Succession of Semi-Natural Grasslands:

Spatially-Explicit, Mechanistic Simulation Considering

Various Forms of Land Use

Von der Fakultät für Mathematik, Informatik und Naturwissenschaften der RWTH Aachen University zur Erlangung des akademischen Grades einer Doktorin der Naturwissenschaften genehmigte Dissertation

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“Predicting the future is a mug’s game,
but any game is improved when you can actually keep the score.”

Douglas N. Adams

Zusammenfassung

Der zunehmende Verlust an Biodiversität erregt weltweit immer größere Besorgnis. Die Form der Landnutzung spielt für den Erhalt und die Pflege von Extensivgrünland, das in Mitteleuropa zu den artenreichsten Biotoptypen gehört, eine wesentliche Rolle – Intensivierung oder Nutzungsaufgabe führen häufig zu hohen Artenverlusten. Auf der Dreiborner Hochfläche, im Zentrum des Nationalparks Eifel, erstrecken sich große ehemals extensiv genutzte Grünlandflächen auf dem Gelände des ehemaligen Truppenübungsplatzes Vogelsang. Als Entscheidungshilfesystem für das zukünftige Management dieser Flächen wurde das GraS-Modell (**Gra**sland **S**ukzessions Modell) entwickelt, welches die dynamische Entwicklung von Grünlandflächen in Abhängigkeit von verschiedenen Landnutzungsformen mechanistisch simuliert.

Das GraS-Modell ist nach einem „Multimodeling“-Ansatz aufgebaut, bei dem verschiedene Modellierungstechniken miteinander verknüpft werden, um die Interaktion auf verschiedenen Skalenebenen von Pflanzen der Baum/Strauch- und Krautschicht in der Landschaft zu berücksichtigen. Die Gräser und Kräuter werden im Modell als Kompartimente behandelt und die Abundanz einer Pflanze bzw. Pflanzengruppe wird als Flächenbedeckung ausgedrückt. Das vegetative Wachstum der Stellvertreterarten sowie der funktionellen Pflanzengruppen wird mit Hilfe von Differenzengleichungen modelliert und in Abhängigkeit von Briemles Nutzungswertzahlen zu Mahd, Weide und Tritt modifiziert. Die Konkurrenzkraft der Arten ergibt sich hierbei aus dem Verhältnis des jeweiligen potentiellen Wachstums zueinander. An einem umfassenden pflanzensoziologischen Datensatz der Dreiborner Hochfläche wurden die Parameter für die Berechnung des Wachstums kalibriert. Gehölze werden im Gegensatz zu den Gräsern und Kräutern individuenbasiert modelliert. Jedes Individuum keimt, wächst, produziert Samen und altert, wobei die Ausbreitung und Etablierung der Gehölze durch die Hemmung des Grasfilzes, durch Wildschweine (*Sus scrofa*) und durch Herbivorie beeinflusst werden.

Das GraS-Modell entnimmt die räumliche Verteilung von Vegetationstypen einer realen Landschaft zu einem definierten IST-Zustand aus GIS-Karten, wobei die Pflanzen in eine räumlich explizite Landschaft aus 10 m x 10 m großen Rasterzellen eingebettet werden. Hierdurch wird die zu modellierende Landschaft als ein kleinräumiges Mosaik abgebildet und die für den Sukzessionsablauf entscheidenden Nachbarschaftsbeziehungen können explizit

berücksichtigt werden. Die musterbasierte („pattern oriented") Evaluierung des Modells hat gezeigt, dass die Simulationsergebnisse sowohl mit der Literatur, als auch mit Expertenerfahrungen und Beobachtungen auf der Dreiborner Hochfläche räumlich und zeitlich übereinstimmen.

Nach der erfolgreichen Evaluierung des Modelles wurden die Auswirkungen von verschiedenen Managementmaßnahmen auf die Vegetationsentwicklung der Dreiborner Hochfläche für einen Zeitraum von bis zu 100 Jahren prognostiziert. Das Modell lieferte unter Berücksichtigung von Nachbarschaftsbeziehungen klare und kleinräumlich hochaufgelöste Entwicklungsszenarien, die in dieser Deutlichkeit ohne Modell nicht annähernd darstellbar wären. So würde z.B. die Waldentwicklung auf der Dreiborner Hochfläche, abgesehen von Mahd, am stärksten durch eine Nutzungsaufgabe in Kombination mit dem Einfluss der aktuell hohen Rothirschdichte verlangsamt, wohingegen eine Beweidung durch Wisente die Entwicklung eines vielfältigen Landschaftsmosaiks aus Grünland, Gebüschen und Baumgruppen förderte.

Aufgrund der hohen Modellkomplexität überstieg eine Simulation der Dreiborner Hochfläche mit ca. 1,500 ha zunächst die Arbeitsspeicherkapazität eines Arbeitsplatzrechners, sodass die Fläche in Teilstücken simuliert wurde. Diese Einschränkung konnte jedoch durch eine Parallelisierung des Modells aufgehoben werden, die es ermöglichte, das Modell auf einem Clusterrechner laufen zu lassen. Dadurch gestaltet sich die Anwendung des Modells auf solch große Landschaften deutlich praktikabler und außerdem nimmt die ökologische Genauigkeit der Prognosen zu.

Die Nutzung des GraS-Modells als Entscheidungshilfesystem bietet vielfältige Vorteile: Die hochaufgelöste, räumlich explizite und in Rasterkarten dargestellte Prognose der Vegetationsentwicklung stellt eine solide Grundlage für Diskussionen und die Entscheidungsfindung für Managementstrategien dar und erleichtert darüber hinaus eine spätere Effektivitäts- und Effizienzkontrolle der beschlossenen Maßnahmen. Außerdem integriert das Modell das Wissen verschiedener Disziplinen und unterstützt die Kommunikation zwischen Wissenschaftlern und Anwendern. Der modulare Aufbau ermöglicht es zudem, das Modell fortwährend dem aktuellen Stand des Wissens anzupassen. So können zukünftig weitere Umweltfaktoren (z.B. Feuchte, Nährstoffe, Licht) integriert oder andere dynamische Modelle (z.B. zu Waldsukzession, Nährstoffkreisläufen, Klimawandel oder der räumlichen Verteilung der Herbivore) in das Modell eingebunden werden.

Summary

Degradation of natural and semi-natural landscapes has become a matter of global concern including for habitats in Western and Central Europe. For maintenance and restoration of grasslands belonging to the most species-rich biotopes in Central Europe, elaborate management is crucial. The Eifel National Park contains vast areas of semi-natural grasslands on the plateau Dreiborner Hochfläche in the area of the former military training site Vogelsang. To support decision-making for the management of this area, we built the GraS-Model (**Gra**ssland **S**uccession Model), which mechanistically simulates the dynamics of grassland vegetation depending on the form of land use.

When dealing with a complex landscape, entities acting at different scales have to be considered. While trees can be distinguished as single individuals, grasses and herbs are rather perceived as the sum of plants building up a certain cover. To cope with these unequal plant types, the GraS-Model is set up using a multimodeling approach. Representative species and plant functional groups of the herbaceous layer are modeled as compartments; their abundance is expressed as cover and only vegetative spread is considered. Difference equations are used to simulate their growth, which is adjusted using Briemle's utilization numbers for cutting, grazing and trampling. Competitive power arises from the growth rate of each species in relation to that of the others. Herbaceous species growth was calibrated based on an extensive community data set of the study site. Trees, in contrast, are modeled using an individual-based approach. Each individual tree germinates, grows, disperses seeds, and ages in a spatially-explicit environment. As factors determining wood encroachment, inhibition by the grasslayer, interference of wild boar (*Sus scrofa*) and of ungulate browsers is considered.

The plants are embedded in a landscape that is simulated as a detailed grid (100 m² cells), which allows inserting spatially-explicit input data from a GIS (geographic information system) so that the model can be easily connected to data of an existing landscape. Due to this raster-based approach, neighborhood relationships can be accounted for and different management regimes can be applied to distinct areas of the landscape. Pattern-oriented model evaluation revealed that the model produces results that are in line with general literature and experiences of local experts, and emulates observed successional pathways on the Dreiborner Hochfläche on the spatial as well as the temporal scale.

After successful evaluation, the GraS-Model was used to predict the landscape developments of the Dreiborner Hochfläche under different management regimes for up to 100 years. It provides a highly detailed, spatially explicit prognosis integrating the initial vegetation composition and resulting neighborhood interactions which would not have been possible without the model. Forest encroachment on the Dreiborner Hochfläche was most strongly delayed by non-interference with the given high abundance of red deer (apart from mowing), whereas grazing by bison promoted a diverse landscape mosaic.

Due to its high complexity, the GraS-Model initially exceeded the available computer main memory of current workstations when applied to the modeled Dreiborner Hochfläche (ca. 1500 ha). The landscape had to be fragmented and modeled separately. Therefore, the model was parallelized so that it can be run on a cluster, improving practicability and enhancing the ecological accuracy of the simulation results.

The benefits of using the GraS-Model as decision support system are multifaceted: It gives highly detailed spatially explicit prognoses providing a strong basis for decision support and facilitating effectiveness and efficiency control; also it combines knowledge of different disciplines and enhances communication between scientists and stakeholders. Due to its modular design, the model can be continuously updated by integrating latest scientific knowledge, which can then be easily communicated. In the future, light, nutrients or moisture as environmental factors could be added in. Furthermore, other raster-based dynamic models (e.g. models of forest succession, nitrogen cycling, climate change, or animal movement) could be coupled.

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1 General Introduction

Degradation of natural and semi-natural landscapes has become a matter of global concern including for habitats in Western and Central Europe (EEC, 1992; Poschlod et al., 2005; Van Calster et al., 2008; CBD, 2010; GBO3, 2010). Semi-natural grasslands belong to the most species-rich biotope types in Central Europe; in Germany, over 50% of vascular plant species occur in these biotope types (Lind et al., 2009). But according to the European Topic Centre for Biological Diversity (ETC-BD), grasslands are one of the habitat types suffering from the highest level of "unfavorably bad" conservation condition. In fact, less than 20% of European grasslands are in a "favorable condition" (EU-COM, 2009). Land use change, leading to habitat loss or degradation, is considered an important driver of biodiversity loss (Sala et al., 2000; Midgley and Thuiller, 2005; Botkin et al., 2007; Van Calster et al., 2008; GBO3, 2010). During the "Green Revolution" in the middle of the 20th century, the management practices on many extensively used grassland areas were intensified, e.g. by amelioration such as drainage or eutrophication, leading to an equalization and a loss of habitat diversity; other sites where intensification was not possible or profitable were in many cases abandoned (Isselstein et al., 2005; Stoate et al., 2009).

For maintenance and restoration of species-rich grassland communities, the type of management is crucial; intensification or abandoning in many cases leads to a severe reduction of species diversity (Bakker, 1989; Pykälä, 2000; Diemer et al., 2001; Dierschke and Briemle, 2002; Tscharntke et al., 2005; Kleyer, 2007; Van Calster et al., 2008; Kleijn et al., 2009; Lind et al., 2009). In case of abandonment, grasslands tend to change into species-poor stands dominated by tall grasses or forbs, which might persist over several decades before woody species encroach upon the open grassland (Ellenberg, 1996; Glavac, 1996; Müller and Rosenthal, 1998). Even so, authorities dealing with landscape management often cannot easily access available scientific knowledge but rather rely on common sense and personal experience (Prendergast et al., 1999; Sutherland et al., 2004; Pullin and Knight, 2005). Yet, insight into ecosystem-functioning and underlying key-processes is essential for a successful landscape management (Brouwer et al., 2005). Furthermore, many restoration projects remain unevaluated and little evidence on the consequence of current practice is collected, so that an evidence-based conservation is hindered (Bratrich, 2004; Pullin et al., 2004; Sutherland et al., 2004; Esselink et al., 2008).

Ecological models are considered to be a potentially powerful tool for ecological forecasting and application facing the growing complexity and extent of environmental problems (Clark et al., 2001; Parker et al., 2002; Jeltsch et al., 2008; Thuiller et al., 2008). They integrate current scientific knowledge and can visualize expected management goals so that an evaluation of the management measure is facilitated. Models simulating a sufficiently large area with a fine resolution, as are needed in landscape management, are still rare (examples are: Jorritsma et al. (1999), Gustafson et al. (2000), Tews et al. (2006), Rammig et al. (2007b) and Kochy et al. (2008)). Mechanistic grassland succession models (e.g. STEPPE by Coffin and Lauenroth (1989), SUMO by Wamelink et al. (2000), PASTUREPOP by Kahmen (2004) and WOODPAM by Gillet (2008)) are often restricted either to a few plants, a small area, or a low spatial resolution, because the number and detail of required parameters is mostly too high for modeling big areas. In less complex, rule-based models (e.g. Matsinos and Troumbis (2002), VDDT by Beukema et al. (2003) or Cousins et al. (2003)), the user defines the rules in which different succession stages turn into one another. Consequently, the knowledge about possible succession stages and about the premises for transitions is mandatory, so that this approach is not suitable when new scenarios are to be predicted.

The Eifel National Park contains vast areas of semi-natural grasslands lying on the plateau Dreiborner Hochfläche in the area of the former military training site Vogelsang. Due to extensive use during military time, diverse mountain hay-meadows and mountain pastures were maintained or developed from formerly tilled fields. When the Eifel National Park was established in 2004, the question arose to what extend and in which way the management of these areas should be carried on. To support decision-making when managing these grassland areas, we built the GraS-Model (**Gra**ssland **S**uccession Model), which simulates the dynamics of grassland vegetation depending upon the form of land use. The unique feature of the GraS-Model is that it dynamically and mechanistically models different plant species' growth with a fine spatial resolution (10 m grid), and is nevertheless capable of predicting the development of an area (up to 1500 ha) typical for landscape management. We chose a dynamic approach since the aim was to simulate not only the succession endpoint of a given management regime but also the development over time, which is essential to gain a deeper understanding of succession processes because the outcome of succession is strongly determined by succession states occurring at earlier time points. To consider the actual vegetation development at a given location, a spatially explicit approach is mandatory. We chose a raster-based approach, to be able to integrate input data from a geographic information system (GIS) and to consider neighborhood relationships and local interactions, which are crucial for local succession (Schreiber, 1997; Kahmen, 2004; Berger et al., 2008). Thanks to the fine resolution (10 m x 10 m) of this landscape model, vegetation patches that can act as propagule sources such as alleys, hedges and small woods can be integrated. The process-oriented (mechanistic) approach requires identifying the most important processes for local grassland dynamics and enables the user to analyze the influence of a given management regime on landscape development. One essential point is, that without a mechanistic model, projections of new scenarios under conditions that were not prestated cannot easily be made (Jeltsch et al., 2008; Jongejans et al., 2008).

The focus of the GraS-Model is to predict and illustrate vegetation development on the Dreiborner Hochfläche over time under different management regimes such as mowing, grazing, and non-interference, to support decision making of the Eifel National Park administration. It is intended to be applied as a decision support system (DSS) for stakeholders dealing with the management of grasslands on a landscape level. Integrating current scientific knowledge, the GraS-Model gives highly detailed, spatially explicit projections providing a strong basis for discussions and decision making. After an ongoing monitoring of the management impacts, the real landscape development can be compared to the simulated maps picturing the desired management goals, so that an efficiency control can be easily performed. Matches as well as mismatches will give deeper insights into key-processes driving vegetation succession to scientists and decision makers.

In this thesis, the preliminary version of the GraS-Model by Lennartz et al. (2006), which was created in close cooperation with the Eifel National Park administration, the MUNLV (Ministry of the Environment, Conservation, Agriculture and Consumer Protection of the State of North Rhine-Westphalia) and the LANUV (North-Rhine-Westphalian Agency for Nature, Environment and Consumer Protection), was refined. This complex simulation model is structured in distinct ecological relevant entities. The simulated landscape is divided into grid cells, in which the herbaceous layer and trees are simulated. Thereby, a multimodeling approach was used: Grasses and herbs were simulated as compartments using difference equations and the trees were modeled using an individual-based approach (see Chapter 3).

Within this thesis, each of these submodels was investigated in detail; in doing so, the model approach for all submodels was recalibrated to real data and tested. The herbaceous layer was re-parameterized and the structure was found to be suitable (Chapter 4). For the tree layer, in contrast, the used model approach was refined to current state of the art in tree modeling and the new submodel was parameterized on a large dataset and tested (Chapter 5). This now well-validated model was used to predict the succession of the Dreiborner Hochfläche within the Eifel National Park under different management regimes at the current state of scientific knowledge (Chapter 6). To overcome computational constraints of the highly detailed spatial simulation of the large landscape, the model was parallelized to be run on a cluster (Chapter 7). Finally, the model's use as a decision support system was discussed (Chapter 8).

2 Study Area

2.1 Eifel National Park

The Eifel National Park was established January 1st 2004 and is located in the West of Germany, bordering on Belgium with its most southern part. It lies in the low mountain range Rureifel about 50 km southwest of Cologne and 30 km southeast of Aachen, covering an area of 10,800 ha. The area rises from 180 m above sea level in the Northeast at the lake Rursee to 630 m above sea level at the southern border.

About 75% of the National Park is covered by forest. While the south is dominated by planted spruce forest, vast areas of the northern part are covered by beech (*Luzulo-Fagetum*) and oak (*Quercetalia*) forests (Fig. 2-1). The main aim of the National Park administration is to develop and protect these natural deciduous forests (Lennartz and Röös, 2006).

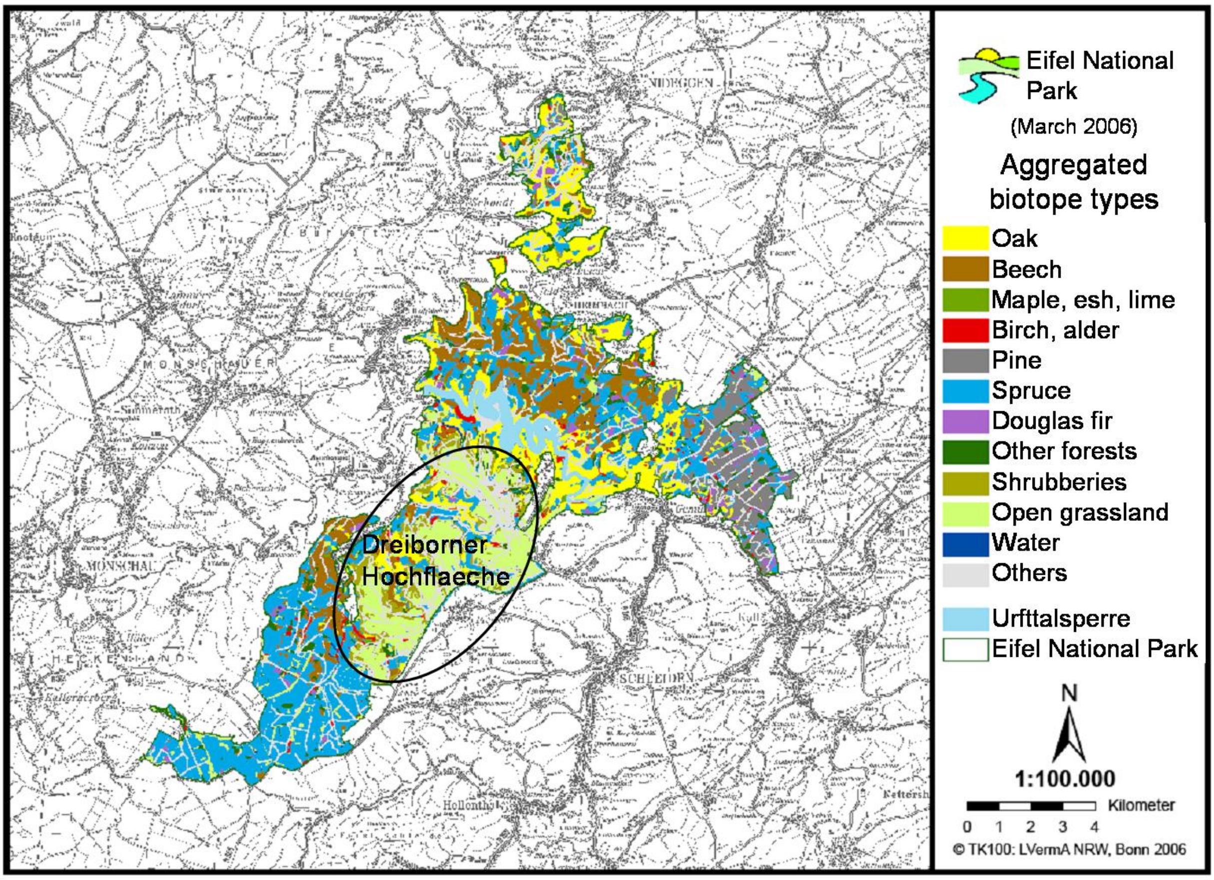

Fig. 2-1: Biotope types in the Eifel National Park. Map: Eifel National Park administration 2006.

Enclosed by this forested landscape, a large area of open grasslands is located in the center of the National Park on the plateau Dreiborner Hochfläche (Fig. 2-1).

2.2 Dreiborner Hochfläche

The plateau Dreiborner Hochfläche lies in the center of the Eifel National Park. This area has been cultivated for centuries and was used as the military training site Vogelsang from 1946 until 2005. The plateau rises from 280 m in northeast to 580 m above sea level in southwest and consists of 1,500 ha of open grasslands and shrubberies (Fig. 2-2). Deep-cut valleys run through the plateau, which are covered by forests at the steep slopes.

Fig. 2-2: View across the Dreiborner Hochfläche. Photo: B. Theissen 2005.

2.2.1 Climate & soil

The Eifel National Park has a subatlantic climate with mild winters and mild summers with high precipitation. Due to the gradient of height and the location at the lee side of the mountain range Hohes Venn, a climate gradient runs through the park. Mean annual temperature and annual precipitation at the Dreiborner Hochfläche range from 7.8°C and 900 mm in the Northwest to 6.8°C and 1100 mm in the Southeast (LÖBF NRW, 2006). Because trees are lacking, protection from strong winds and shade is scarce. Therefore, the shallow soils often desiccate in the summer time in spite of the high annual precipitation.

The parent rock material on the Dreiborner Hochfläche consists mainly of Slate (Meynen et al., 1962). The predominant soil is acid, silty Cambisol (pH_{CaCl2}: 4-5). The soils are shallow and on many places highly eroded due to the former agricultural use and the cruising with heavy military machines. Only in some dells, deeper Colluviums developed (Richter and Hubrig, 2006).

2.2.2 Vegetation

The Dreiborner Hochfläche is characterized by vast semi-natural grassland areas. They have been kept free of forest by agricultural land use and since 1946 by mowing and grazing by sheep at the concern of the military. The grasslands are now dominated by mountain hay-meadows (*Geranio-Trisetetum*) and mountain pastures (*Festuco-* and *Lolio-Cynosuretum*) (c.f. Fig. 2-1). On the fringes of the farmed areas, fallow grasslands dominated by tall grasses such as *Dactylis glomerata, Holcus lanatus, Festuca rubra* and *Arrhenatherum elatius* exist. The establishment of common broom (*Cytisus scoparius*) was enhanced by the so-called "Schiffelwirtschaft", a former type of agricultural land use in the Eifel, at which agriculture, pasturing and frequent burning were alternated. Broom now dominates the scenery of the Dreiborner Hochfläche (Fig. 2-3). Further shrubberies include raspberry (*Rubus idaeus*), bramble (*Rubus* spec.), blackthorn (*Prunus spinosa*) and hawthorn (*Crataegus monogyna*). Forests of spruce (*Picea abies*), birch (*Betula pendula*), beech (*Fagus sylvatica*), oak (*Quercus robur*) and few other deciduous and coniferous species surround the plateau.

Fig. 2-3: Common broom (*Cytisus scoparius*) on the Dreiborner Hochfläche. Photo: S. Engler 2009.

At the establishment of the Eifel National Park, the military retreated. In the northern and central part of the Dreiborner Hochfläche, extensive mowing and grazing by sheep will be continued to conserve the grasslands. The southern part, in contrast, will not be disturbed anymore and is now open to natural succession (Pardey et al., 2008).

2.3 Study sites

In this thesis, vegetation data of the years 2005, 2008, 2009 and 2010 from myself and various other authors (Lennartz et al., 2006; Engler, 2010; Heilburg, 2010; Van Wersch, 2010; Krämer, 2011) were used. An overview over the study sites, which are distributed throughout the Dreiborner Hochfläche, is given in Fig. 2-4.

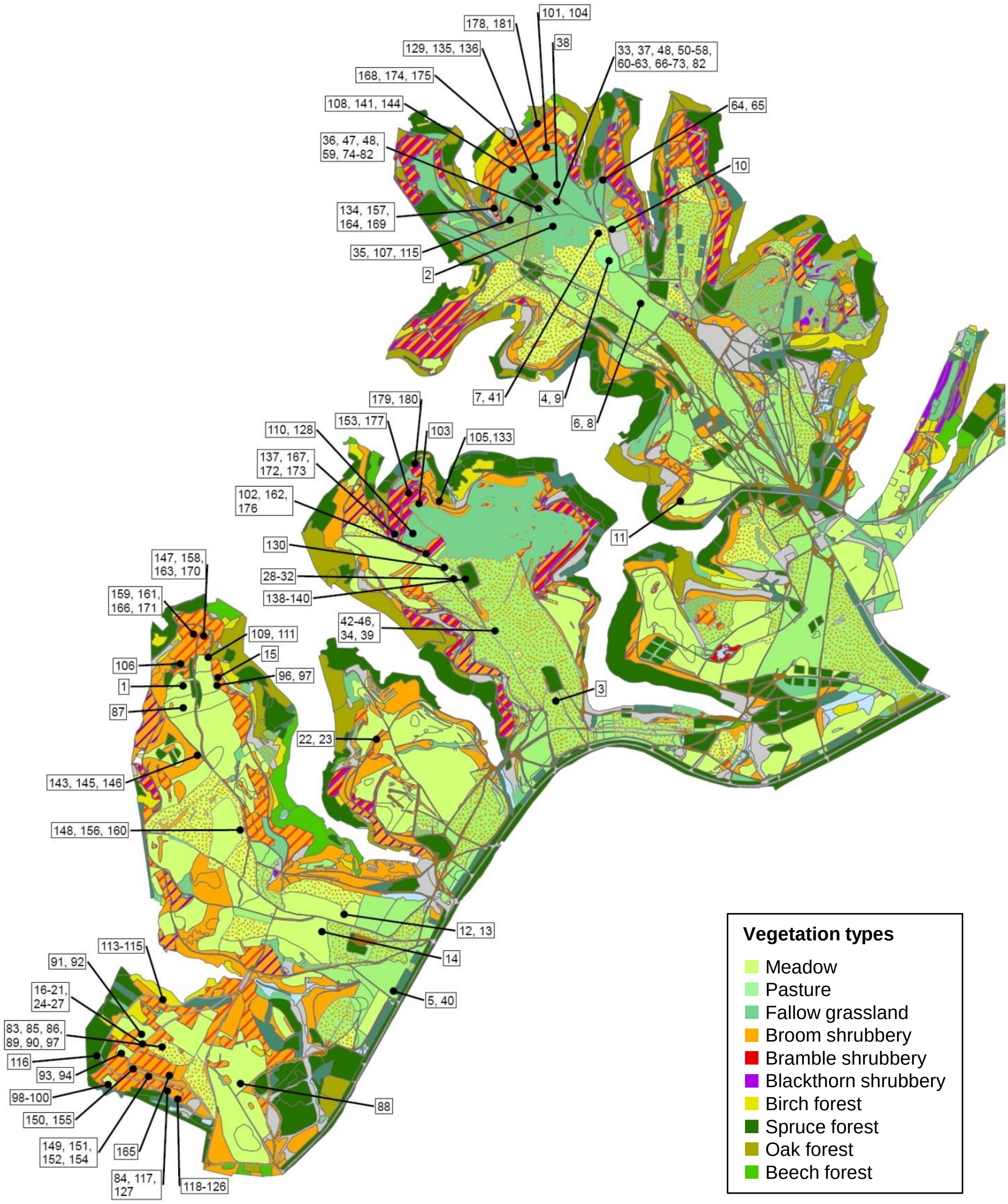

Fig. 2-4: Vegetation types of the Dreiborner Hochfläche (Neitzke, 2005, unpublished) including study sites were data was gathered by different authors. Mixed vegetation types are indicated using stripes or dots of the corresponding colors. Numbers correspond to vegetation relevés in the Appendix (Table A-4 to Table A-8).

3 The GraS-Model: Concept Overview

When dealing with a complex landscape, one has to consider entities acting at different scales. Whereas trees can be distinguished as single individuals within the landscape, grasses and herbs are rather perceived as the sum of plants building up a certain cover. Individual grasses can often not even be distinguished because of their clonal growth. Moreover, generative seed dispersal covers a much bigger area then vegetative spread. In order to cope with these unequal plant types acting at different scales, the GraS-Model is set up using a multimodeling approach (Gross and DeAngelis, 2002). Different modeling approaches are mixed including mutual interactions to simulate different aspects of the landscape (Fig. 3-1).

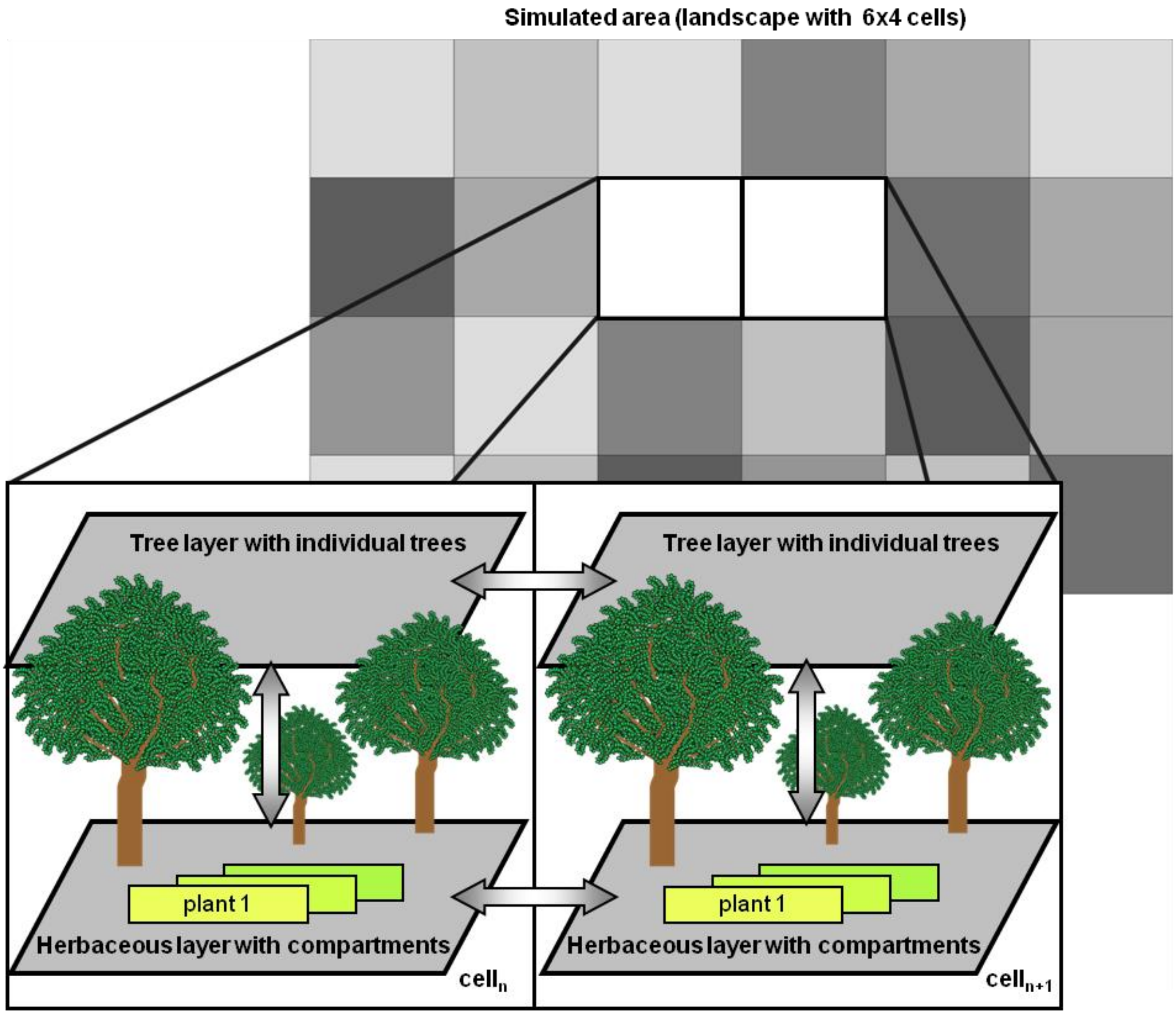

Fig. 3-1: General model concept: the multi-modeling approach. Arrows: interactions.

We divided the vegetation in two layers according to spatial resolution and dispersal mechanisms. Species of the herbaceous layer are modeled as compartments in a difference equation approach. Their abundance is expressed as cover, so that single individuals are not distinguished and only vegetative spread of plants is considered. In the tree layer, in contrast, trees are modeled using an individual-based approach, i.e. each individual is explicitly modeled including its life cycle, individual variability and individual interaction with resources (Grimm and Railsback, 2005). For each tree, seed dispersal over longer distances is simulated.

As the GraS-Model is created to simulate the development of an actual landscape, the herbaceous species and the trees are embedded in a detailed spatially-explicit grid with a cell size of 100 m². We chose such a detailed spatial scale to avoid artifacts which might result from a wider grid (Bithell and Macmillan, 2007), e.g. when small but important features in the initial data such as field paths or small woods cannot be accounted for due to a large cell size, or when seed dispersal distances are shorter then cell length. The raster-based approach enables us to insert spatially-explicit input data of the actual landscape integrating initial vegetation composition and resulting neighborhood interactions, which are crucial for the course of succession of a given landscape (Briemle, 1980; Schmidt, 1981; Ellenberg, 1996; Schreiber et al., 1997; Müller and Rosenthal, 1998; Schupp et al., 1998; Smith and Olff, 1998; Prach and Rehounkova, 2006). It furthermore allows applying different management regimes to distinct areas of the modeled landscape, and the model output can be visualized in detailed raster maps. This possibility of the model to be linked with a GIS is a precondition to be used by stakeholders who want to apply the model to an existing landscape (Rammig, 2005).

In the following chapters, the modeling technique of the herbaceous layer (Chapter 4) and the trees (Chapter 5) are explained. In these chapters, simulation results are also tested in comparison to field data. In Chapter 6, the application of the whole, complex model to the area of the Dreiborner Hochfläche in the Eifel National Park is demonstrated.

4 Simulating the Impact of Land Use Change on Grassland Dynamics Using Ecological Indicator Values

Published in slightly modified form as:

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4.1 Introduction

Plant species communities in semi-natural grasslands are adapted to the given land use form such as cutting or grazing. Once the land use changes or the grasslands are abandoned, the competitive relationship between the species and therefore species composition changes. Whereas adaptation to mechanical disturbance is the primary advantage under land use, the competition for light gains in importance in fallow grasslands (Aerts, 1999). After abandonment, low plants such as rosette or creeping plants, which suffer less from mechanical damage, therefore give way to tall grasses (Ellenberg, 1996; Glavac, 1996; Briemle et al., 2002; Kahmen, 2004).

Few models exist to predict vegetation changes in semi-natural grasslands due to land use change. Individual-based or mechanistic models in general are often restricted to a few plants, a small area, or a low spatial resolution, because the number and detail of required parameters is mostly too high for modeling big areas (e.g. PASTUREPOP by Kahmen (2004)). In less complex, rule-based models (e.g. Matsinos and Troumbis (2002), Cousins et al. (2003)), the user defines the rules at which different succession stages turn into one another. Consequently, the knowledge about possible succession stages and about the premises for transitions is mandatory, so that this approach is not suitable when new scenarios are to be predicted.

The GraS-Model is intended to simulate grassland dynamics under different management regimes on a landscape scale, i.e. for an area >1000 ha over a simulation period up to 100 years. To be able to simulate competition between grasses and herbs, which are very small entities in relation to the considered area, we had to find a way to reduce complexity. Therefore, we chose a set of representative species and plant functional groups (Jeltsch et al., 2008) and simulated their growth using difference equations. To adjust species growth rates to the given land use form, we used utilization numbers by Briemle et al. (2002), integrating the impact of the two most common forms of land use (cutting and grazing) and of non-interference. These ecological indicator values classify plants according to their realized ecological niche regarding mowing, grazing and trampling tolerance. Like the well-known Ellenberg indicator values (Ellenberg et al., 1992), they range over a 9 point scale and are based (and validated) on decade-long experience in grassland habitats (Briemle et al., 2002). Actual growth and thus competitive power in our model arises from the growth rate of each species in relation to that of the others. Spatial and temporal vegetation dynamics emerge from the resulting cover of single species. In order to display results in a spatially explicit map, the vegetation type of each cell is derived from single species' cover. As the model can use input data of a GIS, it can easily be connected to data of an actual landscape, which makes it capable of being used as a decision support system in landscape management.

In this Chapter, the model concept, model testing and simulation results concerning the herbaceous layer of the GraS-Model are described. This submodel is tested using two different data sets. Firstly, simulation results are compared to short-time vegetation data from the year 2005 and pooled data from 2008/09 and, secondly, space-for-time substitution of adjacent succession stages is used to confirm long-time simulation results.

4.2 Model description

In the following sections, the model is described following the ODD (Overview, Design concepts, and Details) protocol as proposed by Grimm et al. (2006). This protocol was originally presented for individual-based models, but it has recently been described as being suitable for any bottom-up simulation model (Grimm et al., 2010) such as our approach.

The source code was written object-orientated in Delphi® using Borland Developer Studio 2009. All objects and processes described in the text correspond to objects and methods in the source code.

4.2.1 Purpose

The GraS-model simulates vegetation dynamics of grasslands in a landscape mosaic containing various forms of land use in a dynamic, process-based manner, which allows analyzing the influence of single processes. The main purpose of the model is to illustrate, analyze and predict the influence of land management on grassland vegetation succession. It is intended to be applied as a decision support system (DSS) for stakeholders dealing with the management of grasslands on a landscape level.

4.2.2 Entities, state variables and scales

To be able to simulate grassland dynamics in a landscape mosaic we mixed two model approaches. The core of the model is a dynamic plant competition model, which simulates the competition between plant species depending on the land use. This competition model is embedded in a raster-based landscape to deal with the mosaic of species distribution and their spatial interaction in the landscape, used for initialization of the model, as well as the spatial explicit land use. The model is therefore structured in three levels: landscape, grid cells and the competing plant species (Fig. 4-1).

We chose a raster-based approach to model the **landscape**, in which the grid cells and their interactions (growth of plant species from one cell to another) are managed. The landscape contains the spatio-temporal information within the model including a loop over the simulated days and cells. The total size of the simulated area depends on the given scenario. The maximal size simulated so far was approximately 1,500 ha, i.e. 150,000 cells.

Each **cell** is characterized by its cell size, its X-/Y-coordinates, and the form of land use (cutting, grazing, trampling) as ecological site-related factors which are determined by the simulated scenario. The usual cell size is 10 m × 10 m, but can be adjusted if necessary. Each cell is a homogenous entity and we did not implement seasonal differences and spatial and temporal heterogeneity at a smaller scale (e.g. for cm² and days). The cells contain the dynamic plant competition model: The growth of each plant species and ingrowth of species from adjacent cells is added up to the potential growth of each plant species. Interaction is calculated in the way that the share of the available space is calculated according to each species' potential growth. From this competition, the cover of each species and therefore species composition emerges. For convenient visualization and comparison with field surveys the current vegetation type in each cell is derived by a decision tree from the cover of all involved plant species (Fig. 4-6). The vegetation type itself has no influence on the model calculation and is only used as a summarizing endpoint.

