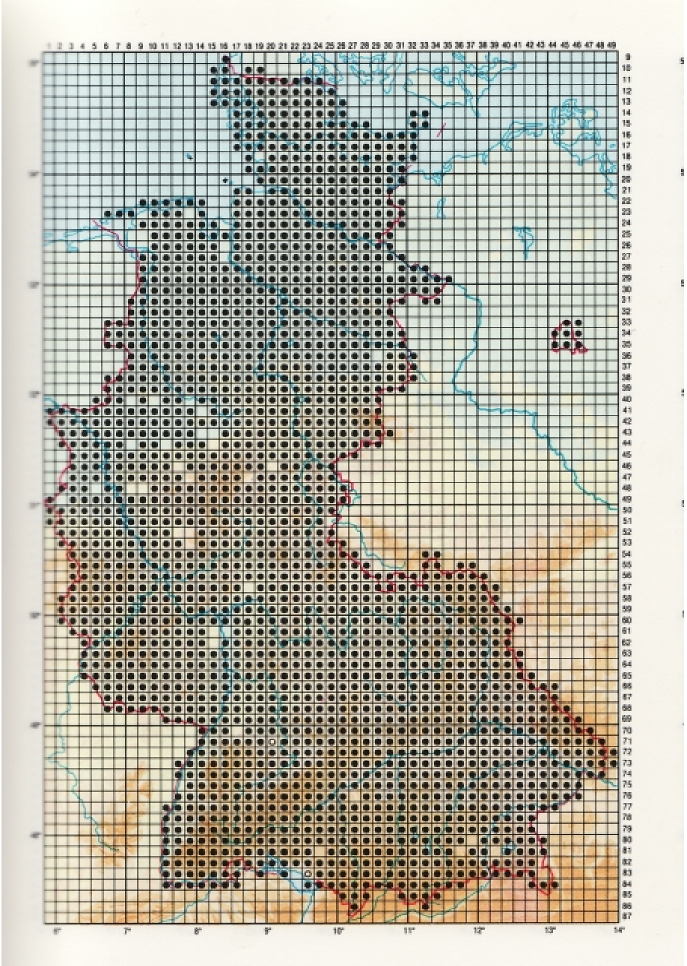


Figure 8: Distribution of *H. pilosella* in Germany (Haeupler et al. 1989)

Hieracium pilosella, the Mouse-ear Hawkweed is a clonal perennial Asteraceae typically forms a rosette of 3-25 leaves which are dull or dark green above and densely grey or white tomentose beneath (BISHOP & DAVY 1994). *H. pilosella* flowers from June to September and reproduces either vegetatively with stolons or sexually with wind dispersed seeds. Its yellow flowerheads develop on leafless 5-30 cm long shoots (ROTHMALER 2005, SCHMEIL-FITSCHEN 2006). The plants form a fine root system close to the soil surface with intense lateral growth and typically one thicker deep growing root of 30 to 40 cm length (WEIGELT 2001). It often occurs in short or sparse grassland vegetation on chalky or acidic soils as well as in maritime cliff communities (BISHOP & DAVY 1994). *H. pilosella* can be found in all areas of Germany.

Ellenberg numbers: Light: **7 Temperature**: - **Kontinental**: **3 F**: **4 Reaction**: - **N**: **2**

1.4 The Study Areas

The parametrization and validation data for the model simulations of this thesis were collected in Northern Bavaria (Franconia) at Eltersdorf (Latitude 49.5418, Longitude 10.9866; WGS 84) in the surroundings of the city of Erlangen and at the Büg natural reserve (Latitude 49.7485, Longitude 11.0530; WGS 84) near the city of Forchheim (see Fig. 10). This region consists mainly of pleistocenic inland sand dunes many of them afforested with pines (JENTSCH 2001). The climate can be described as temperate continental with moderately cold winters. Temperatures range from range 8-9 °C (annual average) with rainfall levels between 650 mm – 750 mm (annual average)(BÖGER 2007). The experiments for part 3 of this work were carried out in a 1.2m deep sandpit near the University of Bielefeld (Latitude: 52.0338 Longitude: 8.4954). The climate in Bielefeld is humid (slightly oceanic) with mean annual rainfall levels of 650-750 mm and temperature between 8 and 9 °C (annual average).

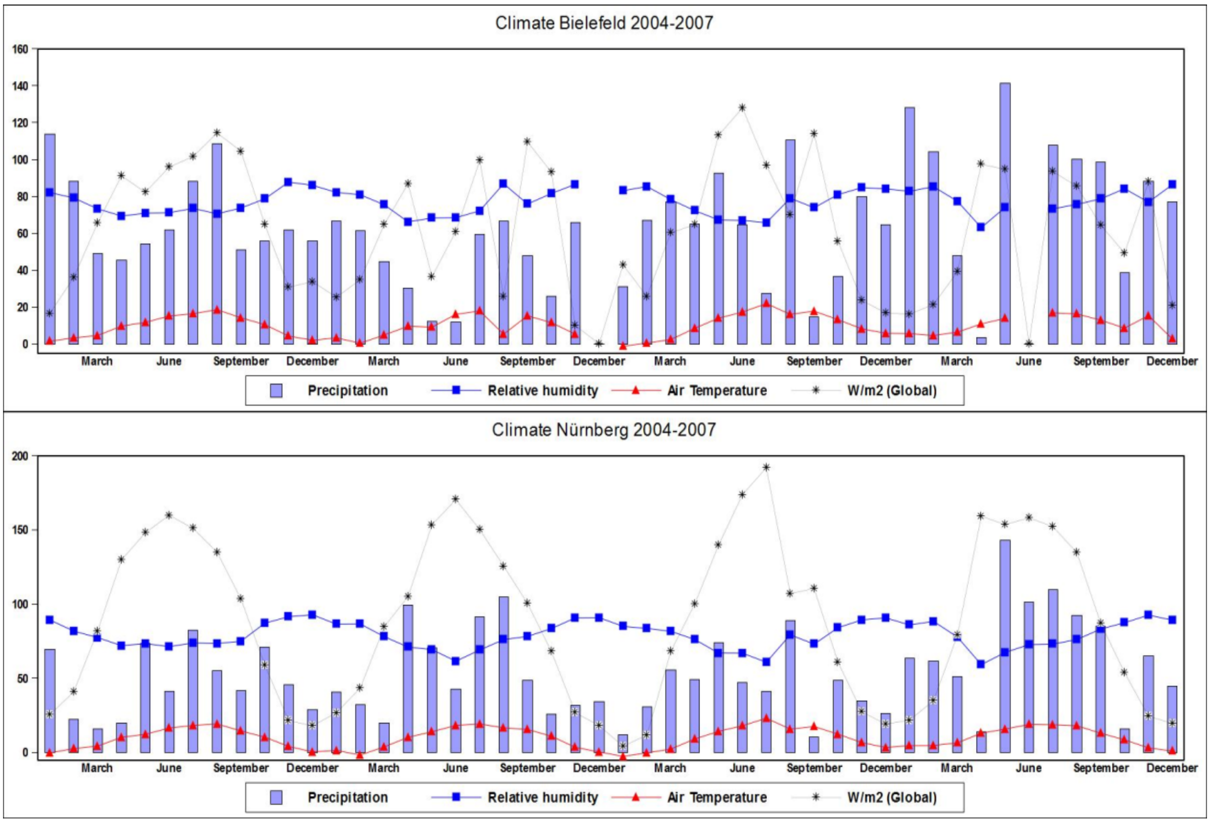


Figure 9: Climate of the two locations in Germany important for this work. Data shows the monthly mean. Data for Nürnberg from weather station Nürnberg-Buch. Data for Bielefeld from the weather station near the University of Bielefeld. Light measured with sensors for global radiation (W/m²).

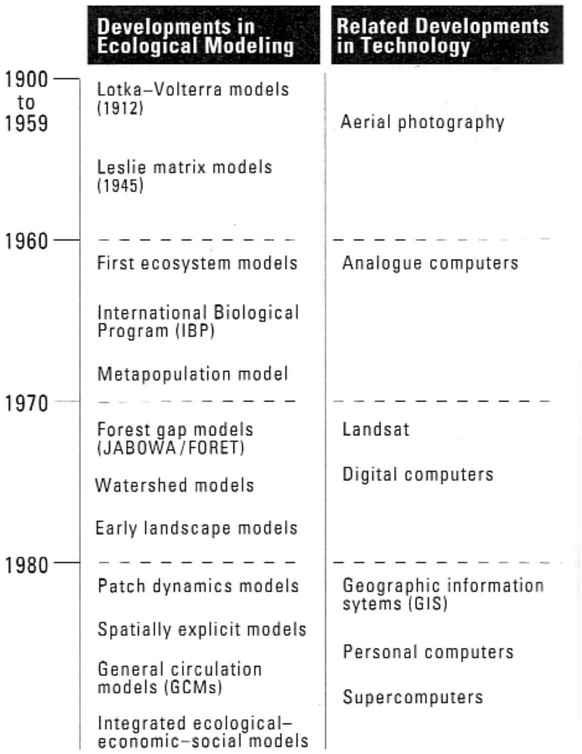
Figure 10: Locations in Germany (near Nuremberg) from which aerial and experimental data were obtained from.
Bottom-left: Büg (Latitude 49.7485, Longitude 11.0530; WGS 84)
Bottom-right: Elterdorf (Latitude 49.5418, Longitude 10.9866; WGS 84)
(image Copyright Microsoft Corporation)

1.5 Models in Ecology

Models are an important tool for the analysis of complex interactions in ecological systems. As stated by Jørgensen & Bendoricchio (2001) it is impossible to analyze all components and their reactions in an ecosystem without the use of models as a synthesis tool. Typically models are a simplified and abstract representation of a system or a process (TURNER et al. 2003). Most authors agree that we are simply not able to get the complete information of all processes within an ecological system. So models are necessary to simplify the reality and bring it into a manageable form for investigation (WISSEL 1989, GAYLER 1998). It is quite interesting that many people think that modeling in ecology is a trend of recent decades starting with the appearance of the first affordable and high-performance computers. However, scientists have always employed models in order analyze complex data as for instance statistical models to deal with the uncertainty of experimental data (Fig. 11).

It is commonly agreed upon, that models in ecology are in the first place useful to create and test scientific hypotheses by comparing real data with model results. Depending on the respective questions models can be either analytical or predictive and can serve as a virtual laboratory. They can reveal unmeasurable system properties and reveal long term dynamics which may be important under the aspect of changing environments. Furthermore they can also serve as integrators within and between disciplines (HAEFNER 1996, JØRGENSEN & BENDORICCHIO 2001, JELTSCH & MOLONEY 2002 WAINWRIGHT & MULLIGAN 2004).

As depicted in Fig. 12 a huge variety of model types has been developed during the last decades for the analysis of all kinds of ecological problems. In the following those of these models which are relevant for the present work, are described in more detail.



	Developments in Ecological Modeling	Related Developments in Technology
1900 to 1959	Lotka–Volterra models (1912) Leslie matrix models (1945)	Aerial photography
1960	First ecosystem models International Biological Program (IBP) Metapopulation model	Analogue computers
1970	Forest gap models (JABOWA/FORET) Watershed models Early landscape models	Landsat Digital computers
1980	Patch dynamics models Spatially explicit models General circulation models (GCMs) Integrated ecological–economic–social models	Geographic information sytems (GIS) Personal computers Supercomputers

Figure 11: History of model development in ecology (from Haefner 1996)

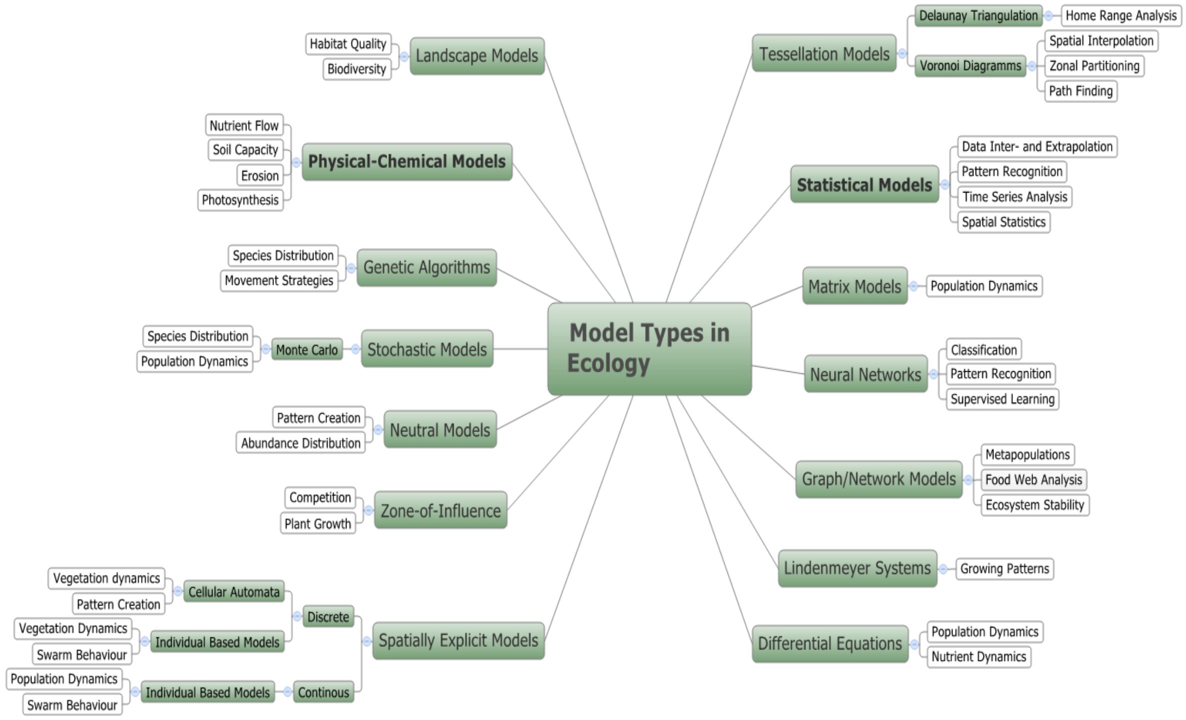


Figure 12: Overview of different popular model types and their use in ecology (more general types are marked bold)

Statistical models (in the context of ecological modeling) certainly belong to the classical type of models researchers successfully use all over the world. Univariate as well as multivariate statistical models are the basis to capture and filter important data from experimental results and to simplify complex interdependencies. As an example frequently used simple statistical models in ecological studies are regressions which allow to estimate parameter values and their standard errors from sample data (CRAWLEY 2007). They typically describe the dependency of one variable from one or many other variables. A linear regression, for example, can be used to to estimate the effect of soil moisture on the abundance of a species (LEYER & WESCHE 2007).

Another classical model type often used in ecology are differential equations. A differential equation is an equation in which beside one or many independent variables and one or many functions of them in addition the derivatives of this functions to the independent variables appear (BRONSTEIN et al. 2001). Differential equations are often used in ecology for mathematical descriptions of population dynamics, predator prey dynamics, ecotoxicological phenomena or nutrient dynamics (LOTKA 1998, JØRGENSEN & BENDORICCHIO 2001, MURRAY 2008). A disadvantage of differential equations in ecology is the generalizing character of this type of models. Ecological processes are often bound to individual properties, variable not fixed events and emergent phenomena, which often cannot be properly addressed by this type of models.

With the increasing availability of powerful digital computers the development of calculation intensive model types (which often produce results because of their emergent and random features whereas the creation of complex patterns is caused by the interaction and interdependence of parts of the system) became possible. In such models patterns and outputs are often caused by self organization similar as in nature ants, termite, bees or even fungal colonies (CAMAZINE 2003). Popular examples for these models are spatially explicit simulation models like grid based models. In a grid based model the modeled area of an ecosystem is divided into a grid of squares in which each square can adopt a (before defined) possible ecological state. In fixed timesteps at each progress rules are applied for changes of the ecological states (WISSEL 2000).

A special case of grid based models are Cellular Automata. Cellular Automata were first developed by John Conway (GARDNER 1970) and later more in detail described by Stephen

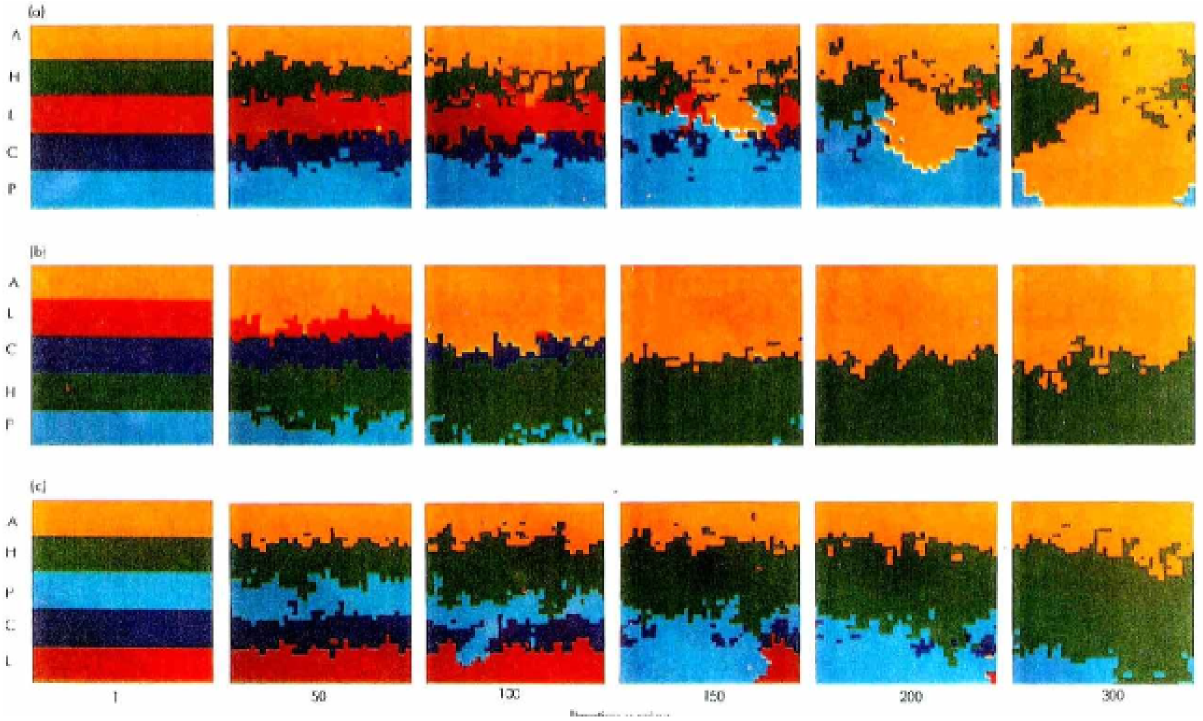


Figure 13: Initial arrangement of Agrostis (yellow), Holcus (green), Lolium (red), Cynosurus (dark blue) and Poa (light blue) in the aggregated model and species' distributions at iterations 1, 50, 100, 150, 200, 300; (a) Agrostis, Holcus, Lolium, Cynosurus, Poa; (b) Agostis, Lolium, Cynosurus, Holcus, Poa; (c) Agrostis, Holcus, Poa, Cynosurus, Lolium (Silvertown et al.1992).

Wolfram (WOLFRAM 1984, WOLFRAM 1986, WOLFRAM 2002). They reveal interesting emergent behaviors and patterns very similar to those which can be found in nature (RIETMAN 1989, GERHARDT & SCHUSTER 1995, WEIMAR 2003, DEUTSCH & DORMANN 2005). Spatially explicit models have been frequently used in ecological research to explore spatio-temporal phenomena within and between populations (Fig. 13; e.g. SILVERTOWN et al. 1992, BALZTER 1998, WINKLER & STÖCKLIN 2002).

The steadily increasing computing power during the last decades made it possible to develop even more complex spatially explicit models, like the so called "individual based models (IBM)" which separately calculate the behaviour of each individual of a population. A popular IBM model is the "Swarm" model, calculating, like the title of the model suggests, the behavior of a swarm. In the implementation of a swarm model the realistic behaviour of a swarm is created by the application of a few rather simple rules for each individual and the effect of self organization (GRIMM & RAILSBACK 2005, REYNOLDS 1987). UCHMANSKI & GRIMM (1996) formulated four criteria which define an IBM: The degree to which the lifecycle is reflected in a model, whether or not the dynamics of resource used by individuals are explicitly represented, whether real or integer numbers are used to represent the size of a population and the extent to which variability among individuals of the same age is considered. Because of the much more realistic implementation and interaction of individual attributes, IBM's became particularly popular in ecological research. Additionally they are easier to understand for scientist with less mathematical knowledge, comprehensible and typically the applied assumptions and rules can be experimental verified (POETHKE 1994).

Similar as cellular automaton models, IBM models are often used to for the analysis of vegetation dynamics (DEUTSCHMAN et al. 1997, SMITH et al. 2001, PICARD & FRANC 2001, SATO et al. 2007, WALLENTIN et al. 2008). This model type is also used in the present work for the analysis of vegetation dynamics of dry acidic grasslands.

Frequently models of a certain type incorporate models of another type (e.g an IBM can contain several statistical models for certain calculations).

1.6 How to Create a Model

Several steps have to be considered in order to create and validate a model (Fig. 15). Detailed descriptions of the modeling process can be found in the ecological modeling literature (e.g. JØRGENSEN & BENDORICCHIO 2001, TURNER & GARDENER 2003, WAINWRIGHT & MULLIGAN 2004, HAEFNER 2005, GRIMM & RAILSBECK 2005).

Most of the authors agree that at the beginning of a modeling process specific questions and hypotheses should be formulated, which a model could help to answer or test. For ecological processes it should be clear which scales should be considered (e.g.: individual scale, community scale see also Fig. 14; WIENS 1989) and which model type seems to be appropriate. In the next step all relevant factors need to be gathered (e.g. experimental results, literature data) in order to identify relevant deterministic, non-deterministic processes, variables and interdependencies. At this step several authors suggest to visualize these factors in a conceptual diagram (e.g. JØRGENSEN & BENDORICCHIO 2001). These diagrams should help to visualize components and their inhibitory or facilitative effects on parts of the modeled system. The next step is the formulation process where the gathered information and insights need to be mathematically or syntactically expressed and translated into an appropriate computer programming language. For many tasks an easy to learn interpreted language may be sufficient. For more complex structured models the newly developed computer program needs to be tested an debugged to make sure that all information is

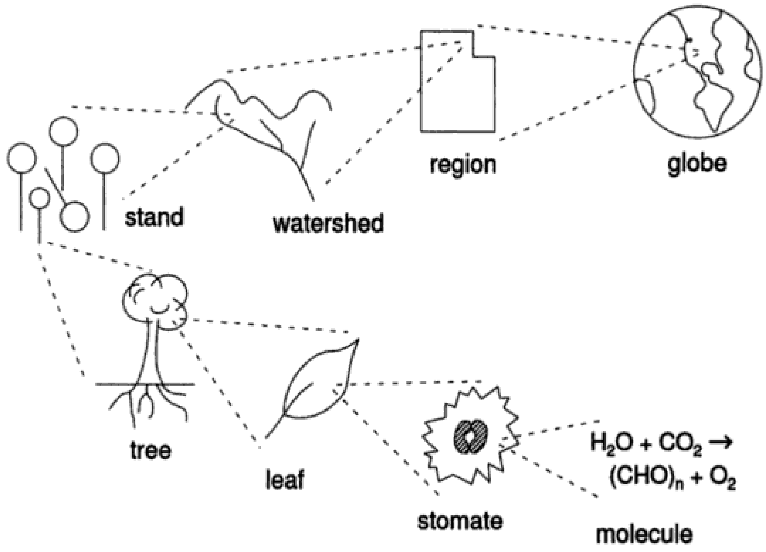


Figure 14: Scales in ecology (from Haefner 2005)

correctly implementated and the code is error free.

Now the model must be validated i.e. the model output has to be compared with measured data in order to proof the reliability of the model results. Frequently this will lead to program changes (mostly implementation of additional information). The next step of the modeling process is the sensitivity analysis where selected parameters are systematically varied to evaluate their impact on the model results (SALTELLI et al. 2000) as well as to systematically analyze the (sometimes) huge combinational space of parameters and to identify critical thresholds.

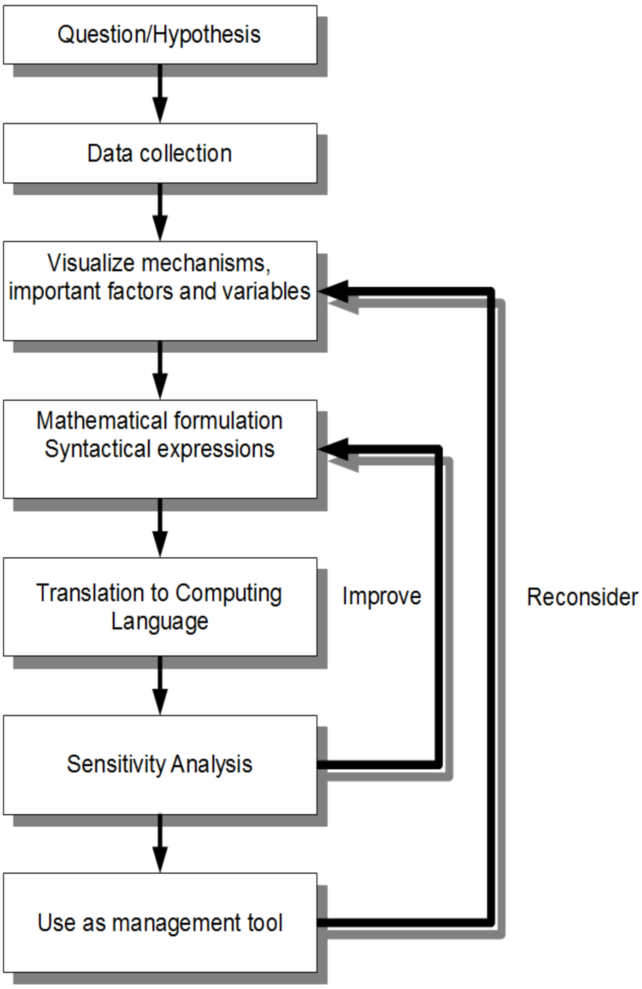


Figure 15: Simplified flowchart of a modeling process.

After successful validation and sensitivity analysis the model can be used to answer the questions and to test the hypotheses. Typically, the application of a model reveals various possibilities for improvements (e.g. removal of redundant parameters).

1.7 Beyond Population Data: Analysis of Spatial and Geometrical data

Besides species lists and classical population analysis, the assessment of spatial and geometrical data adds a new dimension to vegetation analysis, being a necessary precondition for the analysis of all spatio-temporal phenomena and the development of spatially explicit models.

The following section of this chapter provides an overview of established spatial and geometrical analysis methods and their usefulness for ecological problems and ecological modeling. Furthermore some useful summary statistics will be presented to use these methods for modeling and summarizing of plant patterns.

1.7.1 Point Pattern Analysis

A spatial point pattern is defined as locations which are irregularly distributed within a designated region and are presumed to have been generated by some form of stochastic mechanism (CRESSIE 1993, DIGGLE 2003). A simple form of Point Pattern Analysis could for instance be a nearest neighbor analysis of plants assess the nearest neighbor competing for resources.

In ecology Point Pattern Analysis are often used to quantitatively describe spatial distributions of individuals (and their causes). In multispecies systems such distribution patterns can reveal valuable informations on potential competitive interactions (BADDELEY & TURNER 2005, BIVAND et al. 2008). A popular example for a Point Pattern Analysis is Ripley's K method (Fig. 16) , a second-order analysis of point patterns in a two-dimensional space in order to detect if point patterns are clustered, follow a homogeneous Poisson process or are regularly spaced (RIPLEY 1976).

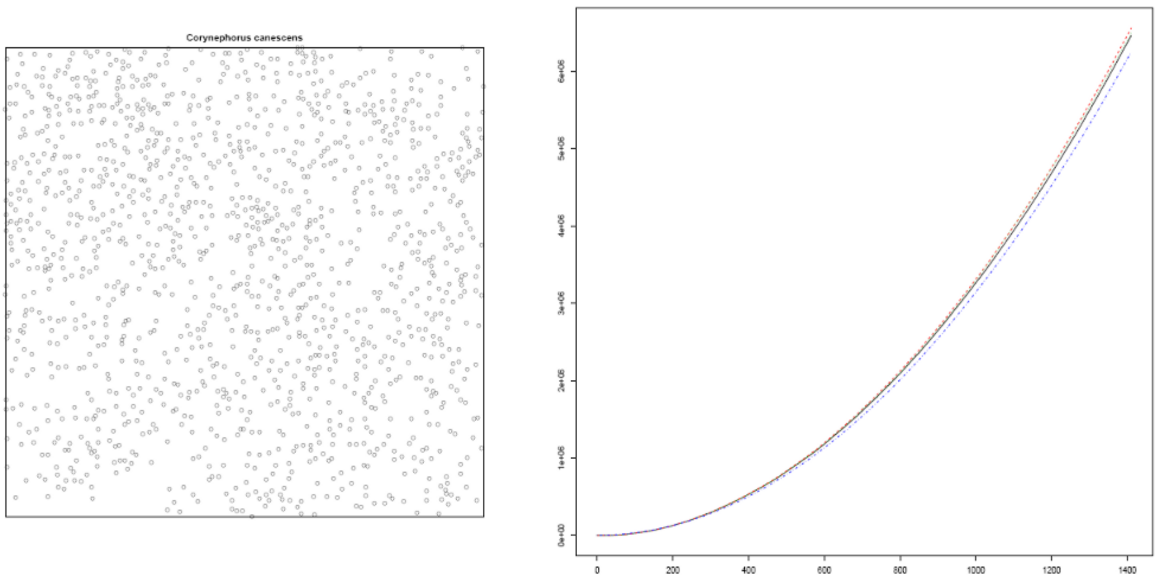


Figure 16: Ripley's K analysis for 1362 locations of *Corynephorus canescens* growing side by side with the moos *Polytrichum piliferum* in Eltersdorf indicating Complete Spatial Randomness (CSR). The points in the graph on the left side are the *C. canescens* location. The graph on the right side shows two dotted lines which indicate CSR within a certain radius (y-axis). The continous line represents the result from the analysis. A line above the dashed lines would indicate aggregation whereas a line below would indicate a more regular pattern.

1.7.2 Morphometrics

Morphometric analysis is the study of shape and size variations and covariations between individuals and their covariations with other variables for a better understanding of the diverse causes of variation and morphological transformations (DRYDEN & MARDIA 1998, ZELDITCH et al. 2004, CLAUDE 2008). Typical examples of morphometrics are the statistical analysis of outlines with the Fourier analysis or the geometrical analysis of shapes based on the configuration of landmarks.

Up to now, morphometrics have rarely been used in connection with vegetation analysis, however, there is quite a potential as the automatic identification species specific outlines of plants individuals providing information of the species composition or the detection and quantification of typical growing patterns (e.g of clonal plants or mosses) moss species. These techniques are particularly valuable for the validation of spatially explicit simulation models.

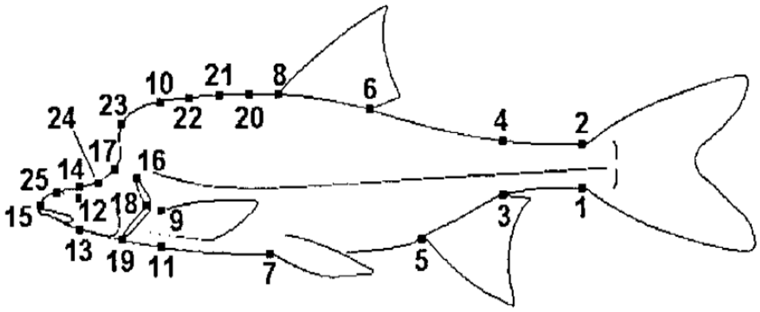
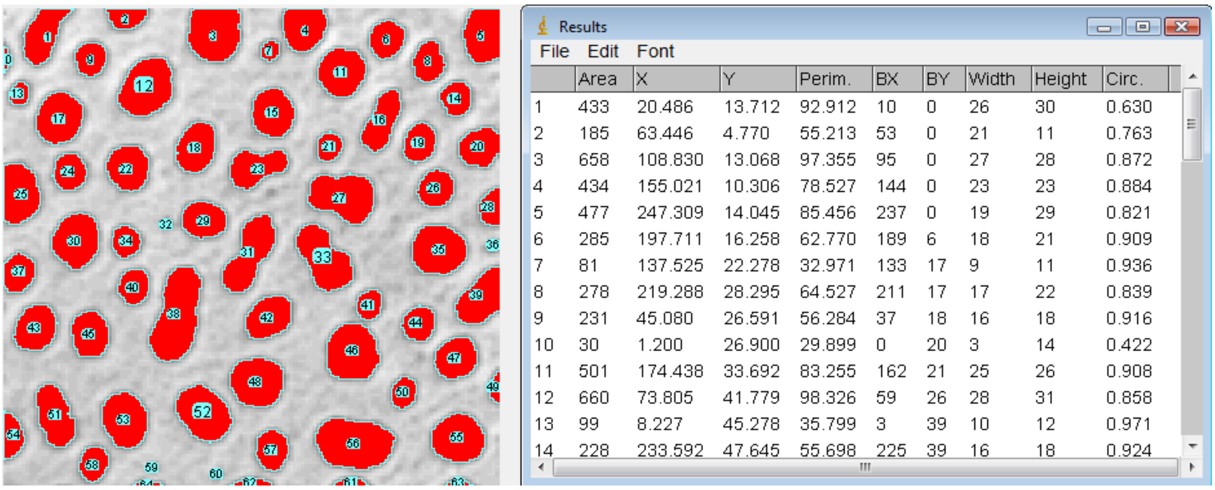


Figure 17: Landmarks from a fish to differentiate Gila (*Cyprinidae*) species (after Douglas et al. 2001)

1.7.3 Geometric Features of Images

This technique certainly belongs to the classical analysis techniques of binary images (BURGER & BURGE 2007). The measurements are quite similar to the measurements of landscape metrics and morphometrics but employ sometimes different algorithms to measure morphological and geometrical features of regions (e.g. cells, leaves etc.). Typical examples are measurements of area, diameter, bounding box, perimeter, roundness of connected regions (Fig. 18). Such measurements are also suitable for the automatical analysis and summary of plant communities.



	Area	X	Y	Perim.	BX	BY	Width	Height	Circ.
1	433	20.486	13.712	92.912	10	0	26	30	0.630
2	185	63.446	4.770	55.213	53	0	21	11	0.763
3	658	108.830	13.068	97.355	95	0	27	28	0.872
4	434	155.021	10.306	78.527	144	0	23	23	0.884
5	477	247.309	14.045	85.456	237	0	19	29	0.821
6	285	197.711	16.258	62.770	189	6	18	21	0.909
7	81	137.525	22.278	32.971	133	17	9	11	0.936
8	278	219.288	28.295	64.527	211	17	17	22	0.839
9	231	45.080	26.591	56.284	37	18	16	18	0.916
10	30	1.200	26.900	29.899	0	20	3	14	0.422
11	501	174.438	33.692	83.255	162	21	25	26	0.908
12	660	73.805	41.779	98.326	59	26	28	31	0.858
13	99	8.227	45.278	35.799	3	39	10	12	0.971
14	228	233.592	47.645	55.698	225	39	16	18	0.924

Figure 18: Measurements of thresholded particles in an greyscale image (left). One row in the table of the right site represent a measurement of one identified particle (one connected region).

1.7.4 Geostatistics

Geostatistics are often used to interpolate spatial data and estimations of spatial averages from continuous spatially correlated data (KALUZNY et al. 1998, BIVAND et al. 2008). A very well known example is Kriging which uses a method of interpolation which predicts unknown values from data observed at known locations (NIELSEN & WENDROTH 2003).

Kriging uses a variogram for the prediction which provides a measure of spatial correlation by describing how sample data are related with distance and direction (KALUZNY et al. 1998) and then minimizes the error of predicted values. This interpolation method reveals trends which for instance predict future states or summarize general trends in spatial datasets.

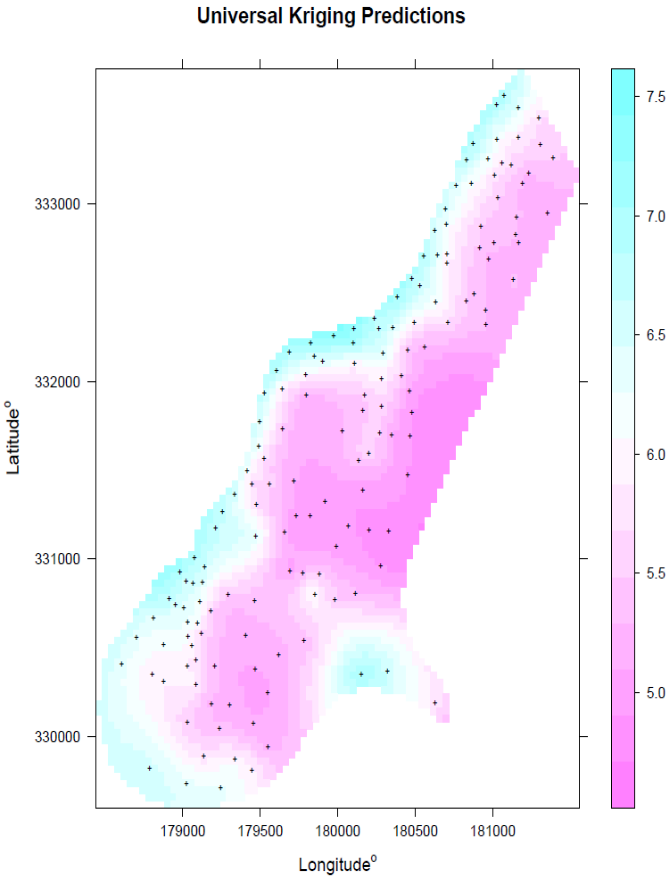


Figure 19: Kriging example (Pebesma 2004) for zinc measurement samples (log(ppm) - black crosses) and their predictions (coloured Quads) for unknown locations. The meuse data set used here as an example is a data set comprising of four heavy metals measured in the top soil in a food plain along the river Meuse (Netherlands; Lat: 50.9703 Lon: 5.7415 – WGS 84). The x,y axis reflecting the geographic locations (Latitude, Longitude - RDM Dutch topographical map coordinates) of the values. The scalebar on the right side of the plot indicates concentrations from low (purple) to high values (green).

1.7.5 Fractal Analysis

Fractals are geometric shapes that can be split into parts, each of which is a reduced-size copy of the whole (MANDELBROT 1967, MANDELBROT 1982, PEITGEN et al. 2004). Fractals are often used to simulate and create landscapes (PEITGEN & BARNSLEY 1988) or create patterns of plants (PRUSINKIEWICZ & LINDENMAYER 1996). Analysis of fractality is a popular method to measure shape complexity and morphometric variability. In ecology Fractal Analysis has been used to analyze vegetation changes (LINARES et al. 2006) landscape complexity (MILNE 1992), forest patches (KRUMMEL et al. 1987) or to examine spider mite movements (DICKE & BURROUGH 1988).

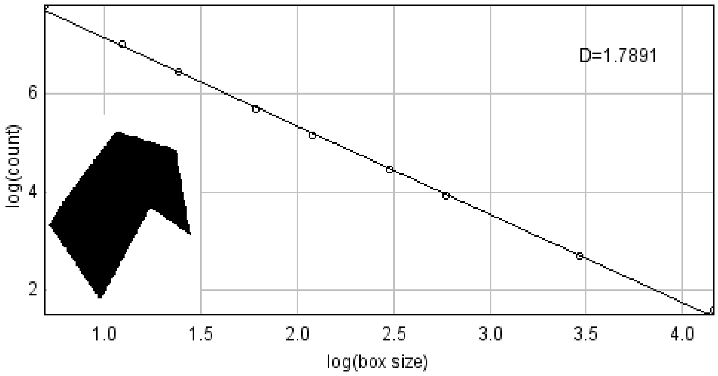


Figure 20: Fractal Dimension of a simple shape (D=1.7891)

1.7.6 Triangulations

A very popular form of triangulation is the Voronoi diagram which is frequently used to visualize spatial relationships between individuals.

They can be constructed geometrically by constructing perpendicular lines from the center of connecting lines between a central point (e.g. plant location) and surrounding points (e.g. competing plants). The closest intersection points from the perpendicular lines forming a Voronoi-Polygon. Given a finite set of distinct, isolated points within a continuous space, all locations within that space are associated with the closest member of the point set. The result is the partitioning of the space into a set of regions. (OKABE et al. 2000). Voronoi diagrams are also used in pattern recognition and path finding routines as well as in Geographical Information Systems (GIS) to interpolate spatial data (NETELER & MITASOVA 2008). In ecology Voronoi diagrams have been used for instance to model forest dynamics and the local competition between trees (MERCIER 1997), to analyze bark beetle attack patterns (BYERS 1992) or to reveal forest age classes (NELSON et al. 2004). Voronoi areas are a good indicator for spatial interactions of individuals (KENKEL 1990, SLETVOLD & HESTMARK 1999, KRISTENSEN et al. 2006). Directly associated to Voronoi diagrams are the so called "Delauney triangulations" which triangulate a set of points. The Delauney triangles are constructed with an method that ensures that the circle circumscribing the points of a triangle contains (within) no points of another triangle. In ecological research they are for instance used to approximate a network of travel paths from a set of animal point locations (DOWNS & HORNER 2007).

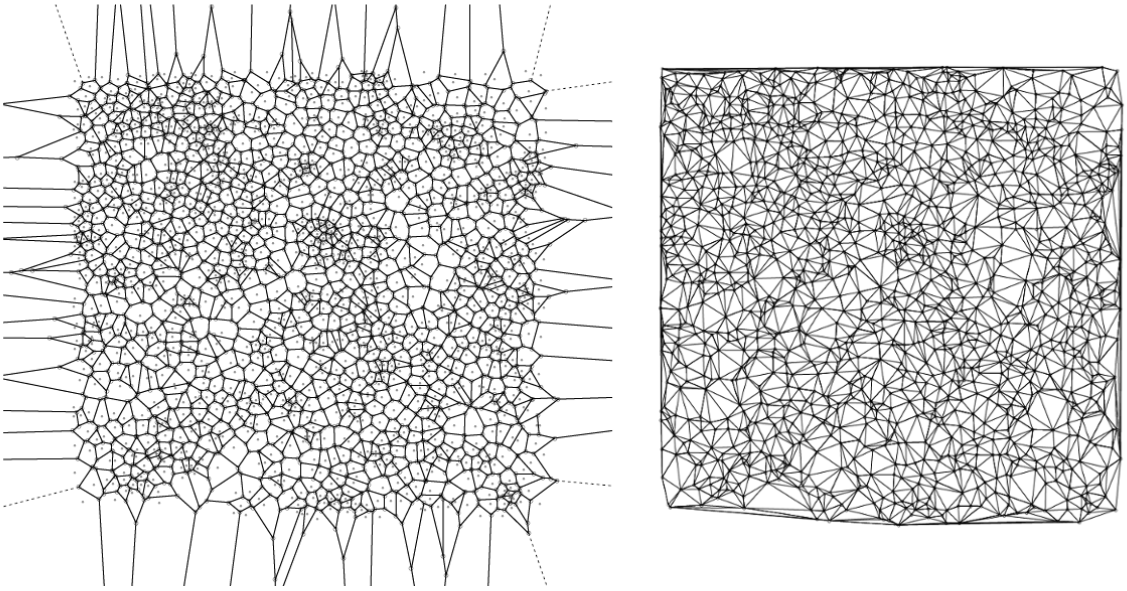


Figure 21: Voronoi diagramm (left) and Delauney triangulation (right) of 1362 locations of *C. canescens* in the Büg. In the left illustration the plant locations building the center (indicated as points) of each polygon. In the right illustration the plant locations are the vertices of the triangles.

1.7.7 Landscape Metrics

Landscape metrics were developed to analyse landscape patterns and to explain spatio-temporal structural changes of different landscapes (TURNER 1989, WIENS et al. 1993, GUSTAFSON 1998, GERGEL & TURNER 2002, TURNER et al. 2003, TURNER 2005). Landscape metrics are defined as algorithms that quantify specific spatial characteristics of patches, classes of patches, or entire landscape mosaics (MCGARIGAL et al. 2002). A patch generally is a landscape component respectively a connected region belonging to one class (e.g open sand). After MCGARIGAL et al. (2002) typical metrics of this kind fall into two categories: those that quantify the composition of the map without reference to spatial attributes (Tab. 1), and those that reflect the spatial configuration of the map (Tab. 2), requiring spatial information for their calculation.

Tabelle 1: Measurements of composition

Composition
Proportional Abundance of each Class The proportion of each class in an entire map.
Richness The number of different patch types.
Eveness Describes the relative abundance of different patch types.
Diversity Diversity is a composite measure of richness and evenness and the computation form varies (e.g. Shannon's and Simpson's diversity indices. Diversity indices can be used to assess the diversity of any population (patch types) in which each member belongs to a unique species (patch).

Tabelle 2: Measurements of spatial configuration

Spatial configuration
Patch size distribution and density Patch size describes the area of a patch whereas the Patch size distribution are summary statistics of this measurment (e.g. mean, median, max, variance, etc.). Patch density is the number of patches per unit area.
Patch shape complexity A general measurement to describe the geometry of a patch (e.g. perimeter-to-area ratio, fractal dimension).
Core Area Describes the area of a patch inside of a buffer zone (e.g after substracting an ecotone or riparian zone).

Isolation/Proximity A general measurement for the distance to other patches of the same class.
Contrast Describes relative differences among patch types.
Dispersion Describes if a patch is regularly or contagiously distributed.
Contagion & Interspersion A relative measurement to analyze whether patch types are spatially aggregated.
Subdivision Describes the general degree to which a patch type is broken up (e.g. fragments).
Connectivity Describes the functional connections among patches.

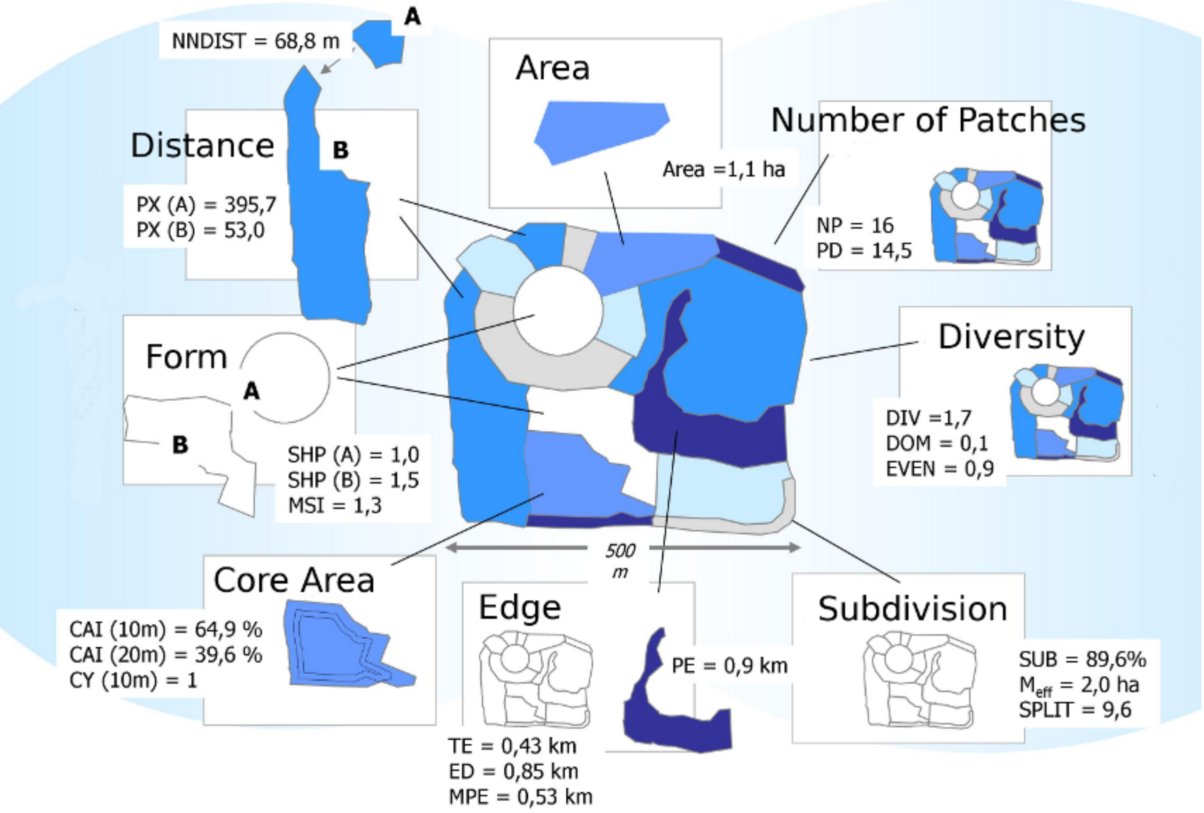


Figure 22: Different landscape metrics for the description of composition and spatial configuration. (Figure from Blaschke, Lang 2007)

Most of these metrics are part of the software package called Fragstats, a computer program designed to compute a wide variety of landscape metrics for categorical map patterns (MCGARIGAL et al. 2002) offering a huge amount (>100) of possible metrics. Since so many landscape metrics are available the question arises which metrics should be used for a specific analysis. Riitters et al. (1995) analyzed some common metrics with a Principal Component Analysis and found out that depending of the type of analysis, often only a few metrics are needed to sufficiently analyze certain landscape patterns.

Since landscape metrics are able to analyze discrete patterns they can also be useful to validate spatially discrete simulation models and to statistically summarize simulated patterns and compare them to real patterns. In this thesis these metrics were used to validate a discrete spatial simulation model with measured data. For the comparison of calculated vs. measured data a statistical method (cluster analysis) was used which is appropriate to extract and arrange spatial data. In the following section some methods beside the cluster analysis are presented, which are useful to analyse spatial data collected from the metrics we introduced in this section.

1.7.8 Summary Results and Classification of Data

In the first place a summary statistic from collected metrics can help to summarize metrics collected from a simulation model and compare them with real spatial data.

If only a few parameters are of importance for the comparison univariate statistical methods (e.g. t-test, ANOVA) are useful and sufficient. However in patterns of ecological systems

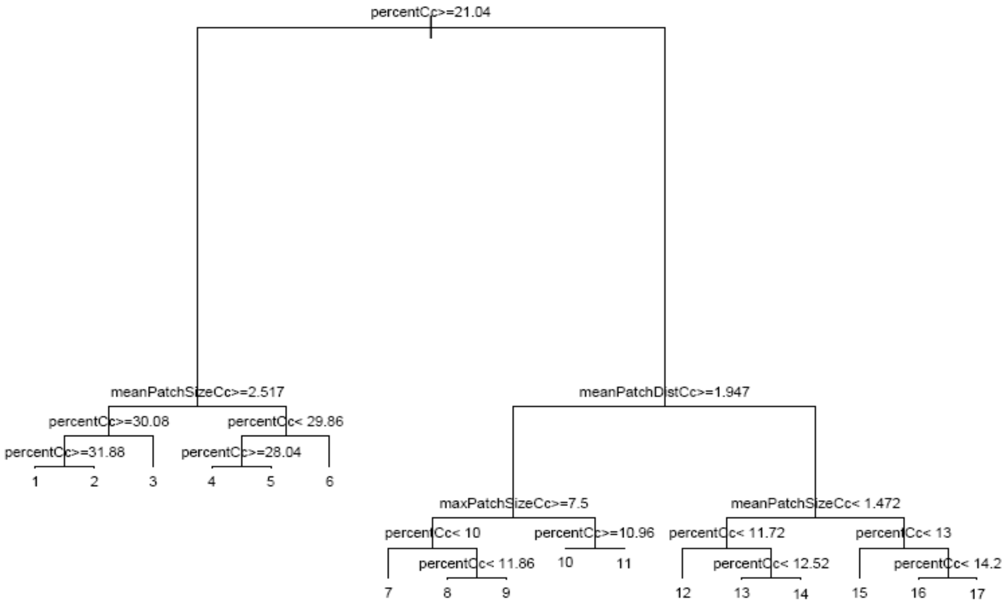


Figure 23: Regression tree result from 17 *C. canescens* patterns (rpart). Patterns can be predicted from classification result.

often more than one attribute has to be analyzed for a comparison. Appropriate for this are multivariate analysis techniques which concern datasets that have more than one response variable for each observational or experimental unit (VENABLES & RIPLEY 2002).

After Venables & Ripley (2002) the main difference in multivariate methods is between those methods that assume a given structure (dividing cases into groups) and those that seek to discover structure from the evidence of the data matrix alone (data mining). They also quote, that in the terminology of pattern recognition there is a difference between supervised and unsupervised methods.

Supervised methods are for example classification and regression trees (CARTs - BREIMANN 1993), Neural networks (see RIPLEY 1996) and Support Vector Machines. CARTs, for example, subdivide the space spanned by the predictor variables into regions for which the values of the response variable are approximately equal, and then estimate the response variable by a constant in each of these regions. In classification trees the dependent variable is categorical, in regression trees it is quantitative. (MOISEN & FRESCINO 2002). CARTs can be useful in analysis to predict unknown patterns out of known spatial data i.e. for example to collect those results (bound to selected parameters) of model simulations which are similar to the patterns found in nature. As example, Fig. 23 shows a regression tree for certain *C. canescens* patterns.
Such classification results can be used to predict unknown patterns (a predict functions generates the probability of one observation belonging to any given group).

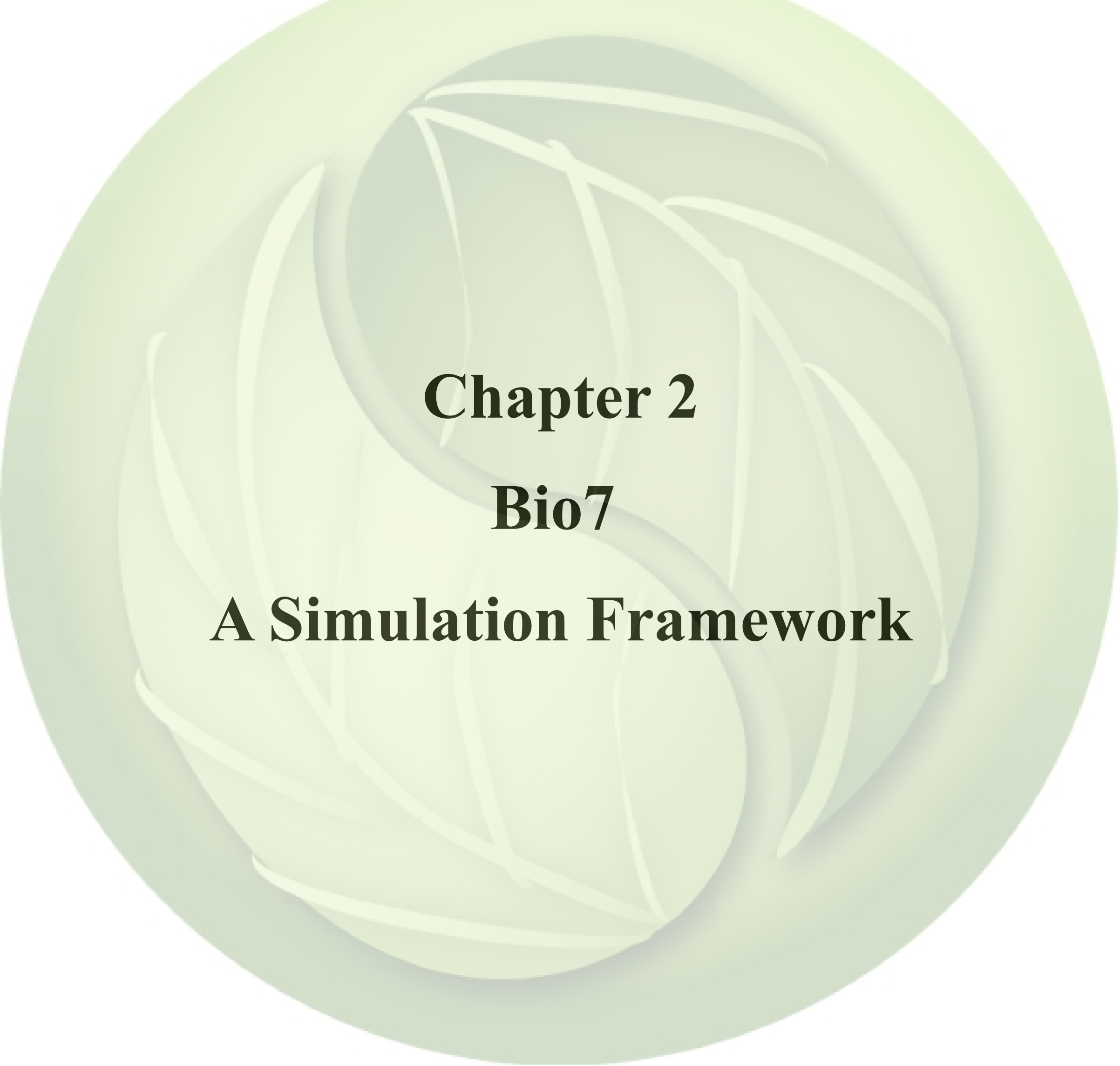
Typical unsupervised methods are cluster analysis, partitioning methods like K-means and factor analysis like the PCA (Principal Component Analysis). A cluster analysis which was particularly important for this thesis (see chapter 3) is a method which discovers groupings among the cases of a n by p matrix.
A cluster analysis can be divided in agglomerative hierarchical methods, optimal partitioning methods and divisive hierarchical methods (HANDL 2002, VENABLES & RIPLEY 2002). For the agglomerative hierarchical methods measures of distances (e.g. Euclidean, Manhatten, Mahalanobis, Hamming distances) are used for measurements of similarity which can be agglomerated with different algorithms (e.g. Single-Linkage, Complete Linkage, Average-

Linkage, Minimum-variance). The minimum-variance (Wards-method) algorithm uses an analysis of variance algorithm to evaluate the distances between clusters. In this thesis patterns of dry acidic grasslands were fusioned with this algorithm (see chapter 3).

Multivariate supervised and unsupervised techniques are presently used in GIS systems to cluster spectral image data in order to detect land use changes or patterns within landscapes (NETELER & MITASOVA 2008).

Generally, the described techniques become increasingly important for the validation of spatial explicit ecological models

There are more methods available in this area of spatial analysis, some of those come from Geographical Information Systems (BÖHNER et al. 2006, NETELER & MITASOVA 2008) others come from the general spatial analysis literature (KALUZNY et al. 1998, BIVAND et al. 2008) and maybe also very useful for summary statistics or multivariate analysis (e.g. analysis of Areal Data, Matrix correlations - e.g Mantel test, Spatial Autocorrelation).



Chapter 2

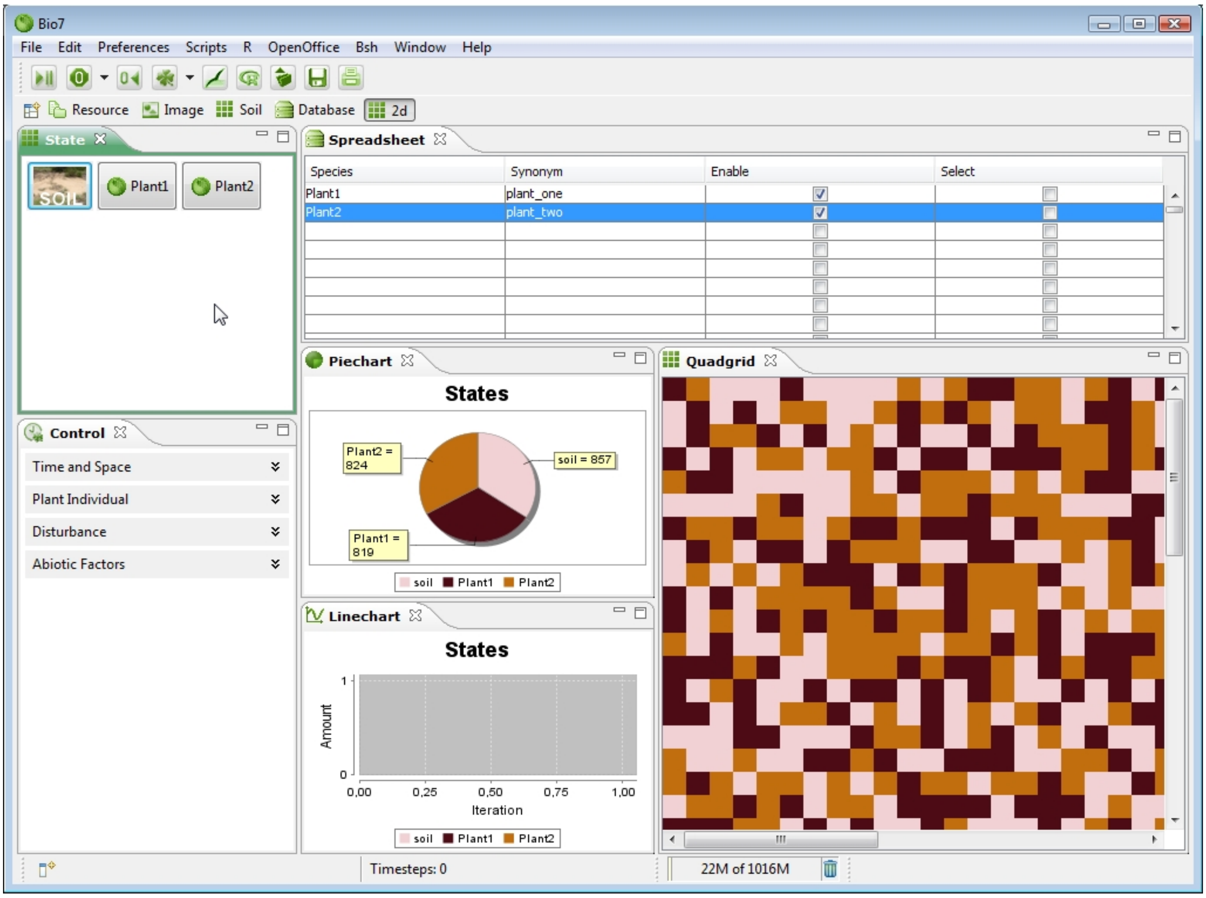
Bio7

A Simulation Framework

2. Bio7 – A Simulation Framework

Creating a model for evaluating a specific ecological problem is typically a time and resource consuming task because the development and testing of the simulation framework, i.e. before the ecological informations are implemented, is a major enterprise per se. Furthermore such frameworks are frequently not scalable i.e. they cannot be used for addressing other ecological problems. To overcome these difficulties and to ease up the general development of ecological models a general simulation framework was developed as part of this thesis, which reduces the developmental work of the scientist to the mere implementation of the particular ecological problem. The newly developed modeling environment, named Bio7 is particularly suitable for the analysis and simulation of spatio-temporal vegetation patterns.

Bio7 (Fig. 24) is an Integrated Development Environment (IDE) for ecological modeling based on a Rich Client platform (RCP) created with the powerful Open Source Java programming tool Eclipse. The RCP Platform is a framework which reuses existing Eclipse



Species	Synonym	Enable	Select
Plant1	plant_one	☑	☐
Plant2	plant_two	☑	☐
		☐	☐
		☐	☐
		☐	☐
		☐	☐
		☐	☐
		☐	☐

Figure 24: Screenshot of the Bio7 user interface

modules, GUI functionalities and libraries. It can be created inside of Eclipse. This platform was chosen because of its high extensibility and plugin structure profiting from its forward-looking modular design and the agile development community of Eclipse in the internet, which is continuously improving this platform and therefore the RCP basis framework. As described below, several powerful tools and panels for the visualization simulation and quantitative analysis of spatiotemporal ecological phenomena were integrated. Further popular applications for image analysis (ImageJ), statistical analysis ("R") and an interface to the "Calc" tool of OpenOffice for the exchange of data were included. Bio7 allows the interactive use of all these tools with their available plugins and thus provides a large variety of advanced analytical methods for the exploration of various ecological phenomena. Several editors for "R", Java and a scripting language (BeanShell) offer the possibility to easily create the code of complete simulation models. In addition an embedded flowchart editor for all created methods and analysis is available. In this special editor scripts can be compiled and interpreted in an ordered sequence which for instance can be used to easily run sensitivity analyses of a particular model or submodel. The main components of Bio7 are illustrated in Fig. 25.

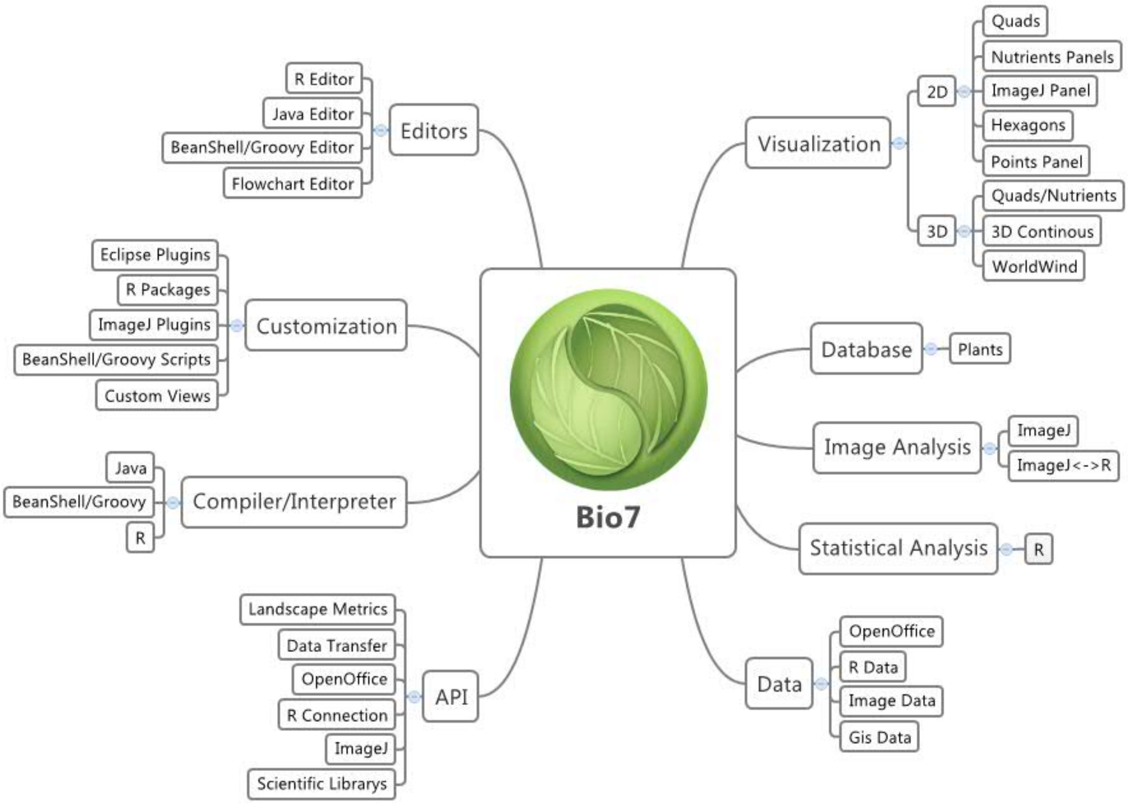
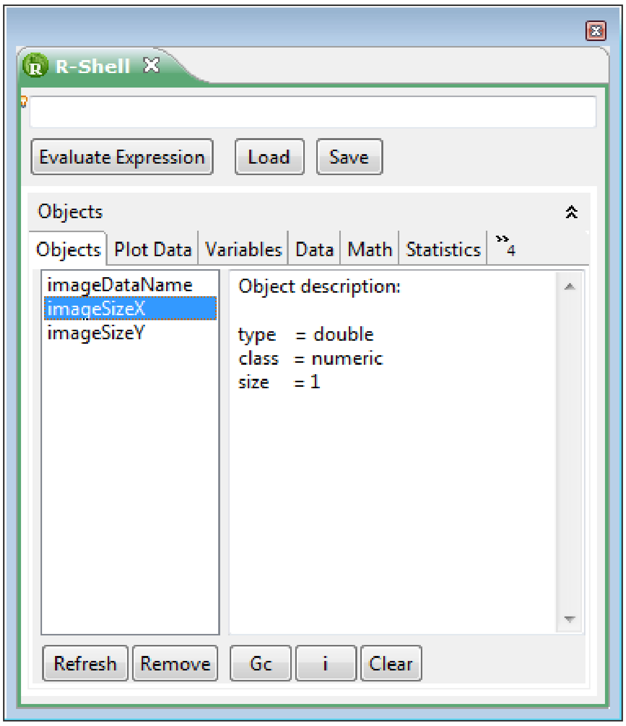


Figure 25: Components of the Bio7 application

2.1. Description of Important Components

2.1.1 Statistical Analysis in Bio7 with "R"

For statistical evaluation of model simulation results Bio7 has an interface to the powerful open source software package "R" together with Rserve, which in Bio7 acts as a local server application. "R" is becoming more and more popular as a tool for ecological modeling and the analysis of complex systems (PETZOLDT 2003, CRAWLEY 2007, PETZOLDT & RINKE 2007, BOLKER 2008, SOETAERT & HERMAN 2009). Rserve provides an interface which can be used by applications to perform computations in "R" (URBANEK 2003) and can be called directly from the programming language Java, the main programming language of Bio7. Because of the speed of this connection it is possible to execute "R" statistics out of a running Java model. Further it is also possible to create models in the "R" scripting language and visualize the results for instance within a Bio7 panel. Bio7 can also be used as a Graphical User Interface to "R" because it includes a full featured "R" script editor and a customized shell to execute "R" commands. "R" offers an enormous amount of valuable statistical methods for ecological analysis which can be installed as separate packages and then interactively be used with Bio7. In the present case special packages for spatial analysis, multivariate data analysis, time series analysis have been used for the modeling work described below.



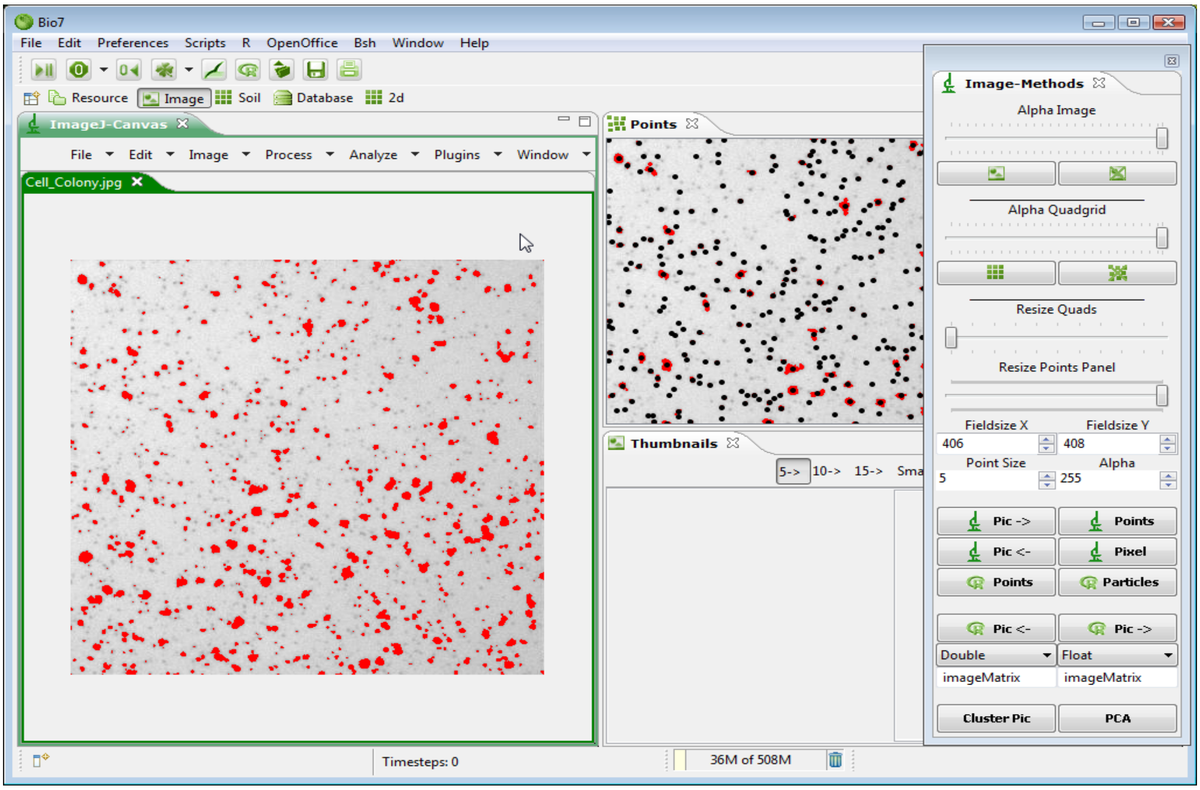
```
Object description:

type  = double
class  = numeric
size   = 1
```

Figure 26: Screenshot of the R-Shell of Bio7

2.1.2 Image Analysis

Bio7 is the first Integrated Development Environment which has fully integrated the open source image analysis tool ImageJ (RASBAND 1997-2009) into a Rich Client Platform.



Fieldsize X: 406
Fieldsize Y: 408
Point Size: 5
Alpha: 255
Timesteps: 0
36M of 508M

Figure 27: Spatial information of marked patters of an image (left side) are transferred as Points to the Points panel (right side - black points illustrated as an overlay)

Thus, ImageJ's sophisticated image analysis methods which can be compiled or interpreted with the integrated Java compiler or the embedded BeanShell script application are available within Bio7. As a scientific image analysis tool, ImageJ provides special methods for morphological measurements, fractal analysis, 3-dimensional analysis (stacks) etc. One of the reasons to implement this particular software into Bio7 was its ability to automatically measure areas of recognized objects (particles) and summarize them in a spreadsheet. Objects in this respect can also be plants which can be measured with its area, location and perimeter etc. useful for a spatial analysis which then can be done in "R". Optional this values can be used tor create spatial interpolations like Kriging, Voronoi diagrams or detect randomness or clumping with methods like Ripley's K for example. The same tools can be applied for a profound analysis of simulation model results calculated within Bio7. Closely associated with ImageJ is a specialized Points panel which allows to easily set points on a resizeable panel.

Points determined by a particle analysis can be transferred to this panel (see Fig. 27). Further points can be mapped on to a grid to simplify spatial information as a basis for a discrete simulation model.

2.1.3 "R" and ImageJ

Bio7 is one of the first applications which contains some special methods to transfer image data (as matrices or vectors) from ImageJ directly into "R". Vice versa vector or matrix data data created in "R" can be transferred back to ImageJ for the creation of images (e.g. Float, RGB, Greyscale). Beside this transfer available image data can be merged in clusters to identify similarities between different images. In the present work this was used to automatically compare measured and calculated vegetation distribution patterns (see Fig. 28). Another available method of image analysis is the Principal Component Analysis which offers the opportunity to preselect only important image information out of several image layers (for example for a cluster analysis).

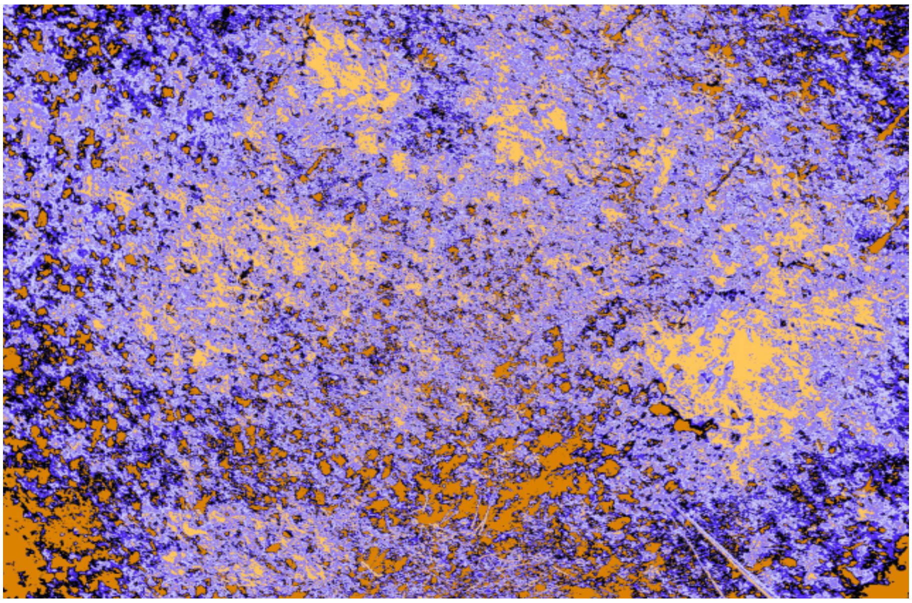
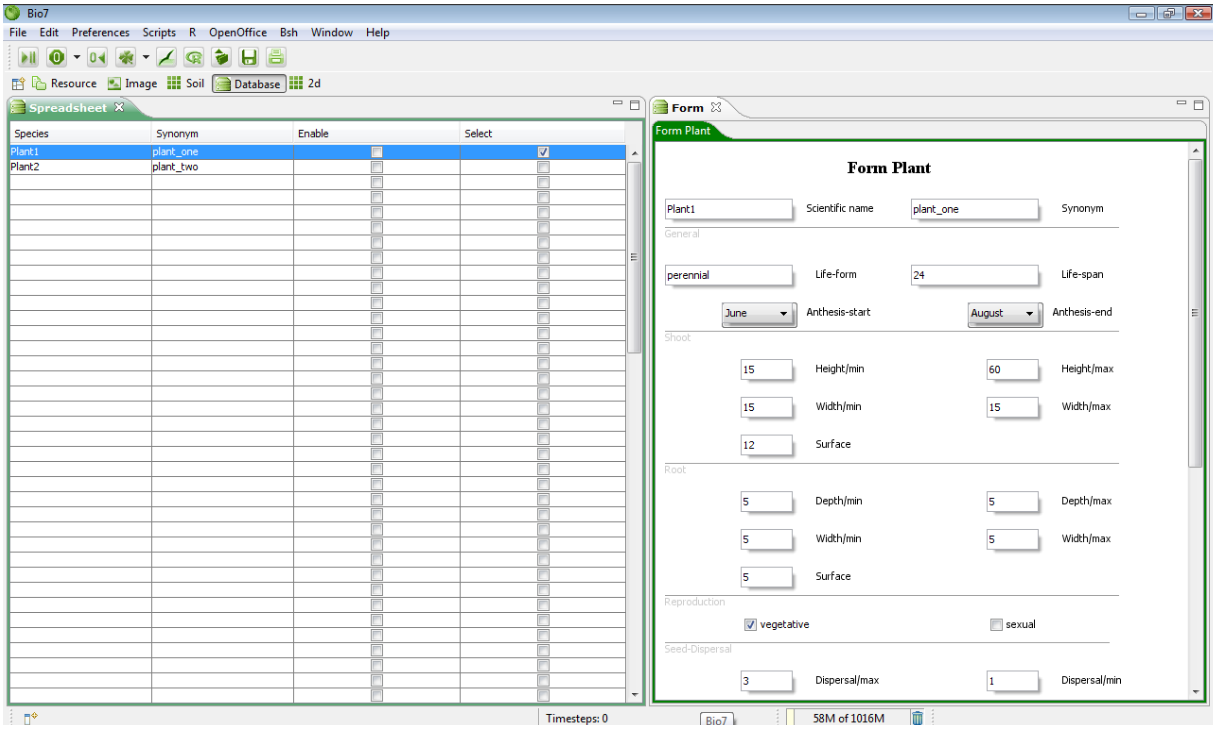


Figure 28: Clustering result of R, G, B image data from an aerial photograph of a Corynephoretum attached to 6 cluster regions. A cluster region in this image represents a vegetation type which could be clearly separated by it's unique R, G, B (spectral) color values. Yellow = sand, blue = moos, orange = *C. canescens*

2.1.4 Database

The integrated object oriented database "dbo4" in Bio7 stores the attributes of the plant objects (species or individuals) used for the model simulation. Information can easily be entered with the help of a questionnaire form which contains entry fields for all necessary attributes. The entire content of this database can be displayed as a spreadsheet from which plant objects can be selected to be used for the model simulations or for editing their attributes. If selected for modeling, plant objects are automatically entered and randomly distributed in a custom sized (e.g. 100*100) 2d-array as a starting pattern for a model run. The dbo4 database is also used for the storage of plant distribution patterns and their individual attributes. So particular patterns can be stored during model runs and can be restored for further analysis or as start configuration for new model runs.