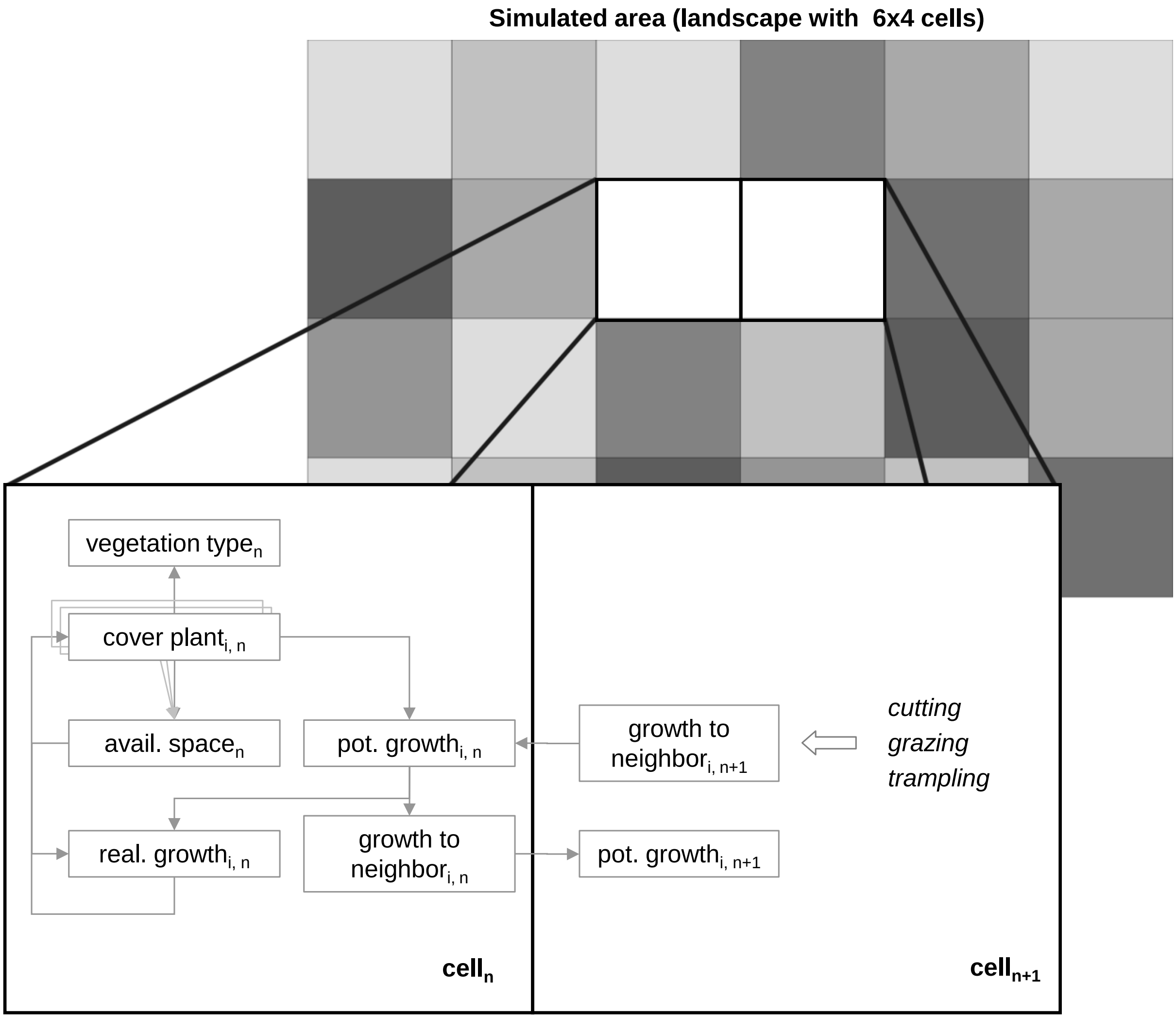


Fig. 4-1: Model concept. Boxes: state variables, arrows: flow of resources (space), italics: disturbance variables.

Each cell contains a set of **plant species**. Plant species are modeled as compartments, so that the whole subpopulation of each plant species within a cell is simulated by one state variable, the cover within that cell. The current cover of each plant species is changed due to a fixed mortality and dynamically calculated growth. Growth is thereby calculated as potential growth, depending on the current cover, the parameters of the species and land use, and realized growth, for which the potential growth is reduced in a manner that the whole community within one cell cannot cover more than 100% of the area. An overview over all model components is given in Table 4-1.

Table 4-1: Model components.

Model component	Type	Abbreviation	Unit
Landscape			
Number of cells	parameter		-
Simulated time	parameter		d
Cells			
Cell size	parameter	A	m²
X,Y-coordinates	parameter		-
Cutting intensity	disturbance variable	I_C	- ; ∈ [0, 100]
Grazing intensity	disturbance variable	I_G	- ; ∈ [0, 100]
Trampling intensity	disturbance variable	I_T	- ; ∈ [0, 100]
Available space	state variable		m²
Vegetation type	state variable		-
Plant species			
Utilization indicator value for cutting	parameter	U_C	- ; ∈ [1, 9]
Utilization indicator value for grazing	parameter	U_G	- ; ∈ [1, 9]
Utilization indicator value for trampling	parameter	U_T	- ; ∈ [1, 9]
Maximum growth rate	parameter	g_{max}	d^{-1}
Competition factor	parameter	F_C	- ; ∈ [0, 10000]
Cover of each species	state variable	c	m²
Potential growth	state variable	$(dc/dt)_{pot}$	$m^2\ d^{-1}$
Growth to neighbor	state variable		$m^2\ d^{-1}$
Realized growth	state variable	$(dc/dt)_{real}$	$m^2\ d^{-1}$

4.2.3 Process overview and scheduling

The model addresses vegetation dynamics at a landscape scale. Species' cover is calculated in steps of 1 day with the modeled time frame ranging up to 100 years. Seasonal differences have not been taken into account. All cells are recalculated each time step from the upper left corner to lower right one. Each day within all cells, each plant behaves in the following order (for an overview see Fig. 4-1):

First, a certain amount of each plant dies creating available space within the cell. Mortality is implemented for the purpose of allowing the processes of competition to take place even when the whole space is used up. Without mortality, the plants could not grow (and thus compete) as soon, as the whole area is covered. The plants are not able to push each other out, but gain competitive power only by their speed of growth into available (uncovered) space.

Afterwards, the species' growth is calculated as a function of its cover, its sensitivity to the given land use (using Briemle's utilization indicator values), its maximal growth rate and its factor for self-regulation (see Formula 4-2 and 4-3). A part of the species' growth is transferred into the adjacent cells simulating vegetative spread; seed dispersal over larger distances is not taken into account. This ingrowth into neighboring cells results either in an additional growth of an already existing species or into a new species immigrating into the cell. If the summed-up, potential growth and ingrowth from neighbor cells of all species exceeds the available space within one cell, the available area is divided according to the species's potential growth (cf. Formula 4-4) and a new, realized growth is calculated. Only in this step, recalculating the potential growth to realized growth, competition between the different species takes place. The competition strength of each plant emerges thereby from the dynamic growth model and depends on the one hand on the species parameters, determining the potential growth, and on the other hand the current plant community, determining the usable space for each plant species.

At the end of each time step, the cover of all species is updated. From the cover of the dominant grasses, the vegetation type of the cell is derived, which can be plotted into raster-maps.

4.2.4 Design concepts

Basic principles

We embedded a dynamic plant competition model into a raster-based landscape. Plants are modeled as compartments with the state variable cover indicating each species' abundance. Difference equations are used to calculate species growth depending on land use. The competition strength of each plant emerges from this dynamic growth model and depends, on the one hand, on the species parameters determining the potential growth and, on the other hand, the current plant community, determining the usable space for each plant species.

To simulate spatial interactions, we used a raster-based approach that allows us to incorporate the spatial spread of plants from a cell to adjacent cells.

Coexistence of plant species depends on niche separation along various environmental axes (Silvertown, 2004). As each cell is modeled as a homogenous entity of 100 m², a factor for self-regulation (F_S) is used to substitute for lower scale competition. It constrains the species to a maximum cover and prevents the best adapted species from taking over all the space. Plants with a low F_S value are reduced in growth at a lower cover than species with a high F_S-value.

As modeling of all existing species will result in overparameterization and chaotic model calibration and output, a set of representatives is chosen. Representatives are either a single plant species or a plant functional group consisting of species with similar traits. For further details about the choice and parameterization of representatives see the section 4.3.2 (species parameterization).

Emergence

Competitive vigor of species emerges from their growth rate in relation to that of the other species in the community of one cell, depending on the form of land use. The cover of single species over the simulation time results from species' growth under competition and influence of neighborhood. Spatial and temporal vegetation dynamics then emerge from the cover of single species.

Sensing & adaptation

The management regime (i.e. different types of land use) is sensed by the plants. According to the applied land use, the growth rate of each plant is adapted by the utilization indicator values of Briemle et al. (2002). Species with a lower utilization number are more sensitive to a certain form of land use and are more heavily restricted in their growth.

Interaction

Species compete for space. Due to interspecific competition, each species cannot always realize its full potential growth but has to share the available space with other species. The share of the available area that each species gets is calculated according to the species's potential growth, which is calculated dynamically based on the species current growth rate (see Formula 4-4). The species with the highest potential growth will achieve the biggest share of the available area and will outcompete the other species over time.

Stochasticity

Since the raster-based approach can only distinguish between different cover of species in different cells, and no information about distribution within a cell is given, the spatial dispersal of plants is modeled stochastically. At each time step, it is randomly chosen whether a plant grows into an adjacent cell. The probability (p) of spread to neighboring cells is implemented as a linear function of species' cover (c), so that the higher the cover, the greater the probability of dispersal to other cells (p = c / cell size). It is randomly chosen, into which one of the adjacent cells the species spreads, as well as the percentage of growth that is transferred to the adjacent cell.

Observation

The main output of the model is the cover of each species in each cell. This information is used to define the vegetation type of each cell. Vegetation dynamics can either be plotted as total cover of species in the whole area over time (cf. Fig. 4-5 and Fig. 4-7) or vegetation types for given time steps can be used to illustrate simulation results in detailed raster-maps using ArcGIS9 (ESRI®) (cf. Fig. 5-16 and Fig. 5-17 in Chapter 5 and Fig. 6-2 to Fig. 6-4 in Chapter 6).

4.2.5 Initialization

Initialization is based either on actual data of a real scenario, or on theoretical test scenarios. For a real scenario the simulation is initialized with data of landscape and form of land use from a detailed GIS-Map of the study site. For a theoretical test scenario, input data can be written into ASCII-Files. Required input data are spatially detailed data of vegetation distribution and land use of the simulated area. For vegetation composition, the cover of each modeled species must be indicated. Initial vegetation distribution in the simulated landscape may influence simulation outcome. Species that would be favored by a certain management regime but do not exist in that part of the landscape might migrate from other parts, therefore influencing vegetation dynamics (see also Chapters 5 and 6). Land use is applied with relative values between 0 and 100 for cutting, grazing and trampling.

4.2.6 Input data

The model does not include any input data that is loaded during the simulation run.

4.2.7 Submodels

The simulation of plant species is divided into four submodels, a constant mortality, a dynamic growth model calculating the potential growth of the species due to its growth rate, and the competition model. These submodels are described in the following sections.

Mortality

A mortality of cover $\times$ 0.55% d^{-1} is assumed to create available space.

Calculation of potential growth

The potential growth of each species is the sum of growth within a cell and ingrowth from adjacent cells. Potential growth is calculated according to the species' growth rate and its cover:

$$\left(\frac{dc}{dt}\right)_{pot} = g \times c$$

Formula 4-1

dc/dt_{pot}: potential growth [$m^2\ d^{-1}$]
g: growth rate [d^{-1}]
c: species' cover [m^2]

This potential growth refers to the capability of a species to grow into an uncovered area. Potential growth is randomly split into the potential growth within the actual cell and to adjacent cells, where it is added to the potential growth of the plant species.

Calculation of growth rate

The growth rate of each plant species is calculated according to its maximal growth rate, its factor for self-regulation and the local land use:

$$g = g_{max} \times \frac{F_S - (\frac{c}{A}) \times 100}{F_S} \times f(C) \times f(G) \times f(T)$$ Formula 4-2

g: growth rate [d^{-1}]
g_{max}: maximum growth rate [d^{-1}]
c: species' cover [m²]
A: cell size [m²]
F_S: factor for self-regulation [-]
f(X): function of land use [-]
C, G, T: cutting, grazing, trampling

The values for maximum growth rate and factor for self-regulation were calibrated on vegetation data from the area under study. Calibration was conducted using scenarios that include the influence on cutting, grazing and trampling (Table 4-5). More information about data and scenarios used for calibration is given in section 4.3.2 (Species parameterization).

The control functions for the form of land use are calculated using utilization indicator values:

$$f(X) = (1 - \frac{U_X}{9}) \times \frac{100 - I_X}{100} + \frac{U_X}{9}$$ Formula 4-3

f(X): control function for the form of land use X
U_X: utilization indicator value for the form of land use X, $\in [1, 9]$
I_X: intensity of the form of land use X, $\in [0, 100]$

The function *f*(X) results in values between 0.1 and 1, decreasing the growth rate of species that are sensitive to the given land use (Fig. 4-2). Since the control function is multiplied with the maximum growth rate a value of 1 signifies that the species is not affected by the form of land use. For single species, the utilization indicator values by Briemle et al. (2002) are used. For grouped species, the medians from the values of the members of the according phytosociological order were calculated (Table 4-6). For a more detailed description see section 4.3.2 (Species parameterization). The degree of growth inhibition furthermore depends on the intensity of land use (Fig. 4-2).

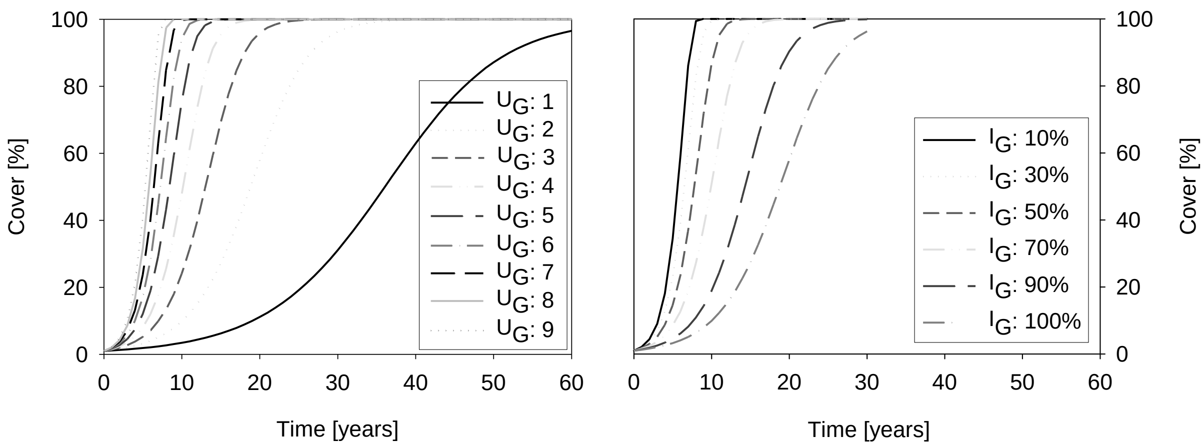


Fig. 4-2: Theoretical growth of plant species at different utilization indicator numbers (left, I_G = 100) or with different utilization intensities (right, U_G = 2). I_G: grazing intensity, U_G: utilization number for grazing.

Competition model - calculation of realized growth

Plant species interact by struggling for the available space. The share of available space each species gets depends on its potential growth in relation to the others. If the summed-up potential growth of all species exceeds the available area, the area is divided between species according to their potential growth, i.e. the sum of growth within the cells and ingrowth from adjacent cells:

$$\left(\frac{dc}{dt}\right)_{real} = g \times c \times \frac{\text{available space}}{\sum \text{potential growth}}$$

Formula 4-4

$(dc/dt)_{real}$: realized growth [m^2 d^{-1}]
g: growth rate [d^{-1}] (see Formula 4-2)
c: species' cover [m²]
available space: uncovered area = cell size - sum of species' cover [m²]
∑potential growth: sum of potential growth of all species at a given time step [m²]

Using this function, we simulate a "simultaneous" growth of all species and their competition for space. The species with the highest potential growth will achieve the biggest share of the available area, where potential growth is dynamically calculated as a function of cover, maximum growth rate, intraspecific competition and sensitivity to the given management regime (Formula 4-2 and 4-3).

This competition model acts in a way that competitive vigor of a species does not only depend on its intrinsic strength, indicated by the parameters g_{max} and F_S, but is strongly influenced by its tolerance of the applied form of land use. Two species with the same values for g_{max} and

F_S, but different indicator values will therefore behave differently according to utilization. In Fig. 4-3, the competition between two theoretic species is displayed. They have the same values for gmax (0.0128 d^{-1}) and FS (4000) but different utilization indicator values (plant 1: $U_C = 6$, $U_G = 3$, $U_T = 3$; plant 2: $U_C = 3$, $U_G = 6$, $U_T = 6$). Consequently, plant 1 outcompetes plant 2 under a cutting regime, whereas plant 2 outcompetes plant 1 under a grazing regime. Thereby, the dynamics of competition in the grazing regime is twice as fast, because in this regime two control functions (f(G) and f(T)) play a role and increase the competition strength of plant 2. The more intense the land use is, the faster the winner outcompetes the looser. When utilization intensities are 0, both species coexist.

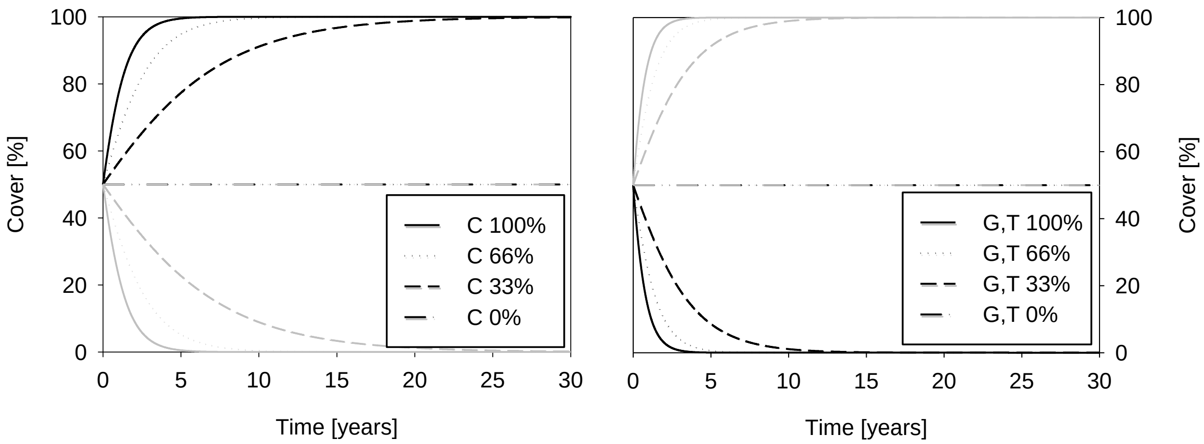


Fig. 4-3: Competition of two theoretical plant species under two scenarios. Plant 1 (black): UC = 6, UG = 3, UT = 3; plant 2 (grey): UC = 3, UG = 6, UT = 6; both: gmax = 0.0128 d-1, FS = 4000. Left: mowing scenario (cutting intensity (C) = 0 to 100), right: grazing regime (grazing (G) and trampling intensity (T) = 0 to 100).

4.3 Model parameterization and calibration

Field data of various authors were used to analyze vegetation succession on the Dreiborner Hochfläche and to determine the most prevalent vegetation types (section 4.3.1). Based on this extensive field survey, a set of representative species and plant functional groups was defined, for which utilization numbers were calculated and the maximum growth rate g_{max} and the factor for self-regulation (F_S) were calibrated (see section 4.3.2).

4.3.1 Generation of vegetation types from field data

The model was calibrated and tested on vegetation data derived from vegetation mapping at the study site (Lennartz et al., 2006; Engler, 2010; Heilburg, 2010). To begin with, aerial photographs, historical maps and interviews with contemporary witnesses were analyzed to gain knowledge on former land use and on vegetation changes over the last decades (Lennartz et al., 2006; Tischler, 2006). The historical data evidenced that fallow grasslands have been existing for at least 30 years in the area, whereas other sites had been under continuous land use by grazing or mowing. Abiotic factors such as soil type and moisture are more or less homogenous in our study site (Richter and Hubrig, 2006). We therefore used space-for-time substitution as often applied in succession research (Foster and Tilman, 2000) concluding on successional processes based on the coexistence of different succession stages on the Dreiborner Hochfläche. Sites with a deviant moisture regime or soil type (e.g. near springs or in dells with deeper colluvial soil) were excluded from our study.

Based on an extensive vegetation mapping (Neitzke, 2005, unpublished) and additional own field surveys, the five prevalent vegetation types at our study site were determined: mountain hay-meadows (*Geranio-Trisetetum*), extensive pastures (*Festuco- Cynosuretum*), intensive pastures (*Lolio-Cynosuretum*), stands dominated by *L. perenne* (sheep pens), and fallow grasslands dominated by tall grasses (mainly *D. glomeratus* and *H. lanatus*) (Table 4-2 and Fig. 4-4).

Table 4-2: Observed grassland vegetation types of the Eifel National Park.

	Vegetation type	Form of land use
Most relevant grassland vegetation types		
GT	*Geranio-Trisetetum*	hay-making
FC	*Festuco-Cynosuretum*	extensive grazing
LC	*Lolio-Cynosuretum*	intensive grazing
Lp-D	Vegetation dominated by *Lolium perenne*	sheep pen
DgHl-D	Vegetation dominated by *Dactylis glomerata* and *Holcus lanatus*, sometime containing *Arrhenatherum elatius*	abandoned for > 30 years
Transitions between vegetation types as used for parameterization and model-testing		
FC-a(4)	Former *Festuco-Cynosuretum* (after 4 years of abandonment)	abandoned for 4 years
FC-mg(4)	Former *Festuco-Cynosuretum* (after 4 years of mowing once per year and grazing by sheep)	extensive grazing and mowing

GT (Photo: I. Heilburg 2008)

FC

LC

Lp-D (Photo: I. Heilburg 2008)

DgHl-D (Photo: S. Engler 2009)

Fig. 4-4: Most relevant grassland vegetation types on the Dreiborner Hochfläche.

GT: *Geranio-Trisetetum*

FC: *Festuco-Cynosuretum*

LC: *Lolio-Cynosuretum*

Lp-D: Vegetation dominated by *Lolium perenne*

DgHL-D: Vegetation dominated by *Dactylis glomerata* and *Holcus lanatus*

Vegetation relevés were collected in these vegetation types and additionally on sites where the form of land use had recently changed so that vegetation was in transition between the defined types (raw data see Appendix Table A-4). To derive the typical cover of the chosen representatives (for definition see section 4.3.2) for each vegetation type, the median of several (n = 2 to 13, see Table 4-3) vegetation relevés were calculated. Vegetation relevés were mostly taken using the Braun-Blanquet-Scale (25 m^2) (in some few cases, species' cover was estimated in percent and the inquired area was > 1000 m^2). To convert the Braun-

Blanquet-Scale into percent, the mean value of each class was taken, as suggested by Ellenberg et al. (1992). The median of the vegetation relevés was then rounded off to the nearest 5% (only once these 5% had to be evenly distributed to two representatives with the same abundance), since a more accurate number based on the Braun-Blanquet-Scale would be inappropriate (Table 4-3).

Table 4-3: Composition of representatives (cover in %) in the used vegetation types (abbreviations for vegetation types see Table 4-2). In brackets: n of vegetation relevés following Braun-Blanquet + n of relevés with %-scale (see text for further explanations).

	GT [1+3]	FC [2+1]	LC [3+2]	Lp-D [2+0]	DgHl-D [13+0]	FC-a(4) [7+6]	FC-mg(4) [5+0]
A. elatius	0	0	0	0	10	0	0
C. cristatus	5	15	20	15	0	1	0
D. glomerata + H. lanatus	20	7.5	5	0	25	15	5
F. nigrescens	35	20	5	0	15	30	35
L. perenne	0	5	15	60	0	0	0
Climbing plants	1	0	0	0	15	5	10
Creeping plants	10	10	20	10	5	5	15
Erect forbs	10	7.5	5	1	10	10	7.5
Rosette plants	5	10	15	10	1	10	7.5
Tufted plants	15	25	15	5	20	25	20
Total cover	101	100	100	101	101	101	100

The so derived typical cover of all modeled species for the vegetation types was now inserted into model parameterization and model testing (see section 4.3.2 species parameterization). We chose different scenarios with either a consistent or a changing land use form. Since no long time data was available, space for time substitution was used. For this purpose the typical cover of the chosen representatives as observed in the field survey for the different land use forms were included as starting point and result of the succession. For example, in the second parameterization scenario “Extensive pasture is abandoned” Fig. 4-5, the typical composition for an extensive pasture in the Eifel National Park was inserted for year 0 and the composition for a typical fallow was included for year 30. In addition to this space-for-time substitution, pooled data of the years 2008 and 2009 were used for scenarios with a changing land use, thus showing not only the equilibrium but also vegetation composition of a transition between two vegetation types three to four years after land use change (see data points at year 4 in Fig. 4-5 and Fig. 4-7).

4.3.2 Species parameterization

As modeling of all existing species would result in overparameterization and model calibration would be impossible, a set of representatives was chosen (Table 4-4): The most abundant grass species which dominate the competition in the study area are *Arrenatherum elatius*, *Cynosurus cristatus*, *Dactylis glomerata* and *Holcus lanatus*, *Festuca rubra* agg. and *Lolium perenne*. Aside from these single species, which are also used to derive the cell's vegetation type, five plant groups including species with a similar ecological behavior were chosen. We grouped species according to the functional trait of growth form (according to Dierschke and Briemle (2002)), which is an important factor for their response to mechanical disturbance by cutting or grazing (Briemle et al., 2002):

- The tufted plants consist of perennial plants that react to mowing or grazing by sprouting of oftentimes numerous new shoots.
- The rosette plants are not beset by mowing or grazing. This group is enhanced by land use whereas they are hardly found in abandoned grasslands.
- The erect forbs are upright plants with only one shoot and are often very tall. They are enhanced by mowing but mostly disappear on grazed or abandoned grassland.
- Because of their entwining character, the climbing plants can survive in dense grass stands and are typical for abandoned grasslands. At our study site, the chamaephyt *Veronica chamaedrys*, classified as erect forb by Dierschke and Briemle (2002), is also able to persist in abandoned grasslands showing a similar ecological behavior as the climbing plants. It is therefore included in this group.
- Branching and creeping plants form long above- or belowground stolons that regenerate fast after mechanical damage. Therefore, they are abundant on mown or grazed grassland but rare in abandoned grasslands.

Members of these plant groups are listed in Table 4-4.

Table 4-4: List of chosen representative species and plant groups.

Single species	
Latin name	**Common name**
Arrhenatherum elatius	Tall oat grass
Cynosurus cristatus	Crested dog's-tail
Dactylis glomerata + *Holcus lanatus*	Cocksfoot grass + Common velvetgrass
Festuca rubra agg.	Red fescue
Lolium perenne	Perennial ryegrass
Grouped species	
Group name	**Characteristics and members considered in calculation of utilization numbers**
Climbing plants	Twining plants, typical for fallow grasslands and the chamaephyt *Veronica chamaedrys*. *Vicia cracca*, *Galium mollugo* agg., *Vicia sepium*, *Lathyrus pratensis*
Creeping plants	Creeping plants, promoted by cutting and grazing. *Stellaria media, Trifolium repens, Ranunculus repens, Poa trivialis*
Erect forbs	Upright high plants with one shoot. Promoted by cutting, very sensitive to grazing and non-interference. *Rumex acetosa, Achillea millefolium, Rhinanthus minor, Trifolium dubium, Leucanthemum vulgare* agg.*, Carum carvi, Ranunculus acris, Malva moschata, Euphrasia officinalis, Knautia arvensis*, *Heracleum sphondylium*
Rosette plants	Not affected by cutting and grazing. *Plantago lanceolata*, *Taraxacum officinale*, *Leontodon autumnale*, *Hypochoeris radicata*, *Bellis perennis*
Tufted plants	Perennial, enhanced by cutting or grazing. *Agrostis capillaris*, *Lotus corniculatus*, *Trisetum flavescens*, *Poa pratensis*, *Trifolium pratense*, *Anthoxanthum odoratum*, *Phleum pratense, Cerastium fontanum, Bromus hordeaceus, Alchemilla* spec.

As parameters for the species' tolerance towards land use, we applied utilization indicator numbers for cutting, grazing and trampling tolerance. The utilization numbers of representative plant species and groups were calculated in the following way: For single species, the original values of Briemle et al. (2002) were used. At our study site, *Festuca rubra* agg. consists mainly of *F. nigrescens* but also contains *F. rubra*. Therefore, utilization numbers for *F. rubra* agg. are calculated as a mean of 75% *F. nigrescens* and 25% *F. rubra*. For *Dactylis glomerata* + *Holcus lanatus*, the mean of both species' indicator values was used. The utilization numbers for the plant groups were calculated in the following way: First, species of each growth form were grouped into phytosociological orders following Ellenberg et al. (1992). As the simulated vegetation types belong to the order *Arrhenateretalia*, only members of this order were considered in further calculations. Second, species that only randomly occurred (degree of presence < 5%) were excluded from the calculation. The median of the utilization numbers of the remaining species was taken as utilization number for the plant functional group.

The parameters g_{max} and F_S for each plant species were fitted by eye in an iterative process, so that the simulated values matched the data points in the calibration scenarios (Fig 4-5). An overview over the scenarios used for calibration and model testing, including the values that the utilization intensities were set to, is given in Table 4-5.

Table 4-5: Scenarios used for model calibration and model testing. For abbreviations of vegetation types see Table 4-2.

Initial vegetation type	Land use (cutting – grazing – trampling)	Resulting vegetation type
Calibration		
GT (hay-meadow)	75-1-1	GT (hay-meadow)
FC (extensive pasture)	0-35-20	FC (extensive pasture)
LC (intensive pasture)	0-50-50	LC (intensive pasture)
Lp-D (sheep pen)	0-85-85	Lp-D (sheep pen)
FC (extensive pasture)	0-1-1	DgHl-D (fallow)
Model testing		
GT (hay-meadow)	0-50-50	LC (intensive pasture)
LC (intensive pasture)	75-1-1	GT (hay-meadow)
FC (extensive pasture)	0-50-50	LC (intensive pasture)
FC (extensive pasture)	75-20-10	Mown pasture (very extensive)
LC (intensive pasture)	0-80-80	Lp-D (sheep pen)
GT (hay-meadow)	0-1-1	DgHl-D (fallow)

g_{max} was calibrated starting with a value of 0.013 d^{-1}. With this value, a plant with a F_S of 500 is able to overgrow an uncovered, fallow area of 1 ha within 10 years, starting from a 10x10 m cell in one corner. Values for F_S were fitted in a range between 50 (where growth rate is reduced to 0 at a cover of 50) and 10000 (where growth rate is only reduced to 99% even at a cover of 100). In a last step, the calibration results were enhanced adjusting the utilization numbers for representatives to the simulated geographic area according to expert knowledge as suggested by Ellenberg et al. (1992), Dierschke (1994) and Briemle et al. (2002) within a maximal change of +/- 0.2.

The outcome of the calibration runs is shown in Fig. 4-5. Calibration was successful for scenarios with one continuing form of land use as well as for one scenario with a land use change. Short term developments as well as the equilibrium situation after a long use of the grassland could be modeled (Table 4-5 and Fig. 4-5). The resulting maximum growth rates (g_{max}) and values for the factor for self-regulation (F_S) for all species are given in Table 4-6.

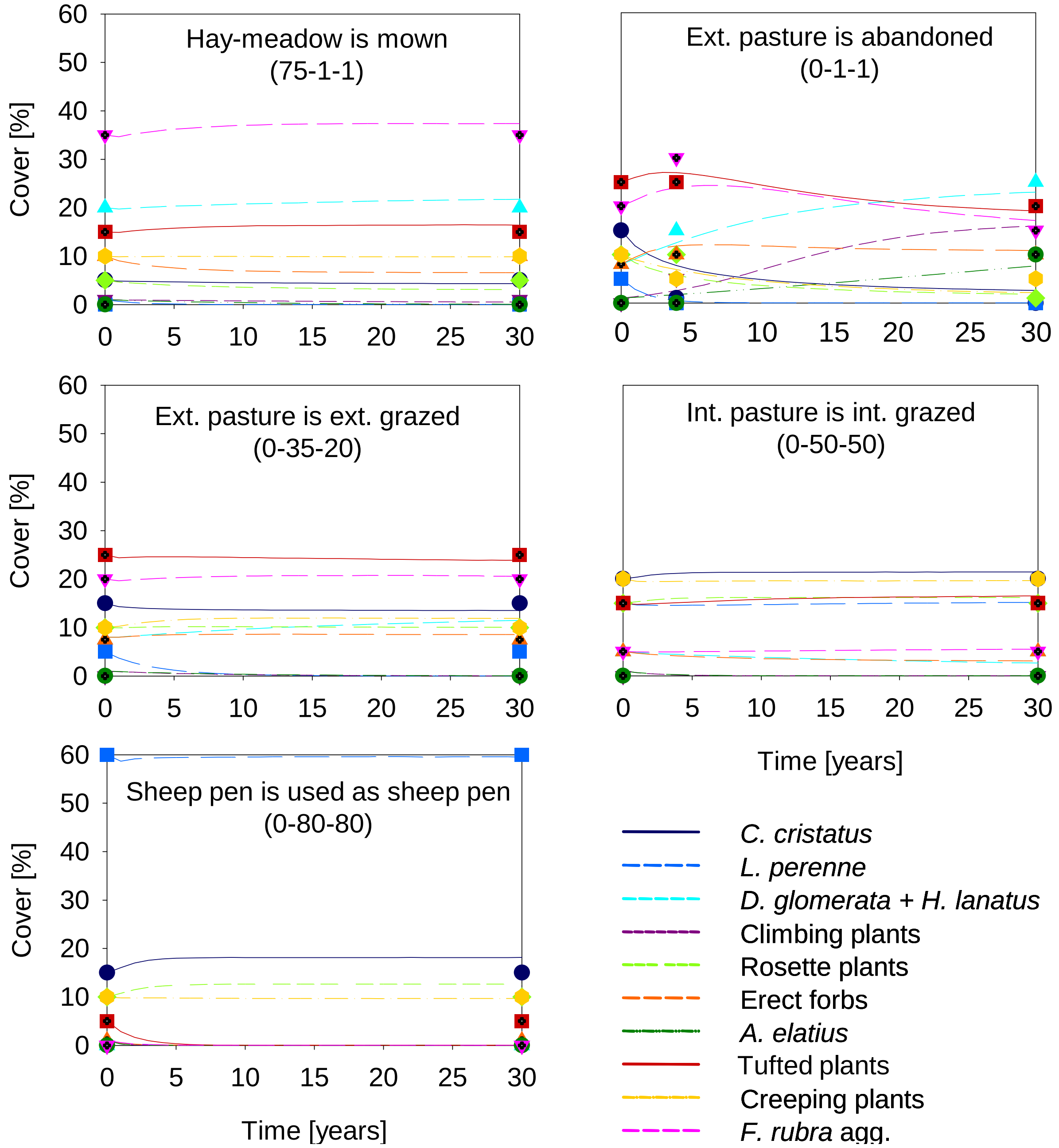


Fig. 4-5: Scenarios used for Calibration, simulating a 1 ha grid (cell size: 10 m x 10 m). Management intensity (mowing – grazing – trampling) is given in brackets.

Table 4-6: Species' characteristics. $U_{C/G/T}$: Utilization number for cutting, grazing or trampling; g_{max}: maximum growth rate, F_S: factor for self-regulation. Utilization numbers are adjusted (maximal change +/- 0.2) for the simulated geographic area according to expert knowledge as suggested by Ellenberg (1992), Dierschke (1994) and Briemle et al. (2002).

Species	U_C [-]	U_G [-]	U_T [-]	g_{max} [d^{-1}]	F_S [-]
Arrhenatherum elatius	6	3	3	0.0128	10000
Cynosurus cristatus	7.2	7.1	6.8	0.0127	80
Dactylis glomerata + Holcus lanatus	6.85	3.8	5	0.0128	4000
Festuca rubra agg.	7.3	4.65	4.3	0.0129	650
Lolium perenne	8	7.9	7.8	0.0084	1500
Climbing plants	6	2	3	0.0135	300
Creeping plants	8	6.3	6.4	0.0125	100
Erect forbs	6.2	3.8	3.8	0.0147	75
Rosette plants	7.2	6.8	6.8	0.0126	65
Tufted plants	6.8	4.7	4.5	0.0134	320

To be able to plot the model outcome in a raster map, species composition of each cell is converted into a vegetation type. We developed a decision tree, to define the simulated vegetation type by the cover of the simulated grasses *Arrenatherum elatius*, *Cynosurus cristatus*, *Dactylis glomerata* and *Holcus lanatus*, *Festuca rubra* agg., *Lolium perenne* and the climbing plants Fig. 4-6. The resulting map of vegetation types can be illustrated in a raster map using ArcGIS9 (ESRI®) (c.f. Chapters 5 and 6).

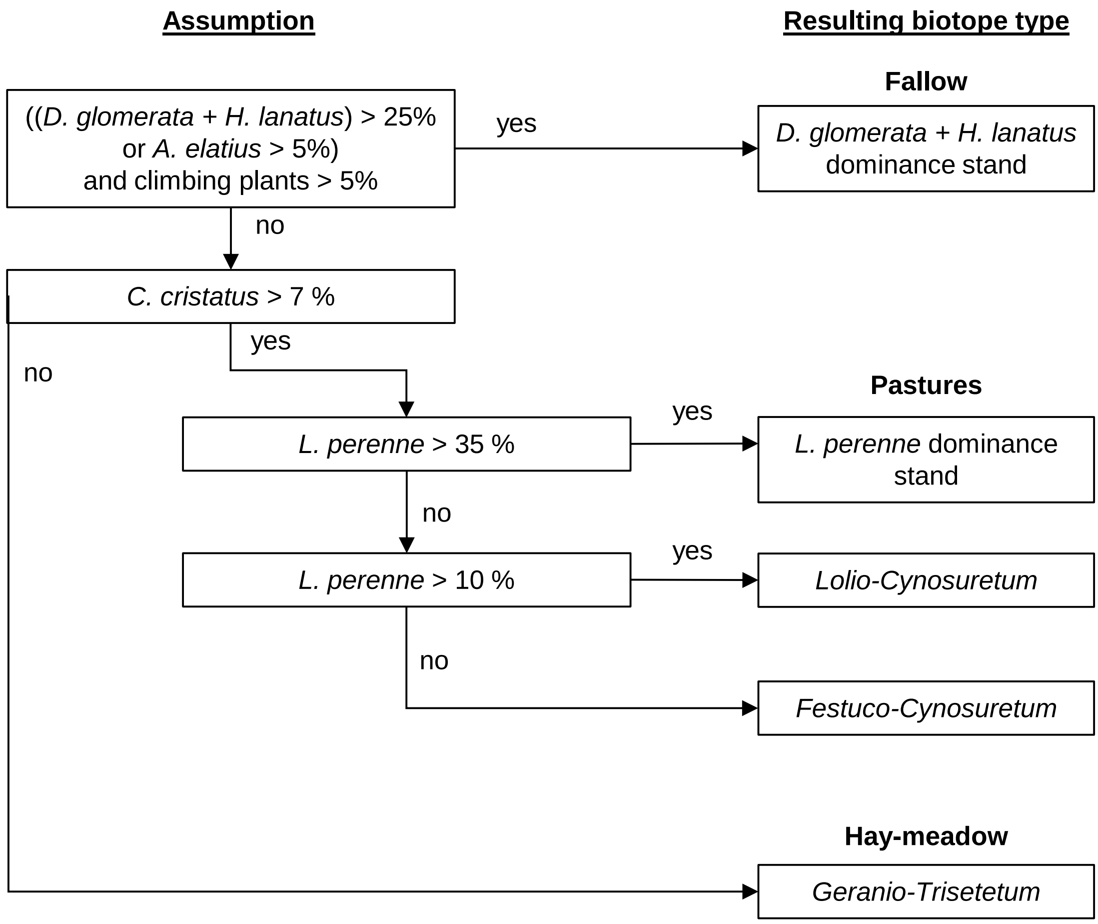


Fig. 4-6: Decision tree for deriving vegetation types from species composition, name of species is referring to their cover.