Species	Synonym	Enable	Select
Plant1	plant_one	☐	☑
Plant2	plant_two	☐	☐

Form Plant

Plant1 Scientific name
plant_one Synonym

General

perennial Life-form
24 Life-span
June Anthesis-start
August Anthesis-end

Shoot

15 Height/min
60 Height/max
15 Width/min
15 Width/max
12 Surface

Root

5 Depth/min
5 Depth/max
5 Width/min
5 Width/max
5 Surface

Reproduction

☑ vegetative
☐ sexual

Seed-Dispersal

3 Dispersal/max
1 Dispersal/min

Figure 29: Screenshot of the database user interface of Bio7

2.1.5 Visualization Tools

Bio7 is particularly suitable for the creation of spatially explicit models. In ecological research such models are typically used to simplify spatial processes and patterns of interaction of individuals. This is achieved by mapping the precise spatial information into a grid and describing the interaction processes by particular rules. Above- and belowground distribution patterns of plant individuals and resources can be simultaneously visualized in several discrete panels (Fig. 30). Plant individuals can either be displayed as quads (Quadgrid panel) or optionally as hexagons (Hexagon panel). Plant species (or individuals) contained in the database can be activated for display in these panels from the database spreadsheet. The attributes of each single individual within the grids can be easily edited by simply clicking on it which will display the respective information from the database. Similarly, the belowground resource or root distribution patterns can be visualized and edited. In a special 3d panel (3Dgrid) both, above- and belowground patterns can be visualized together which allows for instance to explore the spatio-temporal interrelationships between resource and plant distributions.

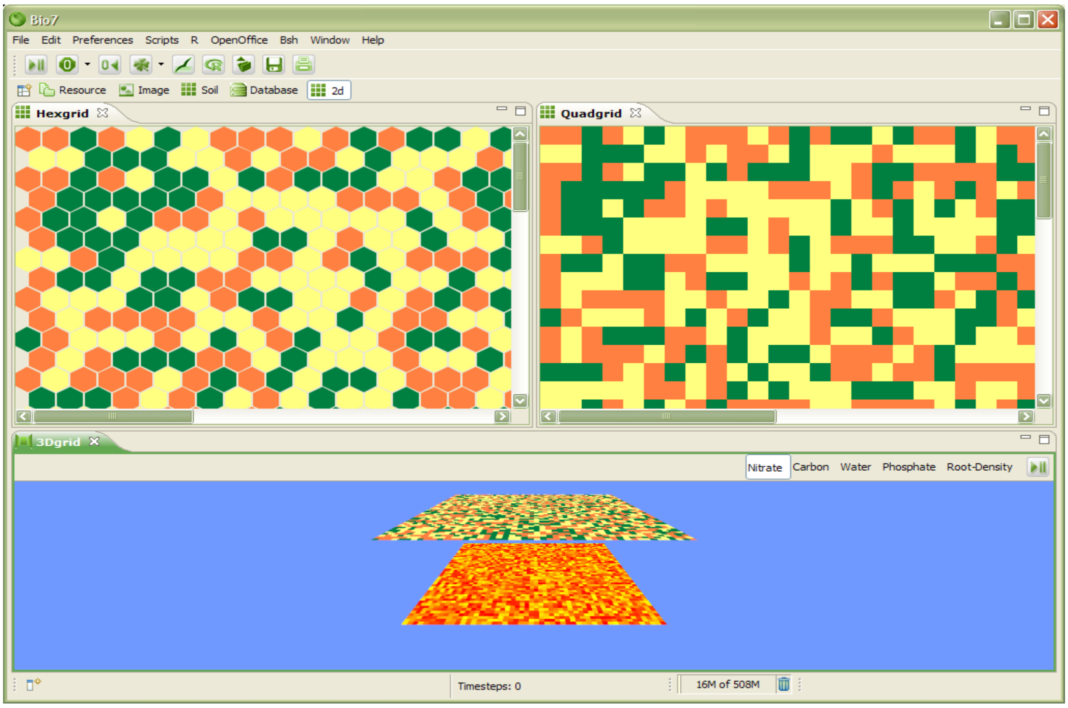
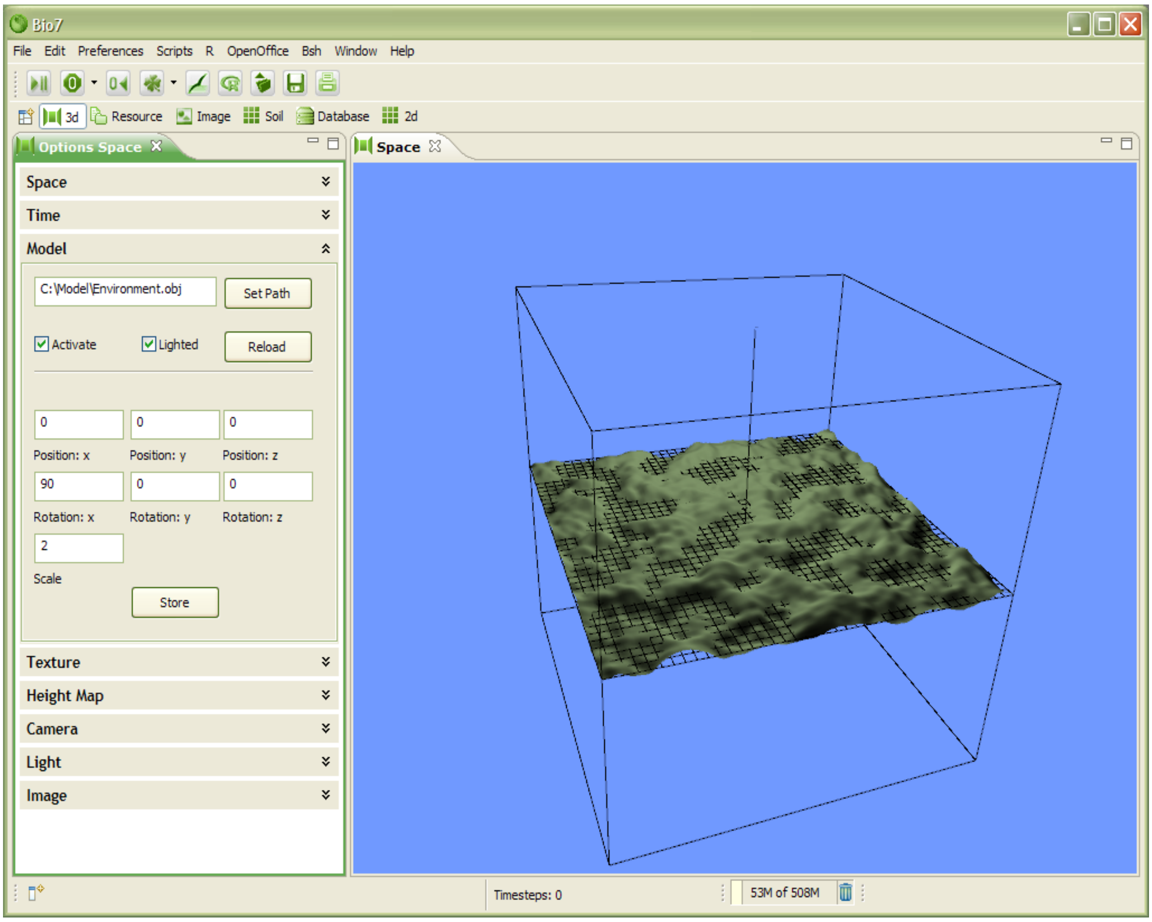


Figure 30: Visualization panels of Bio7: Top-left: Hexgrid panel; top-right: Quadgrid panel; bottom: 3Dgrid panel.

2.1.6 The Spatial Module

Another option to visualize models in Bio7 (which was not used for the present work) is an integrated spatial module. Spatial interactions are of great importance in ecological systems. Spatial models can easily be created in Bio7's spatial module with the embedded Java OpenGL ("JOGL") library's and the available default spatial environment. Several tools and a visualization panel are available to simulate and visualize spatial interaction problems. Using the Java editor of Bio7 simple or complex models can easily be created. Additionally, several specially developed methods and useful libraries are available to measure distances in 3d or to create physics inside a virtual 3d world. The integrated physics library for instance allows the development of soil erosion or seed dispersal models. An easy to use graphical interface (integrated in the Options 3d panel) allows loading of 3d environments and heightmaps for a realistic display of 3d data and supports timing, lightening and camera settings.



C:\Model\Environment.obj

☑ Activate ☑ Lighted

Position: x 0
Position: y 0
Position: z 0
Rotation: x 90
Rotation: y 0
Rotation: z 0
Scale 2

Timesteps: 0

53M of 508M

Figure 31: The 3d perspective which integrates an options panel ("Options Space" - left) to load 3d models, adjust lightening etc. and a visualization panel ("Space" - right) of 3d data. In this example an environment model (green) has been loaded with the help of the user interface into the application.

2.1.7 Virtual Globe

(This option was also not used for the present work.) For the analysis of spatiotemporal phenomena at larger scales (e.g. ecosystem, landscape) it is reasonable to georeference spatial data. This is generally achieved by using Geographical Information Systems. Bio7 is able to load such georeferenced data with the help of "R" and to visualize them as a 2d-plot, with ImageJ or as a 3d virtual globe. This globe is an implementation of the "NASA WorldWind Software Development Kit" (a special library written in Java which offers a complete 3d-globe visualization) and is embedded in a special routine of Bio7. An available options view allows the activation of several layers of georeferenced data from GIS packages. Such data can also be visualized dynamically with OpenGL for Java ("JOGL") commands which allows to run spatial simulations directly and georeferenced on the virtual WorldWind globe (see Fig. 33).

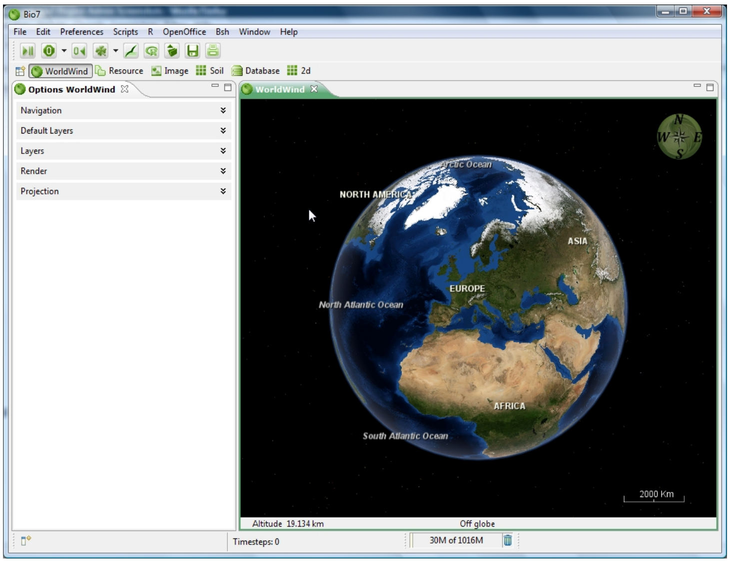


Figure 32: The WorldWind perspective of Bio7. In the "Options WorldWind" panel on the left side some functionalities (e.g. add a dynamic layer) can be controlled and activated.

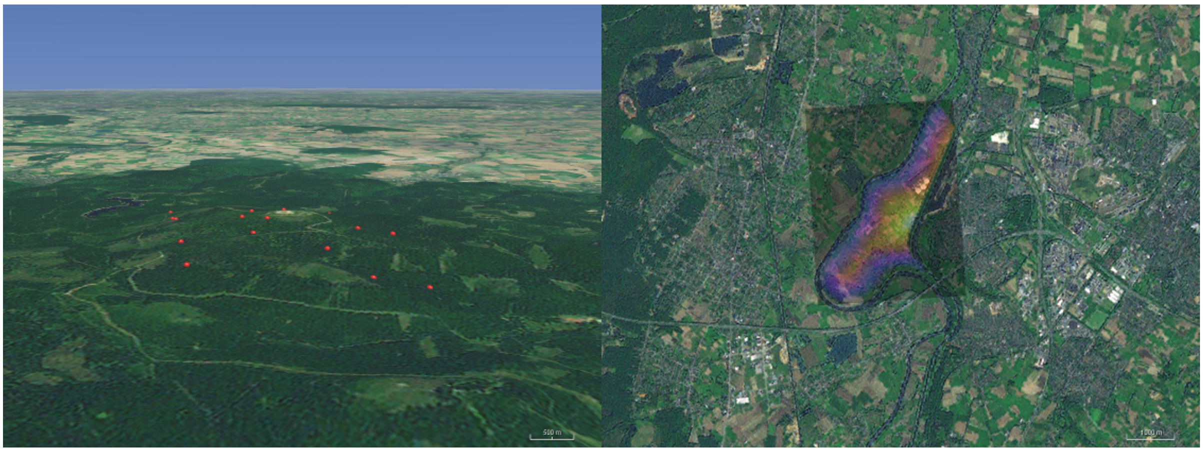
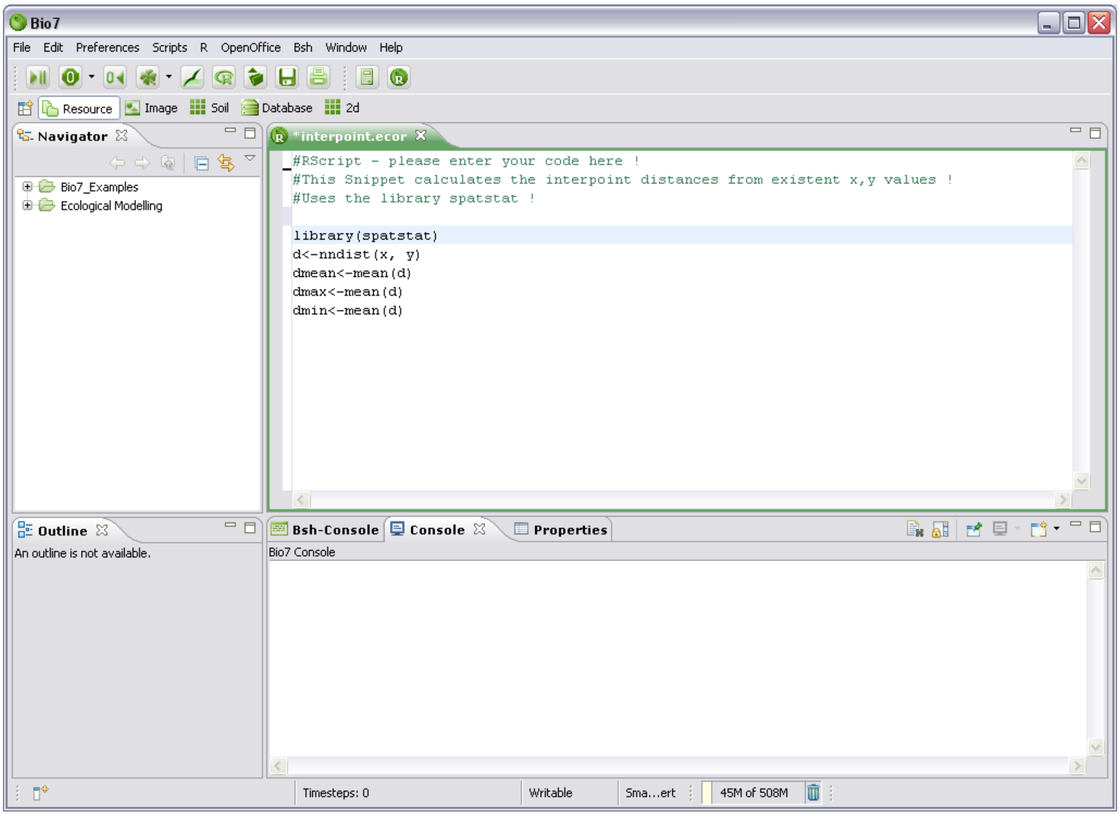


Figure 33: Left: Dynamic data visualized as spheres on the WorldWind globe; Right: Georeferenced data (Meuse data) from "R" and plotted with accurate coordinates on the globe. The meuse data set used here as an example is a data set comprising of four heavy metals measured in the top soil in a food plain along the river Meuse (Netherlands; Lat: 50.9703 Lon: 5.7415 – WGS 84).

2.1.8 Language Editors

The language editors of Bio7 assist the scientist in creating the programming code for his ecological models by offering several editing tools (syntax highlightening, code templates, code formatting etc.) for the integrated programming languages Java, BeanShell and "R". The main programming language of Bio7 is Java which can be easily compiled with the integrated dynamic Java compiler. Since Bio7 uses a dynamic compiler models run "Out of the box" in the Bio7 environment and no intermediate compiled files are created which have to be executed. With the integrated scripting language BeanShell which also can interpret Java, easy to use scripts can be created and for instance be used to extend a special Scripts menu of Bio7 (Scripting languages are easy to learn and allow e.g. a fast prototyping of models). The organization of created files is highly supported inside this Rich Client Platform. The integrated file explorer allows easy storage or loading of created files. The file explorer also supports "drag and drop" of files e.g. into the flow editor (see below).



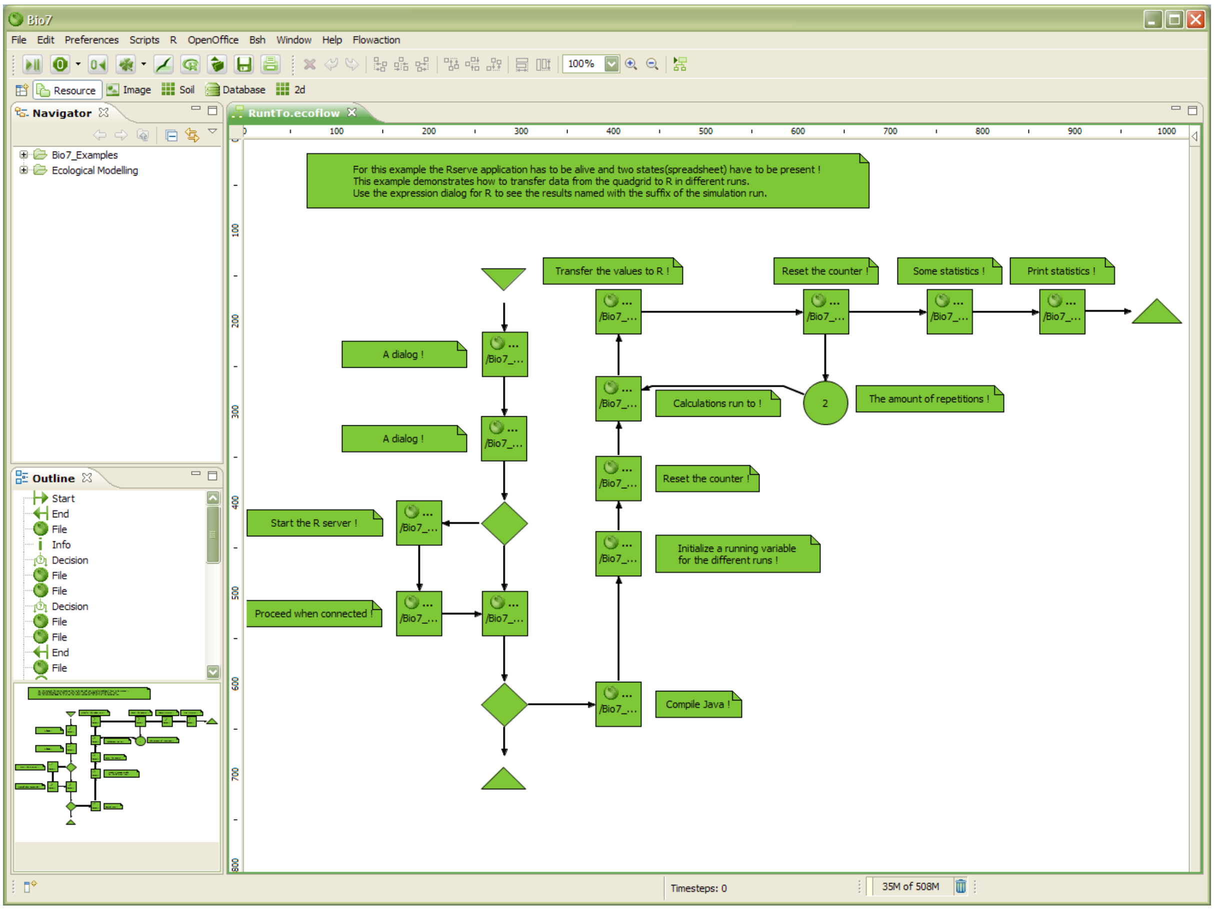
```
#RScript - please enter your code here !
#This Snippet calculates the interpoint distances from existent x,y values !
#Uses the library spatstat !

library(spatstat)
d<-nndist(x, y)
dmean<-mean(d)
dmax<-mean(d)
dmin<-mean(d)
```

Figure 34: Opened "R" editor (top-right) as an example for the language editors in Bio7 (which look similar). In general editor files can be opened from the file explorer (Navigator, top-left). In the Console of Bio7 (bottom-right) error messages (e.g compilation or script errors) are indicated.

2.1.9 Flow Editor

To verify or test different parts a model it is often required to gradually adjust certain parameters or routines. Such a careful analysis of a certain parameter space with a chosen method (e.g. a sensitivity analysis of certain parameters) can be extremely time consuming because the calculation of each scenario requires a complete model run. Furthermore the results of all these model runs need to be statistically analyzed (e.g. compared with measured data from images or population counts for model validation). To accelerate this procedure Bio7 contains a special Flow Editor, in which sensitivity analysis can easily be carried out by simply organizing files in a Flowchart like structure (Fig. 35). With the ability of the Flow Editor to handle nested loops and decisions, a dragged model file (e.g. Java, "R") can be executed and the results systematically be analyzed e.g. with the numerous statistical methods available in Bio7. The Flow editor recognizes different file types ("R", Java, BeanShell, ImageJ macros etc.) which can easily dragged from the available file explorer to the Flow



For this example the Rserve application has to be alive and two states(spreadsheet) have to be present !
This example demonstrates how to transfer data from the quadgrid to R in different runs.
Use the expression dialog for R to see the results named with the suffix of the simulation run.

Figure 35: A flowchart organizing different files for a simulation.

editor and calls the appropriate Compiler or Interpreter for the execution of the file. A typical flow for a sensitivity analysis of a model would at first compile and execute a parametrized model. Then a script would limit the execution of the model to a certain area of interest. A connected statistical script would then calculate and store the data within that area for later analysis. With a connected loop this part of the model would be repeated several times, each time with a different parameter selection defined by a script. At the end of such a routine all collected results then would be analyzed (e.g. using another script) and tested for reliability.

2.2 Sustainable Development

As mentioned above, Bio7 is built upon Eclipse, a very popular tool with a vigor community developing this RCP platform further and further. Newly upcoming tools and concepts developed by this community can easily be implemented into Bio7 if needed. The Bio7 version which was created for this thesis is fully documented with a developers guide, lots of examples and a Java API, making it easy to get started with Bio7. Bio7 is an Open Source application (momentarily available for Windows and Linux) which can be downloaded freely together with all documentation materials from a project website (http://sourceforge.net/projects/bio7/) on the Internet.

2.3 Conclusions

The new development tool Bio7, was built upon the powerful Eclipse framework for sustainable development. In contrast to existing popular OpenSource simulation tools for agent based modeling or numerical computations like Repast, Netlogo, Breve, Swarm, Scilab, Octave (MINAR et al. 1996, WILENSKY 1999, EATON 2002, KLEIN 2003, CAMPBELL et al. 2006, NORTH et al. 2007) Bio7 is particularly suitable for simulations of spatio-temporal phenomena in ecological systems. Many of the integrated algorithms are based on experimental ecological data sources or come from popular OpenSource GIS tools like e.g. Grass, Saga GIS and Fragstats (MCGARIGAL 2002, BÖHNER et al. 2006, NETELER & MITASOVA 2008).

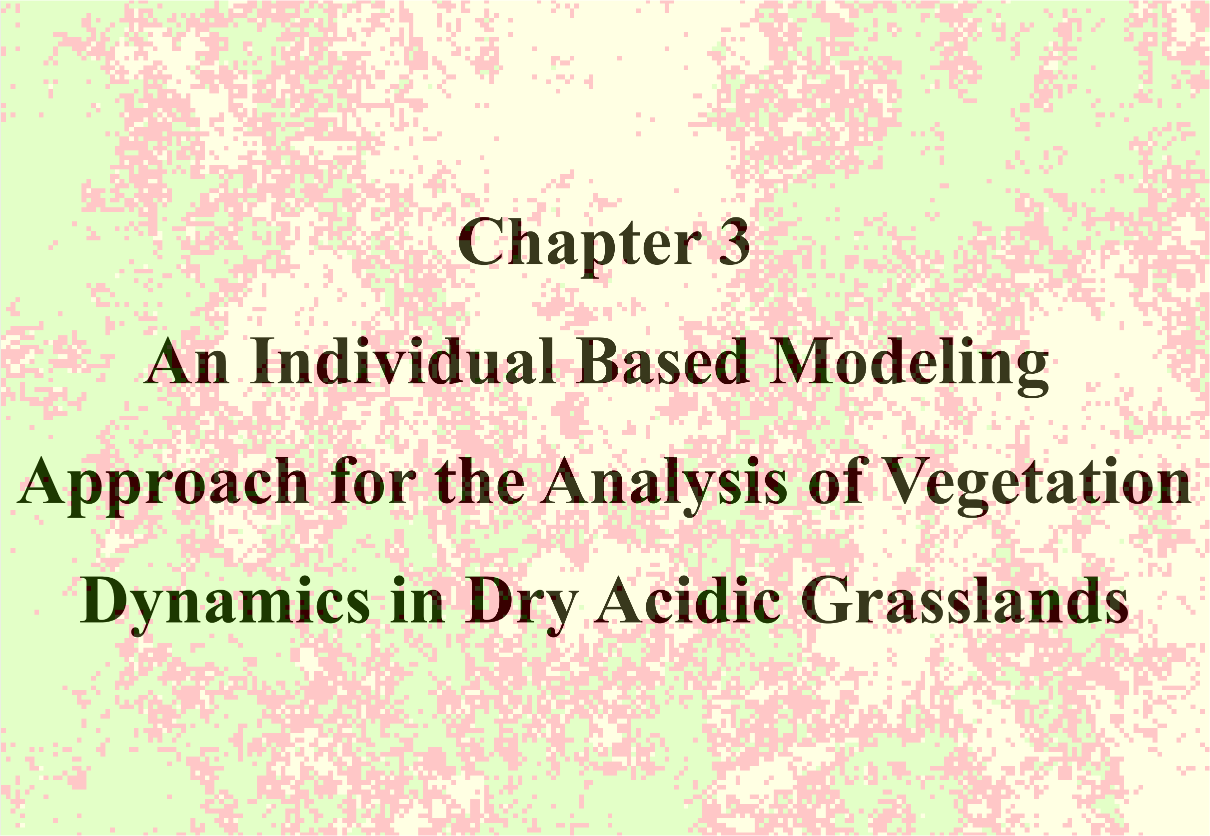
Additionally Bio7 is one of the first simulation tool with an integrated dynamic Java compiler, which makes compiled methods (models) instantly executable thus allowing effective testing of newly created algorithms during model development. A unique feature of Bio7 is the implementation of popular tools like "R" and ImageJ not only used as a library but fully integrated in an Eclipse Rich Client Platform. The ImageJ and "R" components of Bio7 were primarily developed for microscopy and statistics but are presently becoming increasingly popular also for general simulation-workflow environments as well as for pattern recognition or morphological measurements (LUDÄSCHER et al. 2006, BERTHOLD et al. 2006, NORTH et al. 2007).

The widely applicable algorithms facilitate the development of new methods or transfer methods known from e.g. microscopy to scales relevant for spatio-temporal ecological problems. Since both tools have also a huge user base and are well documented, arising problems during model development can quickly be solved. Finally Bio7 offers specialized default visualizations (dynamic charts) which don't have to be created from the programming source which saves valuable development time.

Bio7 is an ongoing effort to create an easy to use general purpose simulation platform for spatio-temporal ecological problems. One can therefore expect, that future versions of Bio7 will integrate even more tools for pattern analysis and will also extend the capabilities of the database. An already finished tool for an upcoming release is a routine which allows to create a different null model with the implemented so-called "midpoint-algorithm" (PEITGEN &

BARNSLEY 1988, GARDENER 1999, GARDENER et al. 2007) which can be combined with random patterns as basis for more realistic start patterns in grid based simulations. Furthermore a tighter integration of "R" with a spreadsheet component inside Bio7 has already been developed, thus allowing to use Bio7 as a complete "R" graphical interface. Certainly future versions will contain more GIS related methods and the already ongoing further development of the general Rich-Client concept will ease up the continuous future development of this platform.

Bio7 integrates concepts of different disciplines like e.g. image analysis and spatial statistics and encourages the application of these concepts in connection with spatio-temporal ecological problems.



Chapter 3

An Individual Based Modeling Approach for the Analysis of Vegetation Dynamics in Dry Acidic Grasslands

3. An Individual Based Modeling Approach for the Analysis of Vegetation Dynamics in Dry Acidic Grasslands

Urban expansion, and other land use changes have been identified to be the major causes for the presently ongoing massive loss of open dry acidic grasslands. But even protected areas of these valuable nutrient poor ecosystems are increasingly endangered by anthropogenic atmospheric nitrogen deposition which destabilizes the competitive equilibrium within this community and elicits an irreversible ruderalization process (BAUERNSCHMITT & GREBE 1997, WEIGELT 2001, 2005). Additionally climatic changes resulting in increased temperatures during the growing season may lower the water availability and, thus, negatively affect mineralization rates and nutrient supply for the plants. In order to evaluate the consequences of such phenomena for the spatio-temporal vegetation dynamics of the early successional stages of such grasslands a spatially explicit individual based simulation model was developed. The rules of this model are based on the available information from previous experimental work as well as on new experimental data particularly collected for this model development. Using this model it should be possible to determine the relative importance of various biotic and abiotic factors for the stability of this plant community, vegetation composition at this successional stage and to determine critical thresholds in this connection. The general working hypothesis was, that besides the already known importance of frequent disturbances (JENTSCH 2001, 2004, FRIEDRICH et al. 2006, HOBBS & TEMPERTON 2006, WARREN et al. 2007) temperature changes and the related changes in water and nutrient availability would play an important role for dynamic equilibrium between the two dominant pioneer species *P. piliferum* and *C. canescens.* Experimentally obtained information on vegetation distribution, growth parameters, dispersal dynamics, disturbance frequencies, competitive interactions and microclimate from two field sites (Eltersdorf and Büg, see chapter 1, Fig. 10) were used for the validation of this model.

3.1 Material and Methods

Individual based models in ecology are defined as models which describe a population of individuals which may differ from each other, thus, taking into account the complexity of the individual's lifecycles. They describe changes in numbers of individuals rather than in population density and typically also consider resource supply (UCHMANSKI & GRIMM 1996).

The Quadgrid option of Bio7 was used for all simulations of the present work. In order to keep the general calculation within reasonable boundaries, the grid size was set to 100*100 cells. The size of the grid cells was set to 10*10 cm which reflects the average diameter of a *C. canescens* bunch. Thus the total grid represented a simulation area of 100 m^2. This scale was chosen because several experimental studies had already shown that an area of 100 m2 was representative to reflect the relevant vegetation dynamics including the important small scale disturbance regime (JENTSCH et al. 2002, JENTSCH et al. 2008). A torus function was used to avoid edge effects in the simulation.

P. piliferum which is much smaller than *C. canescens* and grows in colonies (HOBBS & PRITSCHARD 1987) was modeled as superindividuals (where each grid cell represented multiple individuals but was treated as one GRIMM & RAILSBECK 2005). Each calculation cycle represented a month to resolve the seasonal growth, disturbance and mortality rates of the different plants.

As described in more detail below, the implemented simulation rules for the behavior of the two species were based on the available experimental and literature data on the lifecycle, and the spatial distribution patterns of the two species. The different plant individuals were modeled as objects in an object oriented approach to get a more realistic scenario. In this approach important attributes were assigned to each individual of one of the two modeled species each independent from the other. Additionally a disturbance function which randomly deletes plant individuals and, thus, creates free grid cells (i.e. open sand) at a given frequency was developed to reflect the naturally occurring activities of rabbits and ants in this system which seem to be essential for the stability of these ecosystems (JENTSCH et al. 2002b).

3.1.1 Vegetation Dynamics of *Corynephorus canescens*

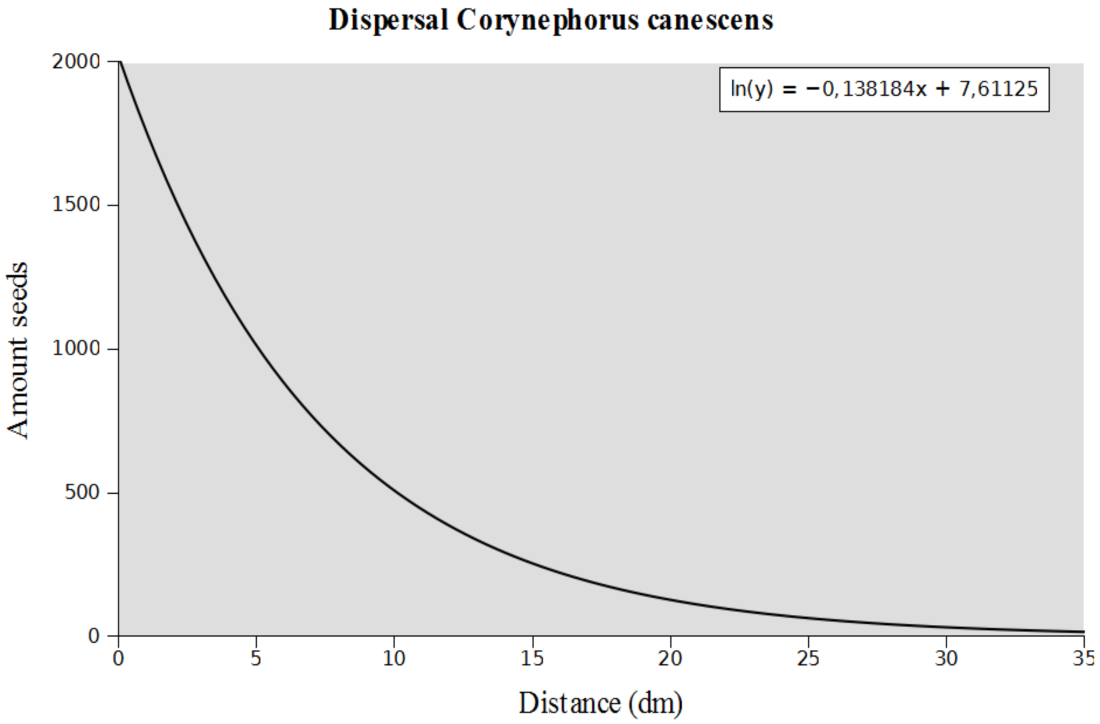


Figure 36: Exponential seed dispersal function, illustrating the decline of dispersed seeds with increasing distance from a dense stand of *C. canescens* based on experimental data from three different sites in Northern Bavaria (Data from Böger 2007).

C. canescens reproduces solely by wind dispersed seeds (BÖGER 2007). Thus the most important aspect for its population dynamics is the dispersal distance. Several authors have shown that the most of the seeds are found within 3-4 m around the mother plant. (ELLENBERG 1996, WOLTER 1996, KUNZMANN 2000, BÖGER 2002, 2007) Only rather few seeds are dispersed over larger distances with the help of wind. Fig. 36 shows an approximated dispersal function (on moos) based on experimental data obtained from three different locations in Northern Bavaria. This function is used in the present model (see below). The number of fertile seeds produced by a healthy individual mother plant of *C. canescens* can reach up to 15.000 fertile caryopses. The numbers for nutrient limited or stressed individuals are typically a magnitude smaller (BÜREN-RIEDER 2000, BÖGER 2007). *C. canescens* is considered to be biennial i.e. its life span amounts to generally 2 (sometimes 3) years (ROTHMALER 2005). They remain vegetative in the first year and typically flower between June and August of the second year. The dispersed caryopses then germinate to almost 100% in the following autumn as soon as the water supply becomes sufficient. There is no evidence for a persistent seed bank (BÜREN-RIEDER 2000, PICKELMANN 2001, JENTSCH 2001) .

These facts were integrated into the model in the following way.

In the simulation model flowering of all individuals occurs in June of their second year. The resulting caryopses are equally dispersed into all directions according to the exponential function from Fig. 36 (see Table 3) . The amount of caryopses reaching the several distances are dependent on an exponential function which is based on the afore illustrated exponential regression function of field data adapted on moos.

The maximum number of produced seeds is ca. 13.000 per individual. However this number can be greatly reduced by a fertility factor, which reflects the nutrient supply of the particular individual which is a combined function of the available nutrients coming from a nutrient availability matrix (see Fig. 37). Nutrient limitations seem to play an important role for the fitness of the plant individuals of this species (WEIGELT 2001, JENTSCH & BEYSCHLAG 2003). Fig. 38 shows the effect of a theoretical nutrient gradient on seed production and dispersal of individual *C. canescens* mother plants. Because there were no spatio-temporal data on nutrient distributions available, the nutrient matrix was randomized each year which comes probably close to the natural situation. If more than one seed is dispersed into an individual grid cell it is assumed that only one seedling will be able to establish itself in this cell.