4.4 Model testing

The predictive potential of the GraS-Model was evaluated using scenarios with different forms of land use, not used for calibration (Table 4-5). These six scenarios covering land-use changes were extracted, in the same manner as for model calibration, from the vegetation relevés as described in section 4.3.1. The predicted development of species' cover over time for these dynamic scenarios is shown in comparison to observed succession in Fig. 4-7.

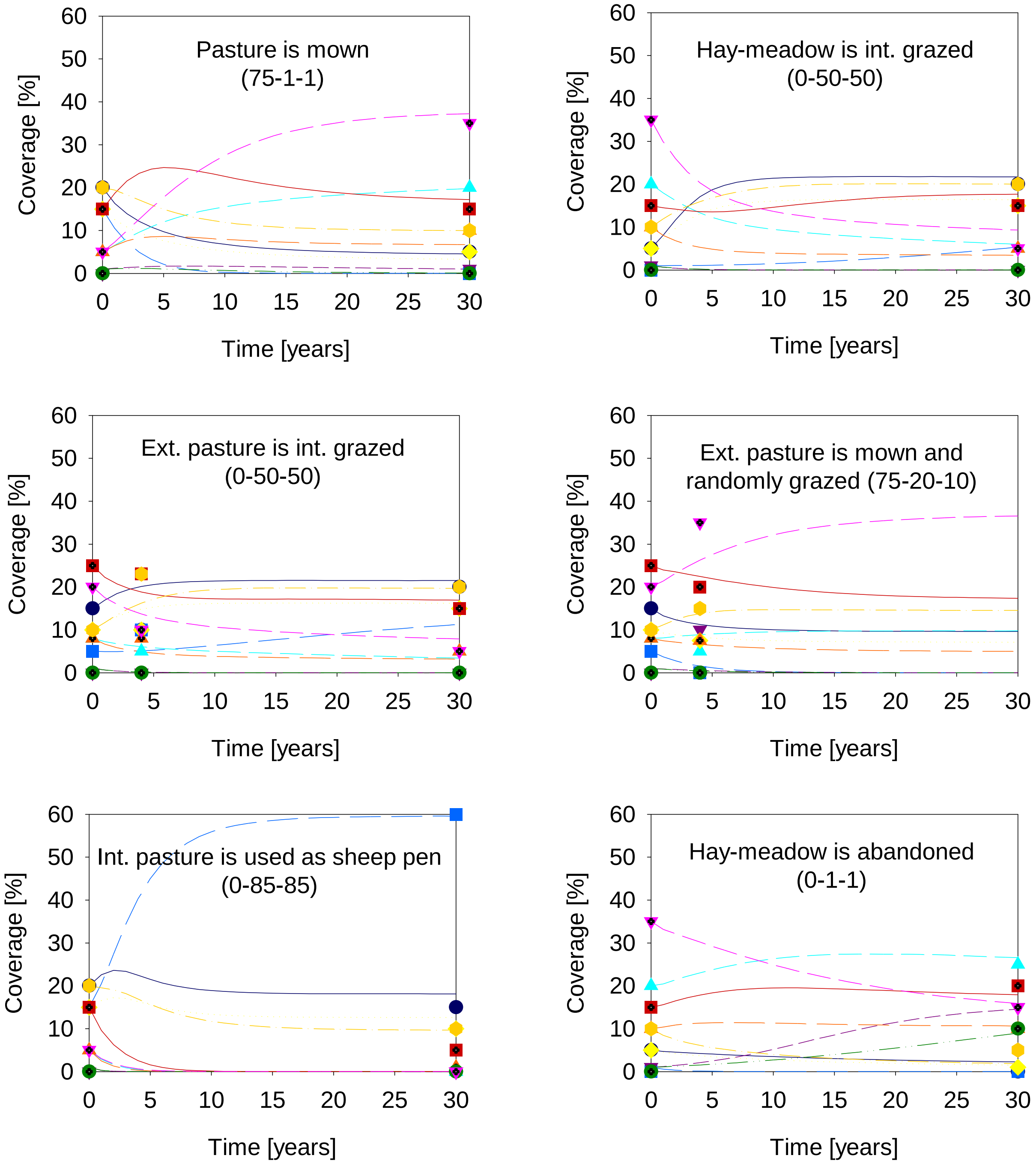


Fig. 4-7: Scenarios used for model testing, simulating a 1 ha grid (cell size: 10 m x 10 m) (legend as in Fig. 4-5). Management intensity (mowing – grazing – trampling) is given in brackets.

Regressions of observed versus predicted cover of the species were plotted (Fig. 4-8). To evaluate model predictions, the r^2 and the root mean squared deviation (RMSD), as proposed by Pineiro et al. (2008), as well as the model efficiency (EF) (Loague and Green, 1991) were calculated for each species. For all species together, we additionally tested the hypothesis that the regression slope is equal to 1 and the intercept equals 0.

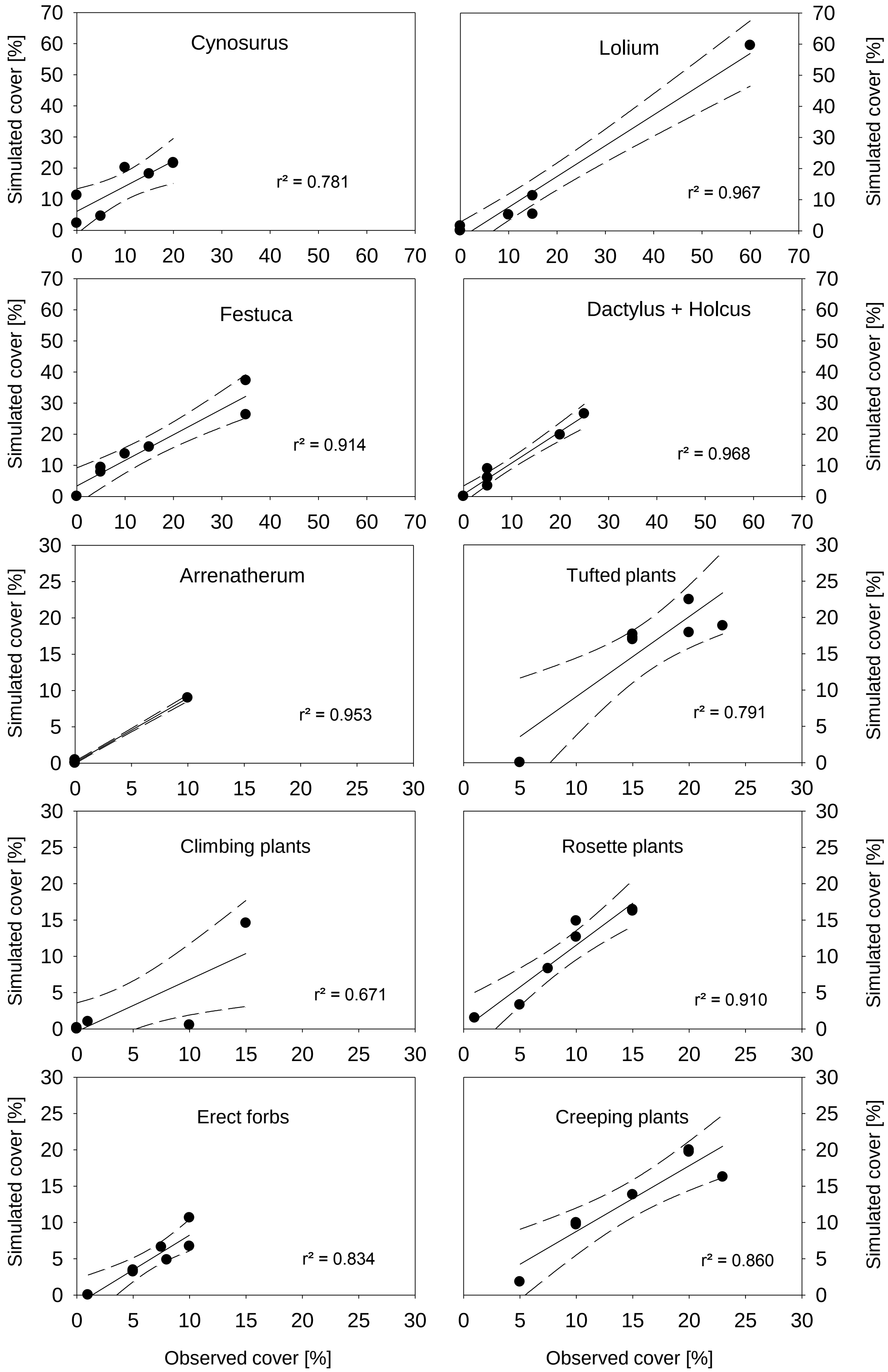


Fig. 4-8: Observed versus predicted cover (simulations as shown in Fig. 4-7) of representative species and plant groups of model testing. Solid line: linear regression, dashed line: 95% confidence level.

Short term as well as long term developments can be predicted with the GraS-model, as indicated by predicted-observed plots including the estimation of r^2, the RMSD and the EF (Fig. 4-8). The most representative species and plant groups show a good correlation between measured and predicted cover (r^2 and EF > 0.8) in the scenarios not used for calibration. Overall, the representative species show higher values than the plant groups with r^2 and EF mostly > 0.9. Only for *C. cristatus*, r^2 and EF are lower with 0.781 and 0.446, respectively. The plant groups in general show a somewhat lower r^2 and EF with a range of 0.671 to 0.910 and 0.535 to 0.968, respectively. Still, in total, a good correlation between observed and predicted cover was found with r^2 = 0.895, EF = 0.892 and RMSD = 3.406 (Fig. 4-9). Parameters of the observed vs. predicted regression for all species did not significantly differ from one and zero in slope (p = 0.637) and intercept (p = 0.870), respectively.

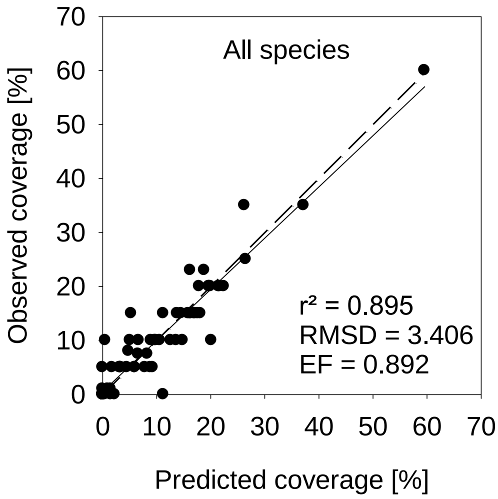


Fig. 4-9: Observed versus predicted cover (simulations as shown in Fig. 4-7) of all species at model testing. Dots represent data, solid line linear regression (y = 0.945 x + 0.52) and dashed line 1:1 reference.

The spread of species over space is presented in theoretical scenarios of 10 × 10 cells (100 × 100 m). We used a scenario with the two single species *F. rubra* and *L. perenne* to illustrate how the plants spread and compete for space (Fig. 4-10) and that initial vegetation distribution in the simulated landscape is crucial for vegetation dynamics. Note that even though *L. perenne* is the more competitive species at the chosen grazing scenario, *F. rubra* is not totally pushed out of the cells that it once occupied. Thus, *F. rubra* retains the potential to regain space, if the land use were to change.

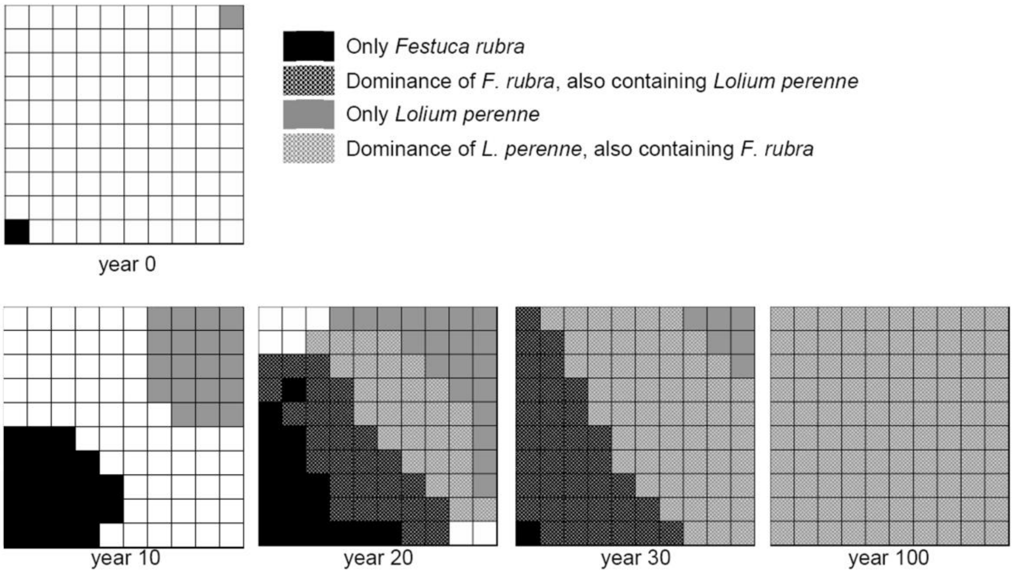


Fig. 4-10: Spread of single plant species within a 1 ha grid (cell size: 10 m x 10 m). Land use: Intensive pasture (mowing 0%, grazing 50%, trampling 50%).

4.5 Discussion

In this section, the results of parameterization and model testing, the benefits and pitfalls of using ecological indicator values, and the simplifications of small-scale dynamics are discussed. We furthermore provide an overview over limitations of our model approach.

4.5.1 Parameterization and model testing

Following the idea of plant phytosociology, we calibrated species' growth for the real species composition under given environmental conditions in the focus area using utilization indicator values. The successful calibration shows, that this approach is suitable to simulate the grassland areas under consideration for different forms of land use. Model testing revealed that the previously calibrated parameter values could also be used to satisfactorily model further scenarios at the given landscape. Most representative species showed a very high modeling efficiency; only *Cynosurus cristatus* showed a lower value. When comparing observed and simulated values for this species, which holds a crucial position for vegetation type classification, there is one case, when the predicted cover (> 11.25%) leads to a classification as a pasture, whereas according to the observed value (0%) the vegetation type would be classified as a hay-meadow. However, in the discussed scenario a mixture of land use forms was applied on the ground: the grassland was randomly grazed as well as mown and therefore the vegetation type can be regarded as a hybrid of pasture and meadow.

When looking at the calibrated parameter values, the maximal growth rates (g_{max}) of *L. perenne* and the erect forbs catches one's eye, with an outlying low and high value, respectively. The low maximal growth rate of *L. perenne* reflects that this grass does not naturally occur in extensively used, semi-natural grasslands, but can only persist on intensively used sites (as is also the case in the simulation runs due to its high utilization numbers). On the contrary, erect forbs are plants that are highly abundant in extensively used semi-natural grasslands. Yet, they disappear at intensively used sites and abandoned grasslands. This is expressed in the model by the high maximal growth rate, but low utilization numbers and factor for self-regulation. The last two are responsible for their suppression on intensively used or abandoned sites in the simulation runs, respectively. In spite of its low maximal growth rate, *L. perenne* is able to build up predominances under high grazing and trampling pressure in the simulation runs. This demonstrates that it is not the fixed parameter maximal growth rate, but rather the dynamically calculated realized growth under the current land use form that is decisive for competitive power.

We did not implement seasonal differences and spatial and temporal heterogeneity at a small scale (e.g. for cm^2 and days, respectively). Yet, coexistence of plant species depends on niche separation along various environmental axes (Silvertown, 2004). The factor for self-regulation (F_S), which substitutes for lower scale competition (Formula 4-2), showed high values (i.e. low competition) for the tall grasses *A. elatius*, *D. glomerata* and *L. perenne* (with descending height and F_S), whereas low values were calibrated for the short grass *C. cristatus*, erect forbs and rosette plants. The latter are usually not dominant in semi-natural grasslands, whereas the tall grasses sometimes dominate the community, especially when the grassland is abandoned (Glavac, 1996; Dierschke and Briemle, 2002) and competition for light gains in importance (Aerts, 1999). In fact, the calibrated factors for self-regulation show a high correlation (Pearson correlation coefficient = 0.885, $p < 0.001$) with the minimal height (Rothmaler, 2000) of the species (Fig. 4-11). We therefore hypothesize that this factor does not only substitute for intraspecific competition – as is explicitly expressed in Formula 4-2, but that also an interspecific competitive advantage for light emerges from a high F_S in the competition model.

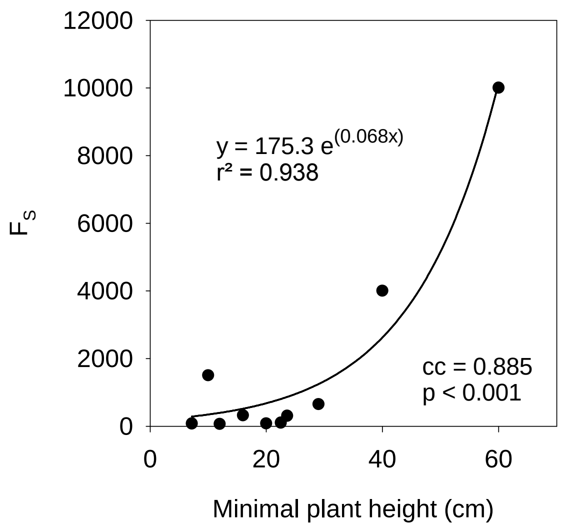


Fig. 4-11: Correlation of factor for self-regulation (F_S) and species minimal height (mean for groups) (Rothmaler, 2000). cc: Pearson correlation coefficient.

4.5.2 Using ecological indicator values

The use of ecological indicator values for mechanistic models is often a controversial subject for discussion (Wamelink et al., 1998; Rowe et al., 2005), especially because they cannot easily be related to the metric units of environmental factors. As we use the indicator values to modify species' growth and thus competitive power *in relation* to the others', we did not have to cope with this problem and achieved good results in modeling the effect of land use on grassland dynamics relying on utilization indicator values (Briemle et al., 2002). As these values exist for most species of Central Europe, we are confident that this approach allows an easy transfer of the model to other regions, without the need of detailed species data except for vegetation characteristics.

Just like Ellenberg indicator values, Briemle's utilization numbers represent the maximum probability of occurrence of each species in the landscape. They do not reflect the physiological optimum or requirements of a species, but its ecological behavior under competition (Ellenberg et al., 1992; Briemle et al., 2002). Therefore, one cannot blindly use the values without bearing the actual species in mind. One crucial point when putting our plants in groups was that species not typically occurring in the phytosociological order under consideration (in our case *Arrhenatheretalia*) were rejected. When we at first tried to integrate all species in the area, calibration was not successful. This was due to the fact, that species growing in unusual places might also show divergent behavior or a divergent indicator value (Briemle et al., 2002), so to speak. For instance, species usually growing on very low-nutrient soils have a low mowing tolerance, just because they are lacking enough nutrients to regenerate from frequent mowing. Yet, if they occur on a more nutrient rich site, they might very well show a higher mowing tolerance. In our case, species not belonging to *Arrhenatheretalia* contorted the median indicator value of the group, so that calibration became difficult. Consequently, when using ecological indicator values for mechanistic models one should bear in mind the fact that local or community specific deviations of the indicator value are likely to occur (Ellenberg et al., 1992; Dierschke, 1994; Briemle et al., 2002).

4.5.3 Simplification of small-scale dynamics to simulate vegetation succession at the landscape scale

Complex mechanistic models are not widely spread in landscape modeling, because they are often assumed to be too data-hungry to be applied for many species on a landscape scale (Jeltsch et al., 2008). To cope with this obstacle, we tried to reduce complexity by different means. First, we chose a set of representative species and merged the remainder into plant groups. Second, to reduce the number of parameters needed, we calibrated species' maximal growth rate (g_{max}) and factor for self-regulation (F_S) for the real species composition under the given environmental conditions in the focus area. Thus, unknown environmental factors are integrated in the phytosociological sense, as plant communities integrate biotic and abiotic factors of the site. The maximum growth rates and the factors for self-regulation implicitly include various environmental parameters like climate and soil conditions. After recalibration, this model is therefore thought to be transferable to other species and landscapes in Central Europe.

4.5.4 Limitations

As shown above, we were able to satisfactorily simulate most grassland types of the former military training site Vogelsang. Still, we were not able to simulate two grassland types at the extreme ends of nutrient levels in this area. In the very south of the area, nutrient-poor grasslands exist, that in phytosociological classification lay in the transition between *Geranio-Trisetetum* and very nutrient-poor *Violio-Nardetum*. At the other end of the nutrient scale, *Arrhenatherum elatius* is capable of building dominance-stands that can at the moment not be simulated. The occurrence of these stands dominated by *A. elatius* is restricted to certain areas with a deeper soil, at which *A. elatius* with relatively high nutrient requirements gains competitive power (Engler, 2010). To be able to simulate these two extremes, nutrient status needs to be added in as another environmental factor. These examples show that the model is able to simulate grassland dynamics in a mosaic of different forms of land use, but only in a homogenous landscape regarding environmental factors such as nutrients and moisture. In a more heterogeneous landscape, the impact of other environmental factors might overlap the impact of land use, so that the accordant factor would have to be modeled explicitly.

The model is not meant to give exact predictions of communities in the environment at finest spatial resolution (e.g. cm^2), because of the high variability of influencing factors (microclimate conditions) as well as the heterogeneity and complexity of soil matrices. Nevertheless the model is able to predict the general patterns of succession. Also, we do not intend to give projections about which species is capable of growing at a certain place (i.e. physiological behavior), but rather to project reactions of a given community to land-use change (i.e. ecological behavior).

To check the model's generality, it still has to be tested to see whether it is transferable to other sites. Yet, we are confident that other species and landscapes in Central Europe could be easily integrated, as we use a general pattern of differential equations and reduced complexity to a few variables. Even so, it is crucial to calibrate the model (i.e. the parameters g_{max} and F_S) with detailed vegetation data of the specific site before use, because local conditions such as soil properties (e.g. nutrients, pH, and moisture), climate and biotic interactions are not integrated explicitly but implicitly in the maximum growth rate and factor for self-regulation.

4.6 Conclusion

This mechanistic model is able to project the reaction of a grassland plant community to a changing management regime. To cope with the trade-off between the fine resolution and the data-hunger of a mechanistic landscape model, we reduced complexity to three parameters that determine species' growth and thus competitive power: maximal growth rate, a factor for self-regulation, and Briemle's utilization numbers. We reduced the number of present species to five representative species and merged the remaining ones into five plant functional groups. Following the principles of phytosociology, we calibrated species' growth based on the community data set for a specific location. As we are using a general pattern of differential equations, we are confident that the model can be easily transferred to other grassland sites.

This model of the herbaceous layer is one submodel of the overall GraS-Model and moves along in all simulations in the subsequent chapters. The interactions between this submodel and the trees will be addressed in the next chapter.

Quintessence:	
✓	Utilization numbers and representative species and groups: suitable to simulate grassland dynamics under different land use forms.
!	Handling utilization numbers: Stay within one phytosociological order!
✓	Model testing: simulation results fit observed data.
✓	Herbaceous layer sufficiently validated → is used in connection with the tree layer in the subsequent chapters.

5 The Influence of Ungulate Browsing and the Herbaceous Layer on Simulated Wood Encroachment

5.1 Introduction

When temperate, semi-natural grasslands are abandoned, their development during secondary succession is strongly site specific. They may either develop into species poor stands dominated by a few grasses or forbs, which can persist over several decades, or woody species encroach leading the successional pathway towards forest development (Ellenberg, 1996; Glavac, 1996). Which course of succession will take place mainly depends on initial conditions and neighborhood interactions (Briemle, 1980; Schmidt, 1981; Ellenberg, 1996; Schreiber et al., 1997; Müller and Rosenthal, 1998; Schupp et al., 1998; Smith and Olff, 1998; Prach and Rehounkova, 2006). For wood encroachment, seed sources must be available and the seeds must be able to germinate and survive up to the age of maturity. Because many trees do not build long lasting seed banks, seed availability depends on seed rain of nearby woods (Smith and Olff, 1998). Germination and establishment of seedlings might be hindered by the herbaceous vegetation (Watt, 1919; Lieffers et al., 1993; Frost and Rydin, 1997; Kochy and Wilson, 2000; Van Auken, 2000; Briemle et al., 2002). In an area with a high abundance of browsing animals, survival of saplings may also depend on “nurse plants” (e.g. thorny bushes) that protect seedlings of palatable species from browsing damage until they reach an age or height to escape or defend browsing (Callaway, 1995; Schupp, 1995; Kuiters and Slim, 2003; Bakker et al., 2004; Callaway, 2007; Smit et al., 2007; Barbosa et al., 2009).

To predict the secondary succession, and especially wood encroachment, on a certain abandoned site is therefore difficult. To integrate all these different processes, including spatial interactions, ecological simulation models can be valuable tools. In recent decades, much research effort has been put into the understanding and simulation of tree establishment and dynamics within forests, so that now whole families of forest models exist, sometimes including the impact of ungulate browsing, e.g. Weisberg et al. (2005), Kramer et al. (2006), Rammig et al. (2007b). For reviews on forest models see Liu and Ashton (1995), Bugmann

(2001), Pretzsch (2001), Scheller and Mladenoff (2007) and Pretzsch et al. (2008). By contrast, models including tree-grassland dynamics have been restricted mainly to arid regions (Weber and Jeltsch, 2000; Peters, 2002; Tews et al., 2006; Kochy et al., 2008); to our knowledge, only a few models exist that simulate the encroachment of wood upon temperate grasslands in a process-based, spatially-explicit way. The model WOODPAM (Gillet, 2008), integrates knowledge on tree-grass interactions in wood-pastures, but consists of a deterministic model based on differential equations where individual trees and stochastic processes are not considered. Peringer and Rosenthal (2011) developed a highly detailed individual-based model of alder encroachment on pre-alpine fen pastures including interactions with the herbaceous layer. This model has been used as decision support system for the given area on a small scale (e.g. < 0.5 ha with a 2 m grid).

The GraS-Model simulates wood encroachment on grasslands on a landscape scale using a multi-modeling approach. Trees are modeled using an individual-based approach. They disperse seeds and grow in a spatially-explicit environment. The tree submodel includes consideration of the interaction with the herbaceous layer, which was described in the previous chapter, and consequent decrease in tree seed availability. Furthermore, the interference of wild boar (*Sus scrofa*) and ungulate browsers with grassland succession is considered. Ungulate browsing is modeled by comparing supply and demand of woody browse, so that wood encroachment depends on the one hand on the density of ungulates and on the other hand also on the potential abundance of sprouting young trees. Spatial aspects of the landscape are taken into account using a raster-based approach. As input data, we can import vegetation maps of the actual landscape as GIS-maps, so that structural landscape elements and neighborhood interactions are considered, which are crucial for the course of succession. For example, initial woods disperse their seeds in the surrounding cells and thorny bushes protect young saplings from browsing damage.

In this chapter, the modeling concept and parameterization of the tree submodel is described in detail. In order to test the model’s predictive capability, the outcome of simulation runs is then compared to vegetation data of our study site. To this end, we use a pattern-oriented modeling approach as proposed by Grimm et al. (2005). The outcomes of simulation runs are evaluated on two hierarchical levels. They are compared on the one hand to counts of individual tree saplings recruiting on the abandoned grasslands of the Dreiborner Hochfläche and on the other hand to emerging patterns in the landscape, providing a strong background for model testing.

5.2 Model description

In the following sections, the tree submodel is described following the ODD (Overview, Design concepts, and Details) protocol as proposed by Grimm et al. (2010). Trees in the GraS-Model are simulated using an individual-based approach sensu Grimm and Railsback (2005), i.e. each individual is simulated including its life cycle and competition with other individuals for the resource space. This individual-based model is combined with the difference equation model of the herbaceous layer (Chapter 4) in a multimodeling approach. Both submodels are embedded and interact within a spatially-explicit, raster-based environment (Fig. 5-1).

The source code was written object orientated in Delphi® using Borland Developer Studio 2009. All objects and processes described in the text correspond to objects and methods in the source code.

5.2.1 Purpose

The main purpose of this model is to simulate the encroachment of woods on a grassland mosaic containing various forms of land use in a dynamic, process-based manner. This approach allows extracting the main processes that are most important for wood encroachment and analyzing the influence of single processes. The model is intended to be applied as a decision support system (DSS) for stakeholders dealing with the management of grasslands on a landscape level.

5.2.2 Entities, state variables and scales

Dealing with a landscape model, one has to account for different scales, e.g. grasses grow and interact on a smaller scale than trees. The GraS-Model is therefore set up as a hybrid model: grasses are simulated as compartments using a difference equation approach (see Chapter 4), whereas trees are modeled using an individual-based approach (see Chapter 5).

Both, grasses and trees, are embedded in a specific **landscape** which contains the spatio-temporal information within the model. It is simulated as a spatially explicit grid (Fig. 5-1) and includes a loop over the simulated years and cells. We chose a fine grid with a cell size of 10 m to be able to take small initial states of woods (e.g. hedges, alleys and small groups of trees or bushes) into account. Within this grid the interactions between adjacent cells are managed, including the spatial dispersal of seeds and the vegetative dispersal of grasses and herbs (see Chapter 4). The total size of the simulated area depends on the given scenario. The maximal size simulated so far was approximately 1,500 ha, i.e. 150,000 cells over a simulation time of 100 years calculated in daily time steps.

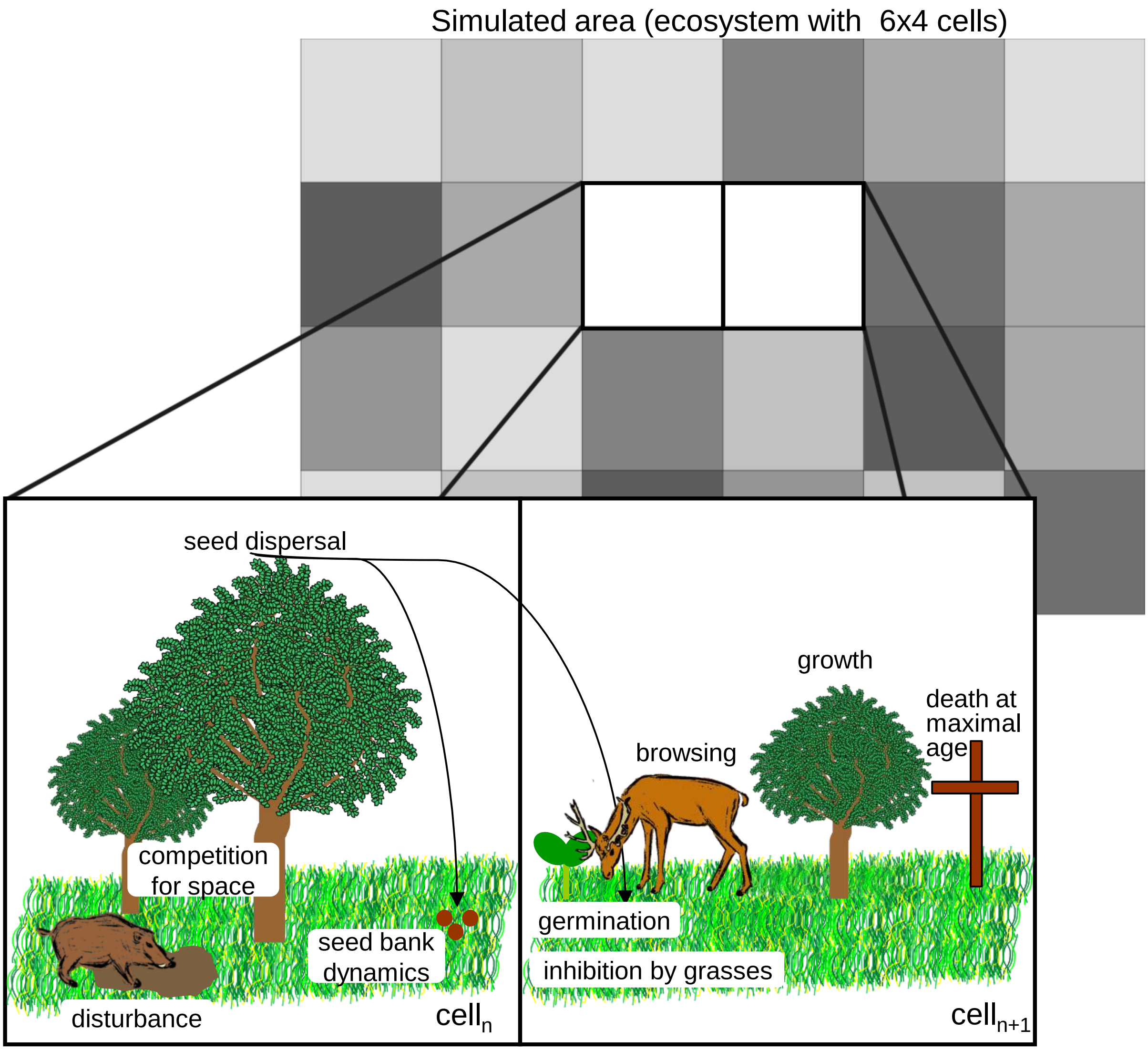


Fig. 5-1: Multimodeling approach: Individually modeled trees are embedded in a grid-based difference equation model. All stated processes may take place in all cells. Dynamics of the grasses are explained in Chapter 4. Images of red deer and wild boar: K. Krämer.

Each **cell** is characterized by its cell size of 10 m x 10 m, its X-/Y-coordinates, and the information about the form of land use (cutting, grazing, trampling), which are determined by the simulated scenario. Land use is most important for grasses and herbs (see Chapter 4), only mowing influences trees directly, as trees between the size of 0.1 and 1 m die, when the area is mown. For trees, the composition of the herbaceous layer in each cell also acts as a further environmental variable. In each cell, the growth of each tree or bush individual and each herbaceous plant species is modeled.

Table 5-1: Model components.

Model component	Type	Abbreviation	Unit
Ecosystem			
Number of cells	parameter		-
Simulated time	parameter		a
Cells			
Cell size	parameter	A	m²
X,Y-coordinates	parameter		-
Cutting intensity	disturbance variable	I_C	- ; $\in$ [0, 100]
Grazing intensity	disturbance variable	I_G	- ; $\in$ [0, 100]
Trampling intensity	disturbance variable	I_T	- ; $\in$ [0, 100]
Vegetation type	state variable		-
Trees			
Growth rate	parameter	G	a^{-1}
Maximal height	parameter	H_{max}	m
Initial height	parameter	H_{ini}	m
Maximal age	parameter	A_{max}	a
Age of maturity	parameter	A_{mat}	a
Allometric constant for crown diameter	parameter	$A_{crownconst}$	–
Allometric coefficient for crown diameter	parameter	$A_{crowncoeff}$	–
Allometric constant for biomass	parameter	$A_{biomconst}$	–
Allometric coefficient for biomass	parameter	$A_{biomcoeff}$	–
Effective seeding distance	parameter	ED	m
Maximum seeding distance	parameter	MD	m
Max. number of seeds	parameter	$Seed_{max}$	–
Seedloss to predators	parameter	P_{loss}	–
Germination rate	parameter	Germ	–
Decay time	parameter	λ	a^{-1}
Grass cover causing 50% inhibition	parameter	I_{50}	m^2
Slope of inhibition by grasses	parameter	S	-
Heigth	state variable	H	m
Crown diameter	state variable	D	m
Cover	state variable	C	m²
Age	state variable	A	a
Inhibition by grasses	state variable	I	–

The agents of this submodel are the individual **trees or bushes**. They are modeled as individuals with a distinct life-cycle. They germinate, grow, suffer from browsing, disperse via seeds to adjacent cells and over longer distances, and die when reaching their maximum age. Each tree is characterized by species-specific parameters (Table 5-1). The individual's state variables are height, crown diameter, cover and age. A further state variable is the current inhibition of seed availability by the grasses emerging from the composition of the herbaceous layer. Grasses (especially in fallows) may build up a thick litter layer that prevents seeds from reaching the soil and hinders the germination and establishment of seedlings (Watt, 1919; Lässig et al., 1995; Ellenberg, 1996; Frost and Rydin, 1997; Diemer et al., 2001; Kuiters and Slim, 2003).

5.2.3 Process overview and scheduling

Vegetation dynamics in the raster-grid are calculated in daily time steps. All cells are recalculated each time step from the upper left corner to the lower right one. Seasonal differences have not been taken into account. The continuous processes of seed decay, browsing, growth, and self-thinning are calculated each day, whereas the discrete events of disturbance by wild boar, seed dispersal, germination, and mortality due to browsing happen only once a year. The processes take place in the following order (⇒: continuous processes, ✧: discrete events):

⇒ The cover of species of the herbaceous layer is updated (see Chapter 4).

✧ A random part of the herbaceous layer is disturbed by wild boar, creating open spots where wood encroachment is not inhibited by the grasses.

✧ Mature trees disperse seeds. Anemochorous dispersal as well as zoochorous dispersal (e.g. by jays and mammals) is considered. The herbaceous layer may prevent seeds from reaching the seed bank.

⇒ Seeds in the seed bank decay.

✧ Seeds germinate.

⇒ Seedlings and young bushes or trees are browsed by red deer.

⇒ Bushes and trees grow.

⇒ Bushes and trees die due to self-thinning or senescence.

✧ Bushes and trees die due to browsing.

5.2.4 Design concepts

Basic Principles

The GraS-Model simulates wood encroachment on grasslands on a landscape scale using a multi-modeling approach. Trees are modeled using an individual-based approach (Grimm and Railsback, 2005). They disperse seeds and grow in a spatially-explicit environment. The mechanistically modeled herbaceous layer (see Chapter 4) interacts with the trees decreasing their seed availability. Furthermore, we integrate the interference of wild boar and ungulate browsers with grassland succession. Ungulate browsing is modeled by comparing supply and demand of woody browse, so that wood encroachment depends on the one hand on the density of ungulates and on the other hand also on the potential abundance of sprouting young trees. Spatial aspects of the landscape are considered using a raster-based approach, so that structural landscape elements and neighborhood interactions are accounted for, which are crucial for the course of succession.

Emergence

Bush and tree encroachment emerges from the interaction of the processes seed dispersal as possibly hindered by the herbaceous layer, seed decay, germination, ungulate browsing, growth, and self-thinning. These processes on the one hand depend on neighborhood interaction (seed dispersal and initial state of the landscape) and on the other hand on the given management regime (influencing the herbaceous layer and the density of ungulate browsers).

Sensing

In the self-thinning submodel, trees sense whether the resource space is limiting or not. When space is limiting, the smallest tree(s) react by dying off. Browsing is sensed in the way that browsed trees cease to grow and may die at the end of the year. Furthermore, trees react to the composition of the herbaceous layer that hinders seeds from reaching the seed bank. The only management regime directly sensed by the trees is mowing, which kills saplings.

Interaction

The resource that the individual trees in the GraS-Model compete for is space. When space becomes limiting, self-thinning takes place and the smallest trees in one cell die (for details see section 5.2.7 (Self-thinning). Trees are superior in succession over the bush *Cytisus scoparius* (common broom), which is modeled in the same way as the trees. Broom is furthermore restricted by bramble (*Rubus* spec.) and blackthorn (*Prunus spinosa*). Therefore, trees only compete with other tree species, whereas broom individuals compete with trees, bramble, blackthorn, and individuals of its own species. Furthermore, seeds only germinate when there is available space in the given cell. For trees, available space is calculated as the space free of all trees not including the bushes broom, bramble and blackthorn. For broom, available space only consists of the space free of trees and all bushes. Competition for space only takes place within a cell, not between adjacent cells.

Tree recruitment can be strongly inhibited by the herbaceous layer, because it prevents the seeds from reaching the seed bank. Once a tree or bush has germinated, it is not hindered by grasses and herbs. Instead, it replaces grasses in the way that space covered by trees and bushes is not available to grasses. Therefore, only the space free of trees and bushes is considered in all calculations concerning the herbaceous layer (Chapter 4).

Stochasticity

To take natural variation into account, several processes are calculated stochastically:

When input data of a landscape is imported from a GIS map, scattered young trees and bushes in grassland or shrubbery vegetation types are randomly clumped. Once a year, some of the non-forest cells are disturbed by wild boar. Which cells are disturbed is randomly chosen (see Chapter 5.2.8 (Wild boar)). Furthermore, the following parameters of the trees' lifecycle are picked from random distributions: For each time step, the growth rate of each tree is randomly drawn from a normal distribution around its mean. For the calculation of number of seed per tree, each year is randomly chosen to be a mast year with 70-100% of maximum amount of seeds, a year with 40-70% of seeds, a year with 10-40% of seeds or even a year without any seeds. The percentage of seeds is then randomly selected from the given range. The maximum age of a tree is varied by +/- 10% of the species' maximum age for each individual. The mortality of trees due to browsing is implemented as a stochastic event (section 5.2.8 (Browsing by red deer)).

Observation

The output of the model contains information about amount, height and cover of each tree or bush in each cell. The cover of the species is used to define the vegetation type of each cell. Vegetation dynamics can either be plotted as cover of species in each cell and total cover of species in the whole area over time (cf. Fig. 5-10) or otherwise vegetation types for given time steps can be used to illustrate simulation results in detailed raster-maps using ArcGIS9 (ESRI®) (cf. Fig. 5-16). These vegetation types are derived from species composition in each cell. The deduction of grassland vegetation types is described in Chapter 4. When the cover of a bush or tree species exceeds 10%, a suffix for that bush /tree species is added to the code for that vegetation type. When more than 50% is covered by one of the tree species, a cell is declared to be "forest". A forest-cell only calculates the process of seed dispersal (i.e. acting as a seed source), but neglects all other processes, as we simulate the succession of grassland towards forest, and not the succession within the forest (e.g. from birch to beech forest).

5.2.5 Initialization

Initialization is based either on actual data of a real scenario or on theoretical test scenarios. For a real scenario the simulation is initialized with data of landscape and form of land use from a detailed GIS-map of the study site. For a theoretical test scenario, input data can be written into ASCII-Files. Required input data are spatially detailed data of vegetation composition and land use of the simulated area. For vegetation composition, the cover of each modeled species must be indicated. Areas with a tree cover over 50% are imported as forest. For grassland or bush areas with scattered young trees or bushes, the amount (x% cover) of young trees and bushes is specified for several age classes (trees: 1, 5 years, broom: 2, 7, 10 years). Trees are supposed to show a clumped distribution. Therefore, x% of cells in that polygon are randomly indicated as completely covered by forest of the given age, whereas the other cells contain no trees. Groups of bushes in the study site mostly do not completely cover an area of 100 m² (= 1 cell). Therefore they are distributed in the way that 4 times x% of the cells in the given polygon are defined to be covered to ¼ by bushes, whereas the rest of the cells remain free of bushes.

5.2.6 Input data

The model does not include any input data that is loaded during the simulation run.

5.2.7 Tree submodels

The simulation of trees is divided in several submodels following the trees' lifecycle. Seeds are dispersed and reach the seed bank if not inhibited by the grass layer. Afterwards, seeds germinate and seedlings and young trees are subject to browsing. If not browsed, trees grow and might die due to later browsing, self-thinning or senescence. If they reach the age of maturity, trees disperse new seeds. These submodels are described in detail in the following sections.

Seed dispersal

Once a year, mature trees disperse their seed. The amount of seeds dispersed is modified according to the amount of seeds in the current year (see section 5.2.4 (Stochasticity)). Seeds are dispersed to the surrounding cells following the LANDIS-II double exponential seed dispersal algorithm (Ward et al., 2004), so that the dispersal kernel is characterized by the effective seeding distance (ED) and the maximum seeding distance (MD) (He and Mladenoff, 1999a). ED is the farthest distance, to which the majority (e.g. 95% for birch) of the seeds are dispersed, whereas the remaining seeds are distributed within the maximum distance (equation as in Ward et al. (2004)) (Formula 5-1, Fig. 5-2). The function is normalized so that its sum over all sink cells is one.

$$p = e^{(x\text{-cellsize})\left(\frac{\ln(1-k)}{ED}\right)} - e^{x\left(\frac{\ln(1-k)}{ED}\right)}$$

Formula 5-1

For x $\in$ [cellsize, ED] and cellsize ≤ ED

$$p = (1-k)\,e^{(x-\text{cellsize}-ED)\left(\frac{\ln(0.01)}{MD}\right)} - (1-k)e^{(x-ED)\left(\frac{\ln(0.01)}{MD}\right)}$$

For x $\in$ [ED, MD] and cellsize ≤ ED

p: proportion of seeds landing in the sink cell
x: centroid-to-centroid distance from the source cell to the sink cell
cellsize: grid cell size (e.g. 10 m)
ED: effective distance
MD: maximum distance
k: probability that the seed will disperse within the effective distance (e.g. 0.95)

For broom, oak and beech, the maximum distance reflects zoochorous dispersal by mammals (e.g. red deer) for broom, and by birds (e.g. European Jay) for oak and beech. As the jay caches seeds preferentially along structured woods (Bossema, 1979), zoochorously distributed acorns and beechnuts only land in the sink cell, when this cell contains at least one tree or blackthorn, but is not a forest-cell.

Before the seeds reach the seed bank in the sink cell, a high proportion (80%) of seeds is lost, due to non-specific predators such as mice (Lischke et al., 2006). Furthermore, grasses may hinder the seeds, so that the number of germinable seeds reaching the seed bank in one cell is calculated as:

$$N_{sb} = N_{in}\,(1 - P_{loss})\,I \qquad \text{Formula 5-2}$$

N_{sb}: number of seeds reaching the seed bank [-]
N_{in}: seeds incoming into the target cell [-]
P_{loss}: proportion of seeds lost to unspecific predators [-]
I: inhibition by grasses [-]; $\in [0, 1]$

Inhibition by grasses

Seeds are prevented from reaching the seed bank by the grasses in the herbaceous layer. We calculate an inhibition factor, as a sigmoid function of grass cover (Formula 5-3). The factors calculated for each single grass species, i.e. *Festuca rubra* agg., *Arrhenatherum elatius*, *Cynosurus cristatus*, *Lolium perenne*, *Dactylis glomerata* + *Holcus lanatus* and the tufted plants (c.f. Chapter 4) are summed up to total inhibition. This inhibition factor I ($\in [0, 1]$) is multiplied by the number of seeds reaching the seed bank.

$$I = \max\left(1; \sum_{i=1}^{n} \frac{1}{1 + e^{\frac{c_i - I_{50}}{S}}}\right) \qquad \text{Formula 5-3}$$

I: inhibition factor [-]
n: number of grasses
c_i: cover of the grass species i [m²]
I_{50}: value of grass cover that causes an inhibition of 50% [m²]
S: parameter defining the slope of the curve [-]

A thick grass felt develops mainly in fallow grasslands (Diemer et al., 2001). When the cell is mown or grazed, biomass is removed so that the grass sward is much weaker (Engler, 2010). Therefore total inhibition is reduced by 30% for mown or grazed grasslands.

Seed decay

Following the model TreeMig (Lischke et al., 2006), the decay of seeds in the seed bank is calculated exponentially:

$$\frac{dN}{dt} = -\lambda N \qquad \text{Formula 5-4}$$

dN/dt: number of seeds decaying per time step
λ: decay constant [a-1]
N: number of seeds

Germination

Once a year, a fraction of the seeds in the seed bank germinates:

$$\text{seedlings} = N\,\text{Germ} \qquad \text{Formula 5-5}$$

seedlings: number of seedlings [-]
N: number of seeds in the seed bank [-]
Germ: germination rate [-]

Seeds only germinate, when there is available space in the given cell. For trees, available space is calculated as the space free of all trees not including the bushes broom, bramble and blackthorn.

$$AS_T = A - \sum \text{trees} \qquad \text{Formula 5-6}$$

AS_T: available space for trees [m²]
A: cell size [m²]
∑trees: sum of cover of all trees [m²]

For broom, available space only consists of the space free of trees and all bushes:

$$AS_C = A - \sum \text{trees} - Ps - Ru - \sum C$$

AS_C: available space for broom (*C. scoparius*) [m²]
A: cell size [m²]
∑trees: sum of cover of all trees [m²]
Ps: cover of blackthorn (*Prunus spinosa*) [m²]
Ru: cover of bramble (*Rubus* spec.) [m²]
∑C: sum of cover of all broom bushes [m²]

The number of seeds germinating is restricted to 35 tree plus 35 broom seedlings per cell to spare simulation time and memory. The surplus of germinating seedlings is memorized and added into the browsing equation. This artificial restriction therefore anticipates browsing or self-thinning.

Height Growth

Growth is modeled following a sigmoid growth curve, using an adapted version of the Bertalanffy equation (Rammig et al., 2006; Rammig et al., 2007a) (c.f. Fig. 5-4):

$$H_{(t+1)} = H_{max}(1-(1-(\frac{H_{(t)}}{H_{max}})^{1/3})e^{-G})^3$$ Formula 5-7

$H_{(t+1)}$: height growth [m a^{-1}]
H_{max}: maximal height [m]
G: growth rate [a^{-1}]

Calculation of crown diameter and cover

Crown diameter is calculated as a function of height, according to the allometric function by Pretzsch (2001) (c.f. Fig. 5-5):

$$D = A_{cd\_const} H^{Acd\_coeff}$$ Formula 5-8

D: crown diameter [m]
H: height [m]
A_{cd_const}: allometric constant to calculate crown diameter [-]
A_{cd_coeff}: allometric coefficient to calculate crown diameter [-]

Based on crown diameter, the cover of the tree is calculated as a circle:

$$C = \left(\frac{D}{2}\right)^2 \pi$$ Formula 5-9

C: cover [m²]

Self-thinning

When space becomes limiting, competition between trees results in self-thinning. Self-thinning is simulated according to Rammig et al. (2006): At the end of each time step (i.e. after growth), the crown area of all trees in one cell is summed up, and if the sum of crown areas exceeds the cell area, the smallest tree dies. Common broom is inferior to trees during succession. Therefore, self-thinning is first calculated for broom, then for tree species. Furthermore, broom competes not only with trees but with bramble, blackthorn, other broom, and with all tree individuals (i.e. sum of crown area is calculated over all broom and tree individuals plus the cover of bramble and blackthorn), whereas trees only compete with other trees. This calculation of competition is a simplification that we need because we do not model the third dimension of height and therefore light reduction for species in lower layers.

Senescence

Once a tree reaches its maximal age (A_{max}), it dies, i.e. the tree-object is deleted.

5.2.8 Wild game submodels

In the GraS-Model, the impact of wild boar (*Sus scrofa*) and ungulate browsers on grassland succession is considered. Wild boar ploughs the ground and creates spots of open ground, where wood encroachment is facilitated. The ungulate browser red deer (*Cervus elaphus*) feeds on young trees that are reduced in growth or even die.

*Wild boar (*Sus scrofa*)*

Wild boar ploughs the ground when searching for food. In the model, 10% of hay-meadows and pastures, 3% of shrubberies and 1% of fallow grassland cells are randomly chosen once a year, at which 45% of the herbaceous layer is freed (percentages as observed by Krämer (2011)). The cover of the grasses is reduced leading to a lower inhibition of seed availability, so that wood encroachment is facilitated.

*Browsing by red deer (*Cervus elaphus*)*

Browsing is calculated based on the demand for woody biomass by red deer and the available wood. First, the weight of a "standard deer" is calculated as the mean weight of an individual in a "standard herd" consisting of five adult males (105 kg each), 10 adult females (70 kg each) and 20 juveniles (42,5 kg each) (average weights: Schulte (1998)). Demand of woody browse (in dry weight, dw) per individual is furthermore calculated as:

$$D = (dsd \times sdays \times sdeer + dwd \times wdas \times sdeer) \times frw$$ Formula 5-10

D: demand of woody browse [kg dw a^{-1}]
dsd: daily summer demand [kg dw (100 kg red deer)$^{-1}$]
sdays: number of summer days [–]
sdeer: weight of a "standard deer" [kg]
dwd: daily winter demand [kg dw (100 kg red deer)$^{-1}$]
wdays: number of winter days [–]
frw: fraction of woody parts of the total food [–]

Data for calculating the demand of woody browse by red deer was gathered from the literature (Table 5-2). When these values are inserted in Formula 5-10, it results in a demand of woody browse of 157.46 kg dw a^{-1} per "standard deer".

Table 5-2: Parameter values for calculating red deer's demand for woody browse.

Parameter	Abbre-viation	Unit	Value	Source
Daily summer demand	dsd	[kg dw 100 kg red deer-1]	2.5	(Schmidt, 2004)
Number of summer days	sdays	[–]	214	(Lennartz et al., 2006)
Daily winter demand	dwd	[kg dw 100 kg red deer-1]	3.0	(Schmidt, 2004)
Number of winter days	wdays	[–]	152	(Lennartz et al., 2006)
Fraction of woody parts of the total food	frw	[–]	0.268	(Gebert and Verheyden-Tixier, 2001)

Trees up to 5 m provide forage (Kalén and Bergquist, 2004), but are only browsed to a height of 1.6 m, which is the maximum browsing height of red deer (Petrak (Forschungsstelle für Jagdkunde und Wildschadenverhütung des Landes Nordrhein-Westfalen), pers. com.). The quantity of available browse that a tree provides is calculated for each tree according to an allometric function which was estimated from Kalén and Bergquist (2004):

$$aB = 0.024\ H^{1.634}$$ Formula 5-11

aB: available browse [kg dw]
H: tree height [m]

At each browsing event, a user-defined length of a branch (here set to 0.1 m) is fed. The browsed part of the tree is converted to biomass following the allometric function (Pretzsch, 2001) (c.f.Fig. 5-6):

$$B = Abiom_{const}\, L^{Abiom_{coeff}} \qquad \text{Formula 5-12}$$

B: biomass [kg dw]
L: length of browsed branch [m]
$Abiom_{const}$: allometric constant to calculate biomass [-]
$Abiom_{coeff}$: allometric coefficient to calculate biomass [-]

When the sum of browsed biomass of one tree reaches its available browse (aB), this tree is not browsed any more in the given year. The browsed biomass from all trees and the surplus of germinating seedlings (see "Germination") are summed up and the red deer keeps feeding until their demand is met. Browsed trees higher than 1.6 m are not further affected by red deer, because their leader shoot is out of reach. For browsed trees smaller than 1.6 m, height growth is set to zero and at the end of the year trees may die according to a species-specific browsing-induced mortality probability. Trees smaller than 0.2 m die immediately when browsed.

To take the feeding behavior of red deer in the Eifel National Park into account, trees are browsed in the order of oak (most preferred) – birch – beech – spruce (least preferred) (Petrak, pers. com.). Common broom seems not to be selectively browsed in the Eifel National Park; therefore no browsing of broom is included in the model.

As thorny bushes such as blackthorn and bramble are known to protect palatable tree species from browsing (Pott and Hüppe, 1991; Olff et al., 1999; Kuiters and Slim, 2003; Bakker et al., 2004; Weber, 2008), the demand of red deer is reduced in cells containing blackthorn and bramble by a factor F ($\in [0, 1]$) according to a sigmoid function of cover:

$$F = \max\left(1; \frac{1}{1 + e^{\frac{C_P - 25}{-5}}} + \frac{1}{1 + e^{\frac{C_R - 50}{-10}}}\right) \qquad \text{Formula 5-13}$$

F: factor [-]
$C_{P/R}$: cover of blackthorn (*P. spinosa*) or bramble (*Rubus* spec.) [m²]

Krämer (2011) found blackthorn to provide a higher protection from browsing in our study area than bramble, as is also calculated using Formula 5-13.

5.3 Tree parameterization

In this section, we describe how the tree submodel was parameterized. For many parameters, values were taken from the literature. Many values, as well as some subroutines in Section 5.2.7 ("Tree submodels"), were obtained from the two forest models TreeMig and LandClim. TreeMig is based on the well-tested model ForClim (Bugmann, 1994) and was itself tested for several scenarios with different temporal and spatial scales (Lischke et al., 2006; Rickebusch et al., 2007). LandClim is based on the well-established model LANDIS (He and Mladenoff, 1999b) and has been tested for different regions (Schumacher, 2004; Schumacher et al., 2004; Schumacher et al., 2006). Remaining data gaps were closed by fitting parameter values to own data collected for this study (see Appendix). An overview over all parameter values used in the tree submodel is provided in Table 5-4. We did not model all tree and bush species existing on the Dreiborner Hochfläche, but chose the most abundant species, namely birch (*Betula pendula*), broom (*Cytisus scoparius*), beech (*Fagus sylvatica*), spruce (*Picea abies*) and oak (*Quercus robur*), as representatives.

Further bushes considered in the GraS-Model are bramble (*Rubus* spec.) and blackthorn (*Prunus spinosa*). As these species distribute vegetatively via stolons, they are modeled in the same way as grasses and herbs (Chapter 4). Seed dispersal via seeds is neglected for these species. The parameters maximal growth rate (g_{max}) and factor for self-regulation (F_s) were set to values at which they slowly replace grasses and herbs in a fallow (Table 5-3).

Table 5-3: Characteristics of bramble (*Rubus* spec) and blackthorn (*Prunus spinosa*). $U_{C/G/T}$: Utilization number for cutting, grazing or trampling; g_{max}: maximum growth rate, F_S: factor for self-regulation.

Species	U_C [-]	U_G [-]	U_T [-]	g_{max} [d^{-1}]	F_S [-]
Rubus spec.	2	3	3	4.7	15000
Prunus spinosa	3	5	9	4.7	15000

Table 5-4: Parameter values for the modeled tree and bush species. $\bar{x}$: mean, s: standard deviation.

Parameter	Abbre-viation	Unit	Birch	Broom	Beech	Spruce	Oak
Growth rate	G ($\bar{x}$ ± s)	[a^{-1}]	0.03 ± 0.007 [f)]	0.3 ± 0.04 [f)]	0.024 ± 0.002	0.021 ± 0.002 [f)]	0.028 ± 0.004 [f)]
Maximal height	H_{max}	[m]	30 [1)]	3.7 [2)]	45 [1)]	45 [1)]	35 [1*)]
Initial height	H_{ini}	[m]	0.05 [f)]	0.05 [f)]	0.05 [f)]	0.05 [f)]	0.05 [f)]
Maximal age	A_{max}	[a]	100 [1)]	12 [2)]	350 [1)]	500 [1)]	800 [1)]
Age of maturity	A_{mat}	[a]	15 [3)]	4 [4)]	50 [3)]	45 [3)]	50 [3)]
Allometric constant for crown diameter	A_{cd_const}	[–]	1.146 [f)]	0.945 [f)]	0.716 [f)]	0.880 [f)]	1.144 [f)]
Allometric coefficient for crown diameter	A_{cd_coeff}	[–]	0.791 [f)]	1.236 [f)]	1.073 [f)]	0.877 [f)]	0.929 [f)]
Allometric constant for biomass	$A_{biomconst}$	[–]	0.0044 [f)]	-	0.0250 [f)]	0.1292 [f)]	0.8172 [f)]
Allometric coefficient for biomass	$A_{biomcoeff}$	[–]	1.247 [f)]	-	2.180 [f)]	2.569 [f)]	3.746 [f)]
Effective seeding distance	ED	[m]	200 [8)]	10 [14)]	30 [8)]	70 [8)]	30 [8)]
Maximum seeding distance	MD	[m]	700 [8)]	500 [g,z)]	200 [9,z)]	250 [8)]	200 [9,z)]
Proportion of seeds in ED	p_{ED}	[–]	95 [8)]	97 [c,z)]	99 [5,z)]	95 [8)]	99 [5,z)]
Max. number of seeds	$Seed_{max}$	[–]	11,775,000 [5)]	10000 [4)]	29000 [5)]	96500 [5)]	27500 [5)]
Seedloss to predators	P_{loss}	[–]	0.8 [5)]	0.8 [5)]	0.8 [5)]	0.8 [5)]	0.8 [=5)]
Germination rate	Germ	[–]	0.1 [5)]	0.8 [7)]	0.7 [5)]	0.75 [5)]	0.75 [5)]
Decay time	λ	[a^{-1}]	0.36 [5)]	0.063 [6)]	0.6 [5)]	0.46 [5)]	0.81 [5)]
Browsing mortality	$Brow_{mort}$	[–]	0.1 [12, 13)]	-	0.2 [10, 11)]	0.1 [10, 12)]	0.2 [11, 12)]
Grass cover causing 50% inhibition	I_{50}	[m^2]	29,0 [c)]	26,1 [c)]	29,5 [c)]	29,3 [c)]	29,8 [c)]
Slope of inhibition by grasses	S	[–]	-10 [c)]	-10 [c)]	-10 [c)]	-10 [c)]	-10 [c)]

References: [1)]Härdtle et al. (2008), [2)]Prevosto et al. (2004), [3)]Burschel and Huss (1997), [4)]Meyer (2008), [5)]Lischke et al. (2006), [6)]Turner (1933), [7)]Tarrega et al. (1992), [8)] Schumacher (2004), [9)]Kunstler et al. (2007), [10)]Vandenberghe et al. (2008), [11)]Harmer (2001), [12)]Bergquist et al. (2009), [13)]Miller and Cummins (1998); [14)]Bossard (1990), Smith and Harlen (1991); an asterisk following a reference indicates, that the source value was adjusted (not exceeding 15% deviation from the original value), [f)]fit to own data, [c)]manually calibrated (see text), [g)]guess; [z)]zoochory.

5.3.1 Seed dispersal

Data for seed dispersal was taken from the literature (Table 5-4). The seed dispersal over space using the double-exponential formula of the model LANDIS (Ward et al., 2004) is displayed for spruce in Fig. 5-2.

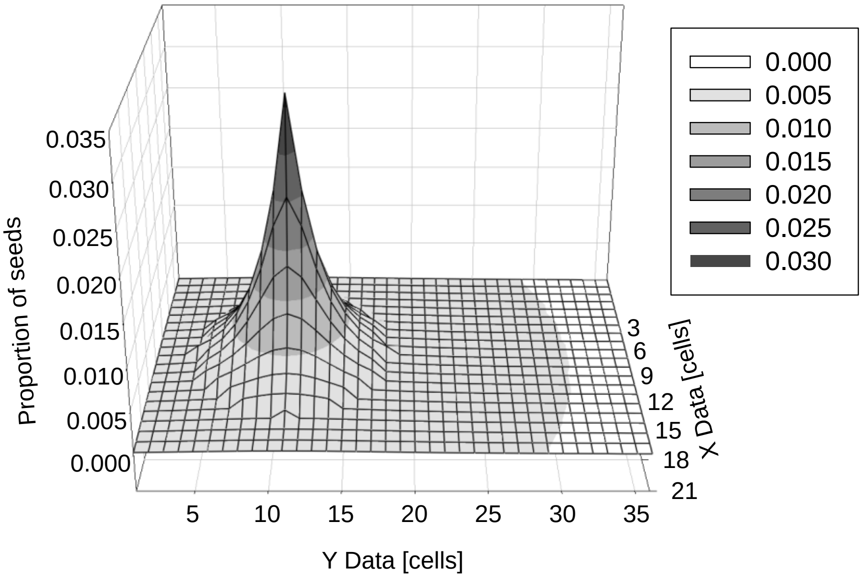


Fig. 5-2: LANDIS II double exponential seed dispersal (Ward et al., 2004) for spruce: ED = 70 m, MD = 250 m with a cell size of 10 m starting from one parent plant.

Seed dispersal along one axis as calculated from the LANDIS II double exponential seed dispersal function (Ward et al., 2004) is illustrated for all species in Fig. 5-3.

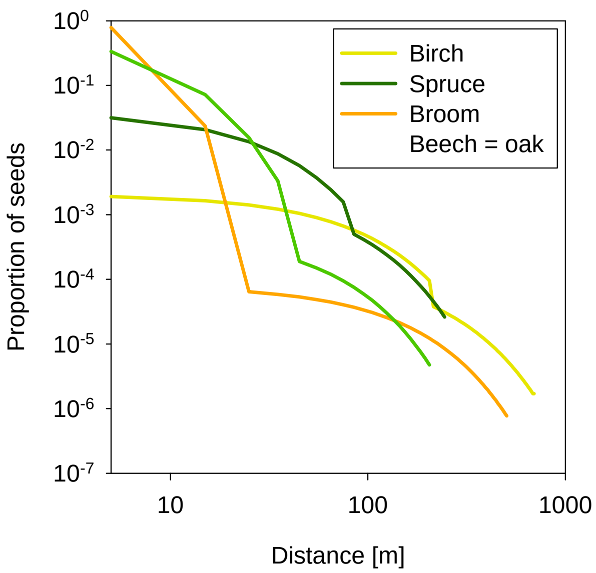


Fig. 5-3: Seed dispersal along one axis for broom and trees starting from one parent plant as calculated from the LANDIS II double exponential seed dispersal function (Ward et al., 2004).

The wind dispersed species, birch and spruce, show a shallow dispersal curve with only a slight bend at the effective seeding distance. Broom, beech and oak, in contrast, disperse the biggest proportion of their seeds in the immediate neighborhood of the parent tree. Only a small part of seeds are distributed zoochorously to further distances resulting in a sharp bend of the curve at the effective seeding distance (Fig. 5-3).

5.3.2 Germination and height growth

Germination rates for trees were taken from the model TreeMig (Lischke et al., 2006). Birch was found to have too high germination rates. The high amount of germinating birch seeds in TreeMig is strongly reduced by a high density-dependent mortality rate. This is not implemented in the GraS-Model. Therefore, the germination rate for birch was halved.

Initial values for height were set to 0.05 m, which was the minimum height found for seedlings of the modeled species in the study area (Krämer unpublished). Mean values for the growth rate (G) of trees were derived by fitting Formula 5-7 (Height growth) to yield tables (Ministerium für Ernährung und ländlichen Raum Baden-Württemberg, 2001) taking mean height values of the yield classes of the Eifel National Park (Vollmer pers. comm.). Data for young spruce (< 10 a) are obtained from Nothdurft (2007). Modeling efficiency (EF) is 0.87 for birch, 0.97 for beech, 0.96 for spruce, 0.72 for oak and 0.999 for broom (Fig. 5-4). The modeling efficiency for broom is high, because the equation was fit to a regression of data from a climatic similar region in France (Prevosto et al., 2004) of which raw data was not available.

To take natural variation into account, even though raw data was not available, values for G were taken from a normal distribution with the fitted value as the mean, and values fitted to the edges of yield classes as one standard deviation. For broom, the mean value for G was derived by fitting Formula 5-7 to the regression provided by Prevosto et al. (2004), whereas values fitted to approx. minimum and maximum values were taken as two standard deviations (Fig. 5-4).

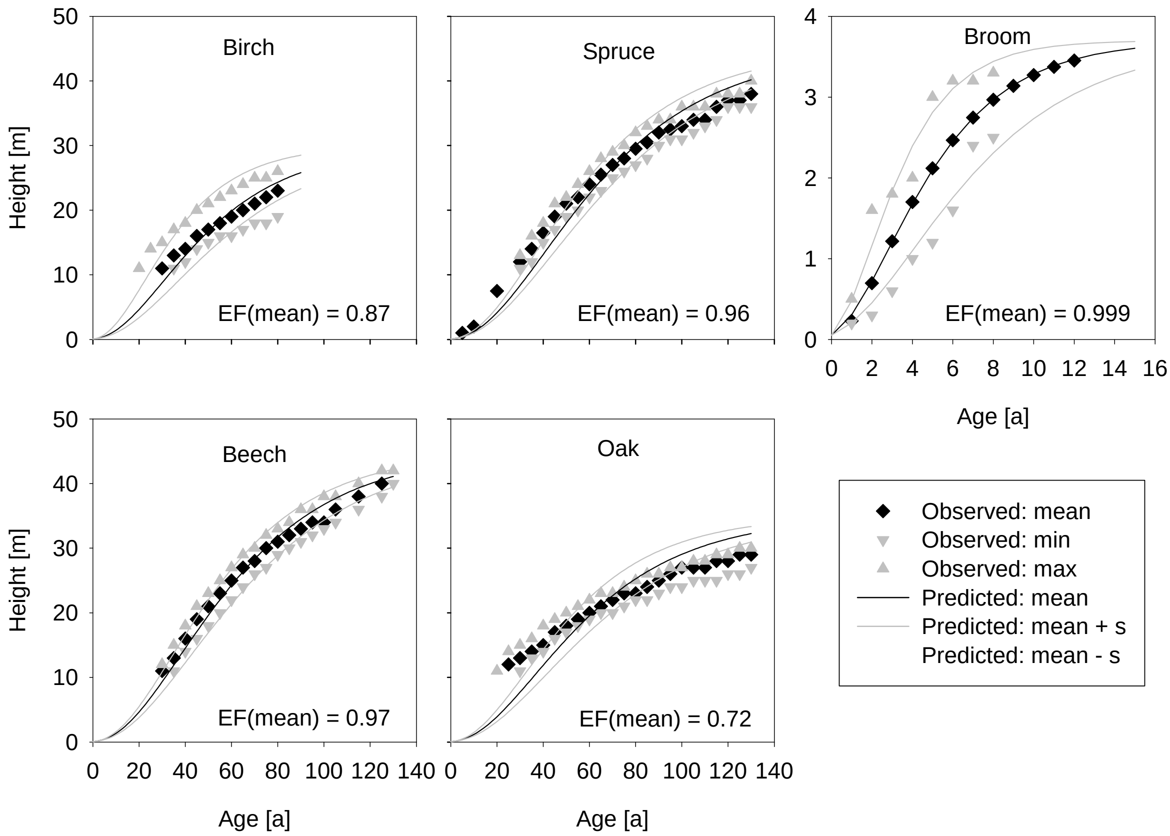


Fig. 5-4: Growth model (Rammig et al., 2006; Rammig et al., 2007a) as fit to data of four tree species (Ministerium für Ernährung und ländlichen Raum Baden-Württemberg, 2001; Nothdurft, 2007) and one bush species (Prevosto et al., 2004). EF: modeling efficiency. s: standard deviation (2s for broom). Further explanation concerning data see text.

5.3.3 Calculation of crown diameter

Parameter values for the allometric constant A_{const} and allometric coefficient A_{coeff} were derived by fitting Formula 5-8 (Calculation of crown diameter) to data of solitary trees in the Eifel National Park (Van Wersch, 2010) and own measurements (Fig. 5-5, raw data see Appendix Table A-1 and Table A-2). Tree height was measured using an optical height meter (Suunto, Finnland, PM-5/1520).

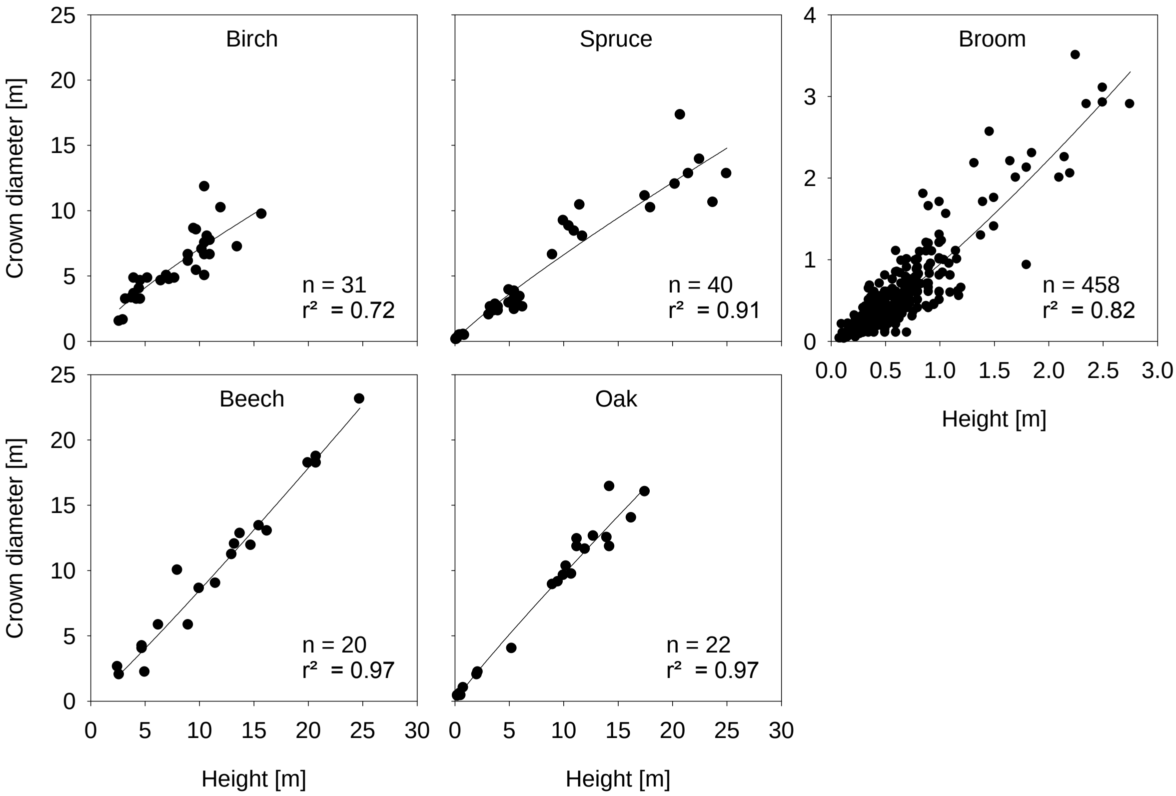


Fig. 5-5: Allometric function for crown diameter (Pretzsch, 2001) fitted to data of solitary trees.

5.3.4 Biomass of twigs

Biomass of browsed twigs is calculated from length according to the allometric Formula 5-12. Values for the parameters allometric constant ($Abiom_{const}$) and allometric coefficient ($Abiom_{coeff}$) were obtained by fitting this formula to own data of collected twigs of trees on the Dreiborner Hochfläche, raw data see Appendix Table A-3 (spruce: n = 26, r^2 = 0.93; birch: n = 21, r^2 = 0.82; oak: n = 22, r^2 = 0.78; beech: n = 16, r^2 = 0.89). Twigs were measured in length, oven dried for one week at 80 °C and weighted (Scale: SCALTEC SBA 31, max. 220g, d = 0.0001 g).

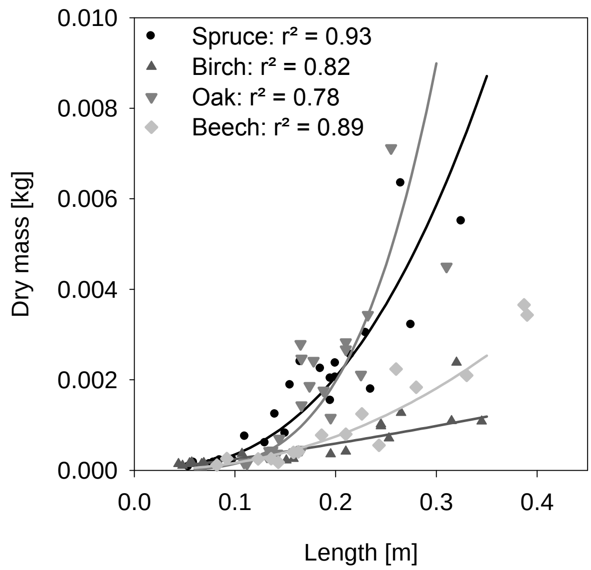


Fig. 5-6: Allometric function for biomass (Pretzsch, 2001) fitted to data of collected twigs (raw data see Appendix Table A-3).

5.3.5 Pattern-oriented calibration of the inhibition by grasses

The parameters I_{50} and S, which determine the inhibition of grasses for trees and broom, and the proportion of seeds in the effective seeding distance p(ED) for broom were calibrated by eye, so that the simulation results met patterns of bush and tree encroachment observed on the Dreiborner Hochfläche. Data used for this calibration include field surveys and analyzes of aerial photographs of various authors (Lennartz et al., 2006; Tischler, 2006; Krämer, 2009; Engler, 2010; Heilburg, 2010; Krämer, 2011) and own data collected for this study (Appendix Table A-5 to Table A-8).

Most data was available for broom; therefore calibration was started with this species. Several meadows and pastures that were recently abandoned were investigated, counting the emerging young broom individuals and calculating the mean abundance per 100 m², i.e. the size of one cell (results see Table 5-5). Broom individuals were counted in the center of pastures. When investigating the meadows, abundance of broom seedlings close to the shrubbery edge was distinguished from the abundance in the center of the meadow. At the edge of the meadows adjoining broom shrubberies, i.e. within the reach of ballistic seed dispersal, many seedlings emerged in the first year after abandonment before a thick grass-felt developed (Table 5-5). In the middle of the abandoned meadows surrounded by broom, a few solitary bushes established due to zoochorous seed dispersal in the first year after abandonment (Table 5-5). In the center of abandoned pastures, a higher number of brooms recruited in the first year after abandonment (Table 5-5). The investigated fallows were surrounded by different amounts of broom shrubberies. For the calibration we therefore created a standard scenario with the mean surrounding broom abundance. In Fig. 5-7, this standard scenario and resulting broom emergence in the cell grid is displayed. For calibration, broom individuals per cell were counted, the mean number of individuals per cell was calculated and compared to observed data (Table 5-5).