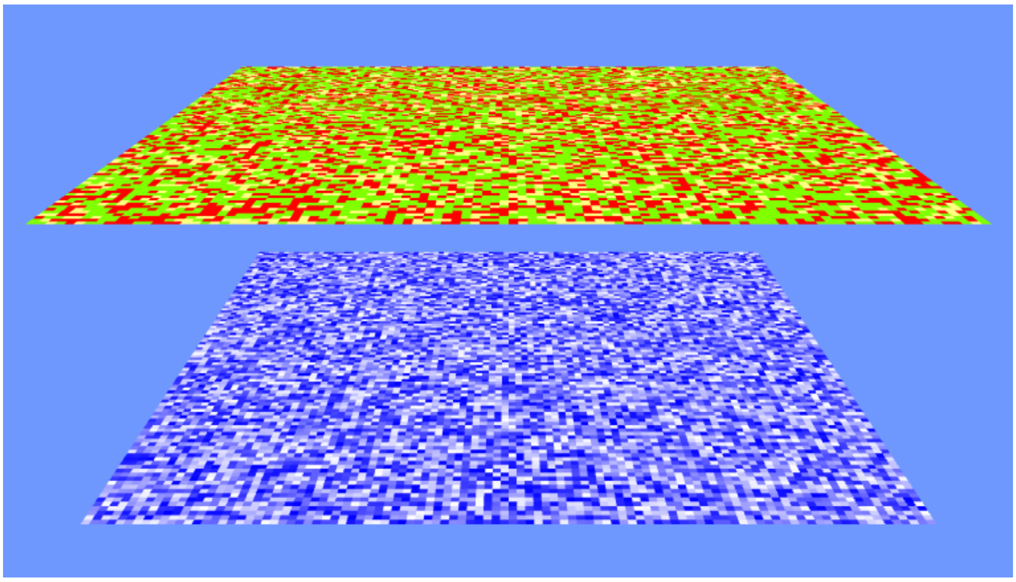


Figure 37: Regular plant grid (top) with the nutrient matrix as a parallel layer below.

Seeds which fall into cells which are already occupied by established plants of either of the two species will not be able to establish themselves. After two years each individual in our simulation died i.e. the respective grid cell was reassigned to the state of open sand.

Table 3: Equations for dispersal and establishment of *C. canescens*

$$Lc_{xy}(t+\Delta t)=P_{xy}*f(d), \quad if\ Lc_{xy}(t+\Delta t)=0$$

Lc$_{xy}$ = A location in the neighborhood distance d of the center cell is occupied by the amount of seeds calculated from the dispersal function f(d) and the fertility factor P$_{xy}$ if not occupied by *P. piliferum or C. canescens* (0 = soil).

t+Δt = Time interval from birth to dispersal.

$$f(d)=\mathrm{e}^{(-0.138184*d+7.61125)}$$

Empirical generalized dispersal function (d=distance), see Fig 36.

$$P_{xy} = 0.01\text{-}1.0$$

Random fertility factor at the given point of the nutrient matrix from which the probability in percent is calculated and is multiplied with the dispersal function.

$$d=\sqrt{(y_{di}-y_c)^2+(x_{di}-x_c)^2}$$

Euclidean distance from the centroid of the center cell *c* to the centroid of the cell in the distance *di*.

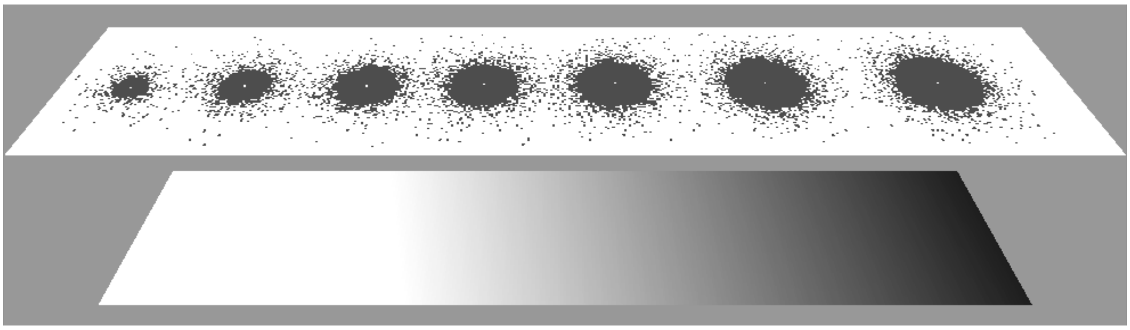


Figure 38: The effect of a (utilizable) nutrient gradient on the dispersal function of *C. canescens.*

3.1.2 Vegetation Dynamics of *Polytrichum piliferum*

The moss *P. piliferum* disperses mostly through clonal growth (HOBBS & PRITCHARD 1987, FREY & HENSEN 1995). In consequence the bryophyte is normally growing in dense circular colonies with a measured yearly radius increase of approx. 5-15 cm (HOBBS & PRITCHARD 1987) depending on the environmental conditions. For the growth of *Polytrichum piliferum* in the simulation model a probability function was created to assess the growth rate of the moss assuming that the cell size of 10*10 cm represents one individual colony of the moss. In this function each individual colony of *P. piliferum* can occupy a neighboring cell as long as it is not occupied by another individual of either plant species. *P. piliferum* shows optimal growth rates under moderately warm (7 to 15 degrees) and wet conditions (annual precipitation between 250 and 650 mm) (CORRADINI & CLÉMENT 1999). To implement this temperature dependency into the model, a polynomial regression was fitted to measured regional air temperature data of the years 2004-2006 (Weather Station Buch, near Nuremberg) to obtain monthly temperature means. In the model simulation growth of *P. piliferum* was only allowed during months with a mean air temperature between 5-15 C. The growth of *P. piliferum* was implemented as a random growth function in all directions. The probability to disperse in the direct neighbourhood (8-cell neighbourhood) was adapted and fixed to match the afore mentioned yearly radius increase (see Fig. 39).

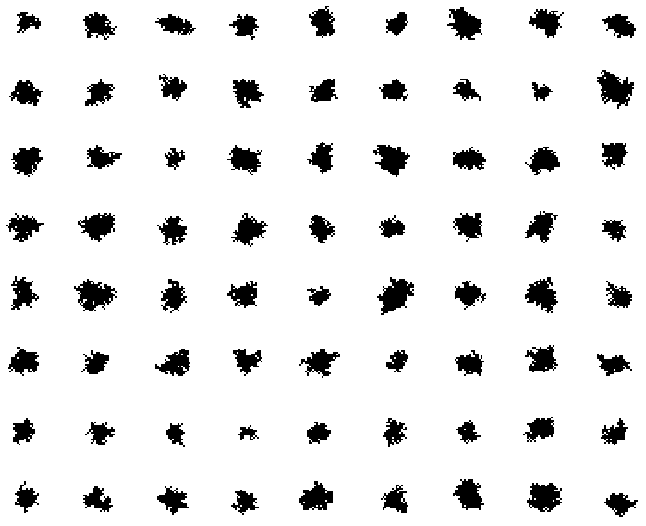


Figure 39: Implemented random growth of P. piliferum (72 colonies as examples) which approx. matches the yearly radius increase experimentally obtained by Hobbs & Pritchard (1987). Illustrated are the different geometries caused by the implemented random growth.

The superindividuals (grid cells) of *P. piliferum* were assumed to be immortal because in in nature all dead material is instantly replaced by a newly formed shoots. Table 4 summarizes the rules for the growth of *P.piliferum*.

Table 4: Equations for the growth of *Polytrichum piliferum*

$$Lp_{xy}(t+1)=P_d*g(t),\quad \textit{if}\ Lp_{xy}(t+1)=0$$

Lp$_{xy}$ = A location in the neighborhood distance d=1 of the center cell is occupied with a fixed probability based on data of yearly radius increase if not occupied by *P. piliferum or C. canescens* (0 = soil).

P$_d$ = fixed probability (0.03).

t+1 = Each timestep.

$$g(t)=1*s \quad s = \begin{Bmatrix} 0 & \textit{for} & f(t)<5, f(t)>15 \\ 1 & & f(t)\geq 5, f(t)\leq 15 \end{Bmatrix}$$

Growth function to only allow the growth of *P. piliferum* colonies at optimal temperature growth conditions.

$$f(t)=4.98578-3.45102\mathrm{t}+1.30274\mathrm{t}^2+0.0634756\mathrm{t}^3-0.0297666\mathrm{t}^4+0.00144329\mathrm{t}^5$$

The fitted temperature function (monthly mean 2004-2006 weather station Buch. t=month 1-12).

3.1.3 Disturbance Dynamics

Since the naturally occurring disturbance activities of rabbits and ants seem to essential for the stability of the ecosystem (JENTSCH et al. 2002b), a disturbance function which randomly deletes plant individuals and, thus, creates free grid cells (i.e. open sand) at a given frequency was implemented into the model. Its activity was limited to the months May – October because this is the time span where ants and rabbits are predominately active in the area (FRIEDRICH 2006). Table 5 contains the rules for this algorithm.

Table 5: Equations Disturbance

$$P_{xy}(t+1) = D_t * P_d \quad P_d = 0.01 - 1.0$$

P_{xy} = The probability that a cell of the whole field is affected by disturbance in the selected months.

P_d = Variable disturbance rates from 1% to 100%.

t+1 = each timestep.

$$D_t = 1 * t_m \quad t_m = \begin{Bmatrix} 0 & for & t < 5, t > 10 \\ 1 & & t \geq 5, t \leq 10 \end{Bmatrix}$$

D_t = The time dependant activation of disturbance based on data about burial activities on dry acidic grasslands.

3.1.4 Initialization of the Model

For initialization the plant individuals and open sand areas were randomly and uniformly assigned to the grid cells of the modeling space using a Mersenne Twister random generator as a pseudo number generator (MATSUMOTO & NISHIMURA 1998). For the distribution of plants and soil the following proportions of grid cells were chosen: 50 % open sand, 25 % *C. canescens*, and 25% *P. piliferum*. This distribution is justified by the results of a cluster analysis where several artificial distributions were compared to measured values (see Fig. 47) showing that this particular random distribution approximately resembles the natural situation. In order to obtain a realistic age distribution, the age of the initial *C. canescens* individuals was randomly shuffled between first year and second year plants. All calculations began in the month of July as a selected seasonal starting point.

3.1.5 Model Validation and Sensitivity Analysis

The general quality of the model was evaluated by means of a sensitivity analysis of important parameters. Each model run for a specific parameter value (starting every time with a randomly different initial distribution of plants and open space) was repeated ten times to obtain a standard deviation for the results. Each run was performed for 600 time steps (months) which represents a simulated time period of 50 years. The final values were collected during the steady state phase in the month of June just before the new dispersal events. The resulting distribution patterns were dynamically collected in a data frame and

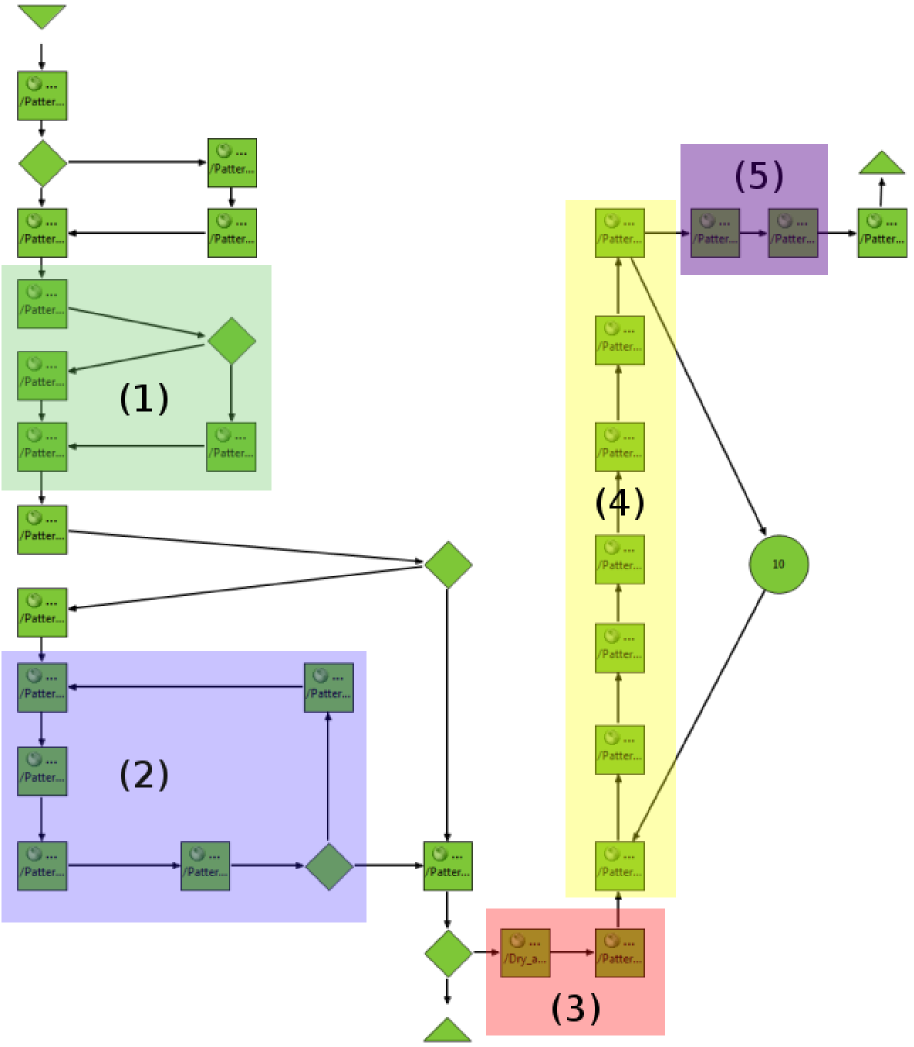


Figure 40: Flow for the pattern analysis of the simulation model. (1) Measured patterns from the Büg and Eltersdorf location are added to a dataframe. (2) Random patterns are created and added to the dataframe. (3) Simulation model is loaded and started. (4) Simulation model repeatedly runs to a specified timestep and the resulting patterns are added to the dataframe. (5) Collected data are statistically analyzed and clustered.

statistically summarized with the software "R". The resulting spatial patterns were analyzed with landscape metrics in order to compare them to experimentally measured patterns from real nature and, thus, validate the model.

These natural distribution patterns of *C. canescens* and *P. piliferum* were obtained from digital photographs taken at about 2 m height above canopy during the summer of 2005 at the Eltersdorf and the Büg site. Additional aerial photographs from approximately 10 m height were taken at different randomly chosen locations of the Büg site during summer of 2006 using a weather ballon with an attached digital camera (see Fig. 41). Before analysis all images were (if necessary) geometrically corrected with the image software GIMP 2.6 to fix spatial distortions (pincushion distortions) caused by the camera lens. Using "Bio7" the obtained spatial information from photographs covering a 10x10m area was then transferred to the model grid (Fig. 42).

Figure 41: Weather balloon with attached digital camera to obtain aerial vegetation images from the Büg site.

Subsequently selected landscape metrics (see Table 6) were calculated for the obtained patterns. The individual bunches of *C. canescens* could be exactly detected from the photographs. The areas of open sand and moss, however were more difficult to quantify. Their percent proportion of the entire area was, therefore, assessed with image analysis.

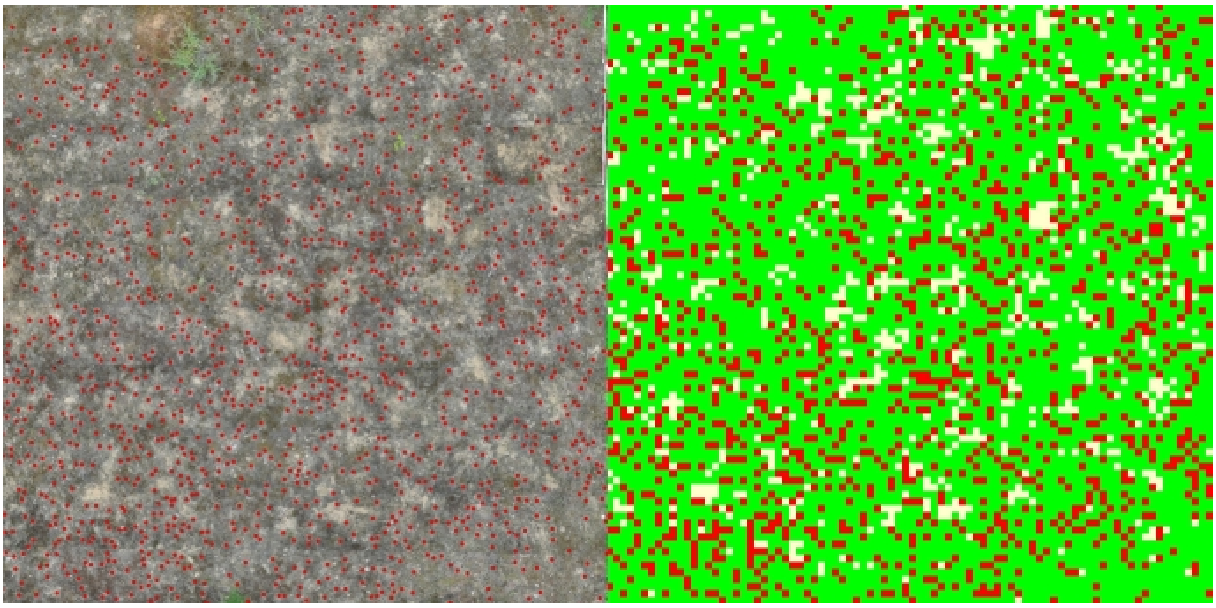


Figure 42: Transfer of distribution patterns from a 10x10m aerial photograph into the modelling grid (Red: *C. canescens*, Green: *P. piliferum*, Yellow: open sand)

Table 6: Left column: Selected Landscape metrics used for the analysis. Right column: Species for which the metrics were measured

Nearest-Neighbor Distance (Patch: **mean**,max) MNN= $\sum_{i=1}^{m}\sum_{j=1}^{n'} h_{ij}$	*C. canescens*
Percent of Landscape $LAND=P_i=\frac{\sum_{j=1}^{n} a_{ij}}{A}$	Soil, *C. canescens, P. piliferum*
Number of Patches $NP=N_i$	*C. canescens*
Patch Density PD = $\frac{n_i}{A}$	*C. canescens*
Patch Size (**mean**, max) $MPS=\frac{\sum_{j=1}^{n} a_{ij}}{n_i}$	*C. canescens*
Nearest-Neighbor Distance (**mean**, max) $MNN=\frac{\sum_{j=1}^{n'} h_{ij}}{n'_i}$	*C. canescens*
Patch Perimeter (**mean**, max) $MPP=\frac{P_{ij}}{n_i}$	*C. canescens*
Perimeter-Area Ratio (mean) $PARA=\frac{P_{ij}}{a_{ij}}$	*C. canescens*
Fractal dimension $FRACT=\frac{(2\ln(.25*P_{ij}))}{\ln a_{ij}}$	*C. canescens*

Subsequently the datasets of the analyzed real patterns and the datasets of the different simulation runs were compared by a cluster analysis in "R" (Wards method with scaled euclidean distances).

3.1.6 Application of the Model

After the verification and evaluation the model was then used to analyze the effect of nutrient availability, different temperature regimes and dispersal distances by varying the respective parameters.

For these simulations the disturbance frequency was adjusted to a value which represented a stable species equilibrium (see Fig. 44). From this stable state the effect of the afore mentioned parameters on the species composition was analyzed.

3.2 Results

3.2.1 The Effect of Disturbance

Assuming a fixed reasonable dispersal distance for *C. canescens* of 3 m and a yearly colony growth of *P.piliferum* of ca. 10 cm colony radius, the disturbance probability was varied between 0.6% and 43.8%. Figs. 43-46 show the impact of different disturbance rates on the population development of the two plant species of concern The y-axis shows the number of individuals with a maximum value of 10.000 (grid cells). The x-axis is a time axis for 50 years simulation time (= 600 time steps à 1 month). After some initial equilibration time stable equilibria between the two species were reached throughout a large range of disturbance rates. With a disturbance rate of about 5-10% per year (low disturbance) the population size of the grass varied between 900 to 1700 i.e. a cover of 9-17 % of the

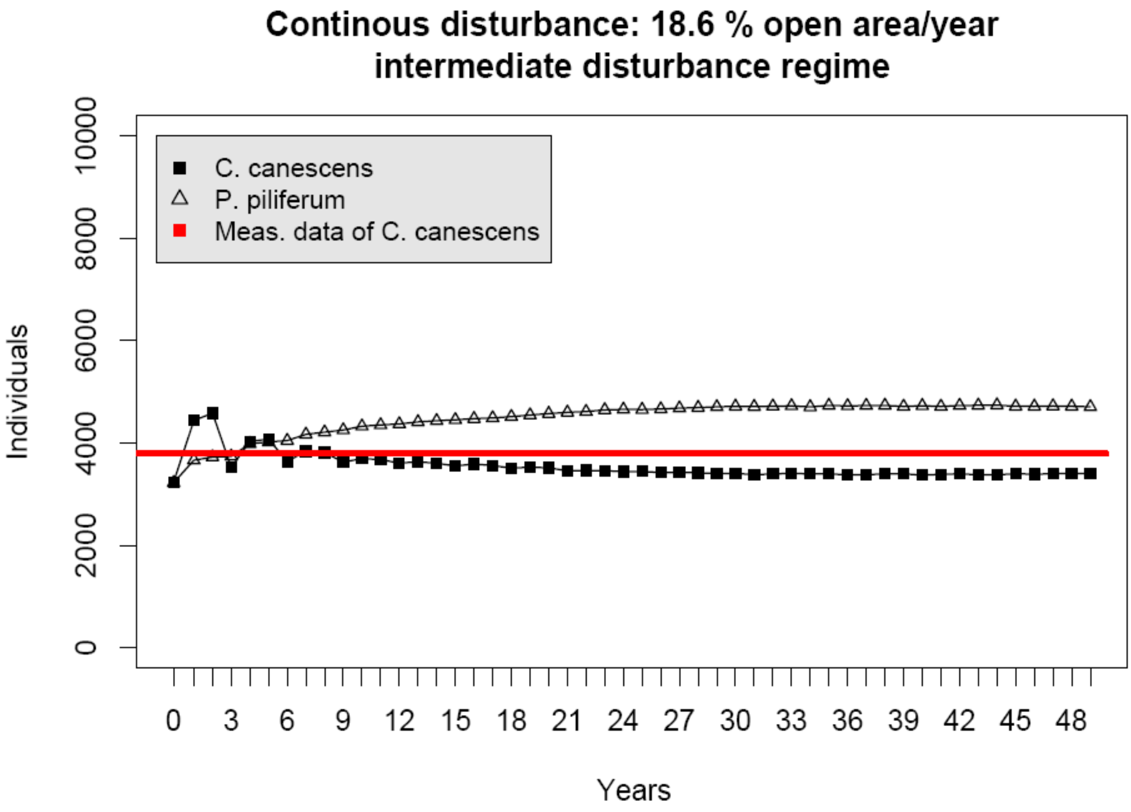


Figure 43: Results from 10 different runs. The y-axis shows the amount of individuals whereas the x-axis shows the time in years (up to 50 years). *C. canescens*: Mean = 3541, sd ± 69.08 (10 repl. including all timesteps!). The red line represents the amount of flowering + non flowering *C. canescens* (3848 individuals) counted in 2004 after ca. 18% disturbances in 2003 (FRIEDRICH 2006).

simulated system while the moss covers almost 85-70% of the available area. At intermediate disturbance rates (10-20 % = medium disturbance) which are close to the disturbance rates reported by Friedrich (2006) for natural systems *C. canescens* increases to 17-35% cover. Whereas *P. piliferum* decreases from 70-43% cover. Under these conditions the calculated data for *C. canescens* match the experimental population data collected by FRIEDRICH (2006) in the same area (Red line in Fig. 43). At about 21-22% disturbance rate (Fig. 44) both species cover roughly the same amount of area.

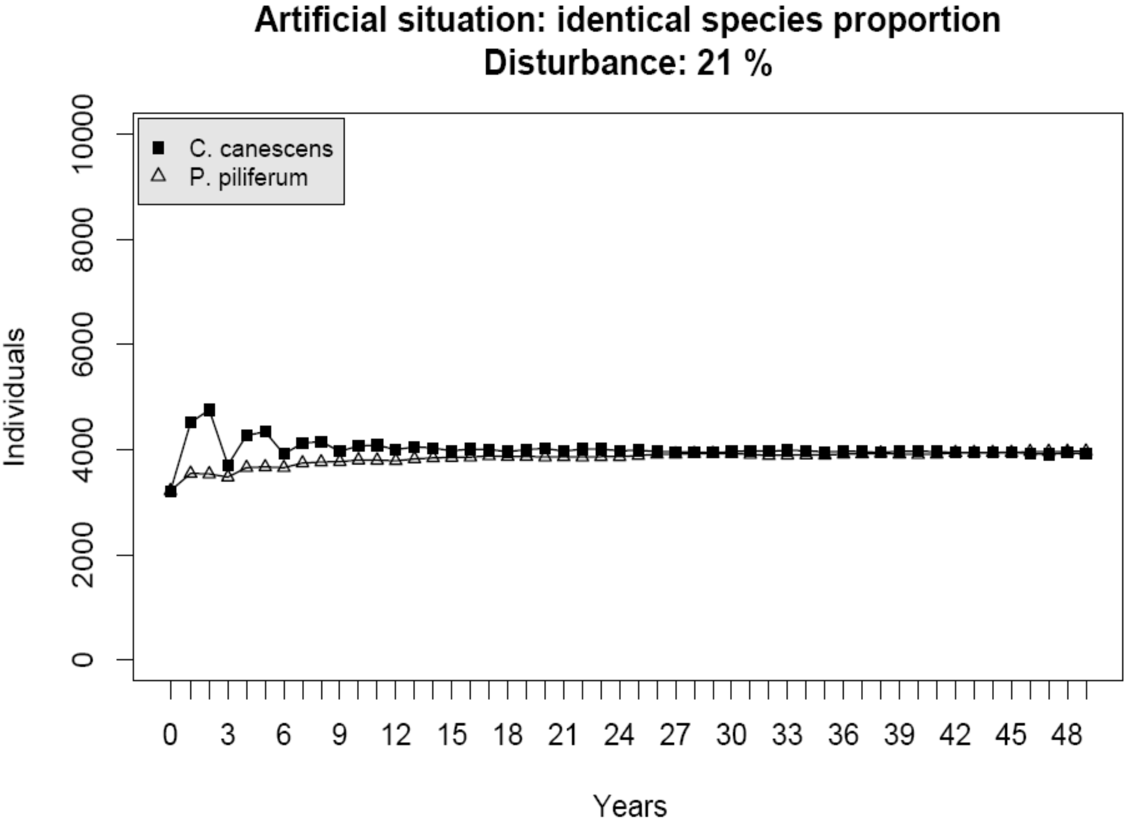


Figure 44: Results from 10 different runs. The y-axis shows the amount of individuals whereas the x-axis shows the time in years (up to 50 years). *C. canescens*: Mean = 3896.71, sd ± 74.13 (10 repl. including all timesteps!)

Higher disturbance rates benefit *C. canescens* which needs open sand for successful establishment and inhibit *P. piliferum*. Lower disturbance rates have the opposite effect. In consequence extremely high or low disturbance regimes lead to the extinction of either one of the species (Fig. 45-46).

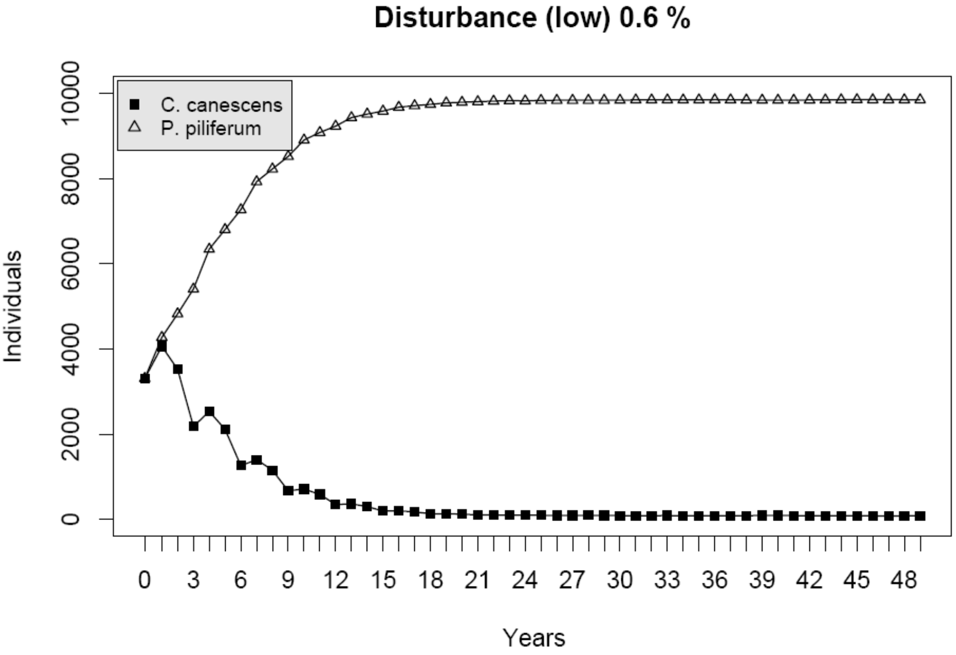


Figure 45: The effect of low disturbance. The y-axis shows the amount of individuals whereas the x-axis shows the time in years (up to 50 years). *C. canescens*: Mean = 575.68, sd ± 19.7 (10 repl. including all timesteps!)

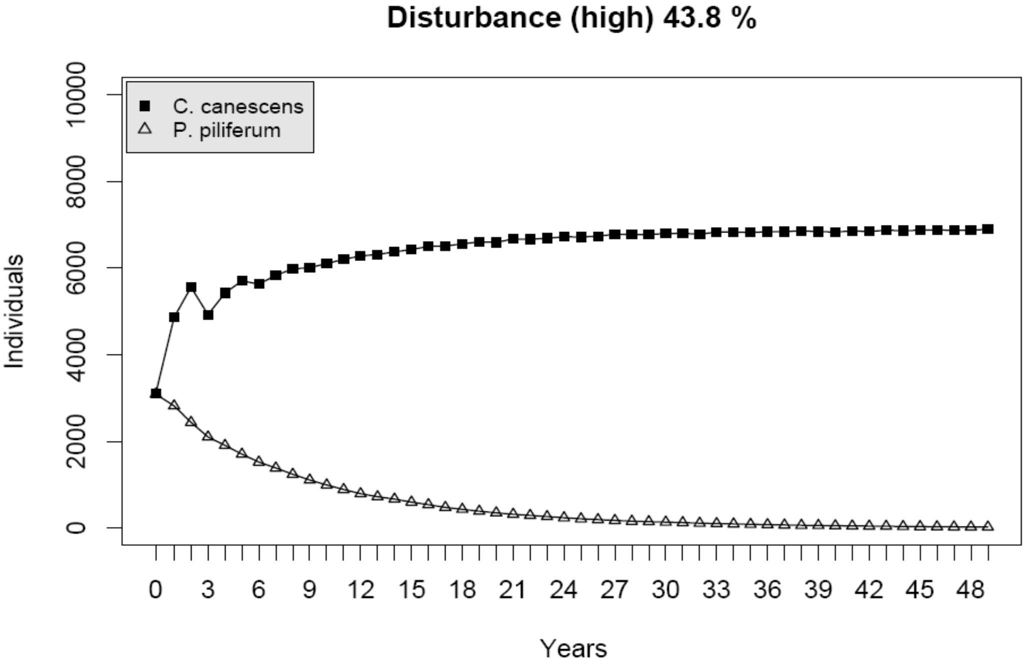


Figure 46: The effect of high disturbance. The y-axis shows the amount of individuals whereas the x-axis shows the time in years (up to 50 years). *C. canescens*: Mean = 5832.5, sd ± 50.38 (10 repl. including all timesteps!)

3.2.2 Model Validation

The resulting distribution patterns from all these simulations were then compared with patterns obtained from the aerial photographs taken at the Büg site (2005, 2006) and the Eltersdorf site (2006) by means of a cluster analysis. As shown in Fig. 47, there is a good accordance between simulated and measured patterns. All measured patterns of Büg and Eltersdorf are found within the same cluster consisting of simulated annual disturbance rates between 0.6-9.6%.

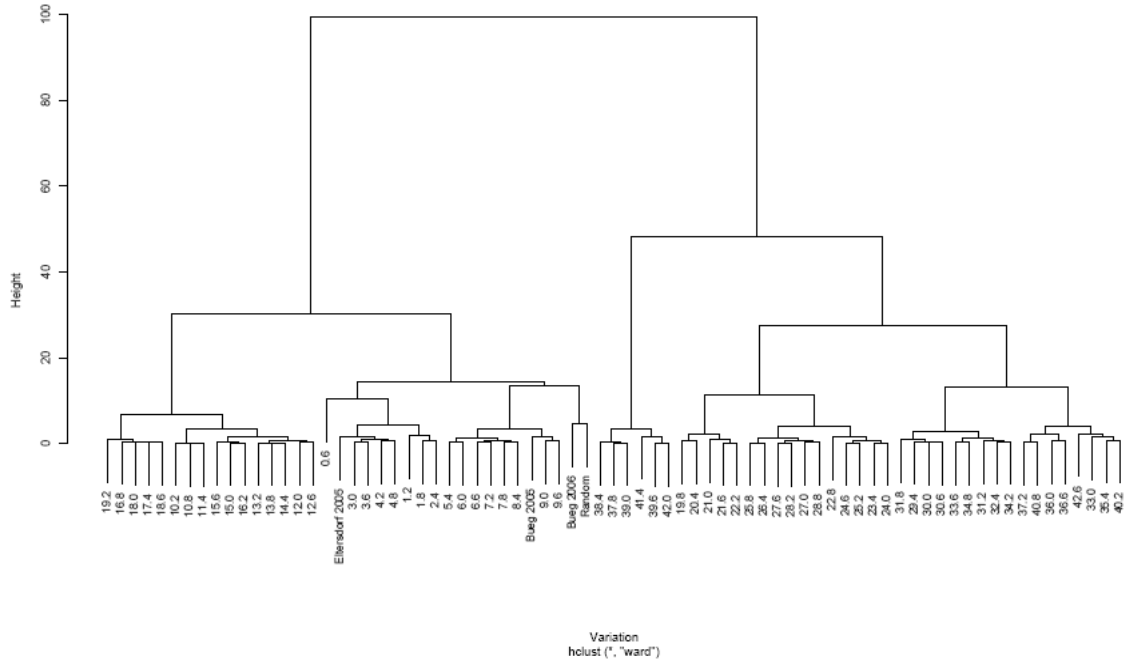


Figure 47: Clustered scaled euclidean distances (ward) of selected Landscape metrics at different disturbance rates. The y-axis reflects the dissimilarities between the clusters. The numbers in the clusters denote the disturbance frequency (%) which are clustered together with the measured spatial patterns of Elterdorf 2005 and the Büg (2005, 2006) and an artificial random pattern.

Within this cluster, a clear distinction between the patterns from the two experimental sites can be observed. This is due to the fact that rabbit activities are less pronounced in Eltersdorf 2005 than in the Büg (own observation). So the Eltersdorf pattern is found in a subcluster together with comparatively low simulated disturbance rates between 3.0-4.8% while the Büg situation belongs to a subcluster with markedly higher disturbance values. Interestingly the measured pattern of Büg (2006) belongs to the same subcluster as the random situation related to a relative high burial activity of rabbits in that year (own observation).

3.2.3 Results of Parameter Variation

Fig. 49 shows the results of model simulations where effects of temperature changes and variations in nutrient supply on the population size of the two species were investigated. The disturbance rate in these scenarios was held constant at approx. 21% resulting in equal populations of *C. canescens* and *P. piliferum* under the standard conditions (see Fig. 44). The data in Fig. 49 represent the steady state population sizes reached after a simulation time of 40 years. Case 1 shows the control situation with equal proportions of the two species. Case 2 shows the effect of an increase of the monthly mean temperature of 5 degrees (Fig. 48 orange line). It was assumed that temperature variations solely affect the length of the growing season of *P. piliferum*.

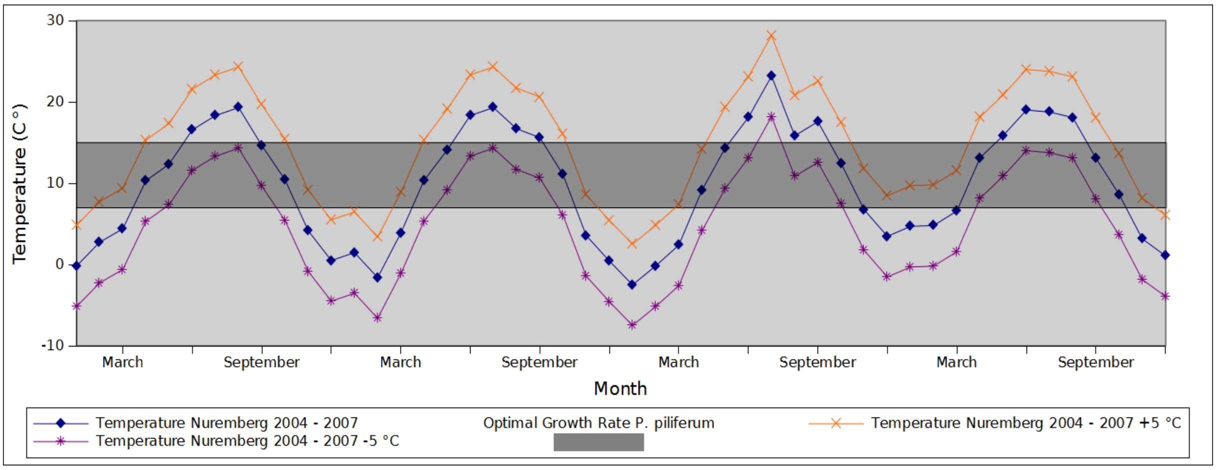


Figure 48: Annual course of air temperature (monthly mean values) as measured at the meteorological station Nuremberg-Buch (blue) as well as the +5 °C (orange) and the -5 °C (purple) courses which were used for the model simulations (see Fig. 49). The dark area indicates the temperature range (7-15 °C) where *P. piliferum* is supposed to exhibit optimal growth rates (CORRADINI & CLÉMENT 1999).

The simulated temperature increase extends the growing period of the moss in spring and fall leading to a higher number of occupied grid cells and in consequence to a decrease of the *C. canescens* population because there is less open sand available for the establishment of its seeds. A temperature decrease of -5 (Fig. 48 purple line) leads to the opposite effect (Case 3). Since *P. piliferum* grows better at low temperatures (see Fig. 48) the optimal growth period of *P. piliferum* falls into the months in which the disturbance activities occur. This is the reason why *C. canescens* dominates slightly in this case. Case 4 illustrates a scenario without temperature limitation for the moss allowing it to grow throughout the entire year without being limited by the temperature optimum, which has major negative effects on *C. canescens*.