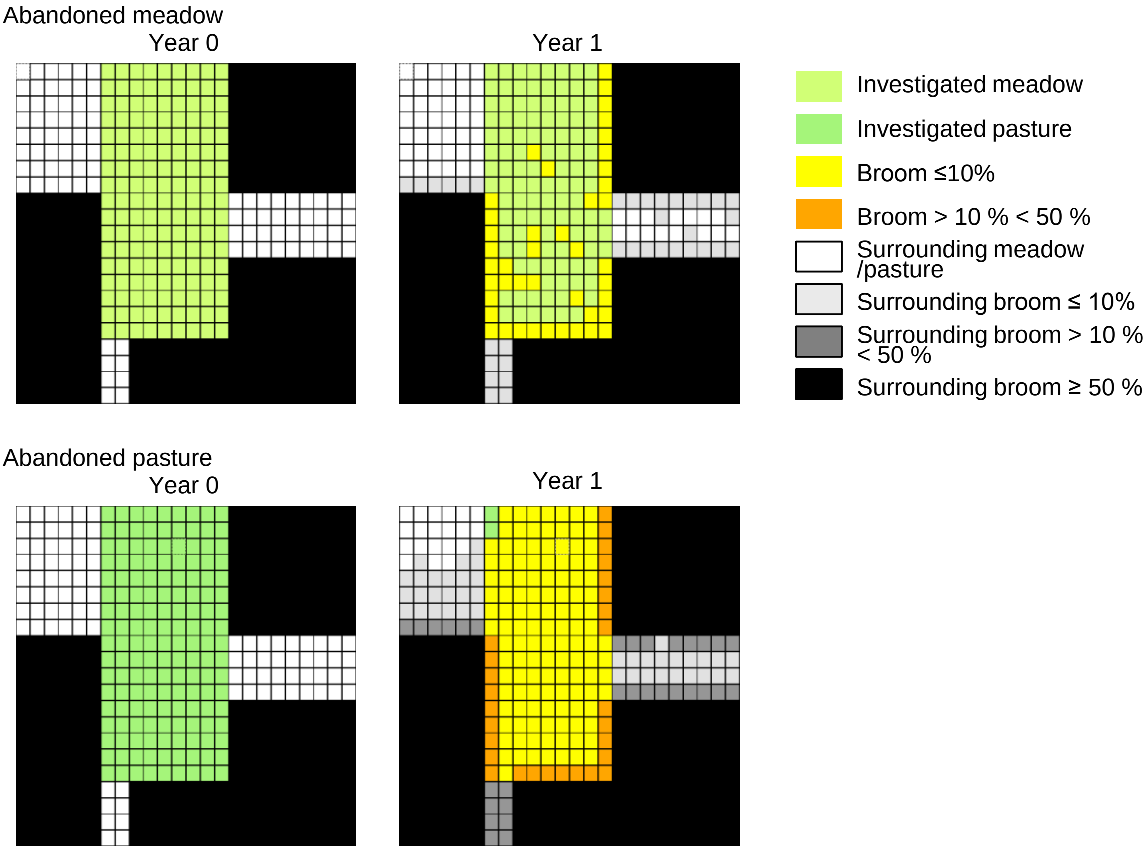


Fig. 5-7: Simulation results (vegetation types and number of individuals) after calibration and observed data (number of individuals) of an abandoned hay-meadow and pasture surrounded by broom after calibration.

Table 5-5: Observed mean number of broom individuals (Ind) in recently abandoned meadows and pastures on the Dreiborner Hochfläche (Heilburg (2008, unpublished), Krämer (2009), Engler (2010) and own data), and simulation results after calibration. n: number of field surveys. Simulations were the same as displayed in Fig. 5-7.

	Observation [Ind 100 m^{-2}] (n)	Simulation results [Ind 100 m^{-2}]
Meadow (edge)	6.5 (6)	8.3
Meadow (middle)	0.2 (10)	0.2
Pasture (middle)	5.2 (16)	5.2

Broom is not able to reproduce in a fallow grassland that has already developed a thick grass-felt as was observed on the Dreiborner Hochfläche (Van Wersch, 2010; Krämer, 2011 and own observations) as well as on other sites (Waloff, 1968; Paynter et al., 2000; Paynter et al., 2003; Prevosto et al., 2004). The parameters I_{50}, S and p(ED) were therefore calibrated so that the simulated mean number of broom individuals per cell recruiting in the first year met the observed data (see Table 5-5) and no further broom recruitment took place in the following simulation years.

The encroachment of broom and trees without any inhibition by the herbaceous layer that emerges from seed dispersal, germination and growth is illustrated in Fig. 5-8 for the area of 1 ha (= 10 cells x 10 cells) starting with one parent plant. The wind dispersed species, birch and spruce, spread fast covering the simulated area in 12 and 16 years, respectively. Beech and oak spread more slowly reaching a maximum cover of 29% in 22 years.

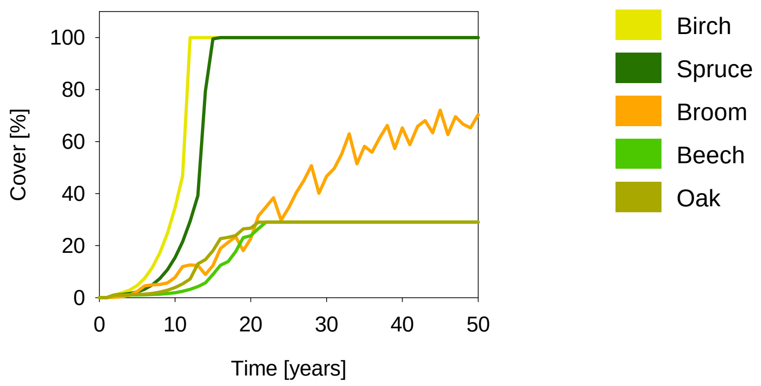


Fig. 5-8: Wood encroachment on a fallow grassland starting with one parent plant in a 1 ha scenario (c.f.Fig. 5-9) without inhibition by the herbaceous layer.

Spread of beech over space for the same simulation run is illustrated in Fig. 5-9 (top). The spread of beech stops when all cells within a distance of 30 m, i.e. the effective seeding distance, are covered by beech. Zoochorous dispersal does not take place in this scenario, because no bushes or woods are present that jays would fly to. A further spread from the newly conquered cells does not happen in the simulated time, because beech trees only reach the age of maturity at 50 years. The same holds true for oak.

Broom shows oscillating population dynamics over time (Fig. 5-8) and space (Fig. 5-9, bottom). It spreads faster than beech and oak because bushes start producing seeds already at the age of four years. The death of broom individuals at the low maximum age of 12 years leads to declines in the population dynamics.

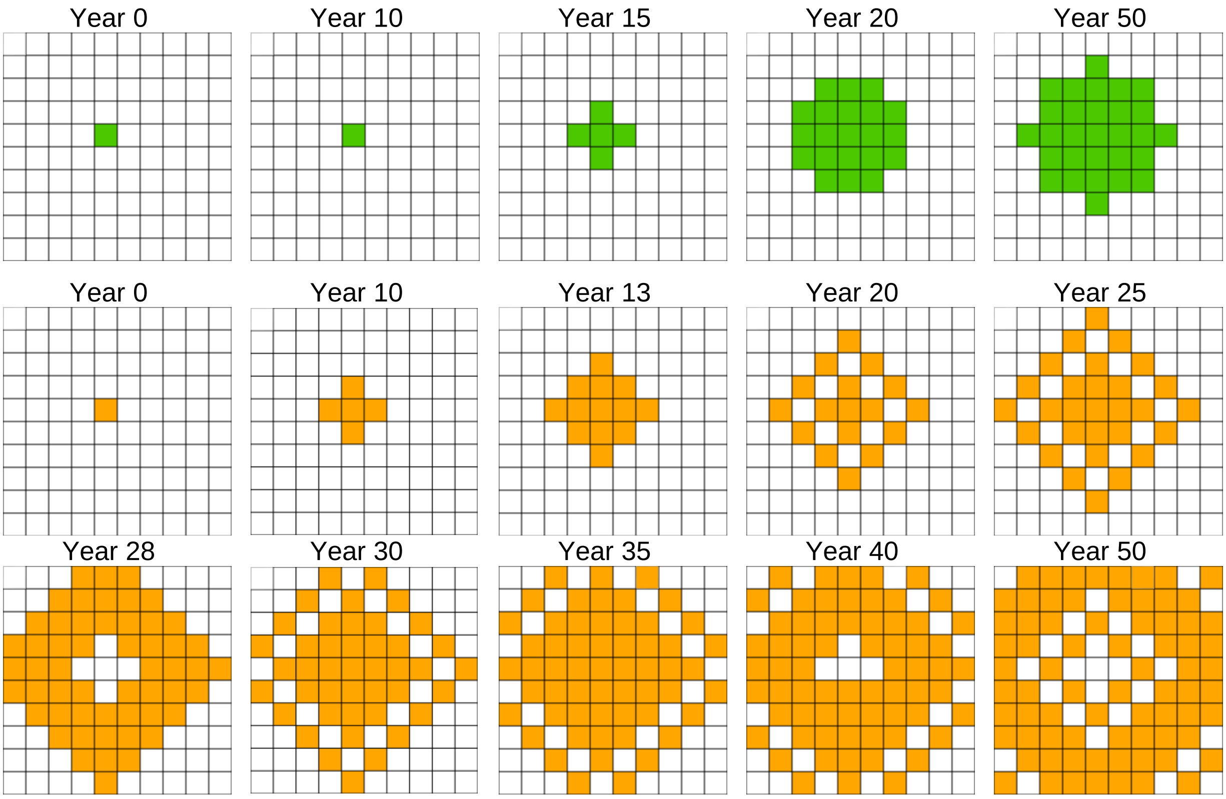


Fig. 5-9: Encroachment of beech (green: cover > 50%) and broom (orange: cover > 50%) on an area of 1 ha starting with one parent plant without inhibition by the herbaceous layer and without red deer.

Without red deer, slow forest development takes place in abandoned grasslands on the Dreiborner Hochfläche (Lennartz et al., 2006; Tischler, 2006), even though it is strongly delayed compared to wood encroachment without inhibition by the herbaceous layer. For calibration of the inhibition of seed availability by grasses, we started with the value I_{50} that was calibrated for broom and then increased the parameter value until a delayed wood encroachment took place in a fallow of 1 ha (= 10 cells x 10 cells) starting with one mature tree or bush. The resulting simulations are displayed in Fig. 5-10.

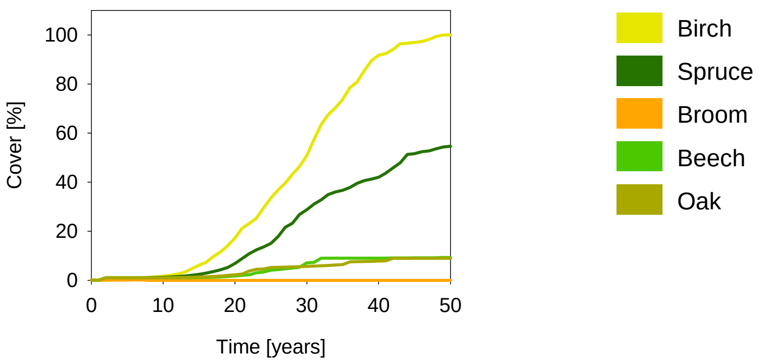


Fig. 5-10: Wood encroachment on a fallow grassland starting with one mature tree in a 1 ha scenario (c.f. Fig. 5-9) without red deer but with the inhibition by the herbaceous layer.

5.4 Pattern-oriented model evaluation

In this section, firstly data of field surveys concerning bush and tree encroachment on the Dreiborner Hochfläche are displayed. Secondly, simulation results are presented, which will be compared to observed data in the discussion (section 5.5.2) in order to evaluate the model's performance.

5.4.1 Observed data

On the Dreiborner Hochfläche, broom (*Cytisus scoparius*) was found in most non-forest vegetation types. It was abundant on sites with disturbed ground and appeared not only in broom shrubberies, but also in mixed shrubberies containing bramble (*Rubus* spec.) or blackthorn (*Prunus spinosa*). Fallow grasslands contained significantly less broom bushes than most other biotope types. Only in blackthorn shrubberies, the number of broom bushes was comparably low (Fig. 5-11).

Tree seedlings were mainly found on sites with spots of bare soil, whereas, significantly, the lowest number of tree saplings was found on abandoned meadows or pastures that developed a thick grass felt (Fig. 5-12 and Fig. 5-13). These fallow grasslands had been abandoned for 3 to more than 40 years. Some saplings were also found in different shrubberies (Fig. 5-13, left).

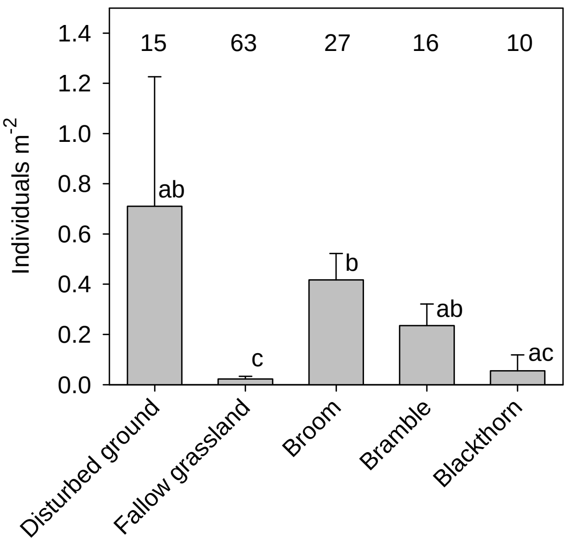


Fig. 5-11: Number of broom individuals (mean + 95% CI) found in different vegetation types on the Dreiborner Hochfläche. Numbers on top indicate number of vegetation relevés. Different letters indicate significant differences (All Pair wise Multiple Comparison Procedures: Dunn's Method). Data from various studies (Heilburg, 2009; Krämer, 2009; Engler, 2010; Van Wersch, 2010; Krämer, 2011) and own data collected for this study (raw data see Appendix Table A-5 to Table A-8).


Fig. 5-12: Left: abandoned meadow with a thick grass felt and no saplings, Photo: S. Engler 2010. Right: Spruce saplings at a site with less grass.

Saplings found in the open areas of grassland and bare soil were smaller than 1 m, the vast majority (> 80%) even smaller than 0.2 m (Fig. 5-13, right). Small saplings were either young, or restricted in growth by heavy browsing (c.f. Fig. 5-14). Tall saplings (> 2 m) were only found in shrubberies, mostly occurring in thorny bushes, where they were protected from browsing (Fig. 5-14).

Krämer (2011) found, that on the landscape scale, patterns of wood encroachment on the Dreiborner Hochfläche occur either along sites with disturbed soil (e.g. fallow field paths), as was observed especially for broom (Fig. 5-15 top), or within thorny bushes, the latter being exclusive for tree recruitment up to a height where trees escape browsing influence (Fig. 5-15 bottom, Fig. 5-13). The establishment of broom on disturbed ground occurred as soon as 5 years after abandonment. In contrast, the establishment of trees in thorny bushes was found on sites that had been abandoned for over 40 years.

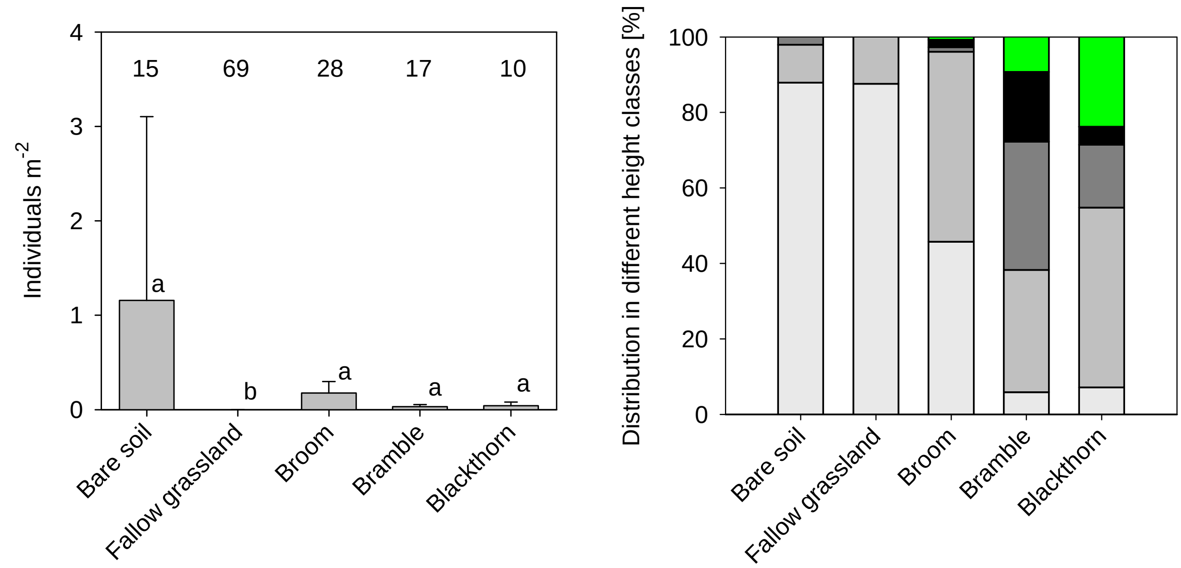


Fig. 5-13: Left: Number of tree saplings (mean + 95% CI) found in different vegetation types on the Dreiborner Hochfläche. Numbers on top indicate number of vegetation relevés. Different letters indicate significant differences (All Pair wise Multiple Comparison Procedures: Dunn's Method).
Right: Distribution of found saplings (data same as left) in different height classes.
Data from various studies (Heilburg, 2009; Krämer, 2009; Engler, 2010; Van Wersch, 2010; Krämer, 2011) and own data collected for this study (raw data see Appendix Table A-5 to Table A-8).

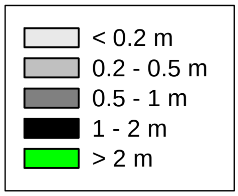


Fig. 5-14: Left: Heavily browsed young beech trees.
Right: Beech sapling protected by a cage of blackthorn. Photos: K. Krämer 2010.

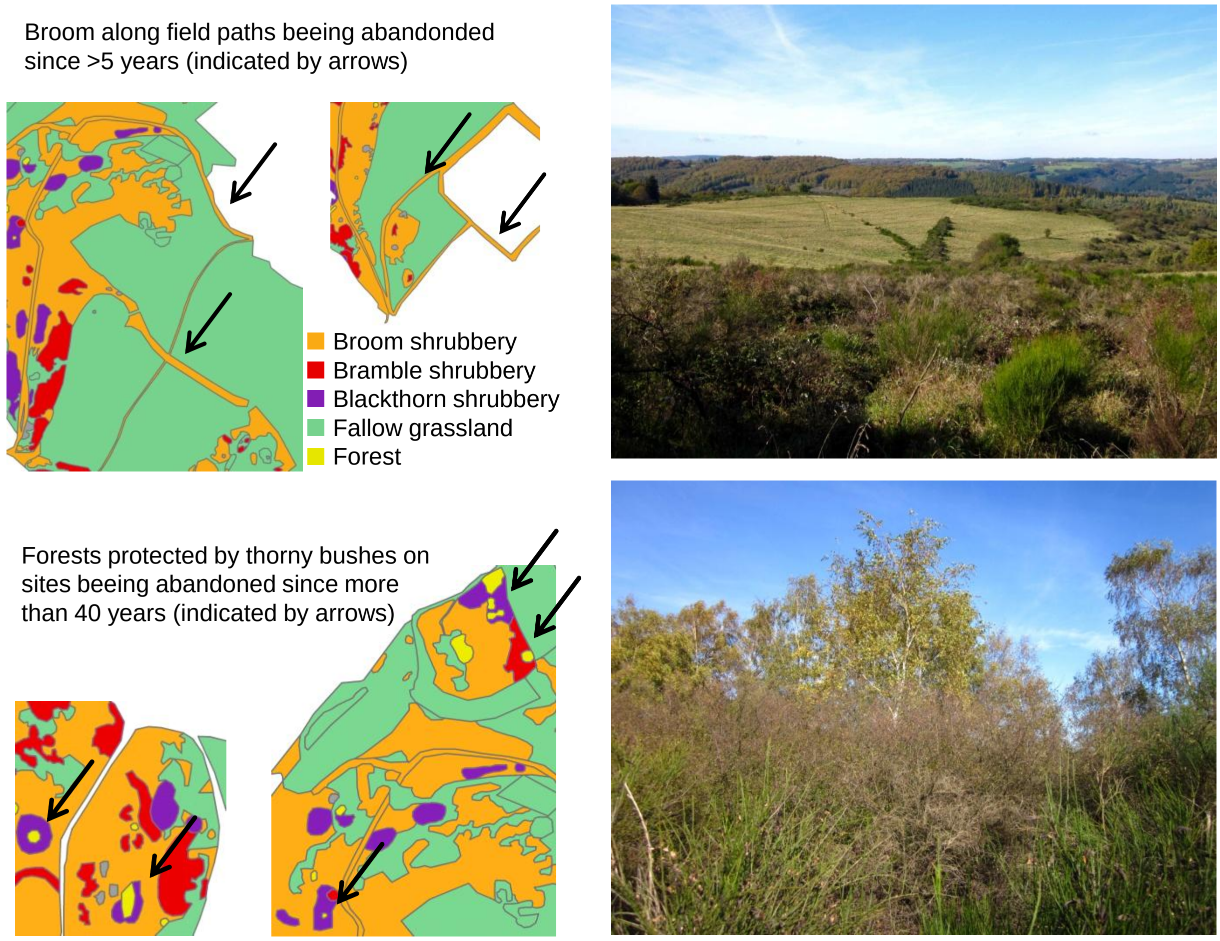
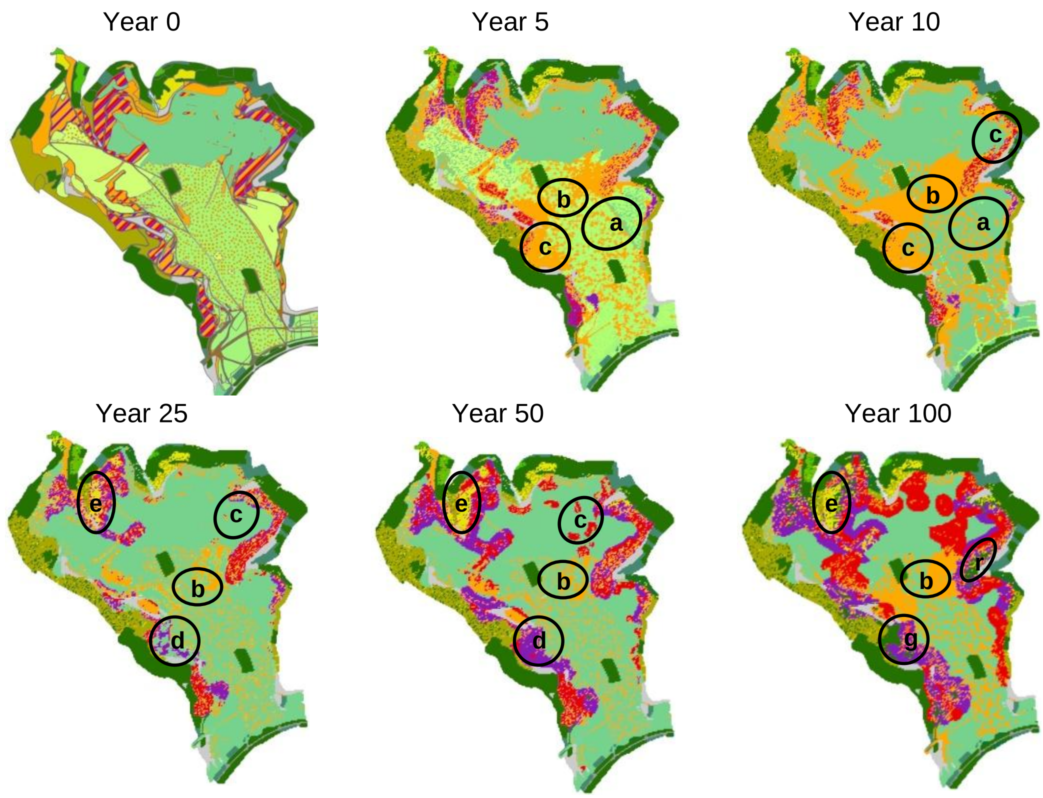


Fig. 5-15: Vegetation types on abandoned parts of the Dreiborner Hochfläche as investigated by Krämer (2011).
Top: Broom along former field paths (vegetation mapping and photo).
Bottom: Young forests protected by thorny bushes. Left: vegetation mapping. Right: photo of a birch preforest protected by a belt of blackthorn.

5.4.2 Simulation results

In order to compare these observed patterns with the model output, two parts of the Dreiborner Hochfläche were simulated under conditions matching the ones in the investigated areas, i.e. under abandonment with a high abundance of red deer (22 animals per 100 ha). As initial vegetation data, an intense vegetation mapping of the Dreiborner Hochfläche was used (Neitzke 2005, unpublished) (Fig. 5-16 and Fig. 5-17, year 0). Simulation results of the whole areas are given in Fig. 5-16 and Fig. 5-17. Details of certain parts of these maps (as indicated by letters) are displayed in Fig. 5-18 to Fig. 5-23, to highlight certain patterns.



a: Meadows and pastures turn into fallow grasslands dominated by tall grasses.
b: Oscillating population dynamic of broom.
c,d: Bramble and blackthorn spread into fallow grasslands, where initials were present.
e: New birch forests develop in blackthorn shrubberies in 25 years.
f,g: New spruce forests develop into blackthorn shrubberies in 50-100 years.

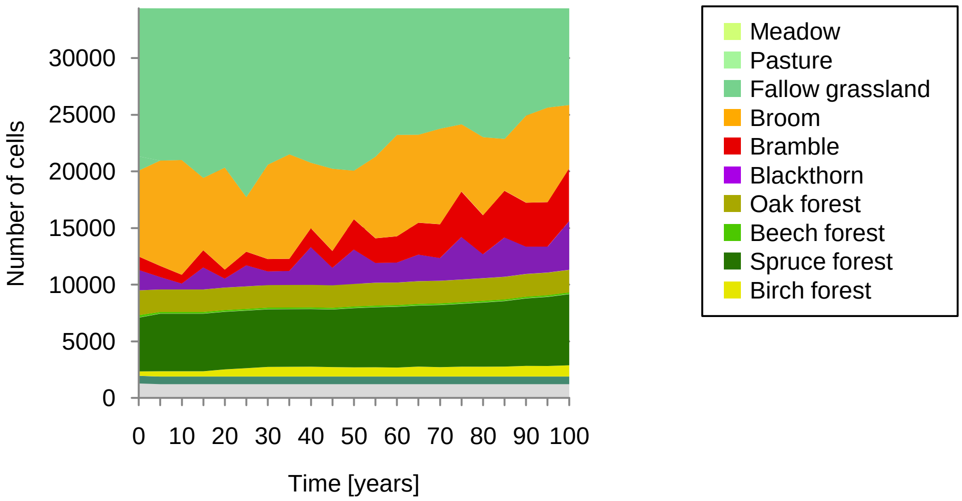
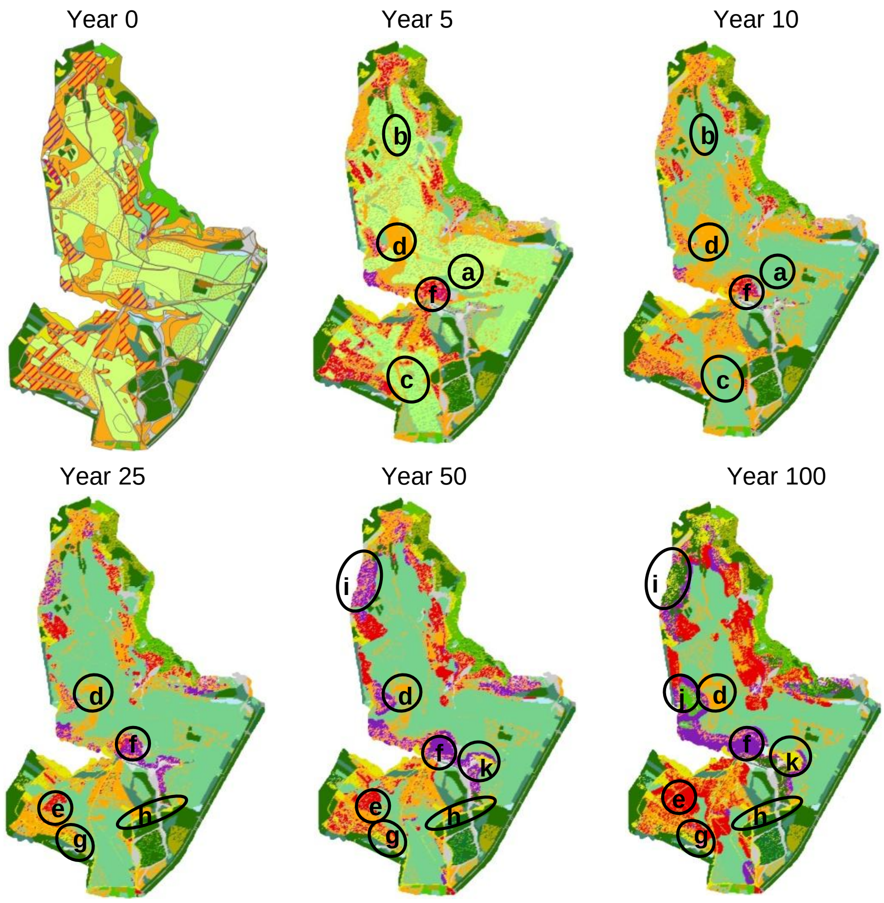


Fig. 5-16: Simulation of a central part of the Dreiborner Hochfläche. Names of bushes refer to shrubberies with a cover of the bush ≥ 10%. Cells with tree establishment refer to cells, where this species has gained a cover ≥ 10%; in forest cells, cover of trees is ≥ 50%.

Top: Landscape development shown in spatially explicit raster maps. Details of the areas indicated by letters are given in Fig. 5-18 to Fig. 5-23.

Bottom: Abundance of different vegetation types over the simulation time. Grassland types are summarized and indicated in the color for fallow grasslands.



a: Meadows and pastures turn into fallow grasslands dominated by tall grasses.
b+c: Broom encroaches on abandoned field paths.
d: Broom populations oscillate.
e+f: Bramble and blackthorn spread into fallow grasslands, where initials were present.
g+h: New birch and few spruce forests develop on abandoned ways and disturbed ground in 25 years.
i-k: New forests (spruce, beech and birch) develop into blackthorn shrubberies in 50-100 years.

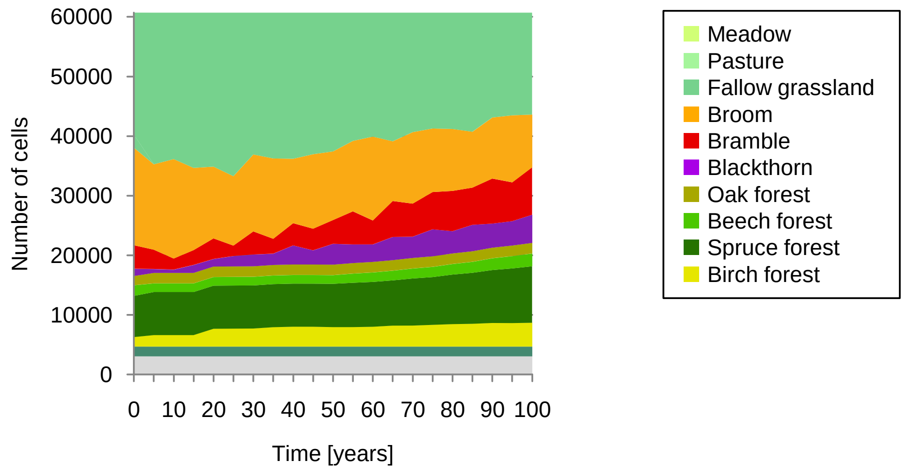


Fig. 5-17: Simulation of the southern part of the Dreiborner Hochfläche. Names of bushes refer to shrubberies with a cover of the bush ≥ 10%. Cells with tree establishment refer to cells, where this species has gained a cover ≥ 10%; in forest cells, cover of trees is ≥ 50%.

Top: Landscape development shown in spatially explicit raster maps. Details of the areas indicated by letters are given in Fig. 5-18 to Fig. 5-23.

Bottom left: Abundance of different vegetation types over the simulation time. Grassland types are summarized and indicated in the color for fallow grasslands.

In both simulations, initial hay-meadows and pastures change into fallows dominated by tall grasses (Fig. 5-16 and Fig. 5-17 a, Fig. 5-18) as was also shown in Chapter 4.

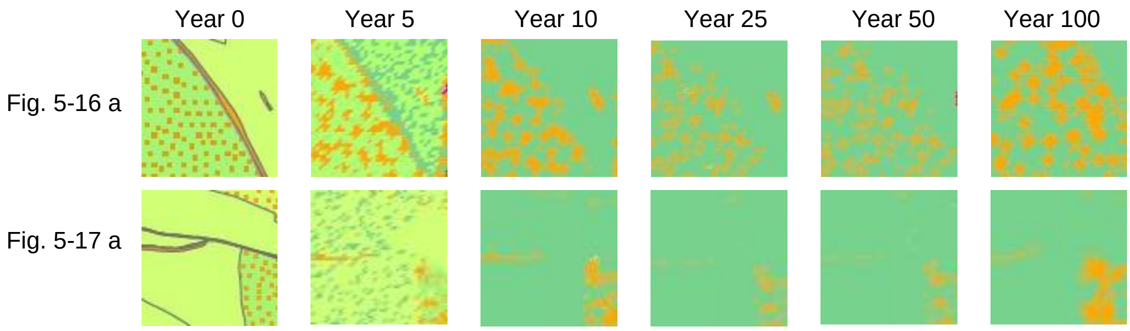


Fig. 5-18: Detail of Fig. 5-16 a and Fig. 5-17 a. Meadows ( ) and pastures ( ) turn into fallow grasslands dominated by tall grasses ( ).

Broom shows oscillating population dynamics. Its abundance fluctuates over time with a slight decreasing trend in both simulations (Fig. 5-16 b and bottom left and Fig. 5-17 c and bottom left, Fig. 5-19).

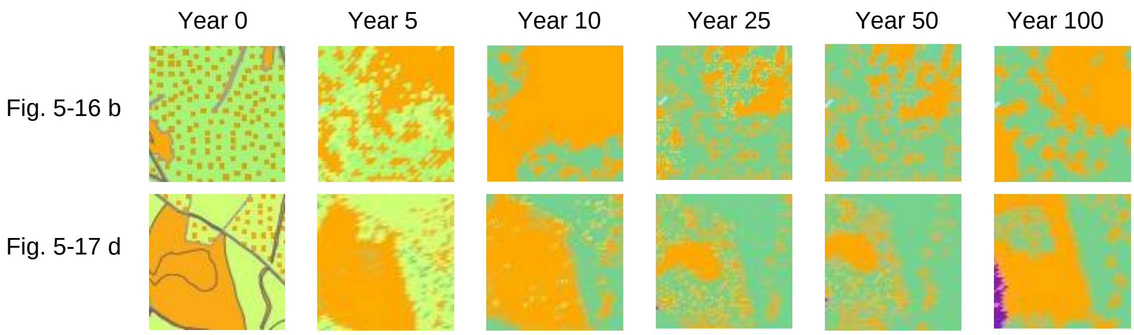


Fig. 5-19: Details of Fig. 5-16 b and Fig. 5-17 d. Broom ( ) populations oscillate.

In the first years, broom establishes on abandoned field paths and disturbed ground (Fig. 5-17 b, c, Fig. 5-20) but unlike blackthorn and bramble, it does not grow into fallow grassland areas.

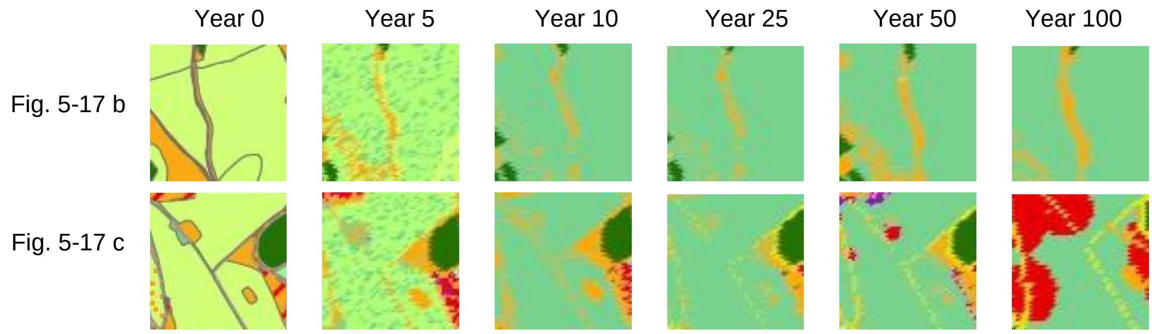


Fig. 5-20: Details of Fig. 5-17 b and c. Broom (■) encroaches on abandoned field paths.

Grassland areas decrease over time, as they are overgrown by bramble and blackthorn (Fig. 5-16 c and bottom left, Fig. 5-17 d and bottom left, Fig. 5-21), where initials of these bushes are present. Yet, wide grassland areas in the center of the sites remain non-forested even after a simulation time of 100 years.

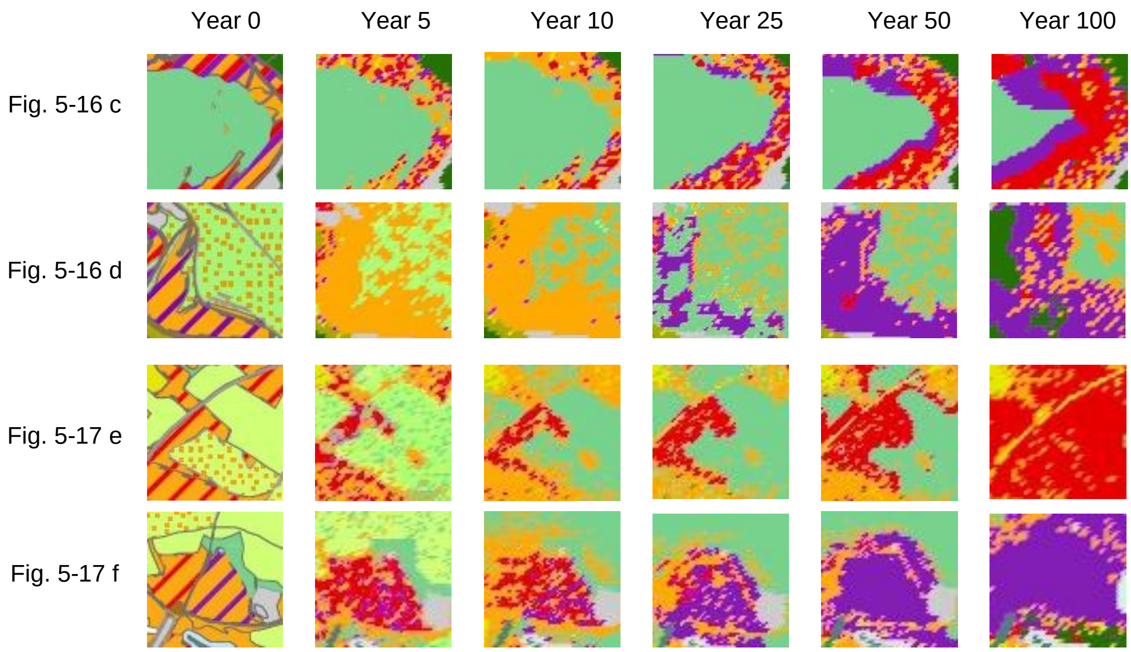


Fig. 5-21: Details of Fig. 5-16 c and d, and Fig. 5-17 e and f. Bramble (■) and blackthorn (■) spread into fallow grasslands, where initials were present.

Tree encroachment in the simulated scenarios strongly depends on the initial spatial distribution of forests and on neighborhood interactions. When blackthorn shrubberies or disturbed ground is located close to birch or spruce forests, new forests develop within 25 years (Fig. 5-16 d and Fig. 5-17 e, respectively, Fig. 5-22).

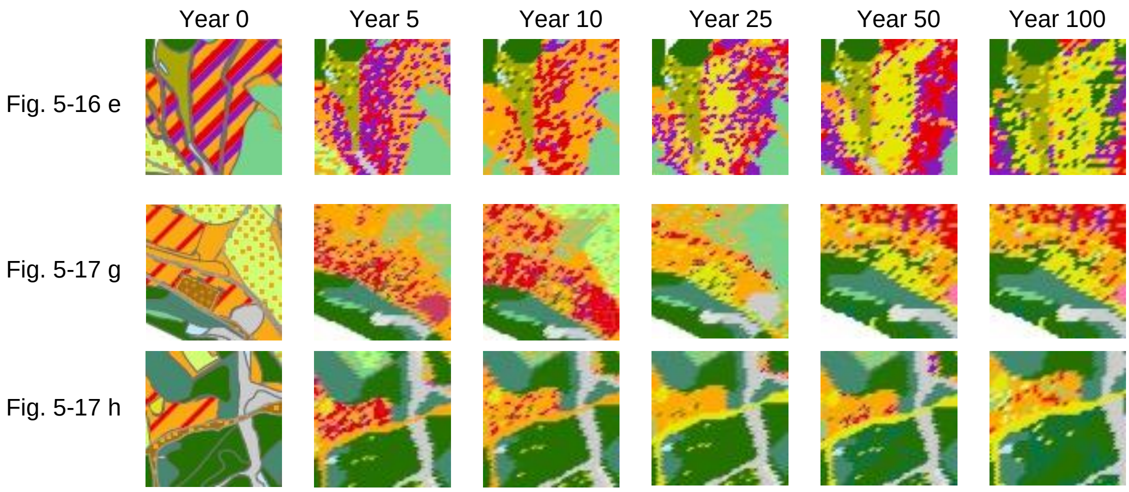


Fig. 5-22: Details of Fig. 5-16 e, and Fig. 5-17 g and h. New birch (■) and spruce (■) forests develop in blackthorn shrubberies (■), on abandoned ways (■) and on disturbed ground (■) in 25 years.

All other wood encroachment takes a longer time. Oftentimes, new forests only arise after blackthorn thickets have developed, therefore taking 50 to 100 years (Fig. 5-16 e, Fig. 5-17 f. Fig. 5-23). These forests consist of different tree species, depending on the forests existing in the neighborhood. Spruce and birch trees establish close to spruce and birch forests, respectively (Fig. 5-16 e, Fig. 5-17 f). In the southern part of the Dreiborner Hochfläche, one new beech forest develops. It develops in a blackthorn thicket already containing a few beech trees at the beginning, which is not close to any other forest (Fig. 5-17 e). This is the only case in the simulation runs, where a new beech forest comes into existence. In both simulation runs, no recruitment of oak was found.

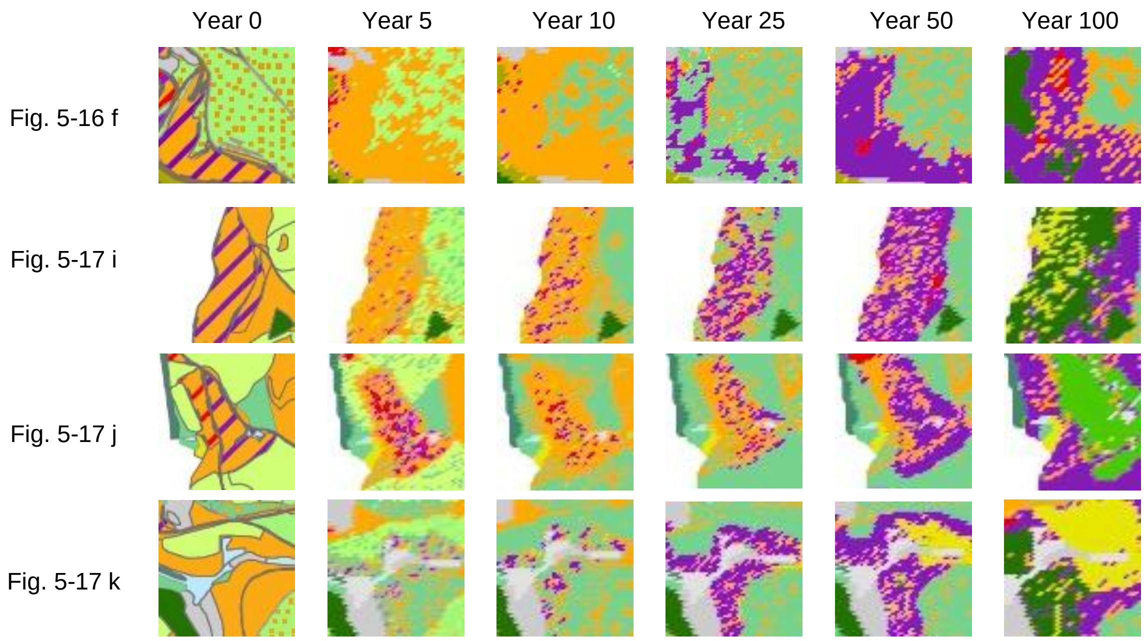


Fig. 5-23: Details of Fig. 5-16 f, and Fig. 5-17 i, j and k. New birch (■), beech (■) and spruce (■) forests develop in blackthorn shrubberies in 50-100 years.

In general, establishment of young trees takes place in thickets of blackthorn or blackthorn associated with bramble (Fig. 5-24). The development of birch forests on disturbed ground is the only exception, when considerable tree recruitment takes place in "grassland" vegetation types. However, this grassland vegetation is <u>not</u> dense, fallow grassland dominated by tall grasses, but grasslands occurring at sites that were field paths or other locations with disturbed ground in the input data (Fig. 5-24 right).

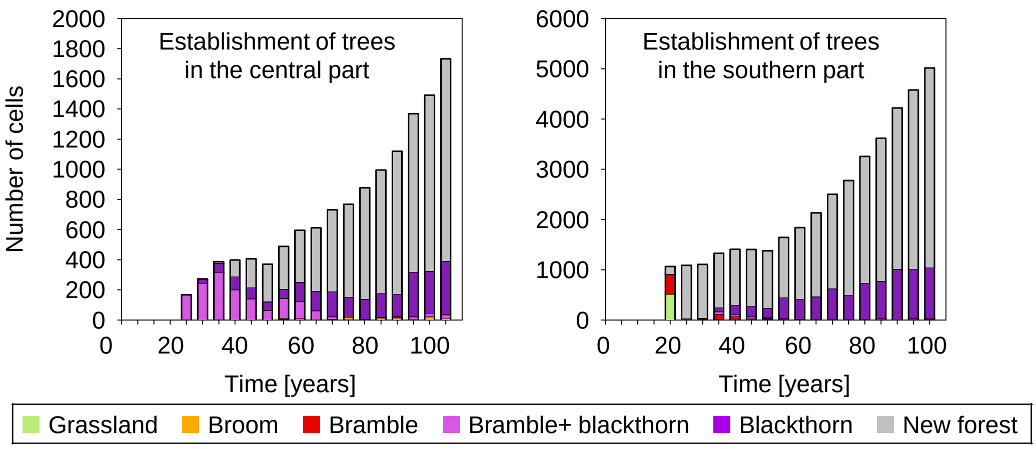


Fig. 5-24: Tree establishment depending on vegetation type in the central and the southern part of the Dreiborner Hochfläche. Simulations are the same as in Fig. 5-16 and Fig. 5-17.

5.5 Discussion

In this chapter, the success and difficulties in parameterization, the pattern-oriented model evaluation and the model design are discussed. We furthermore provide an overview on simplifications and limitations of the model in order to give a better understanding of how to interpret simulation results.

5.5.1 Parameterization

Growth

In order to take site specific growth into account, the parameters of height growth were fitted to yield tables for the Eifel National Park. Thereby we chose a growth function that was developed explicitly to model the entire growth of trees, starting with a size of 0.01 to 0.05 m (Rammig et al., 2006; Rammig et al., 2007a). Most simulation models considering tree growth start with initial heights over 1 or even 2 to 3 m (see reviews by Rammig (2007a) and Bugmann (2005)). However, for smaller saplings that are susceptible to browsing, data for growth is missing for many species. For birch, beech and oak, there was no data on height growth of young trees available. For birch and beech, the overall curve fit is nevertheless good (EF = 0.87 and 0.97, respectively). For oak, in contrast, the curve deviates especially for data of smaller trees so that the fitted curve might not very well emulate the growth of young trees. Oak is the least abundant of the modeled species, so that this impreciseness will not play too big a role in the simulation results. However, survival in young age is a bottleneck for tree establishment, often determining the course of succession. Small trees suffer most from competition and damage by browsing. For our model, this is particularly the case, because browsing is an important factor influencing tree encroachment, and trees only suffer from browsing by growth reduction or mortality at a height smaller than 1.6 m. More data on the growth and survival of young trees and different species is needed to better understand the course of succession.

In our model, the most important state variable for competition is cover. Therefore the height of trees was converted to crown area using the allometric function by Pretzsch (2001). Most parameter values for this function exist for trees growing in dense forests, but as we simulate wood encroachment on the grassland of the Dreiborner Hochfläche, where most young trees develop in scattered small groups, we measured height and crown diameter of solitary trees on the Dreiborner Hochfläche. We achieved a good model fit for this function for most species (EF between 0.82 and 0.97). For birch, the fit only showed a model efficiency of 0.72 as it varied most strongly in growth form and also no tall trees with a height bigger than 16 m were found.

Browsing

To simulate the impact of browsing, we weighted the supply of browsable woody biomass against the demand of red deer for woody food. To our knowledge, this is one of the first approaches to connect the influence of ungulates on tree establishment with the actual animal density in the given area. Other models simulating the impact of browsing are often not linked to animal densities but rather to observed damage probabilities (Rammig, 2005; Weisberg et al., 2005; Didion et al., 2009). Our approach is an important step towards a better understanding of the influence of ungulates on forest development, even though uncertainties remain. Some data exist on the demand of red deer including the portion of woody browse in their diet. Yet, the portion of woody browse might vary strongly between different sites (e.g. within forests or open areas). We chose data for open areas for the parameterization (Gebert and Verheyden-Tixier, 2001). Furthermore, red deer at different sites show different feeding preferences (Gill, 1992; Reif and Gärtner, 2007), often preferring rare tree species over common ones. As site specific knowledge on feeding habits is required, we considered knowledge of a local expert (Petrak pers. comm., Petrak and Steubing (1985), see section 5.2.8).

To estimate the other side of the equation, the available woody browse in a given area, only few data exists. Kalén and Bergquist (2004) performed an extensive study on the available biomass of woody browse of birch (*B. pendula*) and pine (*Pinus sylvestris*) available for moose (*Alces alces*). We converted the biomass given for birch for the reduced maximal foraging height for red deer compared to moose. This biomass was then used for all tree species, because no data was available for spruce, beech and oak. We also did not include seasonal differences in our model. Red deer feed mostly on coniferous browse during the winter time (Palmer et al., 2004), when not much other food is available, whereas deciduous trees are more often browsed in summer time (Gill, 1992). Such peaks in browsing intensity during a certain time of the year might lead to a greater damage than a uniform distribution, especially because trees might react differently to summer and winter browsing (Canham et al., 1994). Furthermore, the frequency of browsing during a year might affect the browsing related mortality (Eiberle, 1989), where shorter trees might suffer from a higher mortality than taller ones (Vandenberghe et al., 2008). More browsing studies with an experimental design (such as the ones by Harmer (2001) and Vandenberghe et al. (2008)) are needed in order to understand the impact of ungulate browsing and to gain a data base to parameterize browsing models for different tree species. A further simplification in our model is that ungulate density remains constant over space and time. Yet browsing intensity is often clumped in space (Gill, 1992) and animal density might vary over time. Earlier simulation studies showed that this variation might influence forest regeneration, creating windows of opportunities for trees to establish (Augustine and McNaughton, 1998; Bugmann, 2005; Didion et al., 2009).

The discussed data gaps and simplifications add impreciseness to our equation comparing supply and demand of woody browse. Yet, integrating all these additional processes and factors would lead to a much more detailed model, which might on the one hand assure more detailed simulation results but would on the other hand hamper the use of the model on a large area and make parameterization even more difficult. The pattern oriented-model evaluation (Section 5.2.2) shows that the GraS-Model is able to emulate observed patterns with the resolution of 100 m² raster cells, so that the loss of detail seems to be acceptable for the simulation on the landscape scale (several 100 ha over 100 years). To be able to simulate browsing effects on a finer scale, one would require a much more detailed model including microclimatic conditions as is realized in the model HUNGER (Weisberg et al., 2005), which is however working on small patches of e.g. 0.001 ha.

Inhibition by grasses

The inhibition of tree encroachment by grasses was simulated using a function that prevents seeds from reaching the seed bank so that they cannot germinate, as described by Watt (1919) and Briemle (2002). This one modeled process substitutes for a row of different ways in that the herbaceous layer may inhibit the establishment of trees. A dense grass sward might not only hinder germination, but also establishment of trees, because grasses compete with young saplings for light, nutrients and water (Lieffers et al., 1993; Frost and Rydin, 1997; Kochy and Wilson, 2000; Van Auken, 2000). It might also suppress the germination and establishment of tree seedlings by allelopathic effects (Jarvis, 1964; Frost and Rydin, 1997). Even though these processes are well known, there is not much available data on the quantity of inhibition under different circumstances. Due to this lack of data and in order to reduce complexity, these different processes were summed up into one inhibition function with the inhibition factor being calibrated to observed patterns.

5.5.2 Pattern-oriented model evaluation

The simulations of secondary succession on formerly used grassland on the Dreiborner Hochfläche produce general patterns that are well-known throughout the literature: Broom shrubberies are slowly overgrown by other shrubberies such as bramble and blackthorn (Glavac, 1996; Schreiber et al., 2000; Harmer et al., 2001; Kratochwil and Schwabe, 2001; Kahmen and Poschlod, 2004). These thorny bushes then act as "nurse-plants" (Schupp, 1995; Kuiters and Slim, 2003; Bakker et al., 2004). They protect young tree saplings from browsing and allow a development towards forested areas even under the given high browsing pressure by red deer. Where no initial shrubberies or disturbed sites exist within the dispersal distance of adult trees, fallow grasslands persist over several decades (Ellenberg, 1996; Müller and Rosenthal, 1998; Schreiber et al., 2000).

However, the model does not only display these patterns in general, but provides a highly detailed picture of succession at the given landscape considering neighborhood relationships. Small structural landscape elements such as abandoned field paths, or initial shrubberies and woods determine the course of succession. These initial landscape elements are considered in the model, because we use input data of a highly detailed grid with a cell size of 10 m. In the simulation results, different parts of the landscape show distinctly different development. A course of succession towards forest is only possible, when adult trees acting as seed sources are within the reach of a site that allows successful establishment of young trees. Such favorable sites are either sites with disturbed ground or existing bramble and blackthorn thickets that protect the seedlings from browsing. Over a longer simulation time, it is enough to have initials of thorny bushes that develop into larger thickets providing protection from browsers.

Succession is often difficult to predict, because it strongly depends on the initial composition of the given landscape (Briemle, 1980; Schmidt, 1981; Ellenberg, 1996; Schreiber et al., 1997; Müller and Rosenthal, 1998; Schupp et al., 1998; Smith and Olff, 1998). Setting up the GraS-Model in a process-based spatially-explicit way helped us to overcome this obstacle. The model uses highly detailed spatially-explicit input data provided in GIS-maps, assuring consideration of the neighborhood relationships of the given landscape. Moreover, it integrates successional processes on a temporal scale as well as on a spatial scale. It considers the speed of growth and the age of maturity of different species determining the ability to disperse seeds. Furthermore, different species-specific dispersal distances as well as the suitability of a sink cell for seedling establishment (e.g. inhibition by grasses or protection from browsing) are accounted for.

Comparing the simulation results with observed data on the Dreiborner Hochfläche proved that the applied model structure and parameterization of tree recruitment, inhibition of tree establishment by the herbaceous layer and ungulate browsing in the GraS-Model are sufficient to emulate observed patterns in a highly realistic way, even though some deviations in detail remain.

Initially used pastures and hay-meadows turn into fallow grasslands under abandonment. A detailed discussion of the dynamics in the modeled herbaceous layer is given in Chapter 4. These fallow grasslands are very stable and even persist in wide areas after a simulation time of 100 years. This simulation result matches the findings at the Dreiborner Hochfläche, where fallow grassland areas persist for over 40 years even close to forests, as well as findings at other sites, especially when no wood initials are found nearby (Ellenberg, 1996; Müller and Rosenthal, 1998).

The dynamics of the herbaceous layer influence the dynamics of wooden species in the model. The development of fallows dominated by tall grasses leads to a strong inhibition of wood encroachment. Broom therefore does not spread into the fallow grasslands but only recruits on disturbed grounds within the dispersal distance of mature bushes. When investigating the recruitment patterns of broom on the Dreiborner Hochfläche, Krämer (2011) also found growth of young bushes at disturbed grounds, even at sites where no mature bushes existed nearby. These broom saplings probably emerged out of a seed bank that might be present at least at parts of the Dreiborner Hochfläche because of the former land use. Broom is known to build up long-lasting seed banks, which can endure over more than 80 years (Turner, 1933; Paynter et al., 1998). As we do not know where exactly on the Dreiborner Hochfläche such seed banks exist, they were not integrated in the model, so that the broom recruitment after disturbance of the herbaceous layer will be underestimated at some sites.

Existing broom stands show oscillating population dynamics, increasing and decreasing in abundance in a fluctuating rhythm. This pattern has been found in broom populations elsewhere (Odom et al., 2003) and is due to its lifecycle characteristics. New bushes recruit on new sites after distinct disturbance events resulting in even-aged stands (Paynter et al., 2003). Soon, a dense stand develops hindering continuing germination of seeds. Because of the short life expectancy of about 12 years (Dancer et al., 1977; Prevosto et al., 2004), these even-aged stands then die more or less at the same time, creating open spots where seeds can again germinate. In the model we assume, as was described for other sites (Weber, 2008), that at the death of a broom bush, open ground is created, because the model is set up in the way that space occupied by the bush and tree layer is not available for herbs and grasses. Yet, it is not totally clear, whether this assumption holds true for the study area. At some sites, old broom stands are degenerating back into fallow grasslands (Krämer, 2011), a phenomenon which was also observed by Waloff (1968). In the absence of soil disturbance, no recruitment of young seedlings is found under dead broom bushes, and grasses are building up a dense sward. The continuing growth of broom in the model might therefore be overestimated to some extend or at least rely more on external disturbance of the ground than is assumed in the model.

Bramble and blackthorn shrubberies coexist with broom bushes, but in contrast to broom they spread into fallow grasslands. As only vegetative spread of these bushes by stolons is modeled, their growth depends on initial thickets. Their dispersal on the Dreiborner Hochfläche is therefore underestimated at sites, where they are not present in the initial input data, because in reality their seeds are dispersed by birds. So far, little is known about the establishment niche of these bushes (Olff et al., 1999; Smit and Ruifrok, 2011). However, these spiny shrubs play an important role in the progression of the open landscape towards forests, as can be seen clearly in the simulation runs as well as in the observed data. They act as “nurse plants” that protect young seedlings from browsing. The importance of thorny bushes in creating a window of opportunity especially for the recruitment of palatable trees has been reported throughout the literature (Pott and Hüppe, 1991; Callaway, 1995; Schupp, 1995; 1998; Olff et al., 1999; Rousset and Lepart, 1999; Kuiters and Slim, 2003; Bakker et al., 2004; Callaway, 2007; Kleyer, 2007; Smit et al., 2007; Barbosa et al., 2009; Smit and Ruifrok, 2011). To our knowledge, this important role that such spiny bushes play for the encroachment of forest during secondary succession has not been integrated into other models, but is one of the major factors explaining patterns of the secondary succession at our study area.

Trees in the simulation runs, as well as in reality, do not recruit on fallow grasslands of the Dreiborner Hochfläche. In the simulation runs, tree recruitment occurs on initially disturbed ground when birch forests are close by. Birches produce such a high amount of seeds, that the abundance of emerging seedlings in such a cell is high enough to meet the demand of red deer and some even survive ungulate browsing and grow up to build new forests. In the field studies, the highest abundance of seedlings was also found on disturbed ground, but they were all small and did not reach a height to escape browsing. This divergence of the simulation results from observed patterns is due to the fact that in the model ungulates are evenly distributed over all cells. Yet, when seedlings emerge on open ground, they are not protected and easy to find, so that they will attract the browsers. Furthermore, when the requirements of deer are not fulfilled in some cells (e.g. in fallow grassland), they do not search for food in other cells in the model. Consequently, this even-distribution of the animals in the model leads to an underestimation of browsing on very attractive sides and allows trees to grow to full height on initially disturbed ground. Except for recruitment on disturbed sites, trees establish almost exclusively on blackthorn or blackthorn plus bramble thickets during the simulation. The same pattern was found in observed data, where saplings with a height > 2 m, which have succeeded to escape browsing, are almost exclusively found in bramble and blackthorn shrubberies. This development of new forests in spiny thickets includes mainly birch and spruce and in one case beech. Birch and spruce are the most abundant species in the forest surrounding the Dreiborner Hochfläche and are also the species with the highest dispersal capability. In the simulations, a new beech forest therefore develops only at one site where there was no other forest nearby that would act as seed source for other species. However, recruitment of birch and spruce in thorny bushes is probably to some extend overestimated. Wind-dispersed pioneer species like birch and spruce are known to germinate mainly on bare soil, whereas beech needs surrounding vegetation to provide shade (Ellenberg, 1996; Smith and Olff, 1998). For this reason, Krämer (2011) found mostly the less light-demanding species oak and beech within dense thickets. New oak forest did not establish during the simulation. Where oak forests are present in the initial vegetation composition, spruce or birch forests are also nearby. As these species are in the model not hindered by low light availability in dense thickets and because oak is preferably browsed, they outcompete oak dispersing and growing faster than oak. The simulation results therefore show mainly the potential spread of pioneer species. As we do not include succession from preforests to later forest stages, oak and beech are not able to displace birch later in the simulation.

The time frame of the patterns in the simulation result fits to the one observed in the field study by Krämer (2011). Broom establishment on disturbed ground takes place early (after 5 years) during the simulation runs and has been observed on fallow field paths after no longer than 5 years of abandonment. Fallow grassland has been found on some sites that have been abandoned for more than 40 years even close to neighboring forests, so that it is not unlikely that fallow grassland persists over 100 years as in the simulation. The establishment of trees in thorny bushes has been found on sites that had been abandoned for over 40 years. Most trees recruiting within these thickets were beech and oak. In the simulation, establishment of birch in blackthorn plus bramble thickets occurs in one spot already after 25 years. All other recruitment of trees in blackthorn shrubberies starts only after 35 simulated years.

In spite of the deviations in detail discussed, the model is generally capable of emulating the observed successional patterns on the Dreiborner Hochfläche at the spatial as well as the temporal scale. The examined patterns resulting from simulation are independent secondary predictions that were not considered during model development and parameterization. Therefore, pattern-oriented model testing provides strong evidence of the predictive capability of the model (Grimm et al., 2005). One big advantage of the GraS-Model is, that it is possible to insert a detailed vegetation mapping as input data, so that initial vegetation composition and consequential neighborhood interactions are accounted for, which are known to highly influence the course of succession (Briemle, 1980; Schmidt, 1981; Ellenberg, 1996; Schreiber et al., 1997; Müller and Rosenthal, 1998; Schupp et al., 1998; Smith and Olff, 1998; Prach and Rehounkova, 2006; Lanta and Leps, 2009; Taylor and Chen, 2011).

5.5.3 Model design

Regarding other existing succession models in forests and grasslands e.g. (Liu and Ashton, 1995; Weber and Jeltsch, 2000; Bugmann, 2001; Pretzsch, 2001; Peters, 2002; Weisberg et al., 2005; Kramer et al., 2006; Tews et al., 2006; Rammig et al., 2007b; Scheller and Mladenoff, 2007; Gillet, 2008; Kochy et al., 2008; Pretzsch et al., 2008), the combination of three outstanding features make up the uniqueness of the GraS-Model:

First, in order to include the influence of the herbaceous layer on wood encroachment upon grassland, we combined the individual-based tree submodel with a mechanistically modeled herbaceous layer (described in Chapter 4). Both submodels work and interact within the same spatially-explicit, raster-based landscape. This multimodeling approach enables us, on the one hand, to simulate the dynamics of herbs and grasses during a changing form of land use (Chapter 4), and on the other hand to integrate the impact of the herbaceous layer on tree encroachment.

Second, we use a highly detailed (10 m x 10 m grid), spatially explicit vegetation mapping of a GIS map as input data, which includes small vegetation patches that may act as propagule sources (e.g. small groups of trees, alleys, hedges and bushes) and other landscape elements such as disturbed ground and field paths. Especially for wood encroachment on grasslands, structural landscape elements and initial vegetation composition are known to determine the course of succession, so that predictions are often difficult to make (Belde and Richter, 1997; Schreiber, 1997; Schupp et al., 1998). Using a raster-based approach, we are able to simulate the neighborhood effects between these landscape elements, and integrate them in our predictions. They have proven to highly influence the course of succession in our observations on our study site as well as in our simulation results. For example, it is crucial for the course of succession, whether forests exist close to disturbed ground or near blackthorn thickets. This raster-based approach furthermore enables the user to depict simulation results in raster maps using ArcGis9 (ESRI), providing detailed spatial-explicit projections of vegetation development.

Third, we weighted the supply of available woody browse against the demand by ungulates. Whereas in most simulation models, browsing demand is not linked with actual ungulate density (one exception is the model FORESPACE by Kramer et al. (2003)), we calculate demand based on the actual abundance of ungulates on the study area. Supply of available browse is calculated based on a spatially-explicit seed dispersal unit, the ability of seedlings to emerge on different ground as influenced by the herbaceous layer, and the simulation of growth of young trees. Especially the influence of the herbaceous layer on seedling emergence and the growth of young trees have rarely been integrated in succession models (examples are Rammig et al. (2007b) and Peringer and Rosenthal (2011)). In our approach, we integrate the interaction of general tree recruitment capability and browsing effect. Augustine and McNaughton (1998) have discussed that the effect that browsing has on wood encroachment is strongly influenced by seed availability, which is also a result of our simulations.

5.5.4 Limitations

To give a better understanding of how to interpret simulation results, we here give a short overview on simplifications and limitations of the model that influence the outcome of the simulations.

Ungulate browsers are evenly distributed over the simulated cells. This may lead to an underestimation of browsing in especially attractive cells such as spots with a weak herbaceous layer on formerly disturbed ground with a high abundance of new seedlings. However, browsing demand in not accessible sites that are caged by thorny bushes is reduced in order to simulate the influence of such “nurse plants”. For the National Park it is also important, that disturbance of the ungulates by visitors along frequently used field paths is not integrated in the model.

Bramble and blackthorn in our model only disperse vegetatively; dispersal of the berries by birds is not accounted for. The development of bramble and blackthorn thickets therefore relies on initials of these bushes in the input layer, whereas in reality their berries will be distributed especially to other shrubberies that are visited by birds. Therefore the occurrence of thorny bushes and their potential to act as “nurse plants” for tree establishment is underestimated in the model.

One important factor that is missing for tree development is light availability. Therefore, the establishment of light demanding species such as birch in thickets is overestimated in the simulation. Yet, a thicket occupied by birch or spruce indicates the suitability of this site for tree establishment in general. It is likely that such a site will in reality be occupied by beech or oak, which are dispersed by birds to those thickets, even though it may take a longer time than the simulated establishment of birch.

Once a cell has developed to forest, i.e. when one tree species covers the cell to over 50%, we do not simulate further dynamics in this cell. The only function of such a forest cell is that it disperses seeds. We therefore do not simulate the succession of forests, e.g. from birch to beech forests, but only the succession of grassland and shrubberies towards forest.

5.6 Conclusion

The GraS-Model is able to project wood encroachment at secondary succession of grassland for our study site. Pattern-oriented model evaluation revealed that the model emulates observed successional pathways on the spatial as well as temporal scale. The parameterization using literature data and additional own data that were collected for the study was successful. Anyhow, some data gaps concerning ungulate browsing and the inhibition of wood encroachment by the herbaceous layer were revealed. Using the multimodeling approach of combining the compartment model of the herbaceous layer and the individual-based tree submodel allows simulating the reaction of agents acting at different scales in a mechanistic way. In the herbaceous layer, the reaction of grasses and herbs to a changing land use is simulated, whereas in the tree submodel, this layer acts as an environmental variable determining wood encroachment. Weighing supply of woody browse against demand allows us to simulate wood encroachment under a given ungulate density. Using a raster-based approach, we are able to integrate a highly detailed vegetation mapping provided in a GIS layer as input data and to consider neighborhood interactions of different elements of the given landscape, which are known to highly influence the course of succession. Simulation results can be depicted in raster maps using ArcGis9 (ESRI), providing detailed spatial-explicit projections of vegetation development.

Quintessence:
✓ Parameterization using literature data and additional own data successful.
✓ Multimodeling approach: mechanistic simulation of the dynamics of the herbaceous as well as the tree layer including their interactions.
✓ Weighing supply against demand of woody browse for ungulates works to simulate the development of the study area.
✓ Pattern-oriented model evaluation: model emulates observed patterns over space and time.
✓ Raster-based approach: Initial vegetation composition and consequential neighborhood interactions are accounted for.

6 Simulated Landscape Development on the Dreiborner Hochfläche as Influenced by Different Forms of Land Use

6.1 Introduction

When the Eifel National Park was established in 2004, the question arose how to deal with the grasslands on the Dreiborner Hochfläche, a former military training site, considering the IUCN regulations for national parks. The GraS-Model was developed to simulate landscape succession of the grassland areas under different management. The overall aim of the model is to build up a decision support tool to assist stakeholders (e.g. politicians, administrative authorities) in choosing suitable strategies regarding open grassland management. In current research it is one of the main tasks to understand the interplay of different processes, from which complex patterns emerge in order to predict the course of secondary succession (Kleyer et al., 2007).

In the GraS-Model, various interacting processes are accounted for, determining the course of succession in a landscape mosaic. Vegetation is divided into the herbaceous layer (including all grasses and herbs) and the woody species (including bushes and trees). The composition of the herbaceous layer is determined by the applied management regime of either grazing & trampling, mowing, or non-interference (Chapter 4). Depending on species composition, the herbaceous layer affects the seed availability of woody species, especially at non-interference, when grasses build up a dense sward. Accordingly, woody species are indirectly affected by the management regime, e.g. seed availability is enhanced at a grazing regime compared to non-interference, because seed availability is less hindered by the herbaceous layer. Direct affects of the management regime on woody species occur at mowing (where trees between 0.1 and 1 m die) and because of browsing, whereby young trees are reduced in growth or even die (for details see Chapter 5).

In the following, we demonstrate how the modeling of these interacting processes results in a detailed prediction of landscape development. The results of simulation runs of the central and southern part of the Dreiborner Hochfläche under different management regimes, as were arranged with the stakeholders, are presented. The input data was derived from an extensive vegetation mapping of the Dreiborner Hochfläche (Neitzke, 2005, unpublished) and additional own mappings of scattered woods, so that initial vegetation composition and resulting neighborhood interactions are taken into account, which are crucial for the course of succession (Briemle, 1980; Schmidt, 1981; Ellenberg, 1996; Schreiber et al., 1997; Müller and Rosenthal, 1998; Schupp et al., 1998; Smith and Olff, 1998; Prach and Rehounkova, 2006). As forms of land use mowing, non-interference with different abundances of red deer (*Cervus elaphus*) and a scenario with grazing by European Bison (*Bison bonasus*) are applied. Regarding their feeding preference, the European Bison (hereafter referred to as bison) is classified as a grazer, feeding to a large extend on fibrous food such as grass, whereas red deer is classified as intermediate type between grazers and browsers (such as roe deer) that feed less fibrous, higher quality diet (Hofmann, 1989; Bunzel-Drüke, 2000). Bison therefore affects the herbaceous as well as the tree layer, whereas red deer impacts only the woody species. Roe deer (*Capreolus capreolus*) plays only a minor role on the Dreiborner Hochfläche (Petrak (Forschungsstelle für Jagdkunde und Wildschadenverhütung des Landes Nordrhein-Westfalen), pers. com.) and is therefore not included.

6.2 Simulated scenarios

In this chapter, simulation results of two parts of the Dreiborner Hochfläche are presented. As initial state of the vegetation, we use a detailed vegetation mapping of the year 2005 by Neitzke (unpublished) (Fig. 6-1). We consider the different zones of the management plan of the Dreiborner Hochfläche (Pardey et al., 2008): the management zone, where mowing is allowed to maintain the hay-meadows, and the core zone, where no interference other than an introduction of endemic animals such as bison is permitted. The results are displayed in detailed raster maps to visualize the projected development of the landscape.

For the <u>central part</u>, including a part of the management zone, we show a scenario of non-interference including 22 red deer 100 ha^{-1}, and a scenario where the management zone is mown. The part of this area indicated as core zone (Fig. 6-1) is simulated with non-interference including 22 red deer 100 ha^{-1} in all shown scenarios. In the initial state, this area consists mainly of extensively grazed pastures with scattered broom bushes, and hay-meadows. The northern part contains some areas of fallows dominated by tall grasses. Along the sides of the plateau grow shrubberies of bramble and blackthorn as well as spruce, oak and few birch forests.

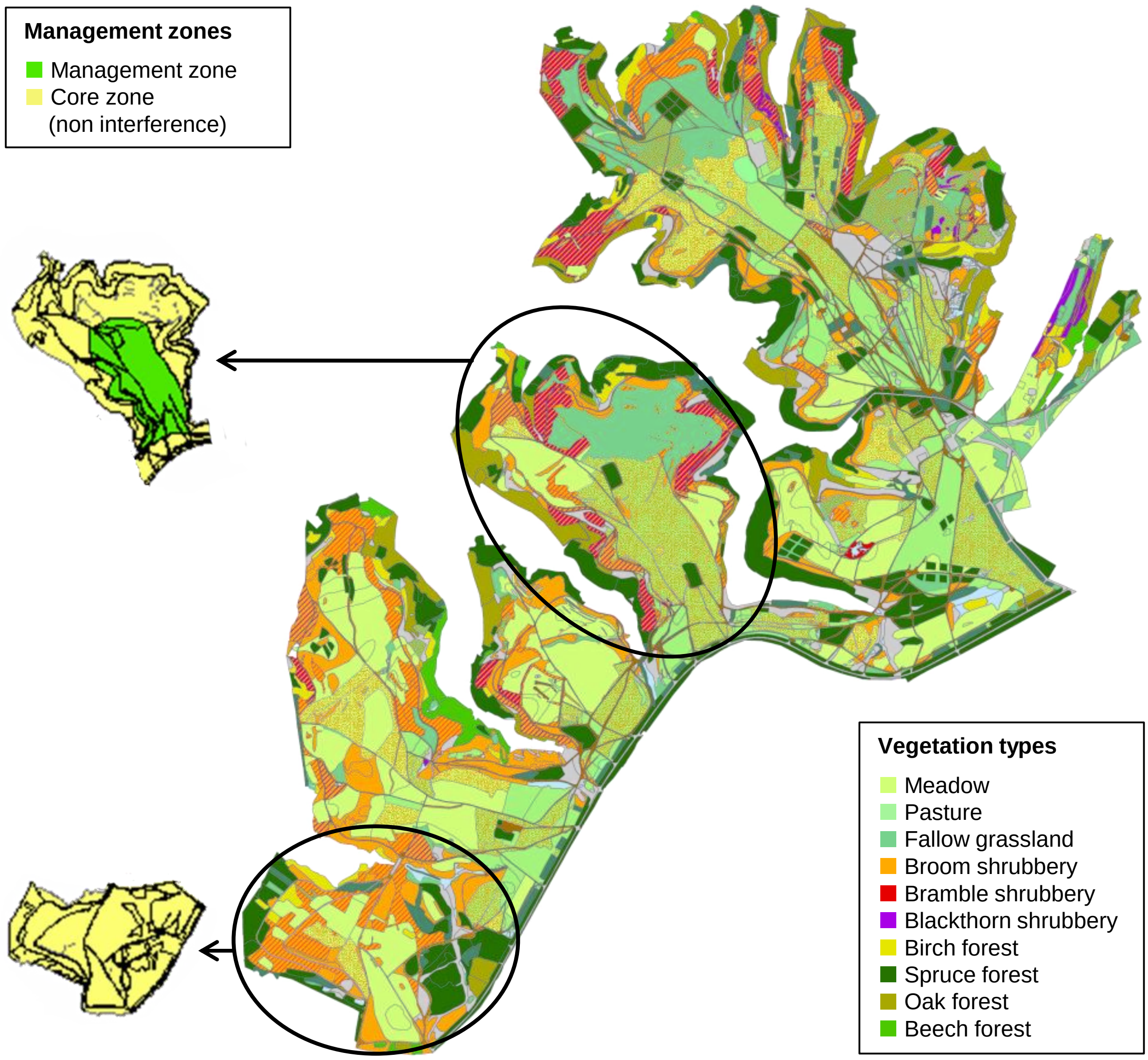


Fig. 6-1: Initial state and management zones of the simulated parts of the Dreiborner Hochfläche. Mixed vegetation types are indicated using stripes or dots of the corresponding colors.

For the <u>southern part</u>, which consists entirely of the core zone where no interference is permitted, we show scenarios with non-interference at different abundances of red deer. As highest abundance we chose the actual density of red deer in the southern part of the Dreiborner Hochfläche (≈ 22 red deer 100 ha^{-1}). We furthermore simulated the development with an abundance of 0, 5 and 10 red deer 100 ha^{-1}. As additional option for the southern part we present a grazing scenario with bison. Bison is endemic to Europe (Pucek et al., 2004) and does not fall under German veterinarian law but is regarded as a wild animal. Therefore it is a possible scenario to re-introduce these herbivores to the core zone of the National Park according to IUCN regulations (Pardey et al., 2008). The re-introduction of such robust herbivores is deemed a cost-efficient possibility to maintain semi-natural grasslands and grass-shrub-tree mosaics, which are of high conservation value (Olff and Ritchie, 1998; Svenning, 2002; Poschlod et al., 2005; Kleyer et al., 2007; Vandenberghe et al., 2008).

In the initial state, this area consists mainly of hay-meadows in the very south and pastures more to the north, some of them including scattered broom bushes. Surrounding these grasslands is a big belt of broom shrubberies including bramble and at few sites some blackthorn. Forests in this area are composed mainly of spruce and birch.

The demand of bison for woody browse was calculated in the same way as was presented for red deer in Chapter 5, Formula 5-10. The average weight of a bison was calculated as the mean weight of individuals in a mixed herd consisting of three bulls (470 kg each), four cows (340 kg each), three adolescents (200 kg each), two calves (100 kg each) plus three free roaming young bulls (200 kg each) (average weights: Krasinska and Krasiniski (2008)). With the parameter values given in Table 6-1, the demand of woody browse in kg dry weight (dw) per "standard bison" results in an amount of 792.74 kg dw a^{-1}.

Table 6-1: Parameter values for calculating bison's demand for woody browse.

Parameter	Unit	Value	Source
Daily summer demand	[kg dw 500 kg $bison^{-1}$]	13.3	(Gebczynska and Krasinska, 1972; Krasinski et al., 1999)
Daily winter demand	[kg dw 500 kg $bison^{-1}$]	9.7	(Gebczynska and Krasinska, 1972; Krasinski et al., 1999)
Fraction of woody parts of the total food	[–]	0.33	(Borowski and Kossak, 1972; Krasinski, 1978)

In contrast to red deer, bison as grazers also have a considerable impact on the herbaceous layer in the grasslands. The grazing and trampling impact for the bison scenario was therefore set to 15 and 9, respectively (c.f. Chapter 4).

6.3 Simulation results

Output data of the Gras-Model consist of vegetation units, which are derived from the cover grade of each species in each cell (c.f. Chapter 4 and 5). The results of simulation runs are presented in spatially explicit maps using the software ArcGIS 9 (ESRI®).

6.3.1 Center: non-interference and mowing of the management zone

In the non-interference scenario including 22 red deer 100 ha^{-1}, initial hay-meadows (*Geranio-Trisetetum*) and pastures (*Festuco-Cynosuretum*) change into fallows dominated by tall grasses (Fig. 6-2, left). Scattered broom shrubberies intermingle those fallow grasslands. Even after 100 simulated years, vast grassland areas remain, although bramble and blackthorn shrubberies slowly encroach from the sides. Shrubberies are rarely replaced by forests, and bramble or blackthorn can locally cover large areas. Only within big blackthorn shrubberies, which protect seedlings from browsing, does forest development take place.