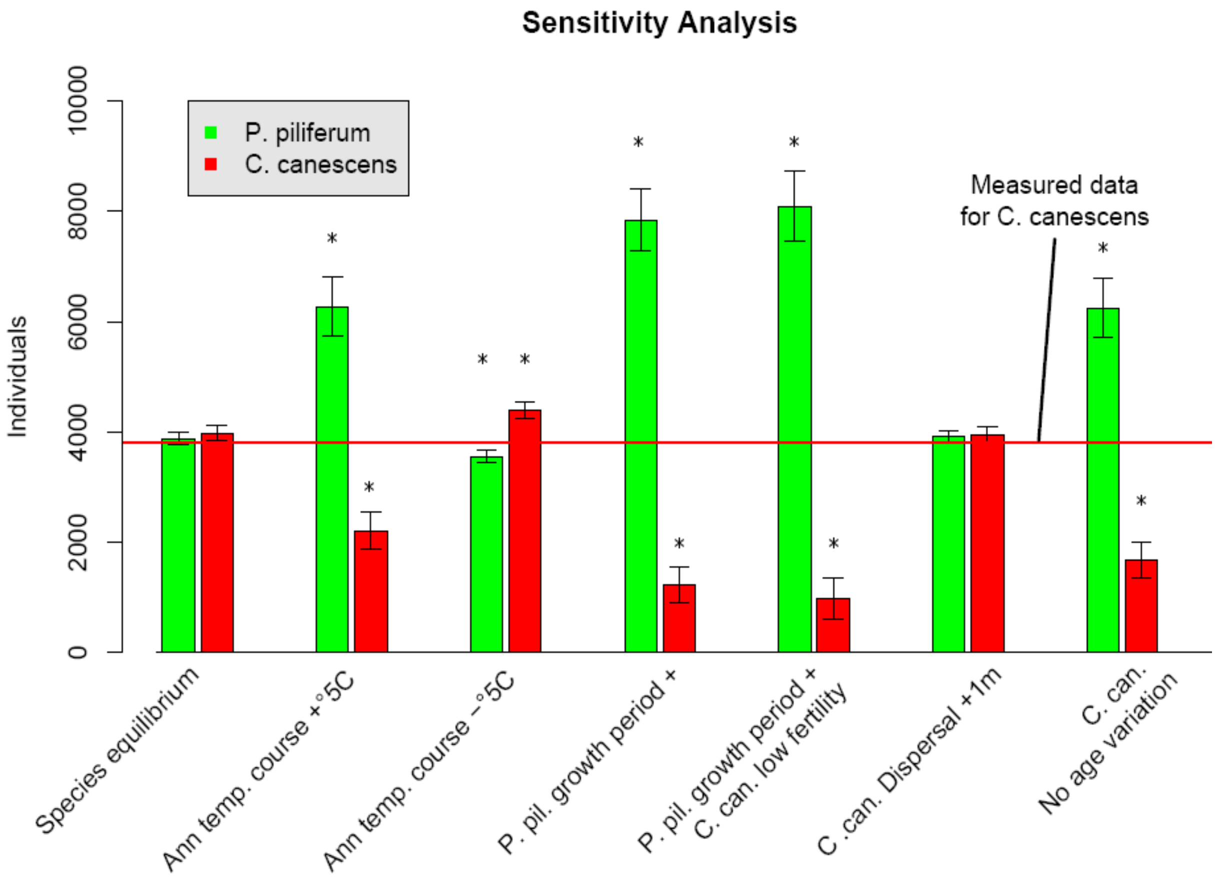


Figure 49: Results from the parameter variation. From left to right the seven grouped barplots denote seven different parameter cases. Case 1 (Species equilibrium) served as a control. "*" Denotes statistical significance using One-way ANOVA with Tukey multiple comparison test at 5% level of significance (Different cases of *C. canescens* tested against *C. canescens* species equilibrium and different cases of *P. piliferum* tested against *P. piliferum* species equilibrium).

Almost the same result was obtained for the situation where the moss grew all year and there was an additional nutrient limitation (Case 5). Variations in nutrient supply were assumed to solely affect the fertility factor of *C. canescens*. The fertility in this case was 99% reduced. The fact that this treatment led to similar results as case 4 indicates that the reduced seed production of *C. canescens* was still sufficient to occupy all available cells of open sand.

In case 6 the dispersal distance of *C. canescens* was increased from 3 to 4 m leading to no significant changes of the species composition. In case 7 finally a homogeneous age structure was assumed for the grass giving the moss the chance to grow without establishment of new *C. canescens* plants for almost two complete vegetation periods. The effect is very similar as in case 2. Both treatments enable the moss to cover plenty of grid cells at the cost of the grass.

3.3 Discussion

The newly developed spatially explicit, individual based simulation model for the simulation of vegetation dynamics in the early successional stages of dry acidic grasslands was used to address questions concerning the long-term stability of this ecosystem under changing environmental conditions. Dispersal events, temperature and nutrient conditions, individual variability and lifecycle are often successfully used and suggested to analyze vegetation patterns in theoretical spatially explicit frameworks (SILVERTON et al. 1992, COLASANTI & GRIME 1993, WINKLER & KLOTZ 1997, CZÁRÁN 1998, WIEGAND et al. 1998, HOVESTADT et al. 2000, WISSEL 2000, JELTSCH & MOLONEY 2002, WINKLER & STÖCKLIN 2002, GROENEVELD 2002, WIEGAND et al. 2003, MAZZOLENI et al. 2004, PERRY & ENRIGHT 2006, NUTTLE & HAEFNER 2007). In the case of dry acidic grasslands these phenomena as well as disturbance dynamics, the role of nutrients, (JENTSCH 2001, WEIGELT 2001, ANDERS et al. 2004, HASSE 2006, FRIEDRICH et al. 2006) dispersal dynamics and life history (HOBBS & PRITCHARD 1987, FREY & HENSEN 1995, ELLENBERG 1996, CORRADINI & CLÉMENT 1999, BÜREN-RIEDER 2000, BÖGER 2007) were intensively studied during the past years. The information from all these studies served as a the basis for the implemented rules.

In a spatially explicit simulation model a critical task is the implementation of spatial information which is even more difficult if the selected species vary extremely in their size for a grid based approach. One strength of the present simulation model is certainly the good approximation of the vegetation distribution data into the chosen resolution of the gridded structure without sacrificing to much spatial detail. For the case of *C. canescens* and *P. piliferum* it was satisfactory to define the grid cell size as the mean bunch size of *C. canescens*.

It is generally agreed upon that one should avoid the development of highly complex models because the huge parameter space will inhibit a systematic test of such models (WISSEL 1989, GAYLER 1998, JØRGENSEN & BENDORICCHIO 2001). Therefore the present application was restricted to only two species and a few carefully chosen important parameters.

It is well known that the disturbance dynamics play an important role for the stability of dry acidic grasslands (JENTSCH et al. 2002, FRIEDRICH et al. 2006). Depending on the respective authors, disturbance events are typically defined as events relatively discrete in time and space which alter the structure of populations, communities and ecosystems, which are a limiting factor for the biomass or a factor which makes resources available or simply a deviation from the normal conditions (GRIME 1979, TILMAN 1982, SOUSA 1984, PICKET & WHITE 1985, FORMAN & GORDON 1986, WALKER 1999). Disturbances can change vegetation distribution patterns and its composition (GRUBB 1977) by benefiting disturbance adapted species like *C. canescens* and *P. piliferum* and thus disrupting the competitive equilibrium.

In dry acidic grasslands and other sand dune communities disturbance events are essential for stability because they inhibit the successional progress towards a nutrient rich grassland community (LACHE 1976, JECKEL 1984, STORM et al. 1998, GELKA 1999, JENTSCH 2001) where the pioneer species adapted to low nutrient availabilities can not survive. In dry acidic grasslands rabbits and ants are the continuously active major disturbance agents (PLATT 1975, JENTSCH 2001, FRIEDRICH 2006).

In the present model application we, therefore, systematically analyzed the role of disturbance to address the question how much disturbance is necessary to preserve this special ecosystem under the present conditions and what would be the consequence of a temperature increase caused by global climate change. Climate change has several effects on the vegetation composition increasing or decreasing the amount of certain species more or less adapted to this changes (BROWN et al. 1997, DUKES & MOONEY 1999, GITAY et al. 2002, CLELAND 2007, WILLIS et al. 2008, BRADLEY 2009) or leading to a complete extinction of species (THOMAS et al. 2004, HARTE et al. 2004). Predictions of possible effects of climate are difficult to derive from experiments. because the predictive value of such experiments is rather limited. In contrast, simulation models like the one which was developed in the present work allow a systematic evaluation and temporal extrapolation of different potential environmental scenarios based on the presently available experimental information. The variation of the selected environmental parameters reflecting climate changes often altered the species composition but did not lead to an extinction or an instable situation of one species in the present analysis (Fig. 49). These results are in good accordance with long term monitoring data of this system which emphasize a high stability of these early successional stages over the last decades (FRIEDRICH 2006, BÖGER 2007).

As shown by the sensitivity analysis for disturbance intensity the model can be used for the determination of upper and lower thresholds for system stability.

A potential future application of this could be to analyze the effect of different disturbance distributions (clumped, regular, random) which would reveal valuable information for the design of necessary management measures in order to prevent succession towards a nutrient rich grassland community.

A still existing weakness of the present model version is the rather rough implementation of the nutrient dynamics due to missing or insufficient experimental data. Typically, the ongoing succession increases the resource availability on sand dunes because of the accumulation of litter (BERGER-LANDEFELDT & SUKOPP 1965, LACHE 1976, JECKEL 1984, Van RHEENEN 1995, STORM et. al 1998, SCHMIDT 1998, HINNENTHAL 2001). In dry acidic grasslands, such nutrient accumulation (nowadays enhanced by anthropogenic nutrient deposition from the atmosphere) threatens the overall stability of the system (JENTSCH & BEYSCHLAG 2003, VAN DEN BERG 2005). So it has been shown that colonies of *P. piliferum* can increase overall nutrient availability by accumulating nitrogen within its dead material (BOWDEN 1991). Further, it is known from controlled field experiments that increased nutrient availability decreases the competitive strength of pioneer species like *C. canescens*. (WEIGELT 2001). Nevertheless, a long term study on nutrient availability and heterogeneity in dry acidic grasslands and it's effect on the vegetation composition would be highly desirable and would certainly improve the quality of related model simulations.

Another important aspect which is presently neglected in the model is the role of the soil microfauna and-flora including mycorrhizal fungi for vegetation composition distribution and dynamics. Common mycorrhizal networks (CMNs) can connect plants and share resources among them (NEWMAN 1988, READ 1997, KENNEDY et al. 2003, PEREZ-MORENO & READ 2004, NARA 2006) and on dry acidic grasslands exploitation of resources, especially nitrate uptake seems to be relevant. (AL-AGELY & REEVES 1995, KOSKE & GEMMA 1997, PERUMAL & MAUN 1999). At present, particularly the role of mycorrhizae and mycorrhizal networks on dry acidic grasslands is not known and lots of experimental work needs to be done before such phenomena can be properly implemented into the model.

In chapter 4 of this thesis we tried to estimate the potential effects of herbivory (i.e. foliage loss) which has been shown to have the possibility of changing vegetation composition

(MCNAUGHTON 1983, ADLER et al. 2001, SWAIN et al. 2007, OLOFSSON et al. 2008, DE KNEGT et al. 2008). While for *C. canescens* and *H. pilosella* there was almost no significant effect, this may be different for other plant species in which case the effects would have to be included into the model simulations.

The presented simulation model deals only with two dominant species in an early successional stage of dry acidic grasslands (*Spergulo morisonii-Corynephoretum canescentis)*. In the future it would be worth to carefully include other typical plant species or plant combinations in order to extend the analysis towards other, more complex successional stages. But as already mentioned the complexity of an model has to be manageable and this has to be considered if e.g. the present model would be extended by new species .

Since the model was created with the help of the integrated development environment (see chapter 2) the implementation of new species is comparatively easy. Nevertheless there is an upper threshold for what the model can do because it is designed to address questions regarding the interactions of plant individuals at the community scale. For ecological questions on higher scales other models (like e.g. GIS models) are more suitable.

In contrast to other existing simulation models the present model was not only validated with experimental population data, but also with collected spatial data. New in this respect was the use of selected landscape metrics to compare measured with simulated distribution patterns. Such a pattern oriented approach to (dynamically) verify simulation results has rarely been employed at the community scale (except for calculations of occupation percentages or summary statistics) because the necessary detailed spatial information is typically lacking.

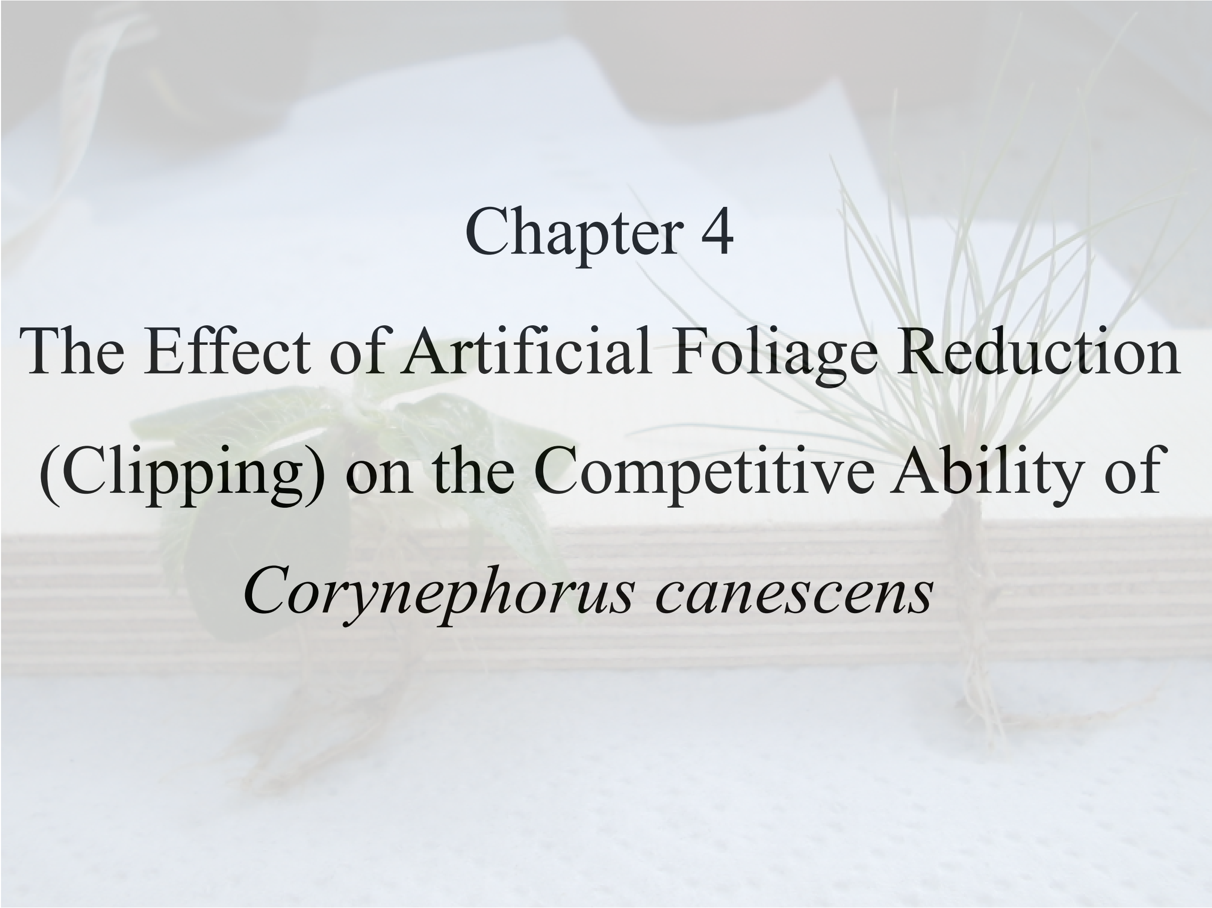
Figure 50: UAV equipped with a digital camera (image from Draganfly Innovations Inc. www.draganfly.com)

Satellite pictures and aerial photographs from planes are costly and do typically not provide the desired resolution. Therefore In the present work, the respective data were collected with an affordable weather balloon and a high resolution digital camera. Future researchers may employ socalled "UAV's" (unmanned aerial vehicles; Fig. 50) which, equipped with high resolution digital cameras, would be ideal for this purpose and would also allow long term monitoring of large areas (HARDIN & JACKSON 2005, SCHMALE et al. 2008, EVERAERT 2008, GURTNER et al. 2009, BERNI et al. 2009).

At present however, such tools are almost unaffordable (>16.000 US$). Additionally new but already available technologies like Light Detection and Ranging (Lidar) (BORK & SU 2007, IM et al. 2008, VIERLING 2008, HILKER et al. 2008, AKAY et al. 2009) will provide even clearer high resolution pictures and even the automatic identification of species seems to be within the range of these new possibilities.

3.4 Synthesis

Analyzing ecological systems is a difficult task because of the complexity of the interdependent biotic and abiotic factors determining the temporal and spatial configuration of animal and plant communities. In this respect dry acidic grasslands because of their comparatively low complexity, provide valuable research sites for a better understanding of the mechanisms of biotic interactions and their emergent patterns in time and space. In order to facilitate the generation of reasonable hypotheses a simulation model was developed using a newly assembled integrated development environment. Due to its very versatile structure the newly developed model can be used for the analysis of numerous ecological problems from a variety of ecosystems In times of changing environmental conditions such models are very useful tools because they can help to analyze and visualize the complexity of the related phenomena and the simulated model scenarios often provide valuable informations for the development of effective management measures.



Chapter 4

The Effect of Artificial Foliage Reduction (Clipping) on the Competitive Ability of *Corynephorus canescens*

4. The Effect of Artificial Foliage Reduction (Clipping) on the Competitive Ability of *Corynephorus canescens*

Up to now, the fitness of a plant individual in our model is solely the function of the species and the nutrient and water supply. Another factor which may have a strong influence on the competitive ability of a plant is herbivory. In dry acidic grasslands the prominent herbivores are grasshoppers, rabbits and small rodents. Additionally grazing by sheep which is frequently part of the management strategy may play a role. It is well known that e.g. grazing has the potential to change distribution patterns, of plant species (MCNAUGHTON 1983, ADLER et al. 2001, OLOFSSON et al. 2008) and species richness (LACEY & VAN POOLEN 1981, BAKKER 1989, PUTMAN et al. 1991, HILL et al. 1992, BULLOCK et al. 1995, PUCHETA et al. 1998, BARBARO et al. 2001). Two contrasting effects of herbivory are discussed. On the one side it is widely believed that herbivory plays a negative role for the general fitness of the affected plant individuals finally leading to a general decrease of biomass (BELSKY 1986, BERGELSON & CRAWLEY 1992, BELSKY et al. 1993, BIGGER & MARVIER 1998). On the other hand many authors found that herbivory can also have a positive stimulative effect on the affected plant finally leading to overcompensation and thus to an increased fitness. Some authors interpret this positive effect also as the result of coevolution (DYER & BOKHARI 1976, OWEN AND WIEGERT 1976, HILBERT et al. 1981, PAIGE & WHITHAM 1987, LENNARTSSON et al. 1997, PAIGE 1999).

Figure 51: Grazed *C. canescens* individual found on an early stage at a dry acidic grassland site near Bielefeld.

Generally compensatory growth can be either overcompensating (cumulative dry weight of the grazed or clipped plants is greater than that of the control plants), or fully compensating (cumulative dry weight of the treated plants equals the weight of the controls, or undercompensating (cumulative dry weight of the treated plants is below the weight of the controls at a defined point in time after the herbivory event (BELSKY 1986). In order to evaluate whether foliage reduction may have substantial positive or negative effects on fitness and competitive ability of *C. canescens* plants (and would, therefore, have to be implemented into the simulation model) a controlled field study was carried out in a sand pit in Bielefeld. At three different timesteps we investigated the effect of foliage removal, on the above and belowground biomass, the spatial distribution of roots and the resulting competitive ability. The effect of competition on root allocation of *C. canescens* has already been investigated by Bartelheimer et al. (2006). They found that *C. canescens* showed a marked root aggregation towards the roots competing neighbor plants. In the present work we used a similar, slightly modified approach to answer the following questions:

4.1 Questions

- Is *C. canescens* able to compensate or even overcompensate foliage removal?
- How does the presence of a competitor affect this behaviour?
- Is there a measurable effect of aggregation or segregation of the roots under herbivory and/or competition?

As a general working hypothesis it was assumed that foliage removal would have a dramatic negative effect on plant fitness and that this effect would be enhanced by the presence of a competitor, due to the limited nutrient supply in this sandy environment.

Figure 52: The sand pit near the University of Bielefeld with the experimental setup

4.2 Material and Methods

4.2.1 Experimental Setup

Figure 53: *Corynephorus canescens* prepared for clipping. 25% or 75% of the Shoot height were clipped.

The experiment was carried out between April and September 2004 in a 20 x 6 m sand pit of 120 cm depth near the university of Bielefeld. The sandpit itself is divided into four identical chambers (Fig. 52). For a detailed description of the sandpit and the available nutrients see Weigelt (2001). *C. canescens* plants were planted either alone (control) or together with an intra- or an interspecific competitor.

Hieracium pilosella was chosen as interspecific competitor because it frequently cooccurs with *C. canescens* in the early successional stages of dry acidic grasslands. At the field sites used in the present thesis *H. pilosella* is typically not majorly affected by herbivores (but see SYRETT et. al 1997).

Two month old young individuals of the two species (cultivated four weeks in a greenhouse and four weeks in a hotbed) were planted either alone or in a 1:1 competition experiment with a 7.5 cm distance between the competitors according to Bartelheimer et al. 2006. The different treatments (Tab. 7) were repeated eight times resulting in 264 single plots and placed in a randomized block design across the area of the sand pit to avoid edge effects and influences of growing position and exposition of the plants. To simulate herbivory on the target species *C. canescens,* either 25% (low herbivory) or 75% (high herbivory) of the aboveground biomass was clipped from the top of the bunches at three different times after planting. A cable strap was used for an exact determination of the foliage proportion to be clipped (Fig. 53).

The first clipping took place in June i.e. three months after planting. In July and August part of the plants were clipped a second and a third time to simulate continuous herbivory. In all cases the removed biomass was oven dried at 80 °C and weighted to obtain its dry weight. In July and August a complete set of plants (8 plants for each treatment) was also harvested from the previous treatment (timestep 1 and timestep 2). The remaining plants including the August treatment were harvested in September timestep 3 (Fig. 54).

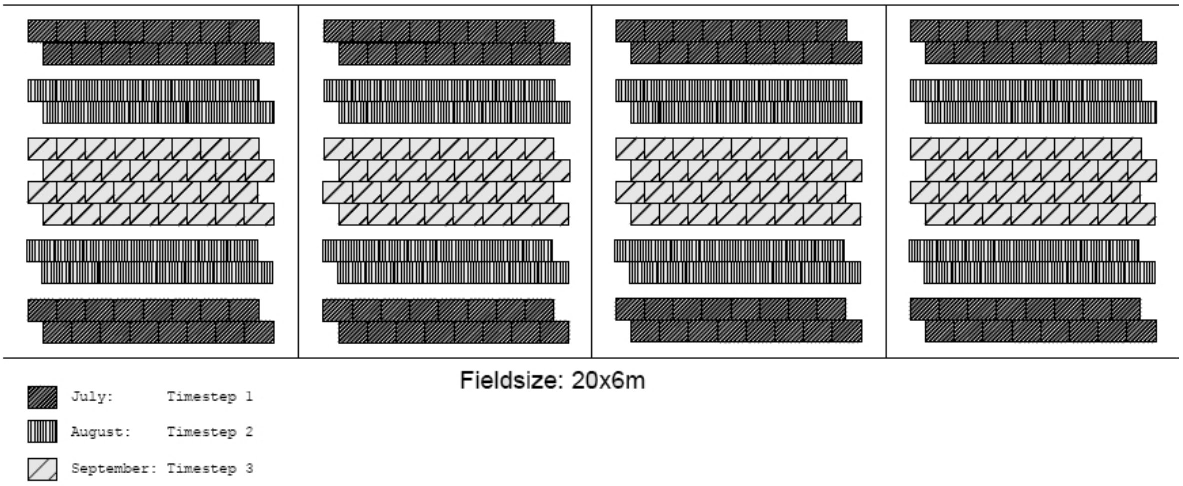


Figure 54: Sandpit harvest plan for the three different timesteps in four chambers of the sandpit (see also Fig. 52). From left to right four different chambers are illustrated. From top, bottom to the middle the three different timesteps are illustrated.

4.2.2 The Harvest

At harvest time, the complete aboveground biomass of all selected plants was removed, oven dried at 80 °C and weighted. The harvest of the belowground plant parts was done fractionally according to Bartelheimer (2005) who used a modified monolith method (BÖHM 1979, CALDWELL & RICHARDS 1986, KÜCKE et al. 1995) in order to obtain informations about the spatial distribution of the root biomass.

As an improvement compared to BARTELHEIMER (2005) a metal box was created which could be opened at one side and could easily be pushed into the rhizosphere of the plot due to its sharpened edges (Figs. 55, 56). To avoid edge effects the box itself was fitted in a gauge to hold an accepted distance to the neighboring plots. The box covered exactly one third of the whole plot down to a depth of 15 cm resulting in a volume 10.125 dm³. According to Bartelheimer a soil layer of this depth contains almost the entire (>80%) root biomass of the plants. Within the opened box it was then possible to divide the contained sand into different layers and volumes from which the contained root biomass was washed out separately (Fig. 56). The washed roots from each subsection were stored in tubes filled with water and transported to the laboratory for later analysis. In the laboratory the root samples were cleaned more carefully and remaining sand particles were removed. Subsequently the roots were placed in transparent glass pan and scanned at 300 dpi with a flatbed scanner with back lighting (AGFA Snap Scan 1236). The resulting scans were analysed with the software WhinRhizo (Version 2002c) whereas the root area was measured. The analysis of the scanned

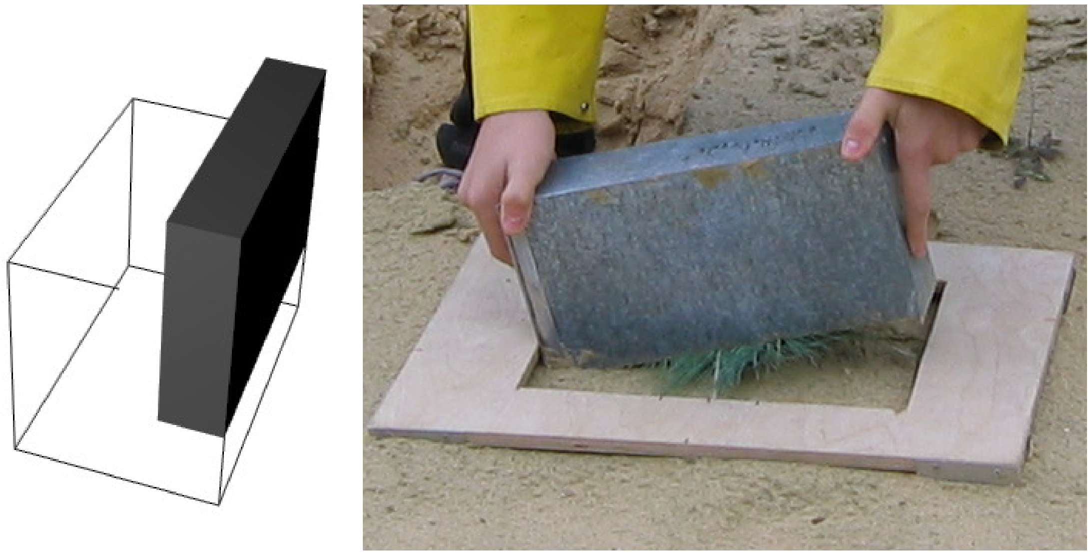


Figure 55: Excavation Box for the fractional harvest of the roots.

images was done as a greyscale image at a threshold value of 235 (greyscale value). Additionally the program was calibrated to ignore objects smaller then 0.01 cm² according to Barthelheimer (2005).

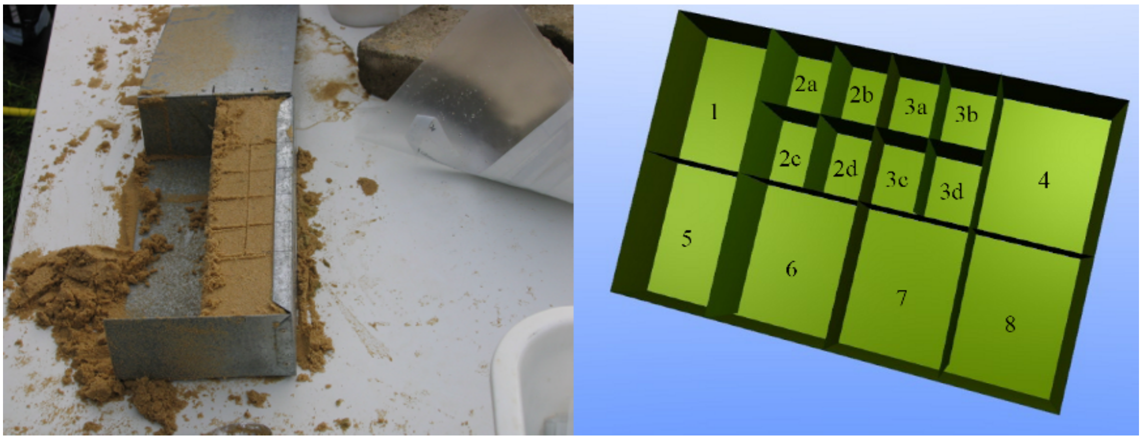


Figure 56: Left: Opened metal box containing one third of the spoil of a plot divided into various depth layers and subsections according to the template shown on the right.

Table 7: Overview of treatments with herbivory and competition of *C. canescens* and *H. pilosella*

Treatment	Clipping	Setup	Repetitions (n)	Time steps	Individuals
Herbivory Monoculture	25.00%	Cc	8	3	24
Herbivory Monoculture	75.00%	Cc	8	3	24
Control		Cc	8	3	24
Control		Hp	8	3	24
Herbivory Competition	25.00%	Hp/Cc	8	3	24*2
Herbivory Competition	75.00%	Hp/Cc	8	3	24*2
Herbivory Competition	25.00%	Cc/Cc	8	3	24*2
Herbivory Competition	75.00%	Cc/Cc	8	3	24*2
Competition		Hp/Cc	8	3	24*2
Competition		Cc/Cc	8	3	24*2
Competition		Hp/Hp	8	3	24*2
Sum					**432** (in 264 plots)

4.2.3 Statistical Analysis

In order to detect significant herbivory and competition effects the measured data from the different treatments were analyzed with an Analysis of Variance (ANOVA) and, if significant values were found, with a Tukey-HSD posthoc test using the statistical Software package "R" vs. 2.8.0. If the assumption of normal distribution and homogeneity of variances were violated for this test, the data were log or square-root transformed. For the detection of root aggregation or segregation patterns a paired t-test was carried out to compare lateral and central fractions in two layers of the root system with their counterparts at the opposite side of the plant. In order to evaluate the effects of competition and clipping on the competitive ability of *C. canescens* a relative indicator was calculated. Because the frequently used Relative Competitive Intensity index (RCI) is not symmetrical around zero a modification of RCI, the so called "Relative Neighbor Effect" (RNE) was used (MARKHAM & CHANWAY 1996, WEIGELT & JOLLIFE 2003).

Table 8: Difference between RCI and RNE calculation.

RCI = $(X_{control} - X_{mix})/X_{control}$.	**Relative competitive intensity** X is an estimation of plant performance in the presence (mix) or in the absence (control) of neighbours
RNE = $(X_{control} - X_{mix})/x$	**Relative neighbor effect** where $x = X_{control}$ if $X_{control} > X_{mix}$ and $x = X_{mix}$ if $X_{mix} > X_{control}$ RNE ranges from - 1 to + 1 with negative values indicating facilitation and positive values indicating competition

For this calculation only the shoot biomass was used because of the not available individual root biomass (The individual root biomass was not available because the roots of two interwoven competing plants couldn't be separated).

4.3 Results

4.3.1 Aboveground Effects

For a comparison the different p-values (to accept or reject the null hypothesis) for all timesteps (p1-p3) relative to the controls are shown. P-values above 0.05 were regarded as not significant. Fig. 57 shows the pure clipping effect on *C. canescens.* Only at the first timestep in July there was a significant reduction of biomass relative to the unclipped controls at the 75% clipping level (p1=0.0012). In August and September the plants had compensated the foliage loss from the previous clipping treatments and showed no significant differences relative to the controls.

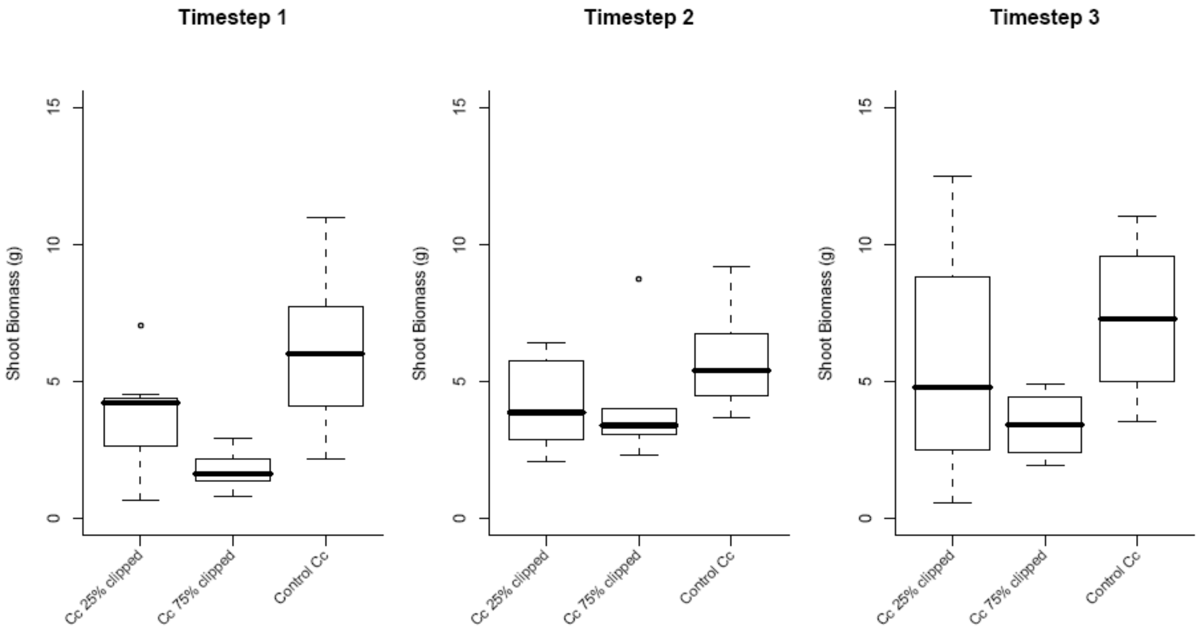


Figure 57: The effect of the two clipping treatments on the shoot biomass of isolated *C. canescens* plants at the three harvest timesteps (July, August and September).
All plants of timestep 1 were clipped in June and harvested in July (clipped one time).
The plants of timestep 2 were clipped in June and July (clipped two times) and harvested in August. Finally all plants of timestep 3 were clipped in June, July and August and harvested in September (clipped three times).
The y-axis shows the harvested shoot biomass. A box indicates the lower quartile (bottom), median (bold line) and upper quartile (top). Whiskers of a box indicate the sample minimum (below) and sample maximum (above). Points indicate outliers.
From left to right in each timestep:
Biomass of C. canescens 25% clipped
Biomass of *C. canescens* 75% clipped
Biomass of *C. canescens* unclipped

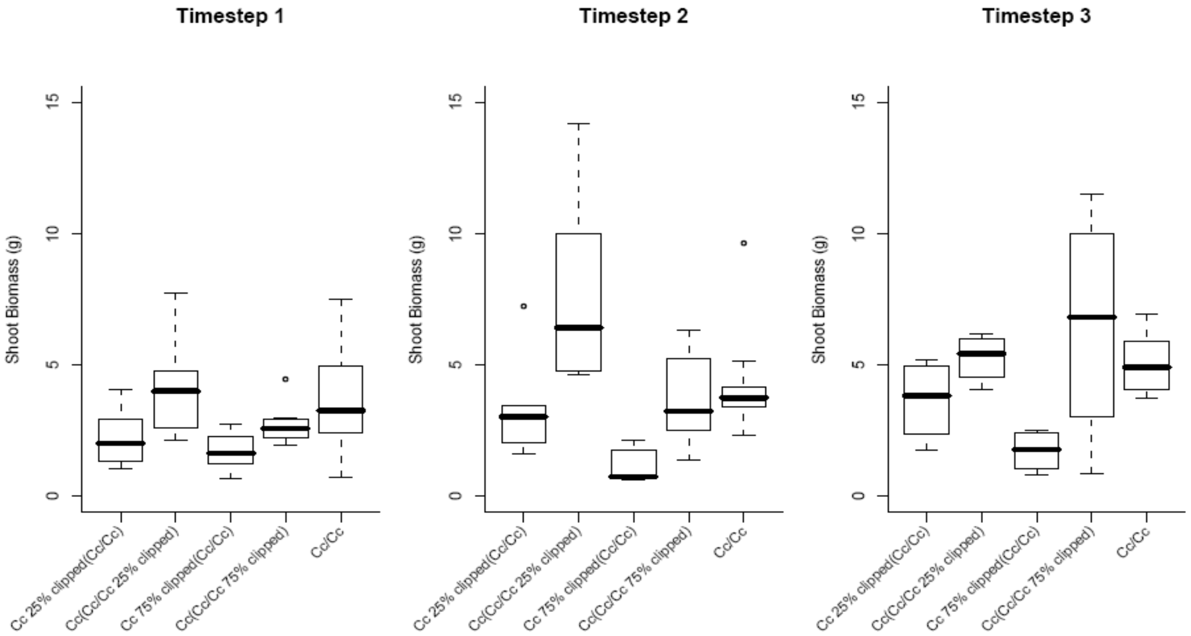


Figure 58: The effects of the two clipping treatments on the shoot biomass of *C. canescens* individuals growing in the presence of an intraspecific competitor at the three harvest timesteps (July, August and September).
All plants of timestep 1 were clipped in June and harvested in July (clipped one time).
The plants of timestep 2 were clipped in June and July (clipped two times) and harvested in August. Finally all plants of timestep 3 were clipped in June, July and August and harvested in September (clipped three times).
The y-axis shows the harvested shoot biomass. A box indicates the lower quartile (bottom), median (bold line) and upper quartile(top). Whiskers of a box indicate the sample minimum (below) and sample maximum (above). Points indicate outliers.
From left to right in each timestep:
Biomass of *C. canescens* 25% clipped (in competition with unclipped *C. canescens*).
Biomass of unclipped *C. canescens* (in competition with 25% clipped *C. canescens*).
Biomass of *C. canescens* 75% clipped (in competition with unclipped *C. canescens*).
Biomass of unclipped *C. canescens* (in competition with 75% clipped *C. canescens*).
Biomass of unclipped *C. canescens* (in competition with unclipped *C. canescens*).

Intraspecific competition (Fig. 58) reduced the aboveground biomass of the unclipped target plants by approx. 32 % compared to the values shown for the control plants in Fig. 57. 25% clipping produced no significant effects neither in the clipped/clipped nor in the clipped/unclipped treatment at all three timesteps (p1=0.087, p2=0.727, p3=0.143). However, the 75% clipped plants, competing with unclipped neighbours were not able to fully compensate the strong simulated grazing pressure and showed a significant reduction in biomass (p1=0.0117, p2=0.0034, p3=0.0002). The unclipped *C. canescens* plants growing in competition with clipped plants did not significantly benefit from this situation at both clipping levels and remained at the level of the control plants. Similar results were found for the plots with interspecific competition (Fig. 59). At the 25% clipping level *C. canescens* was able to fully compensate at all three timesteps (p1=0.077, p2=0.439, p3=0.89) while it showed significantly lower biomass values relative to the unclipped controls for the 75% clipping treatments at the last two timesteps (p1=0.152, p2=0.01, p3=0.0159).

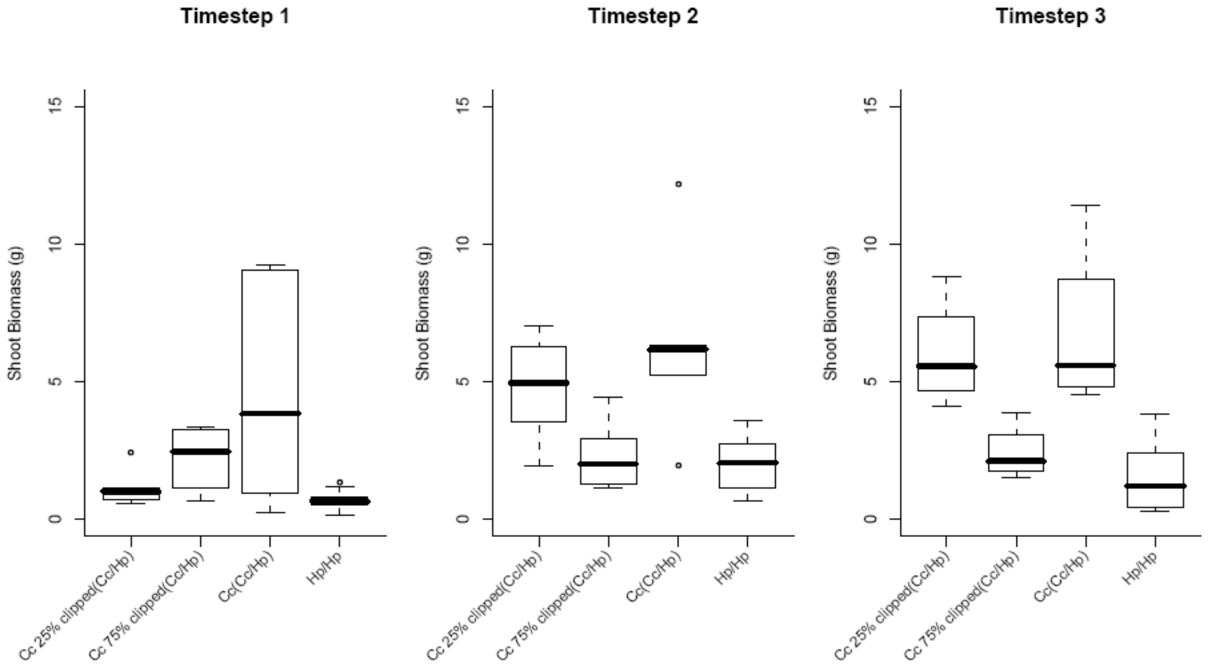


Figure 59: The effects of the two clipping treatments on the aboveground biomass of *C. canescens* individuals growing in the presence of an interspecific competitor (*H. pilosella*) at the three harvest timesteps (July, August and September). All plants of timestep 1 were clipped in June and harvested in July (clipped one time).

The plants of timestep 2 were clipped in June and July (clipped two times) and harvested in August. Finally all plants of timestep 3 were clipped in June, July and August and harvested in September (clipped three times).

The y-axis shows the harvested Shoot biomass. A box indicates the lower quartile (bottom), median (bold line) and upper quartile (top). Whiskers of a box indicate the sample minimum (below) and sample maximum (above). Points indicate outliers.

From left to right in each timestep:

Biomass of *C. canescens* 25% clipped (in competition with *H. pilosella*).
Biomass of *C. canescens* 75% clipped (in competition with *H. pilosella*).
Biomass of unclipped *C. canescens* (in competition with *H. pilosella*).
Biomass of *H. pilosella* (in competition with *H. pilosella*).

4.3.2 Belowground Effects

Figs. 60-62 show the effect of the different clipping treatments on the root area. Since the roots of the competitors could not be separated in the competition treatments the values in Fig. 61 show the total root area of two *C. canescens* plants and in Fig. 62 of one *C. canescens* and one *H. pilosella* individual.

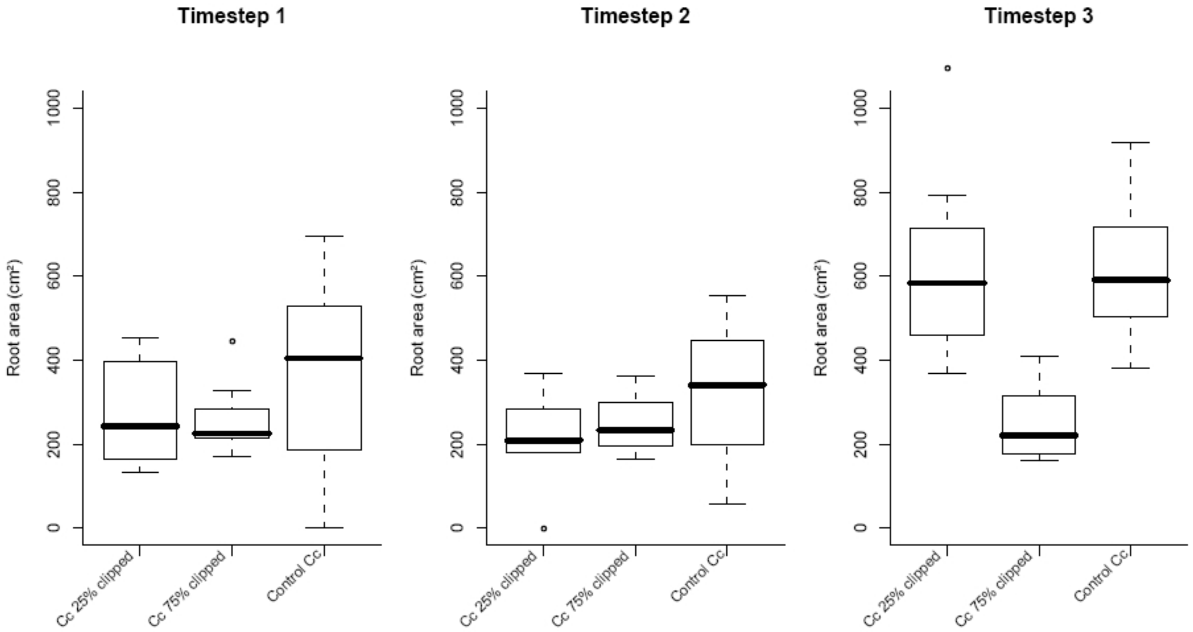


Figure 60: The effects of clipping on the root area of isolated *C. canescens* individuals at the three harvest timesteps (July, August and September). All plants of timestep 1 were clipped in June and harvested in July (clipped one time). The plants of timestep 2 were clipped in June and July (clipped two times) and harvested in August. Finally all plants of timestep 3 were clipped in June, July and August and harvested in September (clipped three times). The y-axis shows the harvested root area (cm²). A box indicates the lower quartile (bottom), median (bold line) and upper quartile (top). Whiskers of a box indicate the sample minimum (below) and sample maximum (above). Points indicate outliers.
From left to right in each timestep:
Biomass of *C. canescens* 25% clipped
Biomass of *C. canescens* 75% clipped
Biomass of *C. canescens* unclipped

Fig. 60 shows the differences between isolated clipped and unclipped *C. canescens* plants. At the first two timesteps no significant differences could be detected between the two treatments and the controls. At timestep 3 there were no differences at the 25% clipping level (p1=0.534, p2=0.51, p3=0.996) but a significant decrease at the 75% clipping treatment.(p1=0.424, p2= 0.78, p3=0.005).

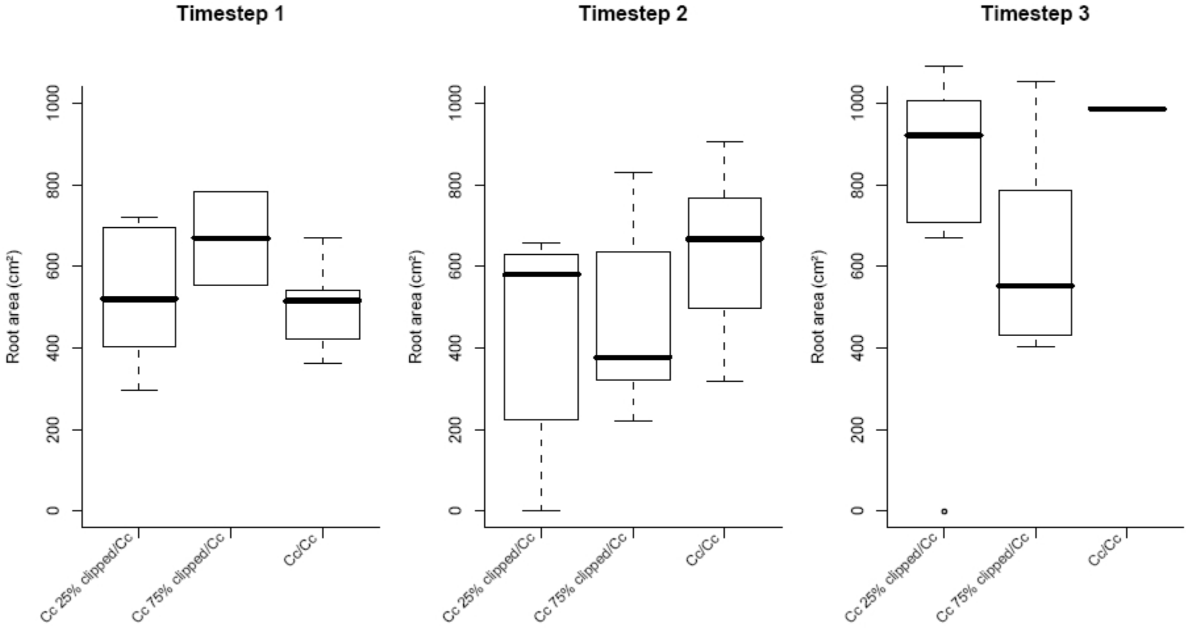


Figure 61: The effects of clipping on the root area of *C. canescens* plants growing in the presence of a intraspecific competitor at the three harvest timesteps (July, August and September). All plants of timestep 1 were clipped in June and harvested in July (clipped one time). The plants of timestep 2 were clipped in June and July (clipped two times) and harvested in August. Finally all plants of timestep 3 were clipped in June, July and August and harvested in September (clipped three times). The y-axis shows the harvested root area (cm^2). A box indicates the lower quartile (bottom), median (bold line) and upper quartile(top). Whiskers of a box indicate the sample minimum (below) and sample maximum (above). Points indicate outliers.

From left to right in each timestep:

Biomass of *C. canescens* 25% clipped (in competition with unclipped *C. canescens*)
Biomass of *C. canescens* 75% clipped (in competition with unclipped *C. canescens*)
Biomass of unclipped *C. canescens* (in competition with unclipped *C. canescens*)

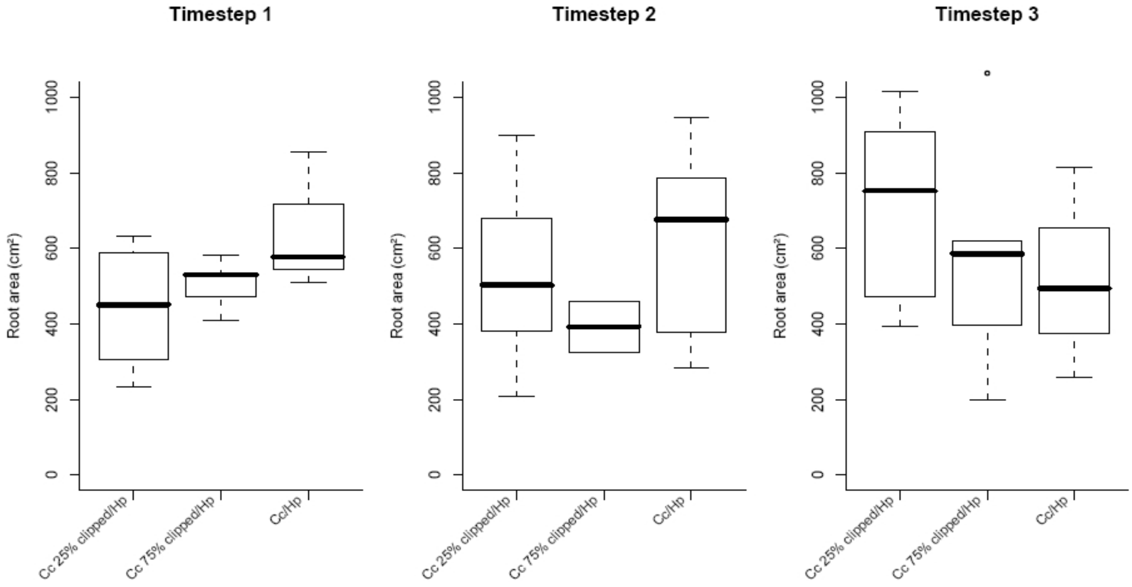


Figure 62: The effects of clipping on the root area of *C. canescens* plants growing in the presence of an interspecific competitor (*H. pilosella*) at the three harvest timesteps (July, August and September).

All plants of timestep 1 were clipped in June and harvested in July (clipped one time). The plants of timestep 2 were clipped in June and July (clipped two times) and harvested in August. Finally all plants of timestep 3 were clipped in June, July and August and harvested in September (clipped three times). The y-axis shows the harvested root area (cm^2). A box indicates the lower quartile (bottom), median (bold line) and upper quartile(top). Whiskers of a box indicate the sample minimum (below) and sample maximum (above). Points indicate outliers.

From left to right in each timestep:

Biomass of *C. canescens* 25% clipped (in competition with *H. pilosella*)
Biomass of *C. canescens* 75% clipped (in competition with *H. pilosella*)
Biomass of unclipped *C. canescens* (in competition with *H. pilosella*)

Fig. 61 shows the combined effect of intraspecific competition and clipping on the total root area of the two competitors. No significant differences between treatments and controls could be found at all three timesteps (25%: p1=0.802, p2=0.65, p3=0.954; 75%: p1=0.298, p2=0.496, p3~0.672). At the third timestep some control plants died. So a statistic evaluation was not possible in this case.

Similar results were obtained for the combination of interspecific competition with *H. pilosella* and clipping (Fig. 62). There were no significant differences for both clipping treatments timesteps (25% clipping: p1=0.058, p2=0.712, p3=0.832; 75% clipping: p1=0.164, p2=0.439, p3=0.992).

Table 9 summarizes the comparisons between treatments and controls from the experiments shown in Figs. 57-62. It contains the respective p-values of the significance tests and indicates the observed trends. An up-arrow marks overcompensation, a zero indicates full compensation and a down-arrow shows undercompensation. p-values which indicate a significant difference ($p < 0.05$) are marked in red. The * denotes the missing samples for the control of intraspecific competition at timestep 3 of Fig 61.

Table 9: Summary of the comparisons between treatments and controls from the experiments shown in Figs. 57-62. Shown are the p-values (p1-p3) of the respective post-hoc tests at the three different timesteps. Values indicating significant differences ($p < 0.05$) are marked in red .

Shoot	**Root**	**Treatment**
Cc (control unclipped)	**Cc (control unclipped)**	
0 p1=0.089, p2=0.289, p3=0.788	**0** p1=0.534, p2=0.51, p3=0.996	**Cc 25% clipped**
0 p1=0.0012, p2=0.422, p3=0.303	↓ p1=0.424, p2=0.78, p3=0.005	**Cc 75% clipped**
Cc/Cc (control unclipped)	**Cc/Cc (*control unclipped)**	
0 p1=0.087, p2=0.727, p3=0.143	**0** p1=0.802, p2=0.65, p3=0.954	**Cc 25% clipped/Cc**
↓ p1=0.0117, p2=0.0034, p3=0.0002	**0** p1=0.298, p2=0.496, p3=0.672	**Cc 75% clipped/Cc**
Cc /Hp (control unclipped)	**Cc /Hp (control unclipped)**	
0 p1=0.077, p2=0.439, p3=0.89	**0** p1=0.058, p2=0.712, p3=0.832	**Cc 25% clipped/Hp**
↓ p1=0.152, p2=0.015, p3=0.0159	**0** p1=0.164, p2=0.439, p3=0.992	**Cc 75% clipped/Hp**

4.3.3 The Effect of Clipping on the Competitive Ability of *C. canescens*

Table 10 and Fig. 63 show the calculated RNE values (based on aboveground biomass) as a relative measure for the influence of clipping on the competitive strength of *C. canescens.*
For the treatments without competition (Tab. 10, Nr. 1-2) a pseudo RNE value was calculated with the RNE formula against the *C. canescens* control as a relative measurement to estimate the effect of clipping.

Table 10: Values from the three time steps of the competition experiments shown in Figs. 57-59. The first two Treatments (1-2) were calculated with the RNE formula (Pseudo-RNE = PRNE) against the *C. canescens* control without competition as a relative measurement to estimate the effect of clipping. The following treatments (3-8) showing the results from the RNE calculations in a competition design.

Nr.	**Treatments**	**PRNE t1**	**PRNE t2**	**PRNE t3**
1	***C. canescens 25% clipped***	0.391	0.28	0.223
2	***C. canescens* 75% clipped**	0.71	0.26	0.53

Nr.	**Treatments**	**RNE t1**	**RNE t2**	**RNE t3**
3	***C. canescens/C. canescens***	0.384	0.294	0.307
4	***C. canescens/C. canescens* 25% clipped**	0.633	0.416	0.499
5	***C. canescens/C. canescens* 75% clipped**	0.718	0.794	0.764
6	***C. canescens/H. pilosella***	0.259	-0.08	0.07
7	***C. canescens/H. pilosella* 25% clipped**	0.805	0.178	0.175
8	***C. canescens/H. pilosella* 75% clipped**	0.642	0.604	0.668

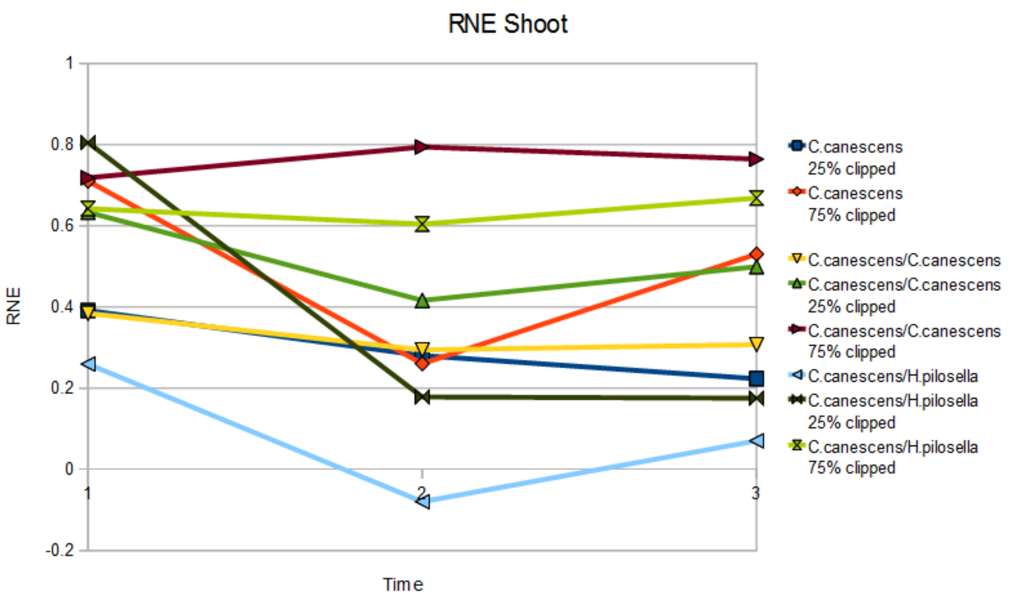


Figure 63: PRNE and RNE values from the three time steps of the competition experiments shown in Figs. 57-59

The RNE values of Table 10 and the plotted RNE values (Fig. 63) show a clear effect for the 75% clipped species indicating once more that the individuals were not able to compensate competition with species of the same kind and strong clipping (Table 10 Nr. 5 -> RNE t3 = 0.764). Comparing this result with the trend of the pure clipping effect (Table 10 Nr. 2 ->PRNE t3 = 0.53) it seems that competition causes an additional negative effect on the treated *C. canescens* target.

There seems to be no effect for the interspecific competition treatment with *H. pilosella* (Table 10 Nr. 6-> RNE t3 = 0.07) indicating no effect on the target. The clipped targets in this setup show higher RNE values (Table 10 Nr. 7, 8 -> RNE t3 = 0.175, RNE t3 = 0.668) caused by the clipping effect. The effect of competition (Table 10 Nr. 3 -> RNE t3=0.307) seems to have the same effect on the shoot biomass as the at least 25% clipped treatments without competition (Table 10 Nr. 1 -> PRNE 3=0.223) .

Generally the results from the RNE values suggest that the effect of intraspecific competition on the target plant equals the effect of soft or medium clipping. The combined effects are strongest with intraspecific competition and 75% clipping.

4.3.4 Results from the Spatial Analysis of Root Distribution

In this section the results from the spatial root analysis are presented. For all timesteps the spatial root allocation was plotted and analyzed (Figs. 64-72).

All figures are separated into two layers. The first layer shows the measured root distribution from 0 cm-7.5 cm depth. The second layer shows the root distribution from 7.5 cm-15 cm. Additionally all layers are separated into four units to enable the comparison of the left-outside of the plots (left-lateral) with the right-outside (right-lateral) and the left-middle (left-central) of the plots with the right-middle (right-central). The smaller harvested central samples (4 sections) were summarized into one section (left-central and right-central) for a sufficient analysis of the data. On the x-axis the different treatments are plotted together with their measured area (cm²) on the y-axis. For an improved visual comparison all treatments are plotted symmetrically around the y-axis for a comparison from the central sections to the lateral sections in both layers (right to left and left to right).

The first three plots show the spatial root distribution under the treatment of intraspecific competition of *C. canescens* and the two clipping factors (25% clipped, 75% clipped) at three different timesteps. In the first three plots the scissor in the legend on top of the plots displays the location of the clipped *C. canescens* plants spatially arranged for the investigation. For this analysis the results from the third timestep represents the most important data with the longest growing period and a continuous clipping pressure.

Generally for the first three plots (*C. canescens/C. canescens*) an increase of the biomass to the left side would indicate a root aggregation in the direction of the weakened clipped concurrent whereas a root aggregation to the right side would indicate an overcompensation of the clipped plants towards the concurrent. A symmetric distribution around the y-axis would indicate no effect of clipping for the spatial distribution of the roots.

For the then following three plots (*C. canescens/H. pilosella*) an increase of the biomass to the left side would indicate a root aggregation in the direction of the clipped *C. canescens* whereas an increase of the biomass to the right side would indicate that *C. canescens* is a strong competitor despite of clipping and is overcompensating. A symmetric distribution around the y-axis would indicate no effect of clipping for the spatial distribution of the roots and no interspecific competition effect.

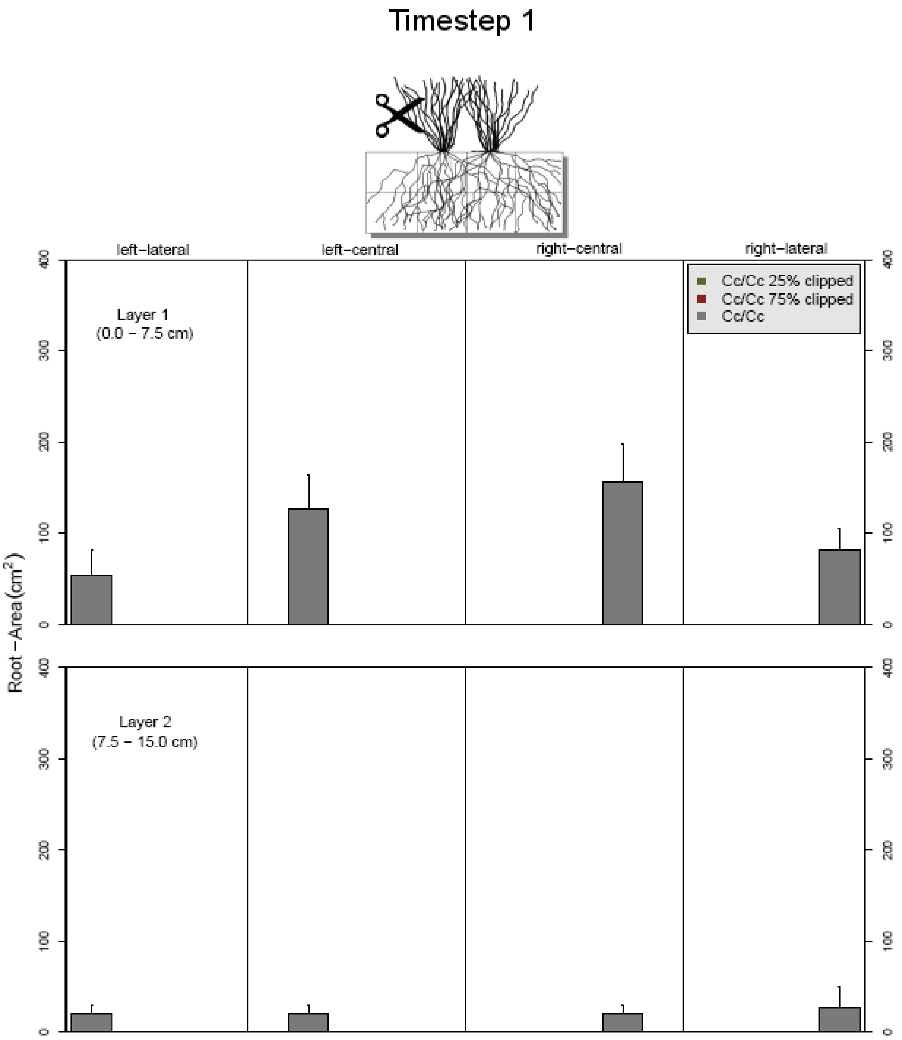


Figure 64: Root area results of two harvested layers after timestep 1. Clipped plant position on the left side. The plants of timestep 1 were clipped in June (clipped one time) and their roots were harvested in July.

In the first timestep (Fig. 64) of the *C. canescens*/*C. canescens* treatments erroneous data was collected and invalid for a further analysis. Generally this plot shows a symmetric distribution (p>0.1) with some significant values to one side in the top-center (p>0.01) and bottom center (p=0.001) but general useless for an interpretation in this early stage.

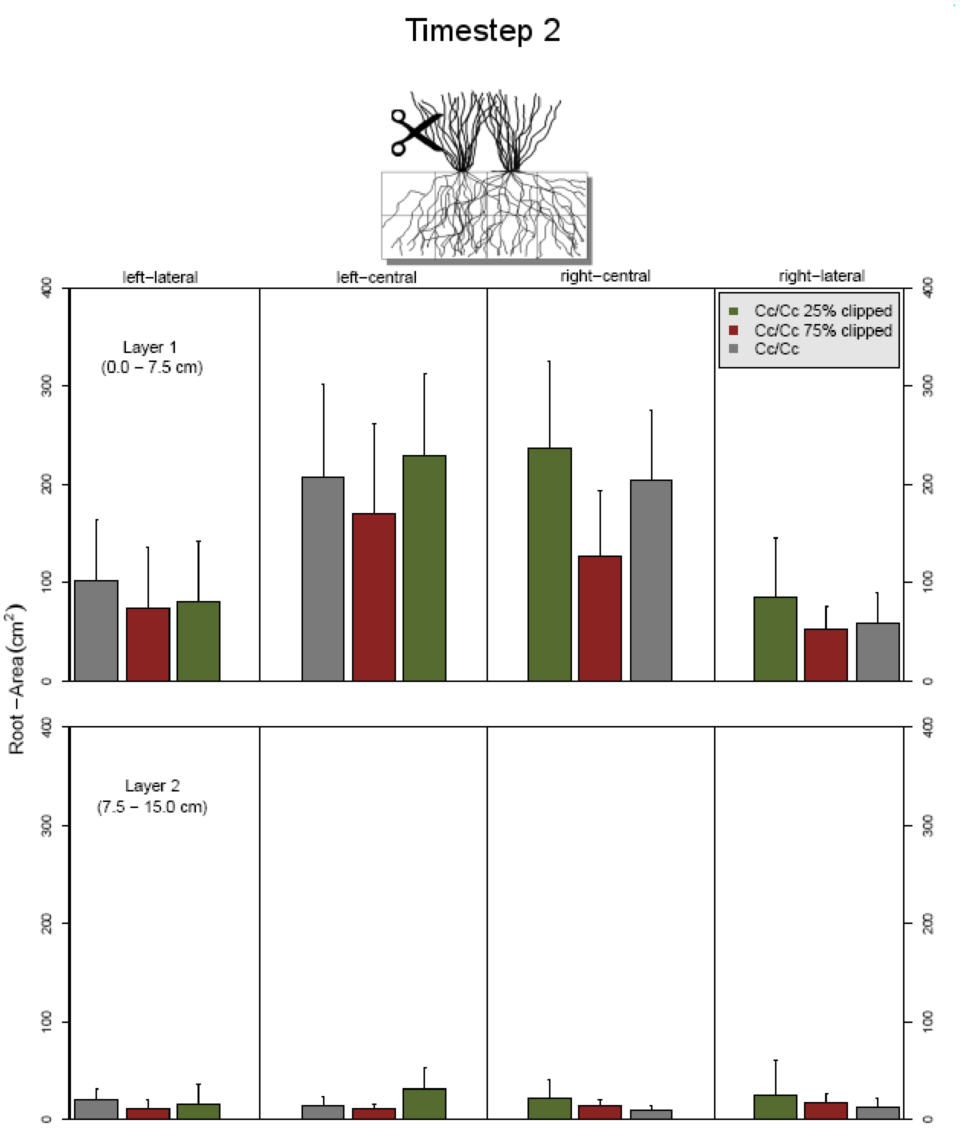


Figure 65: Root area results of two harvested layers after timestep 2. Clipped plant position on the left side. The plants of timestep 2 were clipped in June and July (clipped two times) and harvested in August.

Also in the second timestep (Fig. 65) the statistical analysis revealed no asymmetry between the left and the right side (p>0.1) indicating an aggregation-segregation of roots due to competition and clipping. Once more in the third timestep (Fig. 66) no significant aggregation-segregation (p>0.1; exception is Cc/Hp bottom-lateral with p>0.02) to one side could be found in the analysis despite of the fact that one *C. canescens* individual was continuously clipped and damaged. In this timestep the *C. canescens* control couldn't be used for analysis because of the invalid amount of samples leading to a visual aggregation in this plot.

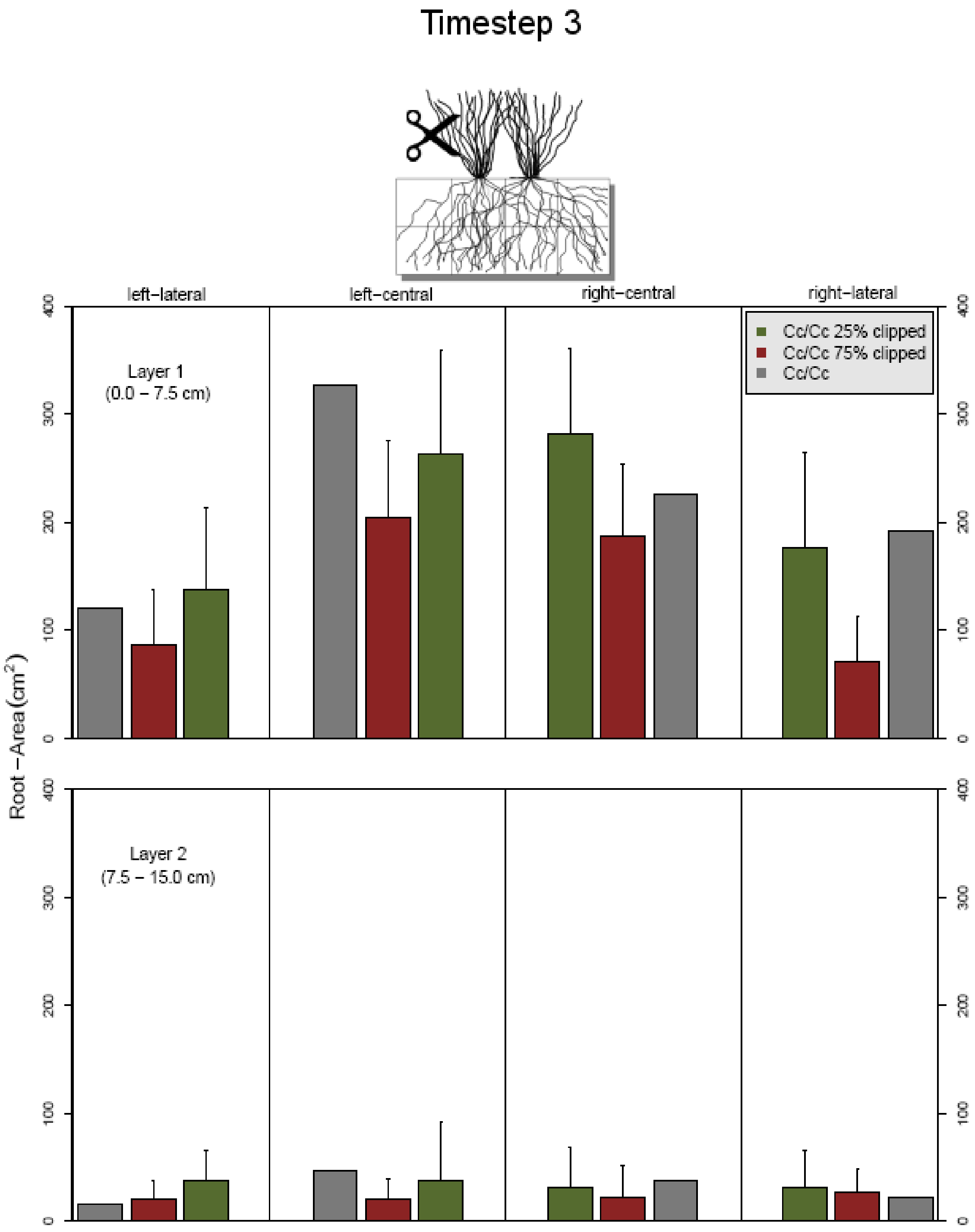


Figure 66: Root area results of two harvested layers after timestep 3. Clipped plant position on the left side. The plants of timestep 3 were clipped in June, July and August (clipped three times) and their roots were harvested in September.

In the next three plots (Fig. 67-69) the results of interspecific competition with *H. pilosella* and the two clipping factors are shown at three different timesteps. The legend on top of the plots displays the location of the species for the analysis. Again the analysis from the early harvested roots in Figure 67 revealed no significant root aggregation or segregation in the first layer as well as in the second layer (p>0.1; 1*0.091).

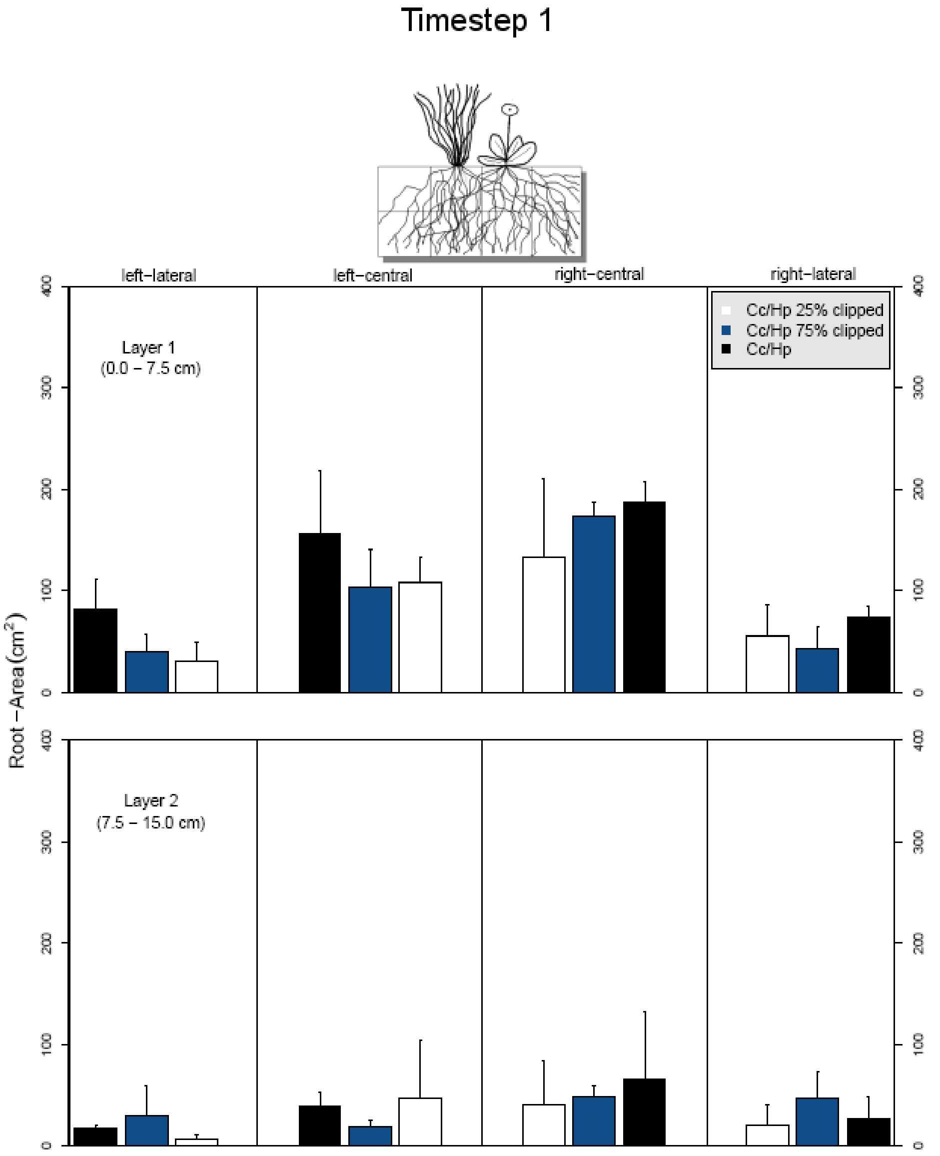


Figure 67: Root area results of two harvested layers after timestep 1. *H. pilosella* position on the right side. The plants of timestep 1 were clipped in June (clipped one time) and their roots were harvested in July.