When the management zone is mown but surrounded by the abandoned core zone, the simulation shows in a fine spatial resolution, how the former pastures (*Festuco-Cynosuretum*) and abandoned grasslands either develop into fallows dominated by tall grasses or turn into hay-meadows, depending on the form of land use (Fig. 6-2, right). Land use is applied in a highly spatially explicit way. Even the field paths running through the meadows can be distinguished, because only there and at the fallow edges of the core zone, broom bushes can establish, whereas the surrounding mown area consist of homogenous hay-meadows. Bramble and blackthorn do not grow into the mown areas but are on the contrary pushed out, where initials were present. Tree encroachment is restricted to blackthorn thickets in the core-zone.

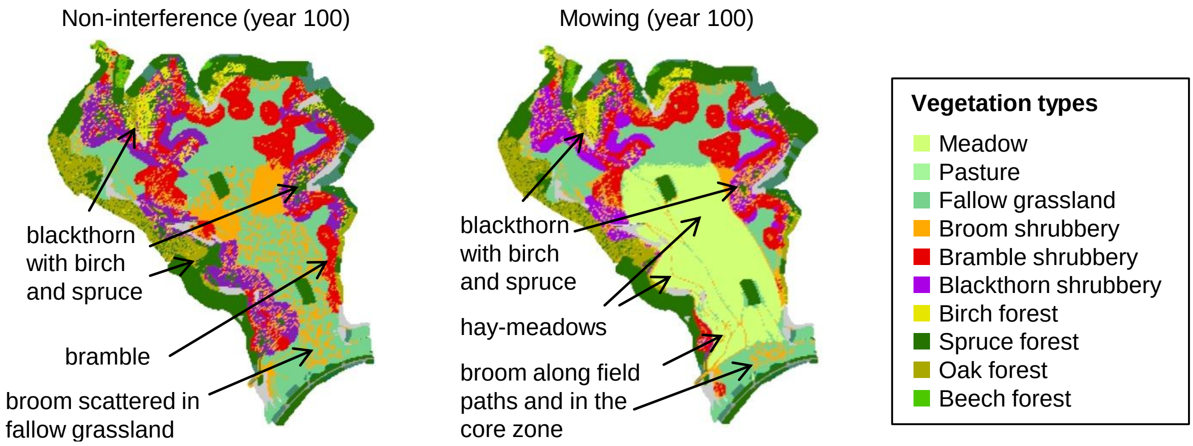


Fig. 6-2: Simulation results after 100 years of the central part of the Dreiborner Hochfläche under non-interference and a mowing regime. Initial vegetation composition and management zones as in Fig. 6-1.

6.3.2 South: non-interference with different abundances of red deer

The predicted development of the landscape under abandonment depends strongly on the density of red deer in the area (Fig. 6-3). With the high density of 22 red deer 100 ha^{-1}, few forests develop first along abandoned field paths and later within blackthorn shrubberies (c.f. Chapter 5). The new emerging forests are birch and to a very small part also spruce forests (Fig. 6-3 and Fig. 6-5). The meadows and pastures develop into fellow grasslands of which big parts remain unforested even over 100 years. From the sides, thickets of bramble and blackthorn spread into former grasslands. While blackthorn is overgrown by forests beginning at the center of the thickets, large bramble shrubberies persist over 100 years. Broom shrubberies persist at sites where they were initially present, but in contrast to bramble and blackthorn do not spread into the fallow grasslands.

With less red deer (10 and 5 individuals 100 ha^{-1}), the amount of new birch forests increases whereas the amount of emerging spruce remains more or less the same (Fig. 6-3 and Fig. 6-5). These new forests overgrow all broom shrubberies and most of the bramble and especially blackthorn thickets, so that only small areas of these thorny bushes remain at the border between forest and fallow grassland. The lower the abundance of red deer, the faster are the shrubberies overgrown by forests.

Without any red deer, almost all shrubberies have turned into birch forests after 50 years, so that the new forests border directly on the remaining area of fallow grasslands. Even though the forests keep on encroaching on the fallow grasslands, big unforested areas remain after 100 simulated years. Oak and beech forests do not increase much in any of the simulations.

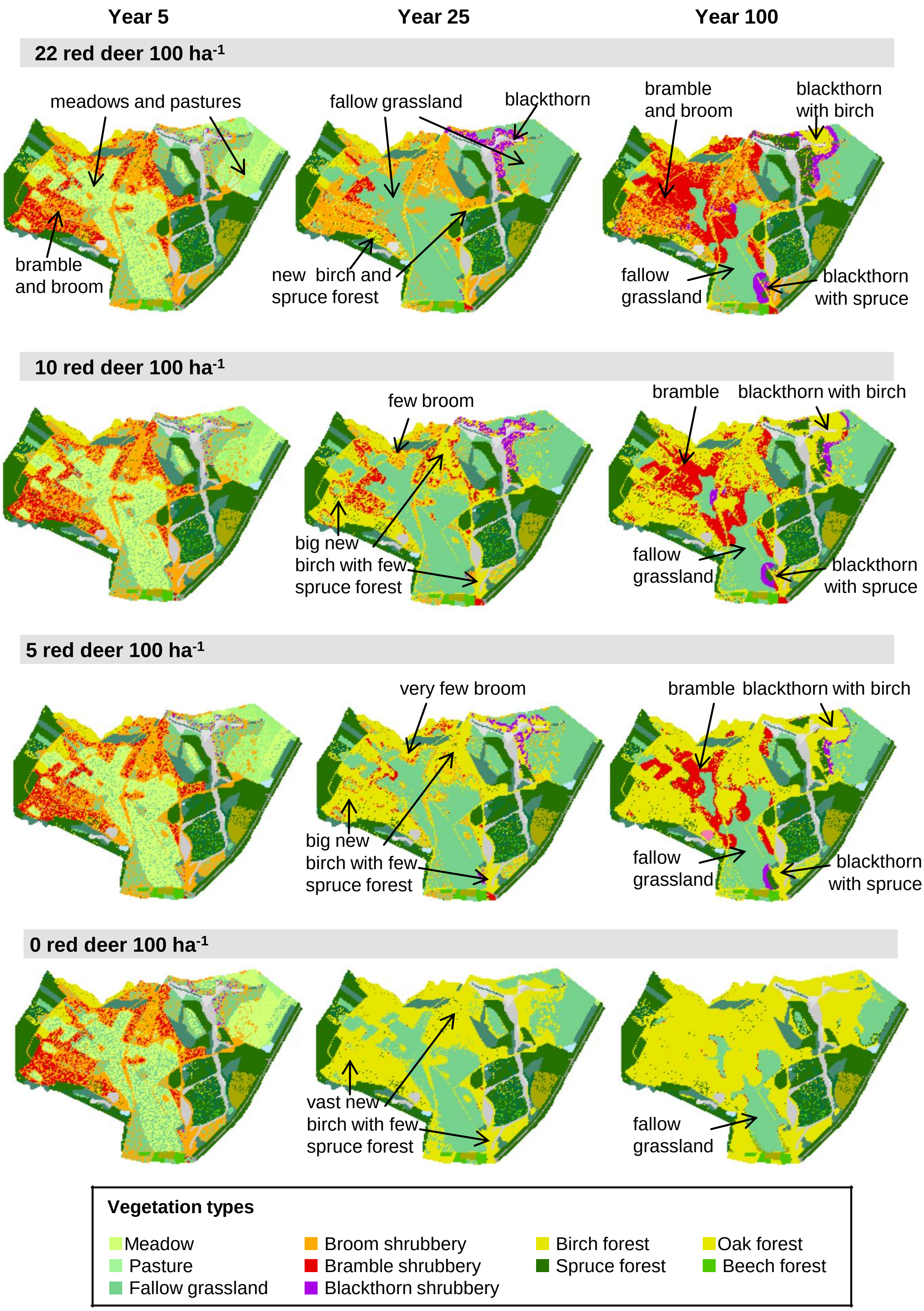


Fig. 6-3: Simulated vegetation development of the southern part of the Dreiborner Hochfläche under abandonment with different abundances of red deer. Note that succession within forests (e.g. from birch to beech or oak) is not included in our model. Initial vegetation composition as in Fig. 6-1.

6.3.3 South: grazing by bison

When the southern part of the Dreiborner Hochfläche is grazed by bison (without red deer), former hay-meadows turn into pastures containing scattered broom bushes (Fig. 6-4). The initial broom shrubberies persist over 100 simulated years, whereas bramble is repressed. New birch and spruce forests emerge first on abandoned field paths and later in the center of blackthorn thickets. They overgrow blackthorn, which persists only at the edge of the new forests. At a few spots, new birch forests also emerge in broom shrubberies.

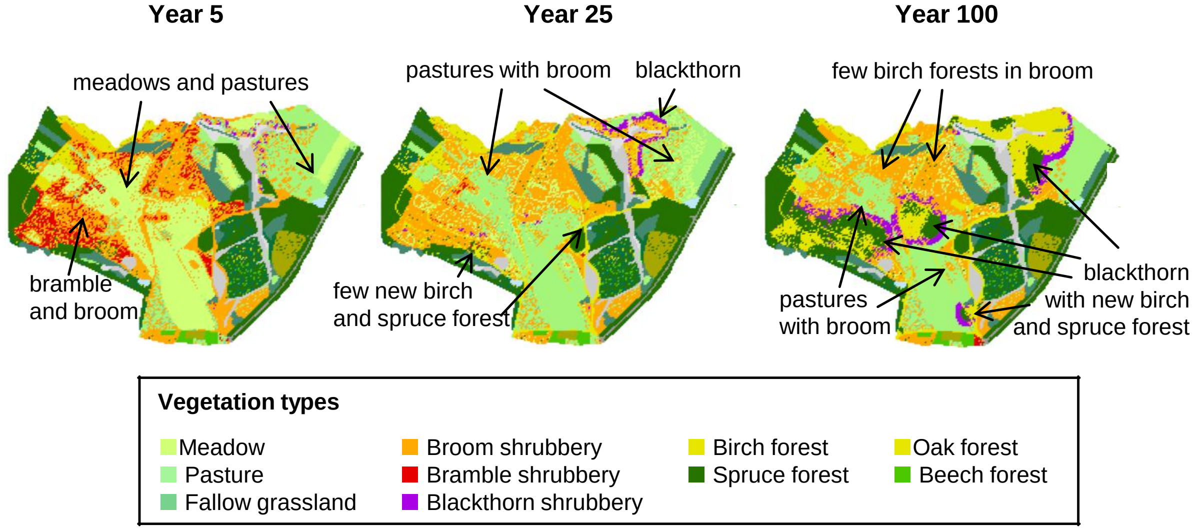


Fig. 6-4: Vegetation development at the southern part of the Dreiborner Hochfläche under grazing by bison. Note that succession within forests (e.g. from birch to beech or oak) is not included in the GraS-Model. Initial vegetation composition as in Fig. 6-1.

Comparing forest encroachment in the non-interference and the grazing scenarios, one can see that emerging forests consist mainly of birch and spruce forest (Fig. 6-5). In the grazing scenario and the scenario with 22 red deer 100 ha^{-1}, spruce forms the biggest part of the emerging forests, whereas in the non-interference scenarios with less red deer, new forests consist mainly of birch.

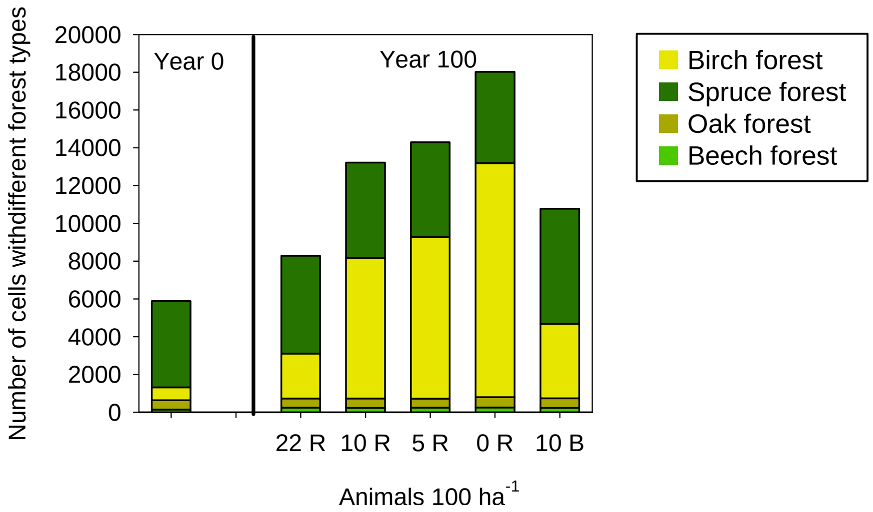


Fig. 6-5: Forest development at the southern part of the Dreiborner Hochfläche under non-interference with different abundances of red deer (R) and grazing by bison (B). Note that succession within forests (e.g. from birch to beech or oak) is not included in the GraS-Model.

6.4 Discussion

In this section, the patterns of landscape development emerging from the integrated processes at the different simulated scenarios is discussed including a plausibility check, and the findings concerning the impact of possible management regimes on landscape development on the Dreiborner Hochfläche are summarized. Furthermore, the limitations of the model are highlighted to provide a better basis for the interpretation of the results and the necessary steps to transfer the model to other sites are discussed.

6.4.1 Patterns of landscape development emerging from the simulated processes

Non-interference with different abundances of red deer

In the non-interference scenario without any red deer, existing shrubberies are rapidly overgrown by forest, and most grassland areas develop into forest over the simulation period of 100 years, which is in line with the general idea of succession (Clements, 1936; Glavac, 1996; Schreiber et al., 2000; Harmer et al., 2001; Kratochwil and Schwabe, 2001; Dierschke and Briemle, 2002; Moog et al., 2002; Hejcman et al., 2004; Kahmen and Poschlod, 2004). The only remaining non-forested sites are fallow grasslands far from seed sources, where inhibition by grasses is high and seed rain is low.

At lower densities of red deer (5 or 10 individuals 100 ha^{-1}), less birch forests develop, being restricted mainly to former broom and bramble shrubberies. After 100 simulated years, bramble and blackthorn shrubberies persist at the edge of the forests and surround outlasting vast areas of fallow grasslands where inhibition of seed availability is high. With increasing browsing pressure, the protection of forests by thorny bushes gains in importance. In the scenarios with intermediate browsing pressure (5 or 10 red deer 100 ha^{-1}), forest encroachment takes place in any kind of bushes (broom, bramble or blackthorn), whereas blackthorn, providing the strongest browsing protection, is essential for trees to establish under heavy browsing (22 red deer 100 ha^{-1}). Even though most forests consist of spruce in the initial state, most emerging forests consist of birch. The spread of spruce is low in scenarios with low browsing pressure and only exceeds birch in the scenario with 22 red deer 100 ha^{-1} and in the grazing scenario. This is due to the fact that birch with its immense dispersal ability beats spruce under lower browsing pressure, whereas the less palatable spruce gains advantage over birch under high browsing pressure. It is important to note that birch forests persist even over 100 simulated years and are not replaced by e.g. beech or oak forests, because succession of birch to other forest types is not modeled. This is also the reason why almost no beech or oak encroachment is shown in the simulations. Beech and oak are climate species with a low dispersal potential that usually predominate later in forest succession. Because of the immense seed rain from birch, this simplification might furthermore lead to an overestimated spread of forests in the last decades of the simulation run, when beech and oak would in reality replace birch.

As already discussed in detail in Chapter 5, the simulation of non-interference with a high abundance of red deer produces successional patterns that meet observations on our study site: Vast areas with fallow grasslands remain, developing a dense sward, which in combination of the high browsing pressure by red deer suppresses forest establishment. Bramble and blackthorn spread into these fallow grasslands. Forest encroachment is restricted to areas with initially disturbed ground and blackthorn shrubberies. The recruitment on disturbed ground is probably overestimated because such unprotected sites are very attractive for the browsers, and in the field studies on the Dreiborner Hochfläche saplings found on such areas never reached a height to escape browsing. Therefore tree establishment can be thought to be exclusive of dense blackthorn shrubberies. Consequently, the developing landscape under abandonment is not characterized by young forests, but mainly by vast shrubberies of broom, bramble and blackthorn. Only because of the exceedingly high abundance of red deer (being one of the highest in Central Europe (Petrak et al., 2006; Nationalparkforstamt Eifel, 2009)), a succession towards forests does almost not take place. Usually, such shrubberies do not persist over such a long time, but are overgrown by trees (Glavac, 1996; Schreiber et al., 2000; Harmer et al., 2001; Kratochwil and Schwabe, 2001; Dierschke and Briemle, 2002; Moog et al., 2002; Hejcman et al., 2004; Kahmen and Poschlod, 2004). It is therefore difficult to assess the further development and to evaluate model predictions regarding this point. It is not clear, whether bramble and shrubberies persist and keep spreading over 100 years as in the simulation run (where they do not age and die of senescence) or whether they degenerate maybe even back into fallow grasslands when no tree encroachment takes place.

Grazing by bison

When the southern part of the Dreiborner Hochfläche is grazed by bison, former hay-meadows turn into pastures and initial pastures remain, which contain few scattered broom bushes. In contrast to non-interference, no fallows dominated by tall grasses develop. Bramble is highly sensitive towards grazing and trampling featuring low utilization numbers (Briemle et al., 2002), so that the big bramble shrubberies in the initial state are strongly reduced by grazing. In their stead either scattered spots of pasture or broom shrubberies develop. Blackthorn, in contrast, which is adapted to grazing (high utilization numbers (Briemle et al., 2002)), is enhanced so that it spreads fast into the grasslands. However, it is overgrown by forests from the center, so that a grass-shrub-tree mosaic emerges, which is typical for wood-pastures (Pott and Hüppe, 1991; Olff et al., 1999; Bakker et al., 2004; Weber, 2008; Van Uytvanck et al., 2010): Pastures are intermingled either with not-palatable bushes (broom) or with bushes that defend themselves with thorns (blackthorn). The latter grow centrifugally via stolons and provide shelter for more palatable woody species so that in their center trees establish, replacing the bushes. Blackthorn therefore forms belts surrounding circular young woods, a pattern emerging from the spatial interactions in the model. Few birch trees also recruit in broom shrubberies, which do not provide protection from browsing, because over the years the seed pressure close to forests gets so high that the browsing of the animals cannot wholly control the growth of the trees.

Even though the significance of thorny bushes for landscape development in grazed systems is well recognized (Schupp, 1995; Callaway, 2007; Van Uytvanck et al., 2008; Barbosa et al., 2009), little is known so far about their lifecycle characteristics and factors facilitating or controlling their growth (Scheper and Smit, 2011; Smit and Ruifrok, 2011). To understand

and predict landscape development in grazed systems it is therefore crucial to investigate the processes leading to an establishment of new bushes as well as the impact of grazing on the growth of existing bushes. In the GraS-Model, only vegetative spread of bramble and blackthorn is included, neglecting ornithochorous seed dispersal. Consequently, their dispersal to sites on the Dreiborner Hochfläche where they were not initially present is underestimated. Yet, so far, little is known about the establishment niche of these bushes, although they are thought to be suppressed by grazers in the early stages, when thorns have not yet developed (Olff et al., 1999; Smit and Ruifrok, 2011). More studies need to be performed to understand their recruitment (Smit et al., 2010). Furthermore, impacts by browsing on the established bushes are not included in the model. However, the centrifugal growth of blackthorn by stolons might be reduced by browsers as was found for rabbit (Smit et al., 2010) and a very high browsing pressure might even affect nurse plants in a way, that their capability to protect tree seedlings is reduced (Smit et al., 2007).

Mowing

When the management zone is mown, the former pastures and shrubberies turn to hay-meadows in the simulations. Bramble and blackthorn shrubberies are pushed back, being highly sensitive to mowing featuring low utilization numbers (Briemle et al., 2002). Wood encroachment is prevented, since young broom bushes and trees die when mown (see Chapter 5), so that only on field paths running through the meadows, broom bushes can establish.

6.4.2 Impact of land use form on the landscape development of the Dreiborner Hochfläche

Regarding the impact of the different forms of land use, forest encroachment is most strongly delayed by doing nothing (apart, of course, from a mowing regime), a phenomenon which has been observed before on fallow grasslands (Ellenberg, 1996; Müller and Rosenthal, 1998; Schreiber et al., 2000). The high browsing pressure of red deer in combination with the dense sward developing in the fallows dominated by tall grasses hinders the establishment of trees. The high density of red deer conceals the processes of wood encroachment in the non-interference scenario with 22 red deer 100 ha^{-1}, because the browsing impact is immense. Only blackthorn as “nurse-plant” is able to facilitate wood encroachment under such extreme circumstances. In order to promote the natural processes of wood encroachment and forest development, the red deer population would have to be regulated to a more “natural” level of e.g. 2-4 individuals 100 ha^{-1}, a density found in the most natural wood in Central Europe, the Bialowieza National Park in Poland (Kamler et al., 2007).

Even at the grazing scenario with 10 bison 100 ha^{-1} (without red deer), more forests emerge than in the non-interference scenario with the high density of 22 red deer 100 ha^{-1} although the bison consume more than twice as much woody browse as the red deer (0.79 vs. 0.35 kg $cell^{-1}$ a^{-1}). This is due to the effect that bison, though they consume a high amount of woody browse, act as grazers as well, reducing the inhibition of seed availability by the herbaceous layer and promoting blackthorn. Grazing results in a diverse landscape mosaic containing grassland intermingled by non-palatable broom and patches of woods encircled by thorny bushes. Such a diverse grass-shrub-tree mosaic is considered to be of high conservation value, because it is discussed as one possible scenario of primeval vegetation in Europe (Vera, 2002; Birks, 2005) and is thought to often promote a high plant and animal diversity (Olff and Ritchie, 1998; Svenning, 2002; Poschlod et al., 2005). Re-introduction of big, robust herbivores is deemed to be a cost-efficient measure to preserve such habitats (Isselstein et al., 2005; Kleyer, 2007; Vandenberghe et al., 2008).

The GraS-Model provides predictions of landscape development that are agreed upon and might have been possibly suggested by local experts. However, the model gives highly detailed, spatially explicit projections integrating the initial vegetation composition and neighborhood interactions (c.f. Chapter 5) which would not be possible without the model. Secondary succession consist of many mutually interacting processes, so that an expert might have difficulties in judging the weight of single processes at different scenarios and predicting the course of succession for a specific site becomes a difficult task. For example local experts might not have considered the delayed forest succession in the non-interference scenario with the actual high abundance of red deer and the comparatively high wood encroachment in the grazing scenario, despite of the high browsing pressure by bison. It is considered an important current research question to understand how landscape patterns emerge from these interacting processes including negative and positive feedback mechanisms (Kleyer et al., 2007). The GraS-Model calculates the quantitative impact of each single process using mathematical formulas, adding contradictive effects up against each other, so that landscape patterns emerge from the interaction of the simulated processes. One further crucial advantage of mechanistic models is that single ecological processes can be modified, so that their influence on the ecological system can be judged (as for example in the scenarios with different abundances of red deer).

6.4.3 Limitations

In order to provide a better basis for the interpretation of the results, four limitations of the model are discussed: Grazers and browsers are evenly distributed, succession of different forest types is not modeled, climate change is not accounted for, and the Dreiborner Hochfläche had to be fragmented for the simulations because of computational restrictions. Furthermore, the necessary steps to apply the model to other sites are discussed.

One important simplification of the GraS-Model is that grazers and browsers are distributed evenly over space and time. In reality, positive feedback mechanisms between grazing and forage palatability occur (Olff et al., 1999; Mouissie et al., 2008). Grazers prefer frequently grazed lawns so that, on the one hand, patches of lawn are maintained even under extensive grazing, whereas, on the other hand, patches with less preferred, tall herbaceous vegetation develop. This patchy grazing pressure results in a spatial heterogeneity of woody as well as herbaceous species. Tall herbaceous stands form suitable establishment niches for thorny shrubs such as blackthorn (Smit and Ruifrok, 2011), which in turn facilitate wood encroachment. The heterogeneity under a grazing and browsing regime in the simulation results is so far mainly induced by heterogeneous initial composition of the vegetation. In reality it might be further enhanced by the described feedback mechanisms.

The simulation of succession in the GraS-Model stops, once a cell becomes forest. The model is intended to predict the development of the grassland towards shrubland or forest; succession of different forest types is not considered. The model has been tested on observations and aerial photographs reaching back for about 60 years. When predicting the further development for the next 100 years, climate change might alter the competition strength of some species such as spruce. So far, no climatic environmental factors are included in the model, so that no statement of the development under climate change can be made.

Due to its high complexity, the high spatial detail, and the large landscape modeled, the GraS-Model exceeds the available computer main memory when applied to the entire Dreiborner Hochfläche. As a consequence raster map of the total landscape consisting of 225,000 grid cells was divided into fragments, which were simulated separately. The area was fragmented in the way that the resulting pieces are mostly separated by valleys forming natural borders and high attention was paid to integrating the neighboring forests in the input data. Nevertheless, this approach may cause errors because neighborhood relationships between the fragments cannot be taken into account. Further analyses such as Monte-Carlo simulations or sensitivity analyses or automatically performed model calibration are also hindered due to memory and time constraints. In the next chapter, we show how a parallelization of the model can overcome these restrictions and evaluate the errors caused by fragmentation of the simulated landscape.

The model was designed, calibrated and tested for the Dreiborner Hochfläche in the Eifel National Park. In order to transfer it to other sites in Central Europe it will have to be adapted in several ways. First, a new set of representative species and groups will have to be identified and data availability for these species must be checked. Yet, as Briemle's utilization numbers exist for most herbaceous species in Central Europe and much data is available on shrubs and trees, we are confident that data gaps will be of an acceptable size. The most crucial point will be to check, if the implemented processes match the most decisive ones at the new side or if additional processes must be included. For the herbaceous layer this could mean that other environmental factors such as nutrient or moisture would have to be integrated, which could be performed using Ellenberg indicator values. For shrubs and trees additional processes such as further dispersal mechanisms or competition for resources that have not been considered so far might have to be included.

6.5 Conclusion

The simulation results provide predictions that are in line with the general idea of succession in abandoned and extensively grazed systems and are agreed upon by local experts. Even though local experts might suggest a similar general prediction, they could, however, not provide such highly detailed, spatially explicit projections, which can be visualized in raster maps. One crucial advantage of the GraS-Model is that it calculates various mutually interacting processes considering initial vegetation composition and neighborhood relationships. The user gains a better understanding of the impact of the processes, because landscape patterns emerge from these amplifying or contradicting processes during the simulation runs. Single processes can be modified to evaluate their influence on the course of succession. In our simulations, thorny bushes acting as “nurse plants” were of high importance. Yet, little is known about their life cycles and more data on processes regulating their establishment and growth is needed. Forest encroachment on the Dreiborner Hochfläche was most strongly delayed by non-interference with the given high abundance of red deer (apart from mowing), whereas grazing by bison promoted a diverse landscape mosaic.

Quintessence:	
✓	Simulation results in agreement with the literature and local experts.
!	More studies on establishment of “nurse plants” needed.
✓	Highly spatially-explicit predictions considering mutually interacting processes and neighborhood relationships.
✓	Single processes can be modified to judge their influence.
✓	Non-interference with the given high abundance of red deer strongly delays forest development on the Dreiborner Hochfläche.
✓	The high browsing pressure by red deer conceals processes of wood encroachment.
✓	Grazing by bison promotes a diverse landscape mosaic.

7 Parallelization of a Grid-based, Mechanistic Grassland Succession Model for Detailed Spatial Prediction

7.1 Introduction

To understand secondary succession of abandoned grasslands, it is crucial to consider neighborhood relationships to the surrounding vegetation, especially bushes and trees as seed sources (Briemle, 1980; Ellenberg, 1996; Schreiber, 1997; Schupp et al., 1998; Smith and Olff, 1998). Establishment of woods depends on many processes such as seed production, seed dispersal, seed bank dynamics, germination and seedling survival (Smith and Olff, 1998; Zimmermann et al., 2008). To integrate the manifold processes that are essential for forecasting landscape development, simulation models are considered to be a potentially powerful tool (Clark et al., 2001; Jeltsch et al., 2008; Thuiller et al., 2008). Yet, spatially-explicit models simulating a large area with a fine resolution, as are needed for landscape management, are still rare because they are often assumed to be too data-hungry to be applied for many species on a landscape scale (Jeltsch et al., 2008) and because they are still limited by computational needs, which increase exponentially with the simulated area (He and Mladenoff, 1999a; Lischke et al., 2006).

The GraS-Model simulates the dynamics of grassland vegetation in a detailed spatially-explicit approach (10 m grid). We chose such a fine grid, to be able to account for spatial heterogeneity and small landscape elements such as hedges and groves which might act as important seed sources determining the direction of landscape development. The unique feature of the GraS-Model is that it dynamically models different plant species' growth at this relatively fine spatial resolution using a multimodeling approach consisting of a herbaceous layer based on difference equations and an individual-based tree submodel, but is nevertheless capable of simulating the development of an area which is typically taken into consideration for landscape management (several 100 to approx. 1500 ha). Due to this high complexity and the large-scale landscape modeled, the GraS-Model initially exceeded the available computer main memory when applied to the whole Dreiborner Hochfläche stretching out over approximately 225,000 grid cells including several millions of trees. Current workstations are equipped with four to eight GB of main memory, which is sufficient even for demanding office applications but not for this kind of fine-grained simulation. Furthermore, the current release of the Delphi programming language compiler supports on 32-bit addressing, which technically limits the memory available for a process instance to 3 GB. Consequently, the total landscape had to be fragmented and modeled separately and the number of individuals (bushes and trees) in each cell had to be restricted. Yet, splitting the dataset into smaller parts to be computed individually may have led to questionable results, since the seed exchange over the artificial boundaries could not be taken into account, standing in contrast to the requirement of considering neighborhood relationships with the surrounding vegetation. The runtime for a 100 year simulation run with daily time steps (i.e. 36,500 iterations) resulted in a highly unpractical total run- and handling time for all fragments of 1 to 2 weeks.

In order to overcome these memory and time constraints of the serial version, the GraS-Model was parallelized with a message passing approach, to employ the combined memory and computing power of multiple nodes. This parallelization enables the GraS-Model to be run on a cluster, i.e. a group of tightly-coupled compute nodes connected with a fast interconnect network, allowing parallel programs to employ the resources of all nodes in the cluster simultaneously. The parallelization therefore provides the means to cut down the runtime significantly and to scale the available main memory with the cluster size.

In this chapter the technical aspects of the parallelization as well as results regarding load balancing and speed up are presented. Furthermore, simulation results of the serial and the parallel version are compared and ecological implications resulting from the landscape fragmentation in the serial version are discussed. Our hypothesis is that especially for species with high seed dispersal distances results will differ in the two versions due to the artificial landscape fragmentation in the serial version. The parallelization was performed in cooperation with the “Institute for Scientific Computing” at the RWTH Aachen University led by Prof. C. Bischof and the Helmholtz-University Young Investigators Group “Performance Analysis of Parallel Programs" at the “Jülich Supercomputing Center” (Forschungszentrum Jülich GmbH) led by Prof. F. Wolf.

7.2 Parallelization

In general, parallelization can be conducted calculating either the different simulated processes or different parts of the landscape separately (i.e. using either functional or geographic decomposition). A functional decomposition is not feasible for our model, because the processes are highly interwoven so that the communication effort would be too great. The raster-based approach of the model facilitates a geographic decomposition, calculating different cells independently on different processes and communicating the plant dispersal between cells using a message passing approach. The geographic decomposition furthermore allows a high flexibility in choosing how many processes are used for a simulation run, depending on the simulated landscape. This has been implemented using the MPI (message passing interface) library, a de-facto standard in High Performance Computing (HPC) to write parallel programs for clusters.

When using geographic decomposition, communication of spatial interactions between different processes has to be provided. Spatial interactions in the GraS-Model occur in the dispersal of plants. Vegetative spread of grasses and shrubs with belowground stolons (i.e. bramble (*Rubus* spec.) and blackthorn (*Prunus spinosa*)) effect only the adjacent cells. Generative seed dispersal of broom (*Cytisus scoparius*) and the tree species beech (*Fagus sylvatica*), oak (*Quercus robur*), spruce (*Picea abies*) and birch (*Betula pendula*) reaches further cells, with maximal dispersal distances ranging from 200 m for zoochorous dispersal of beechnuts and acorns to 700 m for anemochorous dispersal of birch seeds. The number of dispersed seeds also differs strongly with a maximum of 10,000 seeds per broom bush and 11,775,000 seeds per birch tree.

The simulated landscape is represented in a two dimensional, rectangular grid of 10 x 10 m cells. Since the study site (the Dreiborner Hochfläche in the Eifel National Park) is not of a rectangular shape, several fields in the natural grid representation are empty (see Fig. 7-1). All other cells contain a list of species that are present in the cell. The computation for a simulated time step of each cell can be divided into four steps. The computation is performed independently for each cell except for step three where seed exchange between the cells is executed (for more details see Chapters 4 and 5):

1. Growth simulation for each plant contained in the cell: For each plant, the growth per simulated day is computed based on species-specific parameters.

2. Calculating the amount of vegetative growth and seeds to be exchanged with other cells: Depending on the actual plant species, the seed dispersal time(s) in the year and the seed count or vegetative spread varies. Generative seed dispersal is only calculated once a year, whereas vegetative spread into adjacent cells is calculated daily. For the plant species contained in a cell, the amount of seeds or vegetative growth that has been produced is computed as well as to which other cells the seed disperse or the amount of vegetative growth spreads. This information is stored in a three-dimensional array over the species, the amount of seeds or vegetative growth and the XY-coordinates of the sink cell.

3. Execution of the seed exchange: Each simulation process examines for each plant species whether any seed has to be exchanged at all. This information is then exchanged with all other processes and thereby it is derived whether any exchange for that plant species has to be performed or not. If yes, the seed grid containing the amount of seed or vegetative growth to be send to other cells is reduced via the MPI Allreduce functionality, thereby computing the total amount of seeds or vegetative growth to be received for each cell and propagating this information to every process involved. This exchange step takes into account that the seed-dispersing plant species disperse less frequently than plants dispersing via vegetative growth, and avoids the seed array reduction in cases where no exchange happens.

4. Calculation of the impact of seeds or vegetative growth received by other cells: Based on the current state of the cell and the amount of seeds or vegetative growth received by other cells, either new plants start to exist in the cell or vegetative ingrowth is added to the growth of plants already existing in the cell.

7.3 Results

In the following section, results regarding load balancing, speedup and simulated landscape development are presented.

7.3.1 Load balancing

Our first strategy was to split the cell grid into as many equally-sized rectangular areas as MPI processes that the program has been started with. As can be seen in Fig. 7-1 (left) for an example of 16 processes, the overlap of rectangular areas and simulated cells in the dataset of the Dreiborner Hochfläche varied significantly among the MPI processes; there was no simulation work assigned to some processes (e.g. process 0, to which only empty cells were assigned). This led to a bad load balancing as the runtime fluctuated heavily between the different processes as can be seen in Fig. 7-1 (left).

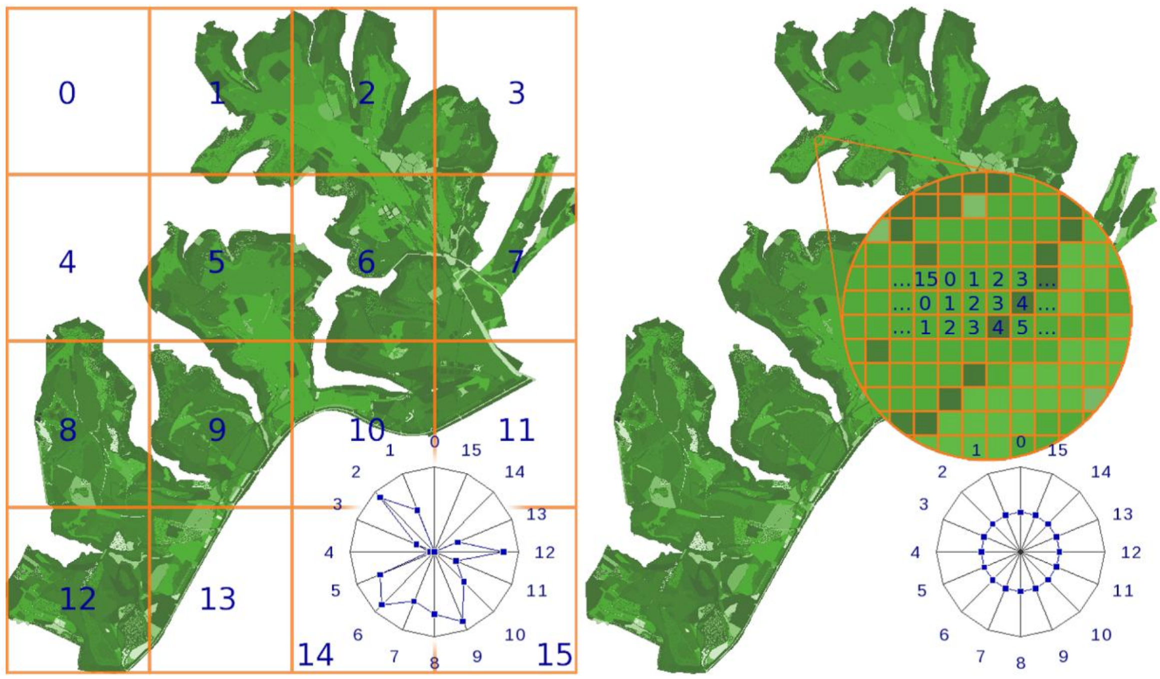


Fig. 7-1: Geographic decomposition of the simulated Dreiborner Hochfläche. Numbered boxes represent the processes 0 to 15. The circular figures show the fluctuation of the runtime for the different processes (center of the circle: no runtime, outer line of the circle: maximal runtime).

Left: Rectangular distribution of cells to 16 MPI processes.

Right: Cyclic distribution of cells to 16 MPI processes.

We improved the load balancing by implementing a cyclic cell distribution: The cells were numbered along the latitude from the north-west corner to the south-east corner of the dataset, and a cell *i* was assigned to the process with the number equaling the modulo of the quotient of *i* and the number of MPI processes as illustrated in Fig. 7-1 (right). This cyclic allocation of cells to the processes led to an equal distribution of empty and simulated cells to the processes resulting in satisfying runtime equality, so that idle time of single processes was avoided. It is noteworthy that in this approach, neighboring cells are distributed to different processes so that cells assigned to one process are not spatially connected to each other.

7.3.2 Speedup evaluation

We examined the scalability of the program using a medium-sized test dataset on a cluster of Intel Nehalem machines, each equipped with two quad-core hyper-threaded Intel X5570 processors running at 2.93 GHz, all connected with a 4x QDR InfiniBand network. The serial runtime of the dataset was about 150 sec per simulated year. The best effort speedup we achieved was 9.1 (i.e. about one order of magnitude) on eight compute nodes with four MPI processes per node, which corresponded to a runtime of 16.5 sec per simulated year. Using more MPI processes per node did not increase performance, since the memory bandwidth was exhausted.

7.3.3 Simulated landscape development

The parallelized version of the GraS-Model simulation code, enabled us to handle the dataset of the Dreiborner Hochfläche as a whole. We compared the results after 100 simulated years - taking about 16 hours of computing time with eight MPI processes – in an abandonment scenario without red deer. We chose this scenario because it is one where trees (especially birch) encroach widely over the area (Fig. 7-2). Without parallelization, the run- and handling time for all fragments of 1 to 2 weeks was highly unpractical and we were only able to simulate the Dreiborner Hochfläche in parts. However, as shown in Fig. 7-2, the simulation results differed when only fragments were calculated compared to the simulation of the area in whole. Birch encroachment was even stronger when the whole area was modeled in one simulation run. When only parts of the area were simulated (Fig. 7-2, bottom), the deviation of the results from the parallel version depended on the initial vegetation composition. At parts of the landscape, where initially only few birch forests existed, some shrubberies remained that were not overgrown by birch even after 100 years (Fig. 7-2 B) or other forest types encroached (Fig. 7-2 C). At parts with more birch in the initial state, results differed less from the parallel simulation of the area as a whole (see Fig. 7-2 A, D).