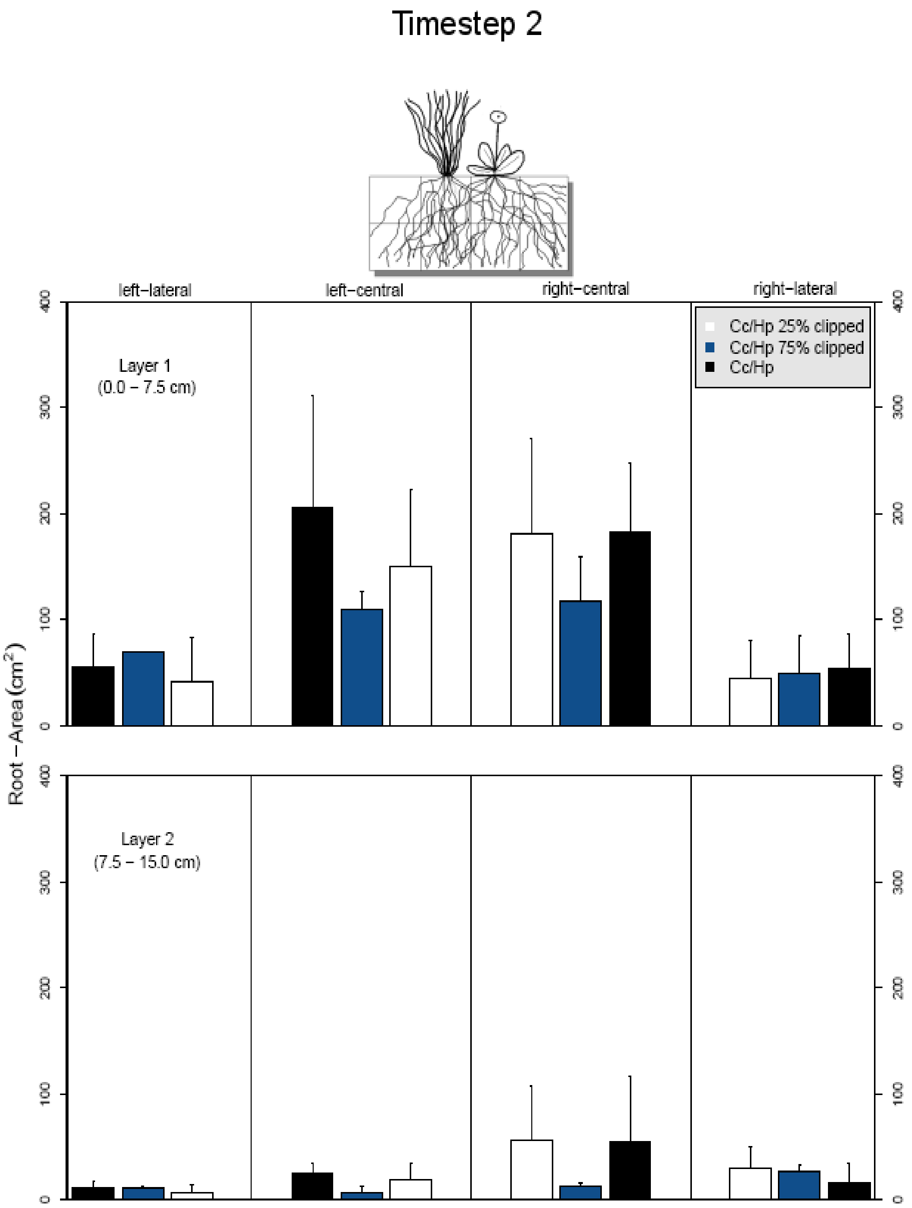


Figure 68: Root area results of two harvested layers after timestep 2. *H. pilosella* position on the right side. The plants of timestep 2 were clipped in June and July (clipped two times) and harvested in August.

In both layers no statistical relevant differences could be found comparing the lateral sections and the central sections. These results were also found for the second timestep in Figure 68 with a longer period of growth. Also this results suggest a strong symmetric distribution from the central sections to the lateral sections in both layers. Finally in the third timestep (Fig. 69) of the interspecific competition treatment between *Corynephorus canescens* and *Hieracium pilosella* with the longest period of growth once more no significant aggregation or segregation occurred.

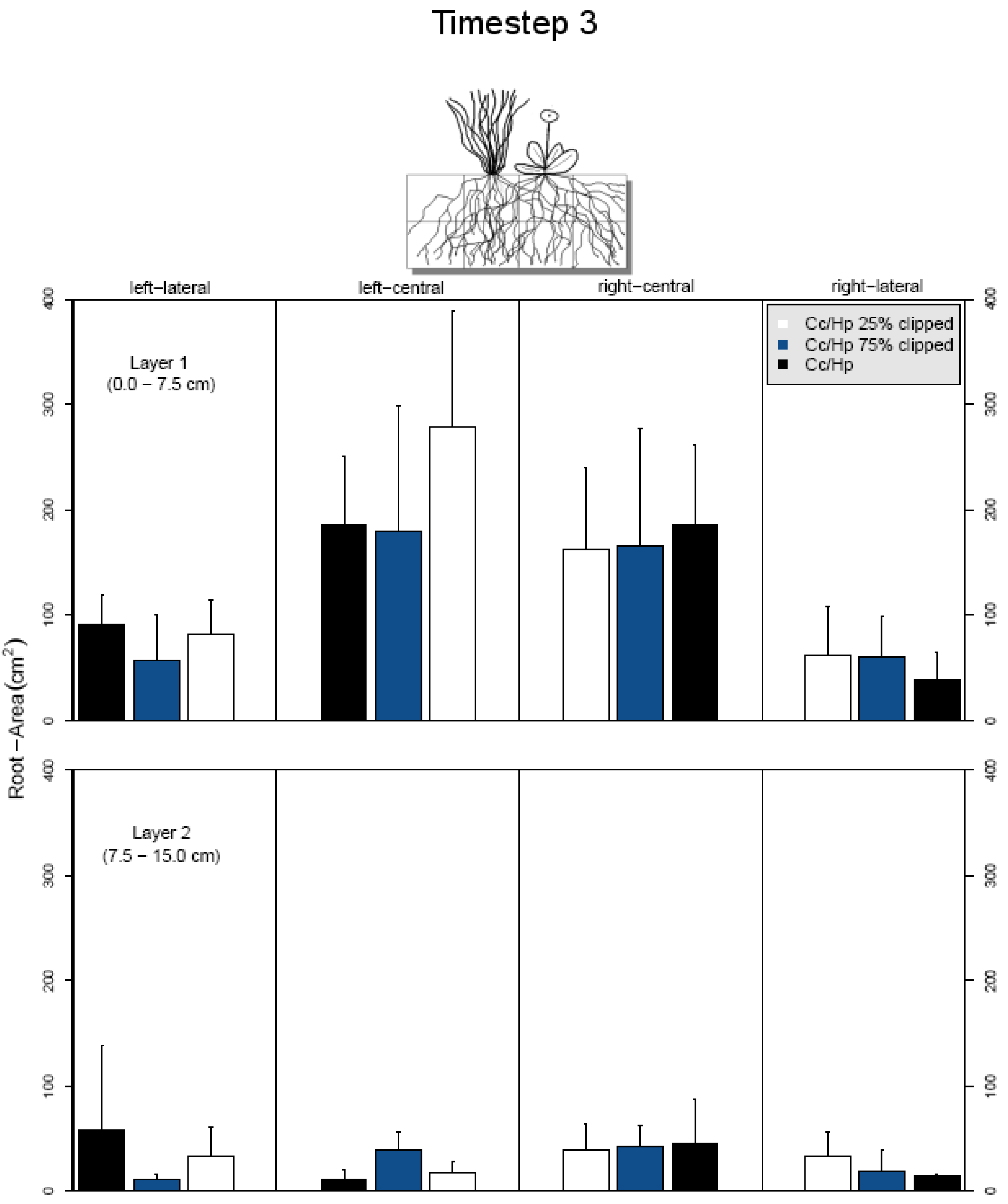


Figure 69: Root area results of two harvested layers after timestep 3. *H. pilosella* position on the right side. The plants of timestep 3 were clipped in June, July and August (clipped three times) and their roots were harvested in September.

The last three plots (Fig 70-72) show the results of *C. canescens* growing without any competition and with two clipping treatments in three different timesteps. Generally the root area decreases under heavier clipping. The root area on the left empty side is generally lower because of the missing neighbor.

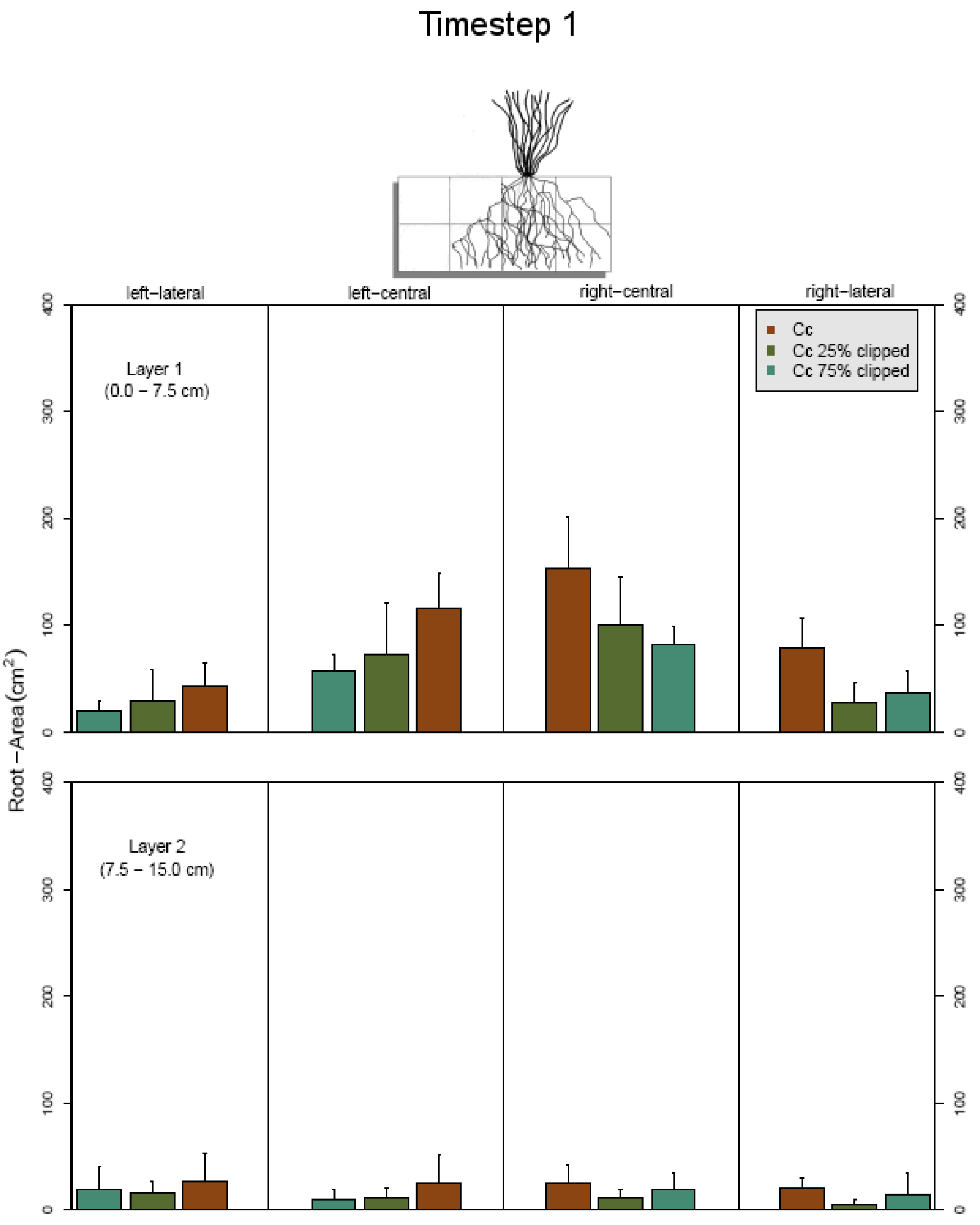


Figure 70: Root area results of two harvested layers after timestep 1. *C. canescens* position on the right side growing without competition. The plants of timestep 1 were clipped in June (clipped one time) and their roots were harvested in July.

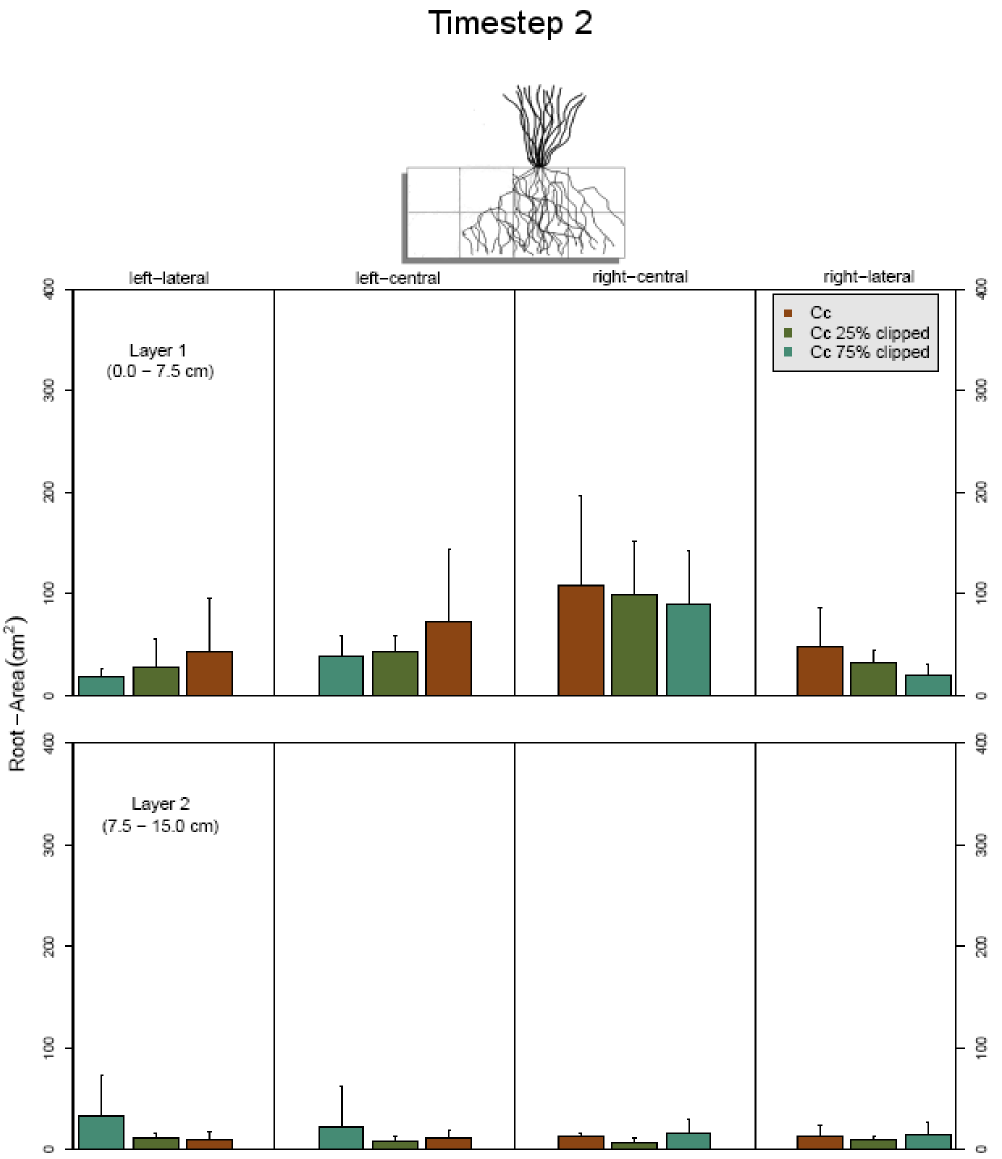


Figure 71: Root area results of two harvested layers after timestep 2. *C. canescens* position on the right side growing without competition. The plants of timestep 2 were clipped in June and July (clipped two times) and their roots were harvested in August.

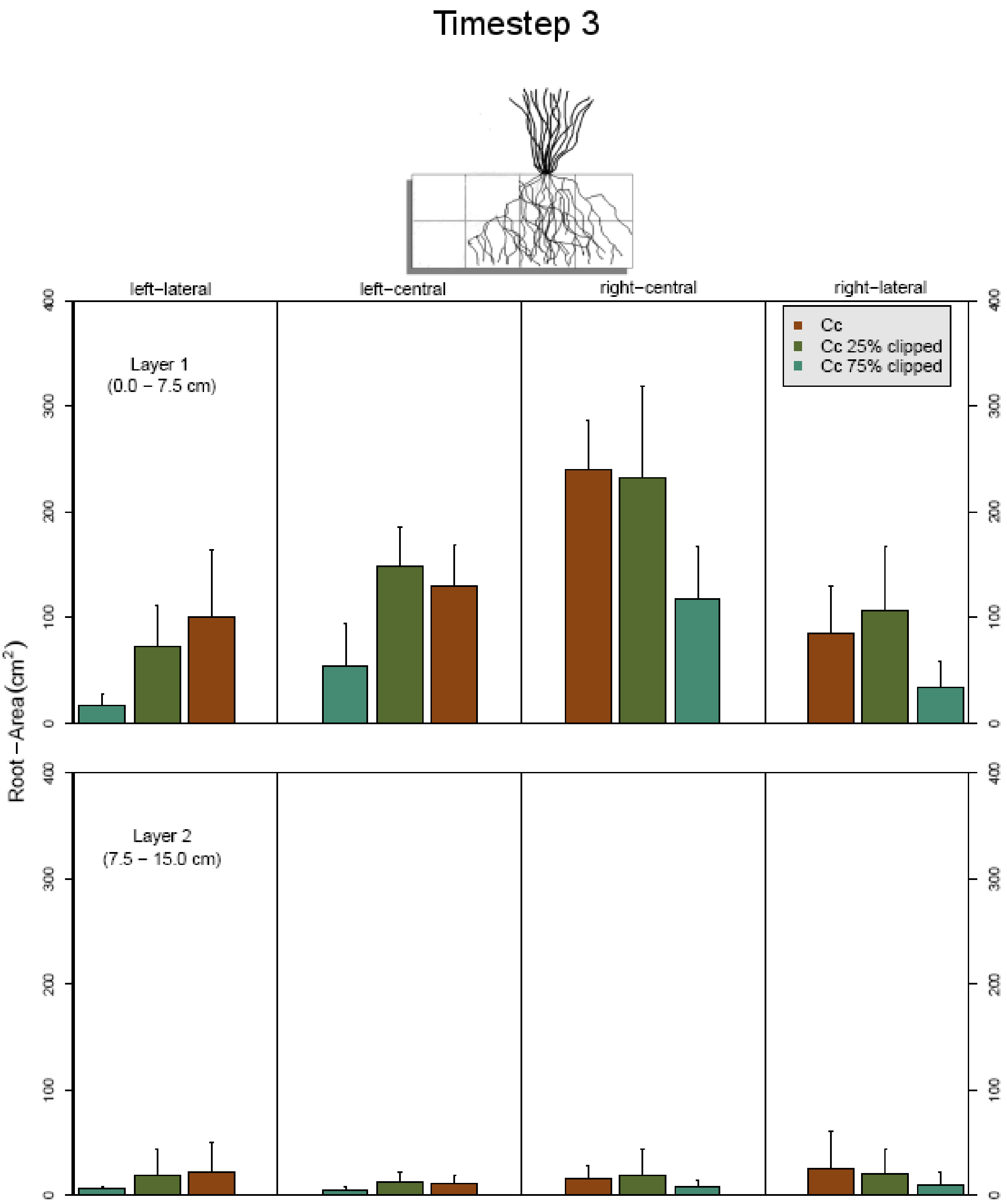


Figure 72: Root area results of two harvested layers after timestep 3. *C. canescens* position on the right side growing without competition. The plants of timestep 3 were clipped in June, July and August (clipped three times) and their roots were harvested in September.

4.4 Discussion

Herbivory reduces living plant material and can be rather disadvantageous for the respective plant individuals (MITCHLEY & WILLEMS 1995, HODGSON & ILLIUS 1998, VALLENTINE 2001). Timing (e.g. before or after reproduction), the amount of foliage removed, the kind of the resulting damage, environmental conditions and also species specific (i.e. genetic) factors are often important determinants for the plants potential to restore itself (MASCHINSKI & WHITHAM 1989, SIMONS & JOHNSTON 1999). Controversial results have been described for the role of simultaneous competitive pressure, which has been found to either amplify the herbivory effects or to have no effect at all. (READER 1992, MCEVOY et al. 1993, WARDLE & BARKER 1997).

4.4.1 Is *C. canescens* able to Compensate or even Overcompensate Foliage Removal?

The above- and belowground data of the present experiment lead to the conclusion that *C. canescens* is obviously able to completely compensate low to medium scale foliage losses. No significant differences were found between the controls and the 25% clipped plants. Further, no significant influence of simultaneous competitive pressure was detectable. These results are in accordance to other grassland studies showing that slight or moderate grazing had no negative effect and could even increase the aboveground biomass and the biodiversity compared to ungrazed areas (MCNAUGHTON 1979, HIK & JEFFERIES 1990, COLLINS et al. 1998, FRANK et al. 2003). It is well known, that compensation of herbivory in grasses works best if the herbivory event (as in the present study) occurs before the reproductive phase (MASCHINSKI & WHITHAM 1989, LEHTILA & SYRJANEN 1995, ESCARRE et al. 1996, LENNARTSSON et al. 1998). *C. canescens* reproduces solely by seeds and the persistence of the species is therefore highly dependent on its flowers. Living as pioneer species in an environment with a high disturbance frequency (FRIEDRICH et al. 2006) including oversanding (LUX 1964) and herbivory, an effective regrowth strategy seems to be a key adaptation in this connection. Overcompensation, a frequently observed phenomenon after herbivory in grasslands (ALWARD & JOERN 1993, LENNARTSON et al. 1998) did not occur which is probably due to the limiting water and nutrient conditions on sand. Heavy grazing typically reduces the biomass production of grasslands (WANG & RIPLEY 1997, SHANG et al. 2003). Accordingly the results of the 75% clipping treatment at timestep 3 (i.e. after repeated heavy foliage loss) show significant negative effects on the aboveground biomass (Fig. 60).

4.4.2 How does the Presence of a Competitor Affect Compensatory Growth?

Looking at the aboveground biomass data and the resulting RNE-values, intraspecific competition had no effect on the regrowth of clipped *C. canescens* plants at the 25% clipping level (Figs. 58, 63). This was different for the 75% clipping treatment which revealed a strong negative effect of at all three timesteps (Figs. 58, 63). Interspecific competition with *H. pilosella* revealed no competitive effect of this species up to a clipping level of 25% (Figs. 59, 63) generally identifying *H. pilosella* as a rather weak competitor.

This finding is in accordance to the results of Weigelt (2001) and Barthelheimer (2005) which came to the same conclusion that *H. pilosella* is a weak competitior on the early stages of dry acidic grasslands. One reason for this result is certainly the low availability of nutrients on the sand whereas *C. canescens* is a strong competitor and grows vigorously under this conditions with an advantage towards *H. pilosella* (WEIGELT et al. 2005). Furthermore the root architecture of both plants differs in morphology. The root morphology of *C. canescens* indicates a high adaption on sand to explore resources from deep soil layers with its extensive root architecture (ELLENBERG 1996).

Root systems of bigger competitors, especially the grasses, grow well into the space of competing smaller plants and use the resources. These bigger neighbor root systems are more likely to co-occupy a plant’s rooting volume and will reduce the nitrate concentration within (TILMAN & WEDIN 1991, BARTHELHEIMER et al. 2006). It's likely that *C. canescens* can use the resources on the *H. pilosella* side to compensate foliage losses. Barthelheimer (2005) found a direct relation between the size of the root system and the ability to affect the nitrate uptake of the neighbouring plant.

In contrast *H. pilosella* with smaller roots shows enhanced clonal growth under these resource poor conditions and seems to invest more biomass towards the exploration of new resources which in consequence again additionally benefits *C. canescens.*

4.4.3 Is there a Measurable Effect of Aggregation or Segregation of the Roots under Herbivory and/or Competition?

The ability of a plant to uptake water and nutrients is bound to a general root plasticity which increases the potential resource availability (BRADSHAW 1965, GRIME 1986, SULTAN 1987, SCHREINER 1993). After Grime (1986) high morphological plasticity is part of the foraging mechanisms which project new leaves and roots into the resource-rich zones of the constantly changing environmental mosaic created by the activity of competing plants. According to several authors competing root systems frequently avoid each other by foraging solely in resource-rich soil areas (HUTCHINGS & DE KROON 1994, KRANNITZ & CALDWELL 1995). Defoliation of plants can change root topology and root branching (ARREDONDO & JOHNSON 1998, 1999) and grazing tolerant plants often temporarily reduce root growth after being grazed (DAVIDSON & MILTTHORPE 1966, RICHARDS & CALDWELL 1985). After Schenk et al. (1999) similar root morphology of two competitors typically suggests an avoiding growth strategy. Weigelt (2001) and Weigelt et al. (2005) found for *C. canescens* no changes in root allocation patterns in response to the presence of a competitor. This contradicts the results of Bartelheimer et al. (2006) who found for the same species and under comparable conditions significant aggregation effects towards a competing root system. The results of the present work, however, support the findings of Weigelt et al. (2005) because there were no significant effects of clipping intensity and/or intra- or interspecific competition on root allocation of *C. canescens* at all timesteps (Figs. 64-69).

Two popular hypotheses have been formulated to explain competition in plant communities along productivity gradients. After Grime (1979) and Huston (1979) competition is stronger in highly productive environments and is lower in less productive sites. For Newman (1973) and Tilman (1982, 1987) the amount of competition interaction is independent of availability of growth resources but the mechanism of competition can differ. In productive systems, plants compete for light or space while in unproductive systems plants compete for water and soil nutrients. The early successional stages of dry acidic grasslands are nutrient and water limited and typically exhibit low plant productivity. The present results couldn't be explained by the theory of Grime (1979) because the results show a clear competition effect at least in the intraspecific competition design (see Tab. 10 and Fig. 63) whereas both species are highly adapted to the nutrient poor conditions. These results are in accordance with the findings of Weigelt et al. (2005) and Barthelheimer (2005) where competition plays an important role in the early stages of dry acidic grasslands and *C. canescens* is a strong competitor under this nutrient poor conditions also for itself.

However the results suggest that moderate foliage loss did not majorly affect the belowground competitive interactions on the early stages of dry acidic grasslands.

The question arises if foliage removal has a stronger effect on the overall fitness than competition. But studies about a comparison between the effect of competition and the effect of herbivory are rare. Results of different works e.g. on temperate salt marshes (DORMANN et al. 2000) suggest a stronger effect of species competition whereas some authors found this effect primarily on sites with relatively low biomass (BONSER & READER 1995).

From the aboveground biomass data in Figs. 57-59 and the RNE values in Fig. 63 it can be concluded that the effect of intraspecific competition approximately balances the compensatory growth at least at moderate (25%) clipping rates. At higher damage rates (75%) it seems that the effect of clipping is stronger.

In conclusion the results of the present experiments reject the introductory hypothesis, that foliage removal would have a dramatic negative effect on plant fitness and that this effect would be enhanced by the presence of a competitor, due to the limited nutrient supply in this sandy environment. Since the effects of foliage removal with or without competition seem to be more or less negligible (but see 4.5) they will not be integrated in the above described simulation model for the time being.

4.5 Outlook

Clipping is not necessarily equal to herbivory. Additional to the loss of foliage real herbivores frequently induce an induction of chemical defenses (BALDWIN & SCHULTZ 1983, KARBAN & BALDWIN 1997, THALER 1999, HEIL et al. 2001, FARMER 2001, HARUTA et al. 2001, ENGELBERTH 2004, HEIL 2004, VAN DAM et al. 2004, KOST & HEIL 2006, MIRANDA et al. 2007). Furthermore, numerous reactions of the plant's immune system induced by the saliva of the grazer have been described (DETLING et al. 1980,

MCNAUGHTON 1985, FELTON & EICHENSEER 1999, ROOKE 2003).

Further the relationship between nutrient supply and herbivory has been investigated by numerous authors revealing a heterogeneous scenario with either positive or negative effects on plant production (JEFFERIES 1988, RICKLEFS & MILLER 2000), and accelerating (MCNAUGHTON 1985, TILMAN 1982, 1988, DEANGELIS et al. 1989, RUESS et al. 1989, HOLLAND & DETLING 1990, STERNER 1994) or slowing down nutrient uptake (NAIMAN et al. 1986, TILMAN 1988, LEIBOLD 1989, BRYANT et al. 1991, PASTOR & NAIMAN 1992, WILSON & AGNEW 1992, WEDIN 1994). This relationship has also been shown to affect biodiversity e.g. by controlling the population of nitrogen fixing species (VITOUSEK & HOWARTH 1991, RITCHIE & TILMAN 1995).

Because information on nutrients has non been collected during the present work we could not directly proof if the applied clipping of the plants changed the activity of nitrogen fixing species and the accompanying nutrient availability. Furthermore the effect of nutrient uptake, chemical responses and metabolistic reactions have not been assessed. So the result that the effect of moderate foliage loss and/or competition seems to be negligible in *C. canescens* needs to be verified under more realistic field conditions (e.g. by means of in situ herbivore exclusion experiments) and in laboratory experiments measuring the chemical responses explicitly.

5. Reference List

Adler PB, Raff DA, Lauenroth WK (2001) The effect of grazing on the spatial heterogeneity of vegetation. Oecologia 128:465–479.

Aerts R, Boot R, Van der Aart (1991) The relation between above- and belowground biomass allocation patterns and competitive ability. Oecologia 1991:551–559.

Akay AE, Oguz H, Karas IR, Aruga K (2009) Using LiDAR technology in forestry activities. Environmental Monitoring and Assessment 151:117–125.

Al-Agely AK, Reeves FB (1995) Inland Sand Dune Mycorrhizae: Effects of Soil Depth, Moisture, and pH on Colonization of *Oryzopsis hymenoides*. Mycologia 87:54–60.

Alward R, Joern A (1993) Plasticity and overcompensation in grass responses to herbivory. Oecologia 1993:358–364.

Anders K, Mrzljak J, Wallschläger D, Wiegleb G (2004) Handbuch Offenlandmanagement. Am Beispiel ehemaliger und in Nutzung befindlicher Truppenübungsplätze. Springer, Berlin.

Arredondo JT, Johnson DA (1998) Clipping effects on root architecture and morphology of 3 range grasses. Journal of Range Management 51:207–213.

Arredondo JT, Johnson DA (1999) Root architecture and biomass allocation of three range grasses in response to nonuniform supply of nutrients and shoot defoliation. New Phytologist 143:373–385.

Baddeley A, Turner R (2005) spatstat: An R package for analyzing spatial point patterns. Journal of Statistical Software 12:1–42.

Bakker JP (1989) Nature management by Grazing and Cutting. Kluwer Academic Publishers, Dordrecht.

Baldwin IT, Schultz JC (1983) Rapid Changes in Tree Leaf Chemistry Induced by Damage: Evidence for Communication Between Plants. Science 221:277–279.

Balzter H, Braun P, Kohler W (1998) Cellular automata models for vegetation dynamics. Ecological Modelling 107:113–125.

Barbaro L, Dutoit T, Cozic P (2001) A six-year experimental restoration of biodiversity by shrub-clearing and grazing in calcareous grasslands of the French Prealps. Biodiversity and Conservation 10:119–135.

Bartelheimer M (2005) Pflanzliche Interaktionen in ressourcenarmen Sandökosystemen: Die Bedeutung funktioneller und morphologischer Wurzelparameter für die unterirdische Konkurrenzfähigkeit. Dissertation, University Bielefeld, Bielefeld.

Bartelheimer M, Steinlein T, Beyschlag W (2006) Aggregative root placement: A feature during interspecific competition in inland sand-dune habitats. Plant and Soil 280:101–114.

Bauernschmitt G, Grebe R (1997) Pflege und Entwicklungsplan Naturschutzgebiet Tennenloher Forst. Gutachten, Planungsbüro Grebe, Nürnberg.

Belsky AJ (Jun., 1986) Does Herbivory Benefit Plants? A Review of the Evidence. The American Naturalist 127:870–892.

Belsky AJ, Carson WP, Jensen CL, Fox GA (1993) Overcompensation by plants: herbivore optimization or red herring? Evolutionary Ecology 7:109–121.

Berendse F, Elberse W (1990) Competition and nutrient availability in heathland and grass ecosystems. In: Grace J, Tilman D, editors. Perspectives on plant competition. San Diego, CA: Academic press. pp. 93–116.

Bergelson J, Crawley MJ (1992) Herbivory and *Ipomopsis aggregata*: The disadvantages of being eaten. The American Naturalist 139:870–882.

Berger-Landefeldt U, Sukopp H (1965) Zur Synökologie der Sandtrockenrasen, insbesondere der Silbergrasflur. Verh. Bot. Ver. Brandenburg:41–98.

Berni JA, Zarco-Tejada PJ, Suarez L, Fereres E (2009) Thermal and Narrowband Multispectral Remote Sensing for Vegetation Monitoring From an Unmanned Aerial Vehicle. IEEE Transactions on Geoscience and Remote Sensing 47:722–738.

Berthold M, Cebron N, Dill F, Fatta G, Gabriel T, Georg F, Meinl T, Ohl P, Sieb C, Wiswedel B (2006) Knime: The Konstanz Information Miner. Technical Report (http://www.knime.org/).

Bigger D, Marvier M (1998) How different would a world without herbivory be? A search for generality in ecology. Integrative Biology 1:60–67.

Bishop GF, Davy AJ (1994) *Hieracium pilosella* L. (Pilosella officinarum F.Schultz & Schultz-Bip.). Journal of Ecology 82:195–210.

Bivand RS, Pebesma EJ, Gómez-Rubio V (2008) Applied spatial data analysis with R. Springer, New York, NY.

Blaschke T, Lang S (2007) Landschaftsanalyse mit GIS. Ulmer, Stuttgart.

Bobbink R, Hornung M, Roelofs JG (1998) The effects of air borne pollutants on species diversity in natural and semi natural European vegetation. Journal of Ecology 86:717–738.

Böger S (2002) Keimlingsbildung und Ausbreitung des Silbergrases *Corynephorus canescens*. Diploma Thesis, University Erlangen-Nürnberg, Erlangen.

Böger S (2007) Ausbreitung, Etablierung und Populationsgenetik des Silbergrases (*Corynephorus canescens* (L.) P.BEAUV.) als Grundlage zur Konzeption eines überregionalen Biotopverbundes für Sandmagerrasen in Deutschland. Dissertation, University Bayreuth, Bayreuth.

Böhm W (1979) Methods of studying root systems. Springer Verlag, Berlin, Heidelberg, New York.

Böhner J, McCloy K, Strobl J (2006) SAGA – Analysis and Modelling Applications. Göttinger Geographische Abhandlungen, Vol.115, 130pp.

Bolker B (2008) Ecological Models and Data in R. Princeton University Press.

Bonser S, Reader R (1995) Plant competition and herbivory in relation to vegetation biomass. Ecology 1995:2176–2183.

Bork EW, Su JG (2007) Integrating LIDAR data and multispectral imagery for enhanced classification of rangeland vegetation: A meta analysis. Remote Sensing of Environment 111:11–24.

Bowden R (Jun., 1991) Inputs, Outputs, and Accumulation of Nitrogen in an Early Successional Moss (Polytrichum) Ecosystem. Ecological Monographs 61:207–223.

Bradley BA (2009) Regional analysis of the impacts of climate change on cheatgrass invasion shows potential risk and opportunity. Global Change Biology 15:196–208.

Bradshaw AD (1965) Evolutionary significance of phenotypic plasticity in plants. Advances in Genetics 13:115–155.

Breiman L (1993) Classification and regression trees. Chapman & Hall, New York.

Bronstein IN, Semendjajew KA, Musiol G, Mühlig H (2001) Taschenbuch der Mathematik, 5. Aufl. Deutsch, Thun.

Brown JH, Valone TJ, Curtin CG (1997) Reorganization of an arid ecosystem in response to recent climate change. Proceedings of the National Academy of Sciences of the United States of America 94:9729–9733.

Bryant JP, Provenza FD, Pastor J, Reichhardt PB, Clausen TP, du Toit JT (1991) Interactions Between Woody Plants and Browsing Mammals Mediated by Secondary Metabolites. Annual Review of Ecology and Systematics 22:431–446.

Bullock JM, Hill BC, Silvertown J, Sutton M (1995) Gap colonization as a source of grassland community change: effects of gap size and grazing on the rate and mode of colonization by different species. Oikos 72:273–282.

Büren-Rieder H (2000) Generative und vegetative Reproduktion bei *Corynephorus canescens*. Diploma Thesis, University Berlin, Berlin.

Burger W, Burge M (2008) Digital image processing. An algorithmic introduction using Java, 1. ed. Springer, New York.

Burkhardt M, Hinrichsen A, Kühling M, Oehlschlaeger S, Wallschläger D, Wiegleb G, Wolters S (2004) Einführung: Offene Sandlandschaften Mitteleuropas, Truppenübungsplätze und Naturschutz. In: Anders, Mrzljak, Wallschläger, Wiegleb -Handbuch Offenlandmanagment. Springer Verlag, Heidelberg, New York.

Byers JA (1992) Dirichlet tessellation of bark beetle spatial attack points. Journal of Animal Ecology 61:759–768.

Caldwell MM, Dawson TE, Richards JH (1998) Hydraulic lift: consequences of water efflux from the roots of plants. Oecologia 113:151–161.

Camazine S (2003) Self-organization in biological systems, 2. print. and 1. paperback print. Princeton Univ. Press, Princeton, NJ.

Campbell SL, Chancelier JP, Nikoukhah R (2006) Modeling and simulation in Scilab/Scicos. Springer, New York, NY.

Claude J (2008) Morphometrics with R. Springer, New York, NY.

Cleland EE, Chuine I, Menzel A, Mooney HA, Schwartz MD (2007) Shifting plant phenology in response to global change. Trends in Ecology & Evolution 22:357–365.

Colasanti RL, Grime JP (1993) Resource dynamics and vegetation processes: a deterministic model using two-dimensional cellular automata. Functional Ecology 7:169–176.

Collins SL, Knapp AK, Briggs JM, Blair JM, Steinauer EM (1998) Modulation of diversity by grazing and mowing in native tallgrass prairie. Science 280:745–747.

Corradini P, Clément B (1999) Growth pattern and modular reiteration of a hardy coloniser *Polytrichum commune* Hedw. Plant Ecology 143:67–76.

Crawley MJ (2007) The R book. Wiley, Chichester.

Cressie N (1993) Statistics for spatial data, Rev. ed. Wiley, New York, NY.

Czárán T (1998) Spatiotemporal models of population and community dynamics, 1. ed. Chapman & Hall, London.

Davidson J, Milthorpe F (1966) The effect of defoliation on the c balance in *dactylos glomerata*. Annals of Botany 30:185–198.

De Knegt HJ, Groen TA, van Vijver C de, Prins HH, van Langevelde F (2008) Herbivores as architects of savannas: inducing and modifying spatial vegetation patterning. Oikos 117:543–554.

DeAngelis D, Mulholland P, Palumbo A, Steinman A, Huston M, Elwood J (1989) Nutrient dynamics and food-web stability. Annual Review of Ecology and Systematics 20:71–95.

Detling JK, Dyer MI, Procter-Gregg C, Winn DT (1980) Plant-herbivore Interactions: Examination of Potential Effects of Bison Saliva on Regrowth of *Bouteloua gracilis* (H.B.K.) Lag. Oecologia 45:26–31.

Deutsch A, Dormann S (2005) Cellular automaton modeling of biological pattern formation. Characterization, applications, and analysis. Birkhäuser, Boston, Mass.

Deutschman D, Simon S, Devine C, Buttel L (1997) Scaling from Trees to Forests: Analysis of a Complex Simulation Model. Science 277:1688.

Dicke Ma (1988) Using fractal dimensions for characterizing tortuosity of animal trails. Physiological Entomology 1988:393–398.

Diggle PJ (2003) Statistical analysis of spatial point patterns, 2. ed. Arnold, London.

Dormann C, van der Wal R, Bakker J (2000) Competition and herbivory during salt marsh succession: the importance of forb growth strategy. Journal of Ecology 88:571–583.

Douglas ME, Douglas, Lynch JM, McElroy DM (2001) Use of geometric morphometrics to differentiate *Gila* (Cyprinidae) within the upper Colorado River basin. Copeia 2001:389–400.

Downs J, Horner M (2007) Joni Downs, Mark Horner, "Network-based Home Range Analysis Using Delaunay Triangulation," International Symposium on Voronoi Diagrams in Science and Engineering, pp. 255-259, 4th International Symposium on Voronoi Diagrams in Science and Engineering (ISVD 2007).

Dryden I, Mardia K (1998) Statistical shape analysis. Wiley, Chichester.

Dukes JS, Mooney HA (1999) Does global change increase the success of biological invaders? Trends in Ecology & Evolution 14:135–139.

Dyer MI, Bokhari UG (1976) Plant-Animal Interactions: Studies of the Effects of Grasshopper Grazing on Blue Grama Grass. Ecology 57:762–772.

Eaton JW (2002) GNU Octave Manual. Network Theory Limited.

Ellenberg H (1996) Vegetation Mitteleuropas mit den Alpen. In ökologischer, dynamischer und historischer Sicht, 5. Aufl. Ulmer, Stuttgart.

Engelberth J, Alborn HT, Schmelz EA, Tumlinson JH (2004) Airborne signals prime plants against insect herbivore attack. Proceedings of the National Academy of Sciences of the United States of America 101:1781–1785.

Escarre J, Lepart J, Sentuc JJ (1996) Effects of simulated herbivory in three old field Compositae with different inflorescence architectures. Oecologia 105:501–508.

Everaerts J (2008) The Use of Unmanned Aerial Vehicles (UAVS) for Remote Sensing and Mapping. In: The International Archives of the Photogrammetry, Remote Sensing and Spatial Information Sciences. Vol. XXXVII. Part B1. Beijing 2008.

Farmer EE (2001) Surface-to-air signals. Nature 411:854–856.

Felton G, Eichenseer H (1999) Herbivore saliva and its effect on plant defense against herbivores and pathogens. pp. 19 – 36 In: A. A. Agrawal, S. Tuzun, and E. Bent, editors. Induced plant defenses against pathogens and herbivores. Phytopathologial Society, St. Paul, Minnesota, USA.

Forman RT, Godron M (1986) Landscape ecology. Wiley, New York.

Frahm JP (2001) Biologie der Moose, 1. Aufl. Spektrum Akad. Verl., Heidelberg.

Frahm JP, Frey W (1992) Moosflora, 3., überarb. Aufl. Ulmer, Stuttgart.

Frank DA, Gehring CA, Machut L, Phillips M (2003) Soil community composition and the regulation of grazed temperate grassland. Oecologia 137:603–609.

Frey W, Hensen L (1995) Spergulo morisonii-Corynephoretum canescentis (Frühlingspark-Silberflur) – Lebenstrategien von Binnendünen- und Lockersandbesiedlern. Feddes Repertorium 106:533–553.

Friedrich S (2006) Bedeutung funktioneller Gruppen für die Systemdynamik offener Sandlebensräume : Störung, Etablierung, Musterbildung. Dissertation, University Bielefeld, Bielefeld.

Friedrich S S, Beyschlag W, Nezadal W, Jentsch A (2006) Vom Wallenstein bis zum Naturschutzpanzer - Vergelich verschiedener Bodenstörungen hinsichtlich der Vegetationsdynamik im Naturschutzgebiet Hainberg bei Nürnberg/Fürth. Anliegen natur. 2006:42–51.

Fromm A, Jakob S, Tischew S (2002) Sandy grassland in former mining areas. Naturschutz und Landschaftsplanung 34:45–51.

Gardener R (1999) RULE: Map generation and spatial analysis program. Pages 280-303 In: Landscape Ecological Analysis: Issues and Applications, J. M. Klopatek and R. H. Gardner, editors. Springer-Verlag, New York.

Gardner M (1970) Mathematical Games: The fantastic combinations of John Conway's new solitaire game "Life". Scientific American 1970:120–123.

Gardner RH, Urban DL (2007) Neutral models for testing landscape hypotheses. Landscape Ecology 22:15–29.

Gayler S (1998) Bewertung computergestützter Umwelt-Simulationsmodelle. Dissertation, University Osnabrück, Osnabrück.

Gelka S (1999) Einfluß von mechanischen Bodenstörungen auf Vegetations- und Stickstoffdynamik ausgewählter Vegetationsbestände von Binnendünen des Naturschutzgebietes "Tennenloher Forst". Diploma Thesis, University of Erlangen, Erlangen.

Gergel SE, Turner MG (2002) Learning landscape ecology. Apractical guide to concepts and techniques. Springer, New York.

Gerhardt M, Schuster H (1995) Das digitale Universum. Zelluläre Automaten als Modelle der Natur. Vieweg, Braunschweig.

Gitay H, Suàrez A, Watson RT, Dokken DJ (2002) Climate Change and Biodiversity: IPCC Technical Paper V. Geneva: Intergovernmental Panel on Climate Change.

Grelka S (1999) Einfluß von mechanischen Bodenstörungen auf Vegetations- und Stickstoffdynamik ausgewählter Vegetationsbestände von Binnendünen des Naturschutzgebietes "Tennenloher Forst". Diploma Thesis, University Erlangen, Erlangen.

Grime JP (1979) Plant strategies and vegetation processes. Wiley & Sons, Chichester, New York, Brisbane, Toronto.

Grime J, Crick J, Rincon J (1986) The ecological significance of plasticity. Symposia of the Society for Experimental Biology 40:5–29.

Grimm V, Railsback SF (2005) Individual-based modeling and ecology. Princeton Univ. Press, Princeton, NJ.

Groeneveld J, Enright NJ, Lamont BB, Wissel C (2002) A spatial model of coexistence among three Banksia species along a topographic gradient in fire-prone shrublands. Journal of Ecology 90:762–774.

Grubb PJ (1977) The maintenance of species richness in plant communities: the importance of the regeneration niche. Biological Reviews 52:107–145.

Gurtner A, Greer DG, Glassock R, Mejias L, Walker RA, Boles WW (2009) Investigation of Fish-Eye Lenses for Small-UAV Aerial Photography. IEEE Transactions on Geoscience and Remote Sensing 47:709–721.

Gustafson EJ (1998) Quantifying landscape spatial pattern: What is the state of the art? Ecosystems 1:143–156.

Haefner JW (1996) Modeling biological systems. Principles and applications, 1. ed. Springer, New York, NY.

Haefner JW (2005) Modeling biological systems. Principles and applications, 2. ed. Springer, New York, NY.

Haeupler H (1989) Atlas der Farn- und Blütenpflanzen der Bundesrepublik Deutschland, 2., durchges. Aufl. Ulmer, Stuttgart.

Handl A (2002) Multivariate Analysemethoden. Theorie und Praxis multivariater Verfahren unter besonderer Berücksichtigung von S-PLUS. Springer, Berlin.

Hardin PJ, Jackson MW (2005) An unmanned aerial vehicle for rangeland photography. Rangeland Ecology & Management 58:439–442.

Harte J, Ostling A, Green JL, Kinzig A (2004) Biodiversity conservation - Climate change and extinction risk. Nature 430:3 p following 33; discussion following 33.

Haruta M, Major IT, Christopher ME, Patton JJ, Constabel CP (2001) A Kunitz trypsin inhibitor gene family from trembling aspen (*Populus tremuloides* Michx.): cloning, functional expression, and induction by wounding and herbivory. Plant Molecular Biology 46:347–359.

Hasse T, Daniels FJ (2006) Species responses to experimentally induced habitat changes in a Corynephorus grassland. Journal of Vegetation Science 17:135–146.

Heil G, Bruggink M (1987) Competition for nutrients between *Calluna vulgaris* and *Molinia caerulea*. Oecologia 73:105–107.

Heil M (2004) Induction of two indirect defences benefits Lima bean (*Phaseolus lunatus*, Fabaceae) in nature. Journal of Ecology 92:527–536.

Heil M, Koch T, Hilpert A, Fiala B, Boland W, Linsenmair K (2001) Extrafloral nectar production of the ant-associated plant, *Macaranga tanarius*, is an induced, indirect, defensive response elicited by jasmonic acid. Proceedings of the National Academy of Sciences (PNAS), Vol. 98, No.3,1083-1088.

Hik DS, Jefferies RL (1990) Increases in the net above-ground primary production of a salt-marsh forage grass: a test of the predictions of the herbivore-optimization model. Journal of Ecology 78:180–195.

Hilbert DW, Swift DM, Detling JK, Dyer MI (1981) Relative growth rates and the grazing optimization hypothesis. Oecologia 51:14–18.

Hilker T, Wulder MA, Coops NC (2008) Update of forest inventory data with lidar and high spatial resolution satellite imagery. Canadian Journal of Remote Sensing 34:5–12.

Hill MO, Evans DF, Bell SA (1992) Long-term effects of excluding sheep from hill pastures in North Wales. Journal of Ecology 80:1–13.

Hinnenthal K (2001) Vergleichende Untersuchungen zur Vegetationszusammensetzung auf ausgewählten Heide- und Sandmagerrasen-Flächen der Oberen Senne. Diploma Thesis, University of Bielefeld, Bielefeld.

Hobbs R, Gimingham C (1984) Studies on fire in Scottish heathland communities. II. Post-fire vegetation development. Journal of Ecology 1984:585–610.

Hobbs VJ, Pritchard NM (1987) Population dynamics of the moss *Polytrichum piliferum* in North-East Scotland. Journal of Ecology 75:177–192.

Hobbs R JA (2006) Restoration as a process of assembly and succession mediated by disturbance. In: Walker L, Walker J, Hobbs R (eds.): Linking Restoration and Succession in Theory and Practice. Springer Series of Environmental Management. Pp. 150-167.

Hodgson J, Illius AW (1998) The ecology and management of grazing systems, Reprinted. CAB International, Wallingford.

Hohenester A (1960) Grasheiden und Föhrenwälder auf Dilluvial- und Dolomitsanden im nördlichen Bayern. Berichte der Bayerischen Botanischen Gesellschaft 33:30–85.

Holland EA, Detling JK (1990) Plant response to herbivory and belowground nitrogen cycling. Ecology 71:1040–1049.

Hovestadt T, Poethke HJ, Messner S (2000) Variability in dispersal distances generates typical successional patterns: a simple simulation model. Oikos 90:612–619.

Huston M (1979) A general hypothesis of species diversity. The American Naturalist 113:81–101.

Hutchings MJ, de Kroon H (1994) Foraging in plants: the role of morphological plasticity in resource acquisition. Advances in Ecological Research 25:159–238.

Im J, Jensen JR, Hodgson ME (2008) Object-based land cover classification using high-posting-density LiDAR data. GIScience & Remote Sensing 45:209–228.

Jeckel G (1984) Syntaxonomische Gliederung, Verbreitung und Lebensbedingungen nordwestdeutscher Sandtrockenrasen (Sedo-Scleranthetea). Phytocoenologia 12:9–153.

Jefferies R (1988) Pattern and process in arctic coastal vegetation in response to foraging by lesser snow geese. In M. J. A. Wergner et al. (eds.) Plant Form and vegetation Structure Adaptiation, Plasticity, and Relation to Herbivory . The Hague: SPB Academic Publishing.

Jeltsch F, Moloney K (2002) Spatially explicit vegetation models: what have we learned? Progress in Botany 63:327–343.

Jentsch A, Friedrich S, Beyschlag W, Nezadal W (2002 b) Significance of ant and rabbit disturbances for seedling establishment in dry acidic grasslands dominated by Corynephorus canescens. Phytocoenologia 32:553–580.

Jentsch A, Friedrich S, Steinlein T, Beyschlag W, Nezadal W (2008) Assessing Conservation Action for Substitution of Missing Dynamics on Former Military Training Areas in Central Europe. Restoration Ecology 17:107–116.

Jentsch A (2001) The significance of disturbance for vegetation dynamics. Acase study in dry acidic grasslands. Dissertation, University Bielefeld, Bielefeld.

Jentsch A, Beyschlag W (2003) Vegetation ecology of dry acidic grasslands in the lowland area of central europe. Flora 198:3–25.

Jentsch A, Beyschlag W, Nezadal W, Steinlein T, Welss W (2002) Bodenstörung – treibende Kraft für die Vegetationsdynamik in Sandlebensräumen. Konsequenzen für Pflegemaßnahmen im Naturschutz. Naturschutz und Landschaftsplanung 34:37–44.

Jørgensen SE, Bendoricchio G (2001) Fundamentals of ecological modelling, 3. ed. Elsevier, Amsterdam.

Kaluzny S, Vega S, Cardoso T, Shelly A (1998) S+SpatialStats. User's manual for Windows and UNIX. Springer, New York. NY.

Karban R, Baldwin IT (1997) Induced Responses to Herbivory. University of Chicago Press, Chicago.

Kenkel N.C (1990) Spatial competition models for plant populations. Coenoses 5:149–158.

Kennedy PG, Izzo AD, Bruns TD (2003) There is high potential for the formation of common mycorrhizal networks between understorey and canopy trees in a mixed evergreen forest. Journal of Ecology 91:1071–1080.

Klein J (2002) breve: a 3D environment for the simulation of decentralized systems and artificial life. Proceedings of Artificial Life VIII, the 8th International Conference on the Simulation and Synthesis of Living Systems. The MIT Press.:329–334.

Koske RE, Gemma JN (1997) Mycorrhizae and succession in plantings of beachgrass in sand dunes. American Journal of Botany 84:118–130.

Kost C, Heil M (2006) Herbivore-induced plant volatiles induce an indirect defence in neighbouring plants. Journal of Ecology 94:619–628.

Krannitz PG, Caldwell MM (1995) Root-growth responses of 3 Great-Basin perennials to intraspecific and interspecific contact with other roots. Flora 190:161–167.

Kristensen L, Olsen J, Weiner J, Griepentrog HW, Norremark M (2006) Describing the spatial pattern of crop plants with special reference to crop-weed competition studies. Field Crops Research 96:207–215.

Krummel J, Gardner RH, Sugihara G, O'Neill RV, Coleman PR (1987) Landscape patterns in a disturbed environment. Oikos 48:321–324.

Kücke M, Schmid H, Spiess A (1995) A comparison of four methods for measuring roots of field crops in three contrasting soils. Plant and Soil 172:63–71.

Kunzmann D (2000) Untersuchungen zur Diasporenbank und des Samenflugs trocken-magerer Standorte als Beitrag zur Definition biotischer Entwicklungspotentiale. - Dissertationes Botanicae Band 326. J. Cramer in Gebr. Borntraeger Verlagsbuchhandlung, Berlin, Stuttgart.

Lacey JR, Van Poollen HW (1981) Comparison of herbage production on moderately grazed and ungrazed western ranges. Journal of Range Management 34:210–212.

Lache D (1976) Umweltbedingungen von Binnendünen- und Heidegesellschaften im Nordwesten Mitteleuropas. Scripta Geobotanica XI, 96 S., Göttingen (Goltze).

Lehtila K, Syrjanen K (1995) Compensatory responses of two Melampyrum species after damage. Functional Ecology 9:511–517.

Leibold MA (1989) Resource edibility and the effects of predators and productivity on the outcome of trophic interactions. The American Naturalist 134:922–949.

Lennartsson T, Nilsson P, Tuomi J (1998) Induction of overcompensation in the field gentian, Gentianella campestris. Ecology 79:1061–1072.

Lennartsson T, Tuomi J, Nilsson P (1997) Evidence for an evolutionary history of overcompensation in the grassland biennial Gentianella campestris (Gentianaceae). The American Naturalist 149:1147–1155.

Leyer I, Wesche K (2007) Multivariate Statistik in der Ökologie. Eine Einführung. Springer Verlag, Berlin, Heidelberg.

Linares J, Esteban FJ, Viñegla B, Carreira JA (2006) A Computational Analysis of Multi-temporal Vegetation Changes Using the Fractal Dimension Spectrum. Harmonic and Fractal Image Analysis 2006:97–100.

Lotka AJ (1998) Analytical theory of biological populations. Plenum Press, New York.

Ludäscher B, Altintas I, Berkley C, Higgins D, Jaeger-Frank E, Jones M, Lee E, Tao J, Zhao Y (2006) Scientific Workflow Management and the Kepler System. Concurrency and Computation: Practice & Experience 18:1039–1065.

Lux H (1964) Die biologischen Grundlagen der Strandhaferpflanzung und Silbergrasansaat im Dünenbau. Zeitschriftenartikel, Angew. Pflanzensoz. Band: 20:5–53.

Mandelbrot B (1967) How long is the coastline of Britain? Statistical self-similarity and fractional dimension. Science 156:636–638.

Mandelbrot B (1982) The fractal geometry of nature. Freeman, San Francisco.

Markham JH, Chanway CP (1996) Measuring plant neighbour effects. Functional Ecology 10:548–549.

Maschinski J, Whitham TG (1989) The continuum of plant responses to herbivory: The influence of plant association, nutrient availability, and timing. The American Naturalist 134:1–19.

Matsumoto M, Nishimura T (1998) Mersenne twister: A 623-dimensionally equidistributed uniform pseudorandom number generator. ACM Trans. on Modeling and Computer Simulations 8:3–30.

Mazzoleni S, Rego F, Giannino F, Legg C (2004) Ecosystem Modelling: Vegetation and Disturbance In: Environmental modelling: Finding Simplicity in Complexity. Wainwright, and M. Mulligan, (Eds). John Wiley & Sons , Ltd. England.

McEvoy PB, Rudd NT, Cox CS, Huso M (1993) Disturbance, competition, and herbivory effects on ragwort *Senecio jacobaea* populations. Ecological Monographs 63:55–75.

McGarigal K, Cushman SA, Neel MC, Ene E (2002) FRAGSTATS: Spatial Pattern Analysis Program for Categorical Maps. Computer software program produced by the authors at the University of Massachusetts, Amherst. Available at the following web site: www.umass.edu/landeco/research/fragstats/fragstats.html.

McNaughton SJ (1983) Compensatory plant growth as a response to herbivory. Oikos 40:329–336.

McNaughton SJ (1985) Ecology of a Grazing Ecosystem: The Serengeti. Ecological Monographs: Vol. 55, No. 3, pp. 259-294.

McNaughton S (1979) Grazing as an optimization process: grassungulate relationships in the Serengeti ecosystem. The American Naturalist 113:691–703.

McNaughton S (1985) Interactive regulation of grass yield and chemical properties by defoliation, a salivary chemical, and inorganic nutrition. Oecologia 65:478–486.

Mercier F, Baujard O (1997) Voronoi diagrams to model forest dynamics in French Guiana. Proceedings of the 2rd International Conference on GeoComputation:161–171.

Meusel H (1935) Wuchsformen und Wuchstypen der europäischen Laubmoose. Nova Acta Leopoldina N.F.3:123–277.

Milne BT (1992) Spatial aggregation and neutral models in fractal landscapes. American Naturalist 139:32–57.

Minar N, Burkhardt R, Langton C, Askenazi M (1996) The SWARM simulation system. A toolkit for building multi-agent simulations. Tech.rept., Santa Fe Institute, Santa Fe, NM.

Miranda M, Ralph SG, Mellway R, White R, Heath MC, Bohlmann J, Constabel CP (2007) The transcriptional response of hybrid poplar (*Populus trichocarpa* x *P-deltoides*) to infection by *Melampsora medusae* leaf rust involves induction of flavonoid pathway genes leading to the accumulation of proanthocyanidins. Molecular Plant-Microbe Interactions 20:816–831.

Mitchley J, Willems JH (1995) Vertical canopy structure of Dutch chalk grasslands in relation to their management. Vegetatio 117:17–27.

Moisen GG, Frescino TS (2002) Comparing five modelling techniques for predicting forest characteristics. Ecological Modelling 157:209–225.

Murray J (2008) Mathematical Biology. I. An Introduction, 3. ed. Springer, New York, NY.

Naiman RJ, Melillo JM, Hobbie JE (1986) Ecosystem alteration of boreal forest streams by beaver (*Castor canadensis*). Ecology 67:1254–1269.

Nara K (2006) Ectomycorrhizal networks and seedling establishment during early primary succession. New Phytologist 169:169–178.

Nelson T, Boots B, Wulder M, Feick R (2004) Predicting forest age classes from high spatial resolution remotely sensed imagery using Voronoi polygon aggregation. GeoInformatica 8:143–155.

Neteler M, Mitasova H (2008) Open source GIS. A GRASS GIS approach, 3. ed. Springer, New York, NY.

Newman EI (1973) Competition and diversity in herbaceous vegetation. Nature 244:310-310.

Newman EI (1988) Mycorrhizal links between plants: their functioning and ecological significance. Advances in Ecological Research 18:243–270.

Nielsen DR, Wendroth O (2003) Spatial and temporal statistics. Sampling field soils and their vegetation. Catena-Verl., Reiskirchen.

North M, Tatara J, Collier N, Ozik J (2007) "Visual Agent-based Model Development with Repast Simphony," Proceedings of the Agent 2007 Conference on Complex Interaction and Social Emergence, Argonne National Laboratory, Argonne, IL USA.

Nuttle T, Haefner JW (2007) Design and validation of a spatially explicit simulation model for bottomland hardwood forests. Ecological Modelling 200:20–32.

Oberdorfer E (1994) Pflanzensoziologische Exkursionsflora, 7., überarb. und erg. Aufl. Ulmer, Stuttgart.

Okabe A (2000) Spatial tessallations. Concepts and applications of Voronoi diagrams, 2. ed. Wiley, Chichester.

Olofsson J, Mazancourt C de, Crawley MJ (2008) Spatial heterogeneity and plant species richness at different spatial scales under rabbit grazing. Oecologia 156:825–834.

Owen DF, Wiegert RG (1976) Do consumers maximize plant fitness. Oikos 27:488–492.

Paige KN (1999) Regrowth following ungulate herbivory in *Ipomopsis aggregata*: geographic evidence for overcompensation. Oecologia 118:316–323.

Paige KN, Whitham TG (1987) Overcompensation in Response to Mammalian Herbivory: The Advantage of Being Eaten. The American Naturalist 129:407–416.

Pastor J, Naiman RJ (1992) Selective foraging and ecosystem processes in boreal forests. The American Naturalist 139:690–705.

Pebesma E (2004) Multivariable geostatistics in S: the gstat package. Computers & Geosciences 30:683–691.

Peitgen HO, Barnsley MF (1988) The science of fractal images. Springer, New York, NY.

Peitgen HO, Jürgens H, Saupe D (2004) Chaos and fractals. New frontiers of science, 2. ed. Springer, New York.

Perez-Moreno J, Read DJ (2004) Ectomycorrhizal fungi, living ties that bind and nurture plants in nature. Interciencia 29:239–247.

Perry GL, Enright NJ (2006) Spatial modelling of vegetation change in dynamic landscapes: a review of methods and applications. Progress in Physical Geography 30:47–72.

Perumal JV, Maun MA (1999) The role of mycorrhizal fungi in growth enhancement of dune plants following burial in sand. Functional Ecology 13:560–566.

Petzoldt T (2003) R as a Simulation Platform in Ecological Modelling. R-News 3:8–16.

Petzoldt T, Rinke K (2007) simecol: An Object-Oriented Framework for Ecological Modeling in R. Journal of Statistical Software 2007:1–31.

Picard N, Franc A (2001) Aggregation of an individual-based space-dependent model of forest dynamics into distribution-based and space-independent models. Ecological Modelling 145:69–84.

Pickelmann I (2001) Untersuchungen zur Diasporen-Langlebigkeit und zum Keimungsverhalten dominanter Arten von Sandtrockenrasen. Zulassungsarbeit, unveröff.

Pickett ST, White P (1985) Natural Disturbance and Patch Dynamics: An Introduction. - In: Pickett, S.T.A. & White, P.S. (eds.): The Ecology of Natural Disturbance and Patch Dynamics. Academic Press, Orlando, FL.

Platt WJ (1975) The colonization and formation of equilibrium plant species associations on badger disturbances in a tallgrass prairie. Ecological Monographs 45:285–305.

Poethke H (1994) Analysieren, verstehen und prognostizieren. Zum Einsatz von mathematischen Modellen und Computersimulationen in der Ökologie. Habilitation, University Mainz, Mainz.

Prusinkiewicz P, Lindenmayer A (1996) The algorithmic beauty of plants. Springer, New York.

Pucheta E, Cabido M, Díaz S, Funes G (1998) Floristic composition, biomass, and aboveground net plant reduction in grazed and protected sites in a mountain grassland of central Argentina. Acta Oecologica:97–105.

Putman RJ, Fowler AD, Tout S (1991) Patterns of use of ancient grassland by cattle and horses and effects on vegetational composition and structure. Biological Conservation 56:329–347.

Quinger B, Meyer N (1995) Landschaftspflege- konzept Bayern. Lebensraumtyp Sandrasen (Bd. II.4). – Bayerisches Staatsministerium für Landesent- wicklung und Umweltfragen, München.

Rasband WS (1997-2009) ImageJ. U. S. National Institutes of Health, Bethesda, Maryland, USA, http://rsb.info.nih.gov/ij/.

Read D (1997) Mycorrhizal fungi - The ties that bind. Nature 388:517–518.

Reader RJ (1992) Herbivory, competition, plant mortality and reproduction on a topographic gradient in an abandoned pasture. Oikos 65:414–418.

Reynolds CW (1987) Flocks, Herds, and Schools: A Distributed Behavioral Model, in Computer Graphics, 21(4) (SIGGRAPH '87 Conference Proceedings):25–34.

Richards JH, Caldwell MM (1985) Soluble carbohydrates, concurrent photosynthesis and efficiency in regrowth following defoliation: A field study with Agropyron species. Journal of Applied Ecology 22:907–920.

Ricklefs RE, Miller GL (2000) Ecology, 4. ed. Freeman, New York.

Rietman E (1989) Exploring the geometry of nature. Computer modeling of chaos, fractals, cellular automata, and neural networks. Windcrest, Blue Ridge Summit, Pa.

Riiters KH, O'Neil RV, Hunsaker CT, Wickham JD, Yankee DH, Timmins SP, Jones KB, Jackson BL (1995) A factor analysis of landscape pattern and structure metrics. Landscape Ecology 10:23–39.

Ripley BD (1976) The Second-Order Analysis of Stationary Point Processes. Journal of Applied Probability 13:255–266.

Ripley BD (1996) Pattern recognition and neural networks. Cambridge Univ. Press, Cambridge.

Ritchie ME, Tilman D (1995) Responses of Legumes to Herbivores and Nutrients During Succession on a Nitrogen-Poor Soil. Ecology 76:2648–2655.

Ritesema CJ, Dekker L (1994) Soil moisture and dry bulk patterns in bare dune sands. Journal of Hydrology 154:107–131.

Rooke T (2003) Growth responses of a woody species to clipping and goat saliva. African Journal of Ecology 41:324–328.

Rothmaler W, Mahn EG, Jäger EJ (2005) Gefäßpflanzen. Grundband, 19., bearb. Aufl. Spektrum Akad. Verl., Heidelberg.

Ruess RW, Hik DS, Jefferies RL (1989) The role of lesser snow geese as nitrogen processors in a sub-arctic salt marsh. Oecologia 79:23–29.

Russel DJ (2002) Endogäische Mikroarthropoden als Reaktionsindikatoren. Bewertung von Pflegemaßnahmen in geschützen Sandfluren. Naturschutz und Landschaftsplanung 34:74–81.

Saltelli A (2000) Sensitivity analysis. Wiley, Chichester.

Sato H, Itoh A, Kohyama T (2007) SEIB-DGVM: A new dynamic global vegetation model using a spatially explicit individual-based approach. Ecological Modelling 200:279–307.

Schenk HJ, Callaway RM, Mahall BE (1999) Spatial root segregation: Are plants territorial? Advances in Ecological Research 28:145–180.

Schmale DG, Dingus BR, Reinholtz C (2008) Development and application of an autonomous unmanned aerial vehicle for precise aerobiological sampling above agricultural fields. Journal of Field Robotics 25:133–147.

Schmeil O, Fitschen J, Seybold S (2006) Flora von Deutschland und angrenzender Länder, 93. Aufl. Quelle & Meyer, Wiebelsheim.

Schmidt A (1998) Nährstoffdynamik (N,P) in Böden ausgewählter Sukzessionsstadien auf Binnendünen der Senne. Diploma Thesis, University of Bielefeld, Bielefeld.

Schreiner S (1993) Genetics and evolution of phenotypic plasticity. Annual Review of Ecology and Systematics 24:35–68.

Shang ZB, Gao Q, Dong M (2003) Impacts of grazing on the alkalinized-salinized meadow steppe ecosystem in the Songnen Plain, China - A simulation study. Plant and Soil 249:237–251.

Shaw AJ, Goffinet B (2000) Bryophyte biology. Cambridge University Press, Cambridge.

Silvertown J, Holtier S, Johnson J, Dale P (1992) Cellular automaton models of interspecific competition for space - the effect of pattern on process. Journal of Ecology 80:527–534.

Simons AM, Johnston MO (1999) The cost of compensation. The American Naturalist 153:683–687.

Sletvold N, Hestmark G (1999) A comparative test of the predictive power of neighbourhood models in natural populations of *Lasallia pustulata*. Canadian Journal of Botany. Revue canadienne de botanique 77:1655–1661.

Smith B, Prentice IC, Sykes MT (2001) Representation of vegetation dynamics in the modelling of terrestrial ecosystems: comparing two contrasting approaches within European climate space. Global Ecology and Biogeography 10:621–637.

Soetaert K, Herman P (2009) A Practical Guide to Ecological Modelling. Using R as a Simulation Platform. Springer-Verlag, New York.

Sousa WP (1984) The Role of Disturbance in Natural Communities. Annual Review of Ecology and Systematics 15:353–391.

Sterner RW (1994) Elemental stoichiometry of species in ecosystems. Pages 240-252 In: C. G. Jones and J. H. Law- ton, editors. Linking species and ecosystems. Chapman and Hall, New York.

Storm C, Herget I, Kappes J, Vormwald B (1998) Nährstofffökologische Untersuchungen im Darmstadt-Dieburger Sandgebiet in (teilweise ruderalisierten) Sandpionierfluren und -rasen. Botanik u. Naturschutz in Hessen 10:41–85.

Strasburger E, Sitte P (2002) Lehrbuch der Botanik für Hochschulen, 35. Aufl. Spektrum Akad. Verl., Heidelberg.

Sultan S (1987) Evolutionary implications of phenotypic plasticity in plants. Evolutionary biology 21:127–178.

Swain DL, Hutchings MR, Marion G (2007) Using a spatially explicit model to understand the impact of search rate and search distance on spatial heterogeneity within an herbivore grazing system. Ecological Modelling 203:319–326.

Symonides E (1985) Population structure of psammophyte vegetation. In: White J. (ed.) The population structure of vegetation. Junk, Dordrecht, Boston, Lancaster.

Syrett P, Smith L, Grosskopf G (1997) Introduction of *Oxyptilus pilosellae* (Lepidoptera: Pterophoridae) into New Zealand. Unpublished Importation Impact Assessment, prepared for The Hieracium Control Trust, by Landcare Research, Lincoln, New Zealand.:32 pp.

Thaler JS (1999) Jasmonate-inducible plant defences cause increased parasitism of herbivores. Nature 399:686–688.

Thomas CD, Cameron A, Green RE, Bakkenes M, Beaumont LJ, Collingham YC, Erasmus BF, Siqueira MF de, Grainger A, Hannah L, Hughes L, Huntley B, van Jaarsveld AS, Midgley GF, Miles L, Ortega-Huerta MA, Peterson AT, Phillips OL, Williams SE (2004) Extinction risk from climate change. Nature 427:145–148.

Tilman D (1982) Resource competition and community structure. Princeton Univ. Pr., Princeton, NJ.

Tilman D (1987) On the Meaning of Competition and the Mechanisms of Competitive Superiority. Functional Ecology 1:304–315.

Tilman D (1988) Plant strategies and the dynamics and structure of plant communities. Princeton University Press, Princeton, New Jersey, USA.

Tilman D, Wedin D (1991) Plant traits and resource reduction for five grasses growing on a nitrogen gradient. Ecology 72:685–700.

Turner MG (1989) Landscape ecology: The effect of pattern on process. Annual Review of Ecology and Systematics 20:171–197.

Turner MG (2005) Landscape ecology: What is the state of the science? Annual Review of Ecology, Evolution, & Systematics 36:319–344.

Turner MG, Gardner RH, O'Neill RV (2003) Landscape ecology in theory and practice. Pattern and process. Springer, New York, NY.

Tüxen R (1967) Corynephoretalia canescentis. Mitt. Pfl.-Soz. Arbeitsgem 11:22–24.

Uchmanski J, Grimm V (1996) Individual-based modelling in ecology: What makes the difference? Trends in Ecology & Evolution 11:437–441.

Urbanek S (2003) Rserve - A Fast Way to Provide R Functionality to Applications. Proc. of the 3rd International Workshop on Distributed Statistical Computing (DSC 2003), ISSN 1609-395X Eds.: Kurt Hornik, Friedrich Leisch & Achim Zeileis.

Vallentine JF (2001) Grazing management, 2. ed. Academic Press, San Diego.

van Dam NM, Witjes L, Svatos A (2004) Interactions between aboveground and belowground induction of glucosinolates in two wild Brassica species. New Phytologist 161:801–810.

van den Berg LJ, Tomassen HB, Roelofs JG, Bobbink R (2005) Effects of nitrogen enrichment on coastal dune grassland: A mesocosm study. Environmental Pollution 138:77–85.

van Rheenen JW, Werger M, Bobbink R, Daniels F, Mulders W (1995) Short-term accumulation of organic matter and nutrient contents in two dry sand ecosystems. Vegetatio 120:161–171.

Venables WN, Ripley BD (2002) Modern applied statistics with S. Springer-Verlag, New York, Berlin, Heidelberg.

Vierling KT, La Vierling, Gould WA, Martinuzzi S, Clawges RM (2008) Lidar: shedding new light on habitat characterization and modeling. Frontiers in Ecology and the Environment 6:90–98.

Vitousek PM, Howarth RW (1991) Nitrogen limitation on land and in the sea: How can it occur? Biogeochemistry 13:87–115.

Wainwright J, Mulligan M (2004) Environmental modelling. Finding simplicity in complexity. Wiley, Hoboken, NJ.

Walker LR (1999) Ecosystems of disturbed ground, 1. ed. Elsevier, Amsterdam.

Wallentin G, Tappeiner U, Strobl J, Tasser E (2008) Understanding alpine tree line dynamics: An individual-based model. Ecological Modelling 218:235–246.

Wang RZ, Ripley EA (1997) Effects of grazing on a *Leymus chinensis* grassland on the Songnen plain of north-eastern China. Journal of Arid Environments 36:307–318.

Wardle DA, Barker GM (1997) Competition and herbivory in establishing grassland communities: implications for plant biomass, species diversity and soil microbial activity. Oikos 80:470–480.

Warren SD, Holbrook SW, Dale DA, Whelan NL, Elyn M, Grimm W, Jentsch A (2007) Biodiversity and the heterogeneous disturbance regime on military training lands. Restoration Ecology 15:606–612.

Wedin DA (1994) Species, nitrogen and grassland dynamics: the constraints of stuff. Pages 253-262 in C. Jones and J. H. Lawton, editors. Linking species and ecosystems. Chapman and Hall, New York, New York, USA.

Weigelt A (2001) Plant competition on inland dunes. Influence of water availability, nitrogen supply and the role of belowground processes. Dissertation, University Bielefeld, Bielefeld.

Weigelt A, Jolliffe P (2003) Indices of plant competition. Journal of Ecology 91:707–720.

Weigelt A, Steinlein T, Beyschlag W (2005) Competition among three dune species: the impact of water availability on below-ground processes. Plant Ecology 176:57–68.

Weimar J (2003) Simulation with cellular automata, 2., überarb. Aufl. Logos-Verl., Berlin.

Wiegand T, Jeltsch F, Hanski I, Grimm V (2003) Using pattern-oriented modeling for revealing hidden information: a key for reconciling ecological theory and application. Oikos 100:209–222.

Wiegand T, Moloney KA, Milton SJ (1998) Population dynamics, disturbance, and pattern evolution: Identifying the fundamental scales of organization in a model ecosystem. The American Naturalist 152:321–337.

Wiens JA, Stenseth NC, Van Horne B, Ims RA (1993) Ecological mechanisms and landscape ecology. Oikos 66:369–380.

Wiens J (1989) Spatial scaling in ecology. Functional Ecology 3:385–397.

Wilensky U (1999) NetLogo. http://ccl.northwestern.edu/netlogo/. Center for Connected Learning and Computer-Based Modeling, Northwestern University. Evanston, IL.

Willis CG, Ruhfel B, Primack RB, Miller-Rushing AJ, Davis CC (2008) Phylogenetic patterns of species loss in Thoreau's woods are driven by climate change. Proceedings of the National Academy of Sciences of the United States of America 105:17029–17033.

Wilson JB, Agnew A (1992) Positive-feedback switches in plant communities. Advances in Ecological Research 23:263–336.

Winkler E, Klotz S (1997) Clonal plant species in a dry-grassland community: A simulation study of long-term population dynamics. Ecological Modelling 96:125–141.

Winkler E, Stocklin J (2002) Sexual and vegetative reproduction of *Hieracium pilosella* L. under competition and disturbance: a grid-based simulation model. Annals of Botany 89:525–536.

Winkler E, Stocklin J (2002) Sexual and vegetative reproduction of *Hieracium pilosella* L. under competition and disturbance: a grid-based simulation model. Annals of Botany 89:525–536.

Wissel C. (1989) Theoretische Oekologie: Eine Einfuehrung. Springer-Verlag.

Wissel C. (2000) Grid-based models as tools for ecological research. In: Dieckmann, U., Law, R. and Metz, J.A.J., editors, The geometry of ecological interactions: simplifying spatial complexity, Cambridge University Press:94–116.

Wolfram S (1984) Cellular automata as models of complexity. Nature 311:419–424.

Wolfram S (1986) Theory and applications of cellular automata. World scientific Publishing, Singapore.

Wolfram S (2002) A new kind of science. Wolfram Media, Champaign, IL.

Wolter B (1996) Lebensstrategieenanalyse am Beispiel der Silbergrasflur (Spergulo morisonii – Corynephoretum canescentis) an ausgewählten Standorten des ehemaligen Mauerstreifens. - Wiss. Hausarbeit Freie Univ. Berlin, 88S.

Zelditch M (2004) Geometric morphometrics for biologists. A primer. Elsevier Academic Press, Amsterdam.

6. Appendix

6.1 CD-ROM

A CD-ROM has been included in this thesis with the created Software Bio7 and the model about Dry Acidic Grasslands.

Erklärung

Hiermit erkläre ich, dass ich die vorliegende Arbeit selbst angefertigt habe und nur die angegebenen Quellen und Hilfsmittel verwendet habe. Alle aus der Literatur ganz oder annähernd entnommenen Stellen habe ich als solche kenntlich gemacht.
Des Weiteren erkläre ich, dass die vorliegende Dissertation weder vollständig noch teilweise einer anderen Fakultät mit dem Ziel vorgelegt worden ist, einen akademischen Titel zu erwerben. Hiermit bewerbe ich mich erstmals um den Doktorgrad der Naturwissenschaften der Universität Bielefeld.

Bielefeld, den 2009