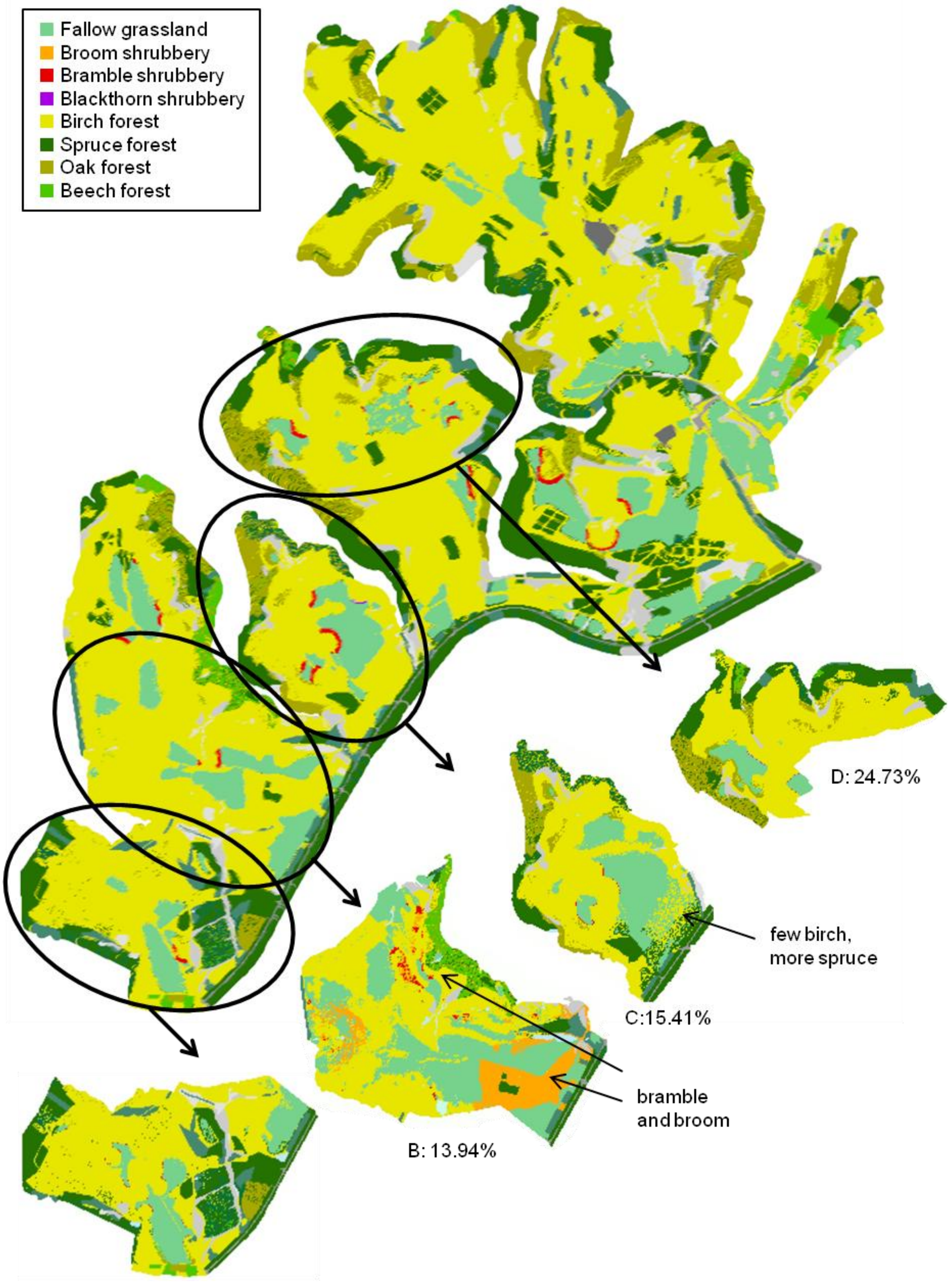


Fig. 7-2: Simulation of the Dreiborner Hochfläche under abandonment without red deer at year 100. Top: area calculated parallel as a whole. Bottom: parts of the area calculated serially. Percentages indicate the initial amount of birch forests in the parts A - D.

7.4 Discussion

The parallelization of the GraS-Model helped to solve the memory problems, so that the entire Dreiborner Hochfläche can now be simulated in one simulation run. The good speedup of 9.1 on eight nodes was achieved distributing the cells cyclically on the processes. Thus, parallelization solved the computational restrictions when modeling a bigger landscape in the required detail of processes and spatial resolution. Additionally, the practicability of simulating the whole Dreiborner Hochfläche was highly enhanced because the work time of illustrating the simulation results in raster maps using ArCGis9 (ESRI) was reduced. The ASCII files that contain the output data of the simulation had to be converted to raster maps with the appropriate legend only once and not several times separately for all fragments.

In order to simulate landscape development for a given area, it is important to consider the initial vegetation composition and especially the occurrence of seed sources (He and Mladenoff, 1999a). However, to include all available seed sources in an area at high spatially-explicit detail requires a high computational performance, which increases exponentially with the simulated area. Some results differed when simulating the development of the Dreiborner Hochfläche over 100 years parallel as a whole compared to fragments with the serial version, even though the area was fragmented in the way that the resulting pieces are mostly separated by valleys forming natural borders and high attention was paid to integrating the neighboring forests in the input data. Results of the serial version deviated mainly for fragments where birch, i.e. the tree with the longest dispersal distance and the highest number of seeds, was not numerous in the initial state. In this case, other species such as shrubs and trees gained in importance in the serial version, because the strength of this highly competitive species was reduced. This shows that, depending on initial vegetation composition, it is important to consider the whole area of interest for the simulation, including important seed sources of species with a high dispersal potential.

In the meantime, the parallel version of the GraS-Model was also linked to a cloud environment (Keller et al., 2011) allowing flexible model calculations and performing Monte-Carlo simulations (Andrich, 2011). It is assumed that in the future, this technique will allow using more sophisticated calibration techniques and analyses of model output.

7.5 Conclusion

The computer simulation of biological systems has become an important instrument for ecological forecasting. Yet, with a growing complexity and area size of the systems under consideration, simulation models are likely to reach the limits of computational possibilities. Restrictions in simulation time and memory can be overcome by parallelization. In this work, the parallelization of the GraS-Model using a geographic decomposition is presented. In this model the computation can be performed in parallel on each raster cell individually, with the exception of the seed exchange representing a synchronization point. Since the landscape cannot be assumed to be rectangular, a good mapping of work onto the MPI processes is important. With the current implementation of the load balancing and the seed exchange we were able to handle the large dataset of the Dreiborner Hochfläche and achieved a speedup of about one order of magnitude. Parallelization did not only highly improve practicability of the model use, but also enhanced the ecological accuracy of the model, since especially for the species with the highest dispersal distance and amount of seeds, results differed between simulations of the whole or partitioned area.

Quintessence:
✓ Restrictions in simulation time and memory overcome by parallelization.
✓ Simulation of the entire Dreiborner Hochfläche only possible with parallel version.
✓ Good mapping of work onto MPI processes essential to reach good speedup.
✓ Parallelization enhances practicability and accuracy of simulation results.
✓ Integrating seed sources especially important for species with a high dispersal distance and amount of seeds.

8 The Use of the GraS-Model as Decision Support System

Land use change, leading to habitat loss or degradation, is considered an important driver of biodiversity loss (Midgley and Thuiller, 2005; Botkin et al., 2007; Van Calster et al., 2008; GBO3, 2010). Thus, authorities managing a certain area need to integrate land use as a major factor. For biodiversity in European semi-natural grasslands, land use change is a major threat (Bakker, 1989; Pykälä, 2000; Diemer et al., 2001; Dierschke and Briemle, 2002; Isselstein et al., 2005; Kleyer, 2007; Van Calster et al., 2008; EU-COM, 2009; Lind et al., 2009; Stoate et al., 2009). Mechanistic models are considered to be a valuable tool to forecast species' responses to environmental changes and facilitate decision making, especially since the complexity and extent of environmental problems are growing larger (Clark et al., 2001; Parker et al., 2002; Choi et al., 2008; Jeltsch et al., 2008; Thuiller et al., 2008). In order to support decision-making by authorities that deal with the maintenance of semi-natural grasslands, the GraS-Model was created in close cooperation with the Eifel National Park administration, the MUNLV (Ministry of the Environment, Conservation, Agriculture and Consumer Protection of the State of North Rhine-Westphalia) and the LANUV (North-Rhine-Westphalian Agency for Nature, Environment and Consumer Protection).

But why use the GraS-Model as a decision support system (DSS)? In the following paragraphs, four major benefits of using the GraS-Model as a DSS will be discussed: It not only gives a highly detailed spatially explicit projections providing a strong basis for decision support and facilitating an effectiveness and efficiency control, but it also combines knowledge of different disciplines, enhances communication, and can integrate and communicate the latest scientific knowledge.

Predictions of landscape development provided by the GraS-Model are agreed upon and might have been possibly suggested by local experts. However, the model gives highly detailed, spatially explicit projections integrating the initial vegetation composition and neighborhood interactions (c.f. Chapter 5 and 6) which would not be possible without the model. Because of its explicitness, the model provides an optimal basis for discussions and decisions of stakeholders dealing with the question of how to manage the open grasslands.

When stakeholders have decided upon a management action, the model can provide projections and maps of the results of that action on grassland condition, which can be generated for different time steps. After an ongoing monitoring of the management impacts, the real landscape development can therefore be compared to the simulated maps and an effectiveness and efficiency control can be easily performed. So far, many restoration projects remain unevaluated, so that evidence-based restoration and learning is hindered (Bratrich, 2004; Pullin et al., 2004; Sutherland et al., 2004; Esselink et al., 2008). When using the GraS-Model (or any detailed spatially-explicit model) as a DSS, the simulated raster maps can be used for an effectiveness control. Resulting matches, and especially mismatches that we can learn from (c. f. Redford and Taber (2000)) will give deeper insights in the system and the key-processes driving vegetation change.

As the GraS-Model is developed for the purpose of being used as a decision support system for stakeholders, we set a high value on the comprehensibility and undertook a reality check by pattern oriented model testing (Chapter 5). Ecological models are often not used or not even accepted by stakeholders, when they are not validated or hard to comprehend (Turner et al., 1995; Midgley and Thuiller, 2005; Botkin et al., 2007; Jeltsch et al., 2008; Thuiller et al., 2008). Yet, even more important for the acceptance of a model is participation of local experts and stakeholders to enhance communication and facilitate learning by debate and exchanging perceptions and ideas (Turner et al., 1995; Clark et al., 2001; Van Kerkhoff and Lebel, 2006; Thuiller et al., 2008; Seppelt et al., 2009; Wassen et al., 2011). When developing the GraS-Model, we therefore worked in close contact with local experts and stakeholders (e.g. the Eifel National Park Administration, the MUNLV (Ministry of the Environment, Conservation, Agriculture and Consumer Protection of the State of North Rhine-Westphalia) and the LANUV (North-Rhine-Westphalian Agency for Nature, Environment and Consumer Protection)). At the beginning of the model development, when deciding which processes to integrate, the model proved to be an ideal basis for communication. Local experts from various disciplines contributed their different viewpoints that were integrated in the model in an objective way (as mathematical formulas), allowing for an objective discussion. For example, foresters provided knowledge about the specific life characteristics of the different tree species, botanists considered the impact of the herbaceous layer and gamekeepers took the influence of wild boar and red deer into account. Only when combining these different factors, did we achieve good simulation results. The model visualizes the projected landscape development in detailed raster maps, so that local experts with a good knowledge of the area under study get a clear idea of the projected landscape developments. The possibility of the model to be linked with a GIS (geographic information system) for input as well as output data is valuable and often a precondition for stakeholders who want to apply the model to an existing landscape (Rammig, 2005).

Current scientific knowledge is often not considered in management decisions because it is not easily available to decision makers (Prendergast et al., 1999; Sutherland et al., 2004; Pullin and Knight, 2005). Ecological models provide an optimal tool to integrate current knowledge of different disciplines. After an ongoing monitoring, the accuracy of earlier model predictions can be checked, and latest scientific insights can be integrated as the model is continuously updated. When applying a model to a new area or another management question, it might be necessary to take other processes into account. Therefore, the model cannot just be handed over from scientists to stakeholders, but close cooperation is required. The scientists will have to adjust the model according to the given landscape and management question, whereas the stakeholders will have to communicate their requirements in detail. In doing so, they can also raise new research question and can convey them directly to the scientists, helping to bridge the mismatch that sometimes exists between science and practice (Prendergast et al., 1999; Griffiths, 2004; Van Kerkhoff and Lebel, 2006; McNie, 2007; Knight et al., 2008). One advantage of the model not to be underestimated is, therefore, its power to support communication between experts of different disciplines as well as between scientists and stakeholders.

Quintessence: Benefits of the GraS-Model as DSS
✓ Highly spatially detailed projections. ✓ Visualization in raster maps. ✓ Optimal fundament for discussions. ✓ Facilitation of an effectiveness and efficiency control. ✓ Support of communication between experts of different disciplines and between scientists and stakeholders. ✓ Integration of latest scientific knowledge.

9 Outlook

The raster-based approach of the GraS-Model allows a coupling of additional static layers of environmental variables (e.g. a heterogeneous landscape concerning nutrients) or of other raster-based, dynamic models (e.g. models of nitrogen cycling, climate change or animal movement). In the following, a short overview of some possible expansions is given. Further expansion especially with other dynamic model components will increase computational needs. Therefore, parallelization is inevitable if large areas of several hundred hectares are still to be simulated.

9.1 Light

In order to simulate the germination and establishment of tree seedlings more precisely, the factor light needs to be included. Different tree species require different light environments during their juvenile phase. As shown in Chapter 5, trees on the Dreiborner Hochfläche mainly recruit in blackthorn shrubberies providing protection from ungulate browsing. Simulation results deviate from reality because they show a high recruitment of wind dispersed species such as birch and spruce within the shrubberies. However, as these pioneer species have high light requirements (Ellenberg, 1996), their seedlings were on the study site mainly found in open areas, whereas trees recruiting within thick blackthorn bushes were mainly climax species such as oak and beech (Krämer, 2011). In order to give a clearer picture of the kind of woods and forests developing, light should therefore be integrated as a factor influencing juvenile tree establishment. Light is also an important factor for succession within forests, because climax species often rely on an already established overstory canopy (Smith and Olff, 1998; Härdtle et al., 2008).

9.2 Forest succession

The aim of the GraS-Model is to simulate succession from grass- or shrubland towards forests; dynamics within forests and a succession from one forest type to another is not included. Many forest models already exist, of which some are spatially-explicit (for reviews see Liu and Ashton (1995), Bugmann (2001), Pretzsch (2001), Scheller and Mladenoff (2007) and Pretzsch (2008)). A possible add-on to the GraS-Model would be the coupling of a spatial-explicit, raster-based forest model such as TreeMig (Lischke et al., 2006) or LandClim (Schumacher, 2004; Schumacher et al., 2004) to integrate forest succession and allow for more realistic simulations over longer time spans.

9.3 Nutrients

When simulating the dynamics of the herbaceous layer of the Dreiborner Hochfläche, the model was able to emulate dynamics within one nutrient level. Yet, vegetation dynamics at a few sites on the Dreiborner Hochfläche either with a higher nutrient level as for example in dells with a much deeper soil or at sites with a very low nutrient level could not be simulated (Chapter 4). To be able to simulate these two vegetation types, a static layer of the nutrient status could be added. The impact of nutrient availability on the herbaceous layer could be modeled in a similar way as the impact of land use, integrating the Ellenberg indicator value for nitrogen, so that the growth rates of species with a high nutrient demand (i.e. a high nitrogen value) would be reduced at sites with a low nutrient availability.

More challenging would be the coupling of a dynamic nitrogen model with the GraS-Model. To this end, the whole nitrogen cycle would have to be integrated in order to achieve the amount of plant available nitrogen (i.e. solute nitrate and ammonium). Such a model extension might be especially important for sites, where abandonment leads to auteutrophication because biomass is no longer removed and nitrogen loads in the depositions are high. In a study at the Dreiborner Hochfläche, Engler (2010) observed only slightly higher amounts of plant available nitrogen at abandoned sites due to mineralization of old biomass remaining at the site. The effect of auteutrophication on the Dreiborner Hochfläche is limited, because the soil is very shallow and nutrient losses due to leaching are high. On other sites, in contrast, eutrophication was found to trigger vegetation changes, e.g. leading to a development of grass dominances in heathlands (Aerts, 1993; Bobbink et al., 1998). This effect can influence the course of succession, because wood encroachment is often delayed on nutrient rich sites, where grasses form a dense sward that inhibits recruitment of woody species (Smith and Olff, 1998).

9.4 Climate

Climate change is likely to alter species composition and therefore successional pathways in future decades. The influence of climate change on the herbaceous layer and on trees could be added in a similar way as nitrogen, relying on Ellenberg's indicator values. For trees, some models already exist that integrate the impact of temperature and moisture on forest dynamics (e.g. ForClim (Bugmann, 1994), LandClim (Schumacher, 2004; Schumacher et al., 2004) and TreeMig (Lischke et al., 2006)). These models could therefore not only be coupled to simulate forest succession, as discussed above, but their moisture and temperature subroutines could also be implemented to take climate change into account.

9.5 Animal movement

So far, the ungulate density in the GraS-Model is uniformly distributed over all cells. However, effects of ungulates on ecosystems are influenced by their behavior. For example, ungulates linger on preferred spots, e.g. near palatable food species, (Hobbs, 1996) or flee from disturbances. Positive feedback mechanisms occur, because ungulates affect vegetation composition and prefer frequently grazed lawns that they created themselves. This can result in structural vegetation diversity, even when abiotic factors are homogenous (Mouissie et al., 2008). Integrating animal movement and behavior into the GraS-Model would therefore provide a more realistic picture of the landscape development. Additionally, it would allow the simulation of management actions focusing on controlled visitor guidance in order to create areas where ungulates are undisturbed. Animal movement could be simulated calculating habitat preferences for the different vegetation types. A possibility to apply animal movement in high detail would be to integrate an individual-based population model with a random walk unit such as e.g. in Vuilleumier and Metzger (2006) or Frost et al. (2009). Yet, this would inevitable require an efficient parallelization as it would immensely enlarge computational needs.

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Appendix

Table A-1: Measured solitary trees: height (H) vs. crown diameter (CD)

Picea abies		Betula pendula		Fagus sylvatica		Quercus robur	
H [m]	**CD [m]**	**H [m]**	**CD [m]**	**H [m]**	**CD [m]**	**H [m]**	**CD [m]**
0.19	0.115	4.6	4.6	6.25	5.8	10	9.6
0.25	0.175	4.25	3.2	13.75	12.8	9.5	9.1
0.82	0.48	4.6	3.2	4.75	4	12	11.6
0.9	0.435	7.75	4.8	13.25	12	0.28	0.4
0.12	0.11	3.25	3.2	5	2.2	10.25	10.3
0.17	0.18	4	3.6	2.65	2	2.15	2.2
0.52	0.44	5.25	4.8	8	10	0.8	1
0.44	0.43	2.65	1.5	10	8.6	0.28	0.36
11.75	8	3	1.6	13	11.2	0.5	0.56
11.5	10.4	4.5	4	11.5	9	12.75	12.6
10	9.2	11	6.6	4.75	4.2	9	8.9
3.6	2.3	10.5	11.8	2.5	2.6	0.56	0.4
4	2.6	3.8	3.3	20.75	18.2	10.75	9.7
5	2.9	6.5	4.6	15.5	13.4	17.5	16
4	2.3	9	6.6	20	18.2	14.25	11.8
18	10.2	7.25	4.7	16.25	13	5.25	4
23.75	10.6	10.5	5	14.75	11.9	11.25	11.8
20.25	12	13.5	7.2	20.75	18.7	2.05	2
21.5	12.8	12	10.2	24.75	23.1	11.25	12.4
22.5	13.9	10.5	6.6	9	5.8	14	12.5
25	12.8	4	4.8			14.25	16.4
5.5	2.4	7	5			16.25	14
5.5	3.8	9.5	8.6				
5	3.9	9.75	8.5				
3.4	2.4	9	6.1				
3.75	2.8	9.75	5.4				
3.3	2.6	15.75	9.7				
3.15	2	10.75	8				
5.75	2.9	10.5	7.5				
5.5	3.2	11	7.7				
5.25	3	10.25	7				
6.25	2.6						
6	3.4						
5.75	3.3						
5.5	3.6						
9	6.6						
10.5	8.8						
11	8.4						
20.75	17.3						
17.5	11.1						

Table A-2: Measured *Cytisus scoparius* bushes. Height (H) [m] vs. crown diameter (CD) [m].

Cytisus scoparius																	
H	**CD**	**H**	**CD**	**H**	**CD**	**H**	**CD**	**H**	**CD**	**H**	**CD**	**H**	**CD**	**H**	**CD**	**H**	**CD**
1.15	1.10	0.20	0.10	0.50	0.30	0.30	0.20	0.40	0.30	0.48	0.37	1.06	1.56	0.40	0.33	0.88	1.20
0.80	0.70	0.60	0.60	0.35	0.30	0.30	0.20	0.30	0.15	0.19	0.08	0.36	0.68	0.44	0.19	0.93	1.10
0.70	1.00	0.60	0.60	0.40	0.25	0.30	0.20	0.50	0.50	0.16	0.12	0.24	0.11	0.54	0.25	0.27	0.21
0.65	0.70	0.60	0.60	0.40	0.30	0.35	0.20	0.50	0.30	0.08	0.03	0.22	0.31	0.50	0.43	0.40	0.17
0.65	0.40	0.60	0.60	0.40	0.20	0.30	0.20	0.50	0.80	0.16	0.05	0.45	0.36	0.70	0.52	0.66	0.33
0.45	0.20	0.60	0.60	0.30	0.30	0.30	0.20	0.65	0.50	0.11	0.10	0.37	0.24	0.72	0.63	0.56	0.32
0.95	0.45	0.60	0.60	0.70	0.50	0.40	0.40	0.30	0.20	0.23	0.12	0.23	0.17	1.20	0.65	0.23	0.15
0.50	0.35	0.50	0.15	0.90	0.70	0.70	0.50	1.00	1.00	0.26	0.23	0.88	1.10	0.90	1.19	0.27	0.27
0.35	0.50	0.40	0.15	0.90	0.70	0.35	0.20	0.75	0.60	0.70	0.58	0.47	0.35	0.60	0.84	0.34	0.24
0.60	0.60	2.50	3.10	0.60	0.60	0.40	0.30	0.60	0.30	0.23	0.17	0.33	0.18	0.82	1.09	1.10	0.59
0.50	0.20	0.60	0.30	0.80	1.00	0.80	0.60	0.50	0.60	0.23	0.11	0.34	0.26	0.75	0.69	0.20	0.09
0.60	0.40	0.20	0.20	0.80	0.90	1.10	0.80	0.40	0.30	0.11	0.06	0.76	0.36	0.73	0.46	0.27	0.09
0.30	0.25	0.30	0.15	0.60	0.40	0.60	0.50	0.35	0.15	0.80	0.60	0.55	0.27	0.79	0.73	0.17	0.11
0.60	0.50	0.45	0.20	0.70	0.40	0.40	0.60	0.40	0.30	0.20	0.09	0.75	0.30	0.57	0.58	0.72	0.53
1.00	1.70	0.40	0.20	0.90	0.90	0.50	0.60	0.53	0.28	0.29	0.23	0.47	0.47	0.44	0.46	0.54	0.33
0.90	1.65	0.90	0.60	0.80	0.60	0.50	0.40	0.27	0.17	0.81	0.82	0.59	0.43	0.37	0.41	0.25	0.09
0.55	0.35	1.00	0.60	1.00	1.20	0.40	0.30	0.42	0.43	0.77	0.77	0.57	0.32	0.39	0.16	0.45	0.43
0.55	0.35	0.50	0.40	0.90	0.65	0.25	0.10	0.30	0.30	0.48	0.42	1.38	1.29	0.44	0.26	0.79	0.88
0.60	0.40	0.80	0.70	0.50	0.60	0.60	0.35	0.31	0.25	0.50	0.14	0.32	0.20	0.20	0.12	0.36	0.27
0.60	1.10	0.40	0.40	0.80	0.50	0.30	0.40	0.25	0.21	0.40	0.27	0.46	0.30	0.25	0.19	0.63	0.45
0.60	0.40	0.50	0.30	0.80	0.80	0.60	0.30	0.09	0.03	0.39	0.57	0.36	0.27	0.43	0.23	0.35	0.28
0.85	1.80	0.40	0.25	0.60	0.60	0.70	0.60	0.42	0.41	0.60	0.40	0.20	0.15	0.25	0.12	0.42	0.35
0.45	0.70	0.50	0.25	0.30	0.10	0.60	0.60	0.29	0.21	0.29	0.31	0.47	0.48	0.28	0.12	1.17	0.61
0.40	0.20	0.80	0.40	0.30	0.30	0.40	0.20	0.23	0.05	0.37	0.47	0.48	0.37	0.30	0.17	0.30	0.17
0.30	0.30	0.40	0.40	0.30	0.40	1.00	0.80	0.33	0.35	0.32	0.42	0.54	0.40	0.35	0.26	1.80	0.93
0.70	0.70	0.50	0.45	0.30	0.30	0.60	0.20	0.25	0.10	0.65	0.98	0.64	0.83	0.38	0.38	0.78	0.78
0.50	0.60	0.40	0.30	0.70	0.70	0.40	0.10	0.15	0.04	0.60	0.46	0.35	0.17	0.23	0.11	1.18	0.55
0.50	0.60	0.35	0.15	0.50	0.20	0.50	0.40	0.44	0.50	0.65	0.38	0.49	0.36	0.95	0.44	0.70	0.41
0.50	0.60	0.20	0.10	0.80	0.50	0.50	0.30	0.45	0.55	0.65	0.54	0.31	0.32	0.57	0.64	0.23	0.28
0.50	0.60	0.30	0.10	0.30	0.10	0.90	0.90	0.36	0.24	0.53	0.23	0.60	0.44	0.53	0.21	0.25	0.24
0.50	0.60	0.30	0.20	0.70	0.90	1.00	1.20	0.38	0.22	0.56	0.43	0.37	0.53	0.61	0.85	0.23	0.16
0.50	0.50	0.60	0.30	0.40	0.30	1.00	1.30	0.91	0.82	1.16	1.00	1.00	1.01	0.53	0.60	1.00	0.59
0.60	0.40	0.90	0.40	0.40	0.30	0.30	0.30	0.54	0.43	0.75	0.71	0.72	0.76	0.35	0.64	0.79	0.59
0.50	0.20	0.50	0.20	0.40	0.40	0.50	0.40	0.13	0.03	0.36	0.12	1.09	0.95	0.40	0.23	0.83	0.70
0.60	0.60	0.35	0.25	0.60	0.30	0.70	0.60	0.24	0.16	0.34	0.12	0.68	0.61	0.57	0.75	0.49	0.36
0.60	0.60	0.35	0.20	0.60	0.40	0.70	0.10	0.25	0.21	0.52	0.34	0.47	0.36	0.49	0.51	1.46	2.56
0.50	0.50	0.30	0.20	0.60	0.60	0.60	0.10	0.42	0.38	0.40	0.15	1.04	0.99	0.42	0.28	2.50	2.92
0.50	0.50	0.30	0.15	0.70	0.60	0.80	0.60	0.33	0.23	0.60	0.54	0.43	0.33	0.45	0.39	2.20	2.05
0.50	0.50	0.80	0.80	0.80	0.70	0.60	0.60	0.17	0.17	0.55	0.28	0.48	0.34	0.37	0.48	2.25	3.50
0.50	0.50	0.35	0.15	0.50	0.10	0.30	0.20	0.16	0.21	0.35	0.24	0.58	0.53	0.41	0.37	1.80	2.12
0.70	0.50	0.35	0.15	1.00	1.00	0.25	0.20	0.42	0.24	0.35	0.34	0.69	0.79	0.24	0.29	2.15	2.25
0.70	0.50	0.70	0.50	0.40	0.30	0.40	0.30	0.18	0.15	0.61	0.50	0.21	0.17	0.63	0.27	2.75	2.90
0.70	0.50	0.45	0.30	0.50	0.60	0.40	0.20	0.10	0.21	0.92	0.95	0.45	0.37	1.03	0.84	2.10	2.00
0.70	0.50	0.40	0.25	0.70	0.70	0.40	0.30	0.40	0.47	0.38	0.47	0.40	0.27	1.32	2.18	2.35	2.90
0.70	0.50	0.30	0.40	0.50	0.40	0.40	0.20	0.36	0.36	0.32	0.26	0.24	0.18	1.02	1.23	1.85	2.30
0.40	0.30	0.20	0.10	0.30	0.30	0.50	0.50	0.34	0.33	0.38	0.41	1.10	0.80	0.78	0.99	1.40	1.70
0.40	0.30	0.80	0.60	0.50	0.30	0.35	0.25	0.18	0.18	0.67	0.69	0.33	0.16	0.50	0.20	1.70	2.00
0.60	0.30	0.50	0.30	0.40	0.30	0.50	0.20	0.42	0.36	0.44	0.37	0.50	0.43	0.38	0.34	1.50	1.40
0.30	0.30	0.80	0.80	0.50	0.30	0.30	0.30	0.56	0.55	0.22	0.11	0.40	0.16	0.88	0.43	1.50	1.75
0.40	0.20	1.00	0.50	0.30	0.30	0.35	0.10	0.24	0.07	0.39	0.25	0.17	0.20	0.54	0.37	1.65	2.20
0.20	0.10	0.55	0.55	0.40	0.40	0.40	0.30	0.51	0.43	0.78	0.77	0.29	0.18	0.89	0.70		

Table A-3: Length (L), wet weight (WW) and dry weight (DW) of measured twigs.

Picea abies			Betula pendula			Fagus sylvatica			Quercus robur		
L [m]	**WW [kg]**	**DW [kg]**	**L [m]**	**WW [kg]**	**DW [kg]**	**L [m]**	**WW [kg]**	**DW [kg]**	**L [m]**	**WW [kg]**	**DW [kg]**
0.098	0.00063	0.00023	0.107	0.00086	0.00037	0.082	0.00021	0.00012	0.137	0.00098	0.00044
0.085	0.00067	0.00022	0.067	0.00039	0.00014	0.092	0.0005	0.00026	0.166	0.00098	0.00046
0.081	0.00039	0.00013	0.067	0.00039	5.8E-05	0.123	0.00087	0.00025	0.159	0.00095	0.0004
0.082	0.00050	0.00019	0.057	0.00046	0.00014	0.136	0.00044	0.00026	0.134	0.00097	0.00043
0.054	0.00021	0.00007	0.044	0.00036	0.00014	0.143	0.00087	0.00017	0.109	0.0004	0.00017
0.079	0.00044	0.00017	0.069	0.00049	0.00016	0.28	0.00369	0.00184	0.132	0.00061	0.00031
0.081	0.00036	0.00012	0.057	0.0005	0.00017	0.26	0.00422	0.00224	0.142	0.00077	0.00037
0.075	0.00038	0.00013	0.055	0.00042	0.00016	0.243	0.00103	0.00055	0.112	0.00038	0.00015
0.059	0.00049	0.00017	0.048	0.00028	0.0001	0.33	0.00382	0.0021	0.144	0.00146	0.0007
0.2	0.00525	0.00205	0.21	0.001	0.00042	0.21	0.00159	0.0008	0.21	0.00578	0.00268
0.275	0.00808	0.00321	0.315	0.00249	0.00109	0.226	0.00255	0.00125	0.174	0.00405	0.00187
0.23	0.00798	0.00303	0.253	0.00173	0.00071	0.186	0.00145	0.00078	0.21	0.00601	0.00283
0.2	0.00606	0.00236	0.158	0.0006	0.00026	0.387	0.00748	0.00366	0.225	0.00476	0.00211
0.325	0.01401	0.00550	0.195	0.00087	0.00036	0.158	0.00082	0.0004	0.195	0.00254	0.00116
0.195	0.00525	0.00202	0.151	0.00053	0.00022	0.163	0.00081	0.00041	0.232	0.0077	0.00344
0.235	0.00466	0.00179	0.245	0.00197	0.00098	0.39	0.00618	0.00343	0.255	0.01503	0.00712
0.155	0.00548	0.00188	0.345	0.00215	0.00108				0.31	0.00972	0.0045
0.265	0.01704	0.00634	0.32	0.00414	0.00238				0.166	0.00524	0.00247
0.13	0.00160	0.00060	0.265	0.00283	0.00127				0.166	0.00295	0.00144
0.215	0.00711	0.00255	0.245	0.00196	0.00102				0.188	0.00376	0.00176
0.195	0.00444	0.00154	0.16	0.00087	0.00039				0.165	0.00567	0.00279
0.165	0.00651	0.00240							0.178	0.00483	0.00242
0.14	0.00336	0.00123									
0.185	0.00607	0.00224									
0.11	0.00200	0.00074									
0.15	0.00211	0.00081									

Table A-4: Cover of species used for the simulation of the herbaceous layer for continuous (a) and recently changed land use (b), sorted by representative species or plant functional groups.

Biotope types: FC: Festuco-Cynosuretum
LC: Lolio-Cynosuretum
Lp-D: Lolium perenne dominance stand
DgHl-D: Dactylus glomerata and Holcus lanatus dominance stand
FC-f: young fallow of former Festuco-Cynosuretum

Authors: L: Lennartz et al. (Lennartz et al. 2006)
H: Heilburg (Heilburg 2009, 2010)
E: Engler (Engler 2010)
S: Siehoff, own data

° direct estimation of % (not indicated relevés: Braun-Blanquet scale transformed to %)
d.o.p.: degree of presence
(A): occuring in Arrhenatheretalia or generally in Molinio-Arrhenatheretea (Ellenberg 1992)
(x): indifferent phytosociological behavior (Ellenberg 1992)
*: belonging to a different group according to Dierschke & Briemle, but rearranged due to its behavior on the Dreiborner Hochfläche

Table A-4 a: Continuous land use

Biotope type	**FC**			**LC**					**Lp-D**		**GT**				**DgHl-D**													
Author	**H**	**S**	**S**	**H**	**H**	**H**	**S**	**S**	**L**	**H**	**H**	**S**	**S**	**S**	**L**	**L**	**H**	**H**	**H**	**H**	**H**	**H**	**H**	**E**	**E**	**E**	**E**	
Current number	**1**	**2**	**3°**	**4**	**5**	**6**	**7°**	**8°**	**9**	**10**	**11**	**12°**	**13°**	**14°**	**15**	**16**	**17**	**18**	**19**	**20**	**21**	**22**	**23**	**24°**	**25**	**26**	**27**	
Year	**2008**	**2009**	**2009**	**2008**	**2008**	**2008**	**2009**	**2009**	**2005**	**2008**	**2008**	**2009**	**2009**	**2009**	**2005**	**2005**	**2005**	**2008**	**2008**	**2008**	**2008**	**2008**	**2008**	**2009**	**2009**	**2009**	**2009**	
Single species																												**d.o.p.**
Arrhenatherum elatius (A)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	10	10	-	-	-	2.5	10	10	10	3	20	-	20	0.34
Cynosurus cristatus (A)	10	15	30	10	10	20	20	20	20	-	-	7.5	7.5	3	-	-	-	-	-	-	-	-	-	-	-	-	-	0.43
Dactylis glomerata (A)	2.5	5	1	0.2	2.5	-	1	1	0.2	-	0.2	7.5	5	3	10	20	10	10	37.5	20	37.5	10	2.5	25	38	63	38	0.92
Festuca rubra agg. (A)	10	30	20	2.5	2.5	2.5	10	5	-	-	37.5	25	40	60	10	37.5	37.5	10	2.5	10	10	37.5	37.5	7.5	20	20	20	0.97
Lolium perenne (A)	10	1	5	20	10	10	15	20	37.5	62.5	-	-	-	-	0.2	-	-	-	-	-	-	-	-	-	-	-	-	0.20
Holcus lanatus (A)	2.5	10	5	-	2.5	2.5	10	10	0.2	-	2.5	40	40	10	2.5	0.2	2.5	2.5	2.5	2.5	2.5	-	-	7.5	20	10	2.5	0.82
Cirsium arvense	2.5	10	5	2.5	-	-	5	5	-	-	-	-	-	-	2.5	-	-	-	-	-	-	-	-	-	-	-	-	0.19
Tufted plants																												
Achillea ptarmica (A)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2.5	-	-	-	-	-	-	-	0.02
Agropyron repens	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2.5	-	-	-	-	-	-	-	-	0.08
Agrostis tenuis (A)	2.5	5	20	2.5	2.5	20	5	5	0.2	-	2.5	-	1	2	0.2	0.2	2.5	2.5	2.5	2.5	2.5	2.5	2.5	-	-	0.2	2.5	0.94
Alchemilla spec. (A)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2.5	-	-	0.2	0.07
Alopecurus pratensis (A)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.01
Anthoxanthum odoratum (x)	-	1	-	-	-	-	-	-	-	-	2.5	7.5	7.5	10	2.5	2.5	-	-	-	-	-	-	-	2.5	-	0.2	1	0.51
Bromus hordeaceus (x)	-	-	-	2.5	-	0.2	-	-	0.2	-	-	-	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.08
Cerastium fontanum (A)	2.5	1		2.5	2.5	2.5	1	-	-	-	-	-	3	3	-	-	2.5	-	-	-	-	-	-	2.5	-	-	-	0.39
Deschampsia flexuosa (x)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2.5	-	-	-	-	-	-	2.5	-	-	-	0.04
Festuca pratensis (A)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	20	-	-	-	-	-	-	-	-	7.5	-	10	-	0.01
Galium verum	2.5	1	-	-	-	-	-	-	-	-	2.5	-	-	1	2.5	-	-	-	-	-	-	2.5	2.5	-	-	-	-	0.42
Holcus mollis	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2.5	20	2.5	10	2.5	2.5	2.5	7.5	-	-	10	0.24

Table A-4 a (continued)

Current number	1	2	3°	4	5	6	7°	8°	9	10	11	12°	13°	14°	15	16	17	18	19	20	21	22	23	24°	25	26	27	
Lotus corniculatus (A)	2.5	5	-	-	2.5	-	5	1	-	-	-	-	3	5	0.2	0.2	2.5	2.5	2.5	-	2.5	2.5	10	2.5	2.5	0.2	2.5	0.64
Luzula campestre	-	-	-	-	-	-	-	-	-	-	2.5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.17
Luzula multiflora	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.2	-	-	-	-	-	-	-	-	-	-	-	0.02
Phleum pratense (A)	-	1	-	2.5	2.5	0.2	-	-	-	-	-	-	-		0.2	-	2.5	2.5	2.5	2.5	2.5	-	-	2.5	0.2	0.2	-	0.51
Poa pratensis agg. (A)	-	-	5	2.5	2.5	2.5	-	-	2.5	2.5	-	-	5	-	10	37.5	-	2.5	-	2.5	2.5	2.5	2.5	2.5	10	2.5	10	0.58
Potentilla erecta	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.03
Rumex acetosella agg. (x)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.01
Trifolium pratense (A)	10	10	5	0.2	2.5	2.5	5	5	2	-	-	-	-	15	2.5	2.5	2.5	-	-	2.5	-	-	-	2.5	-	-	-	0.56
Trisetum flavescens (A)	2.5	-	-	-	-	-	1	-	-	-	2.5	-	0.1	<1	10	2.5	-	-	-	2.5	-	-	-	-	-	-	-	0.61
Veronica arvensis	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.02
Viola tricolor (A)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.2	-	-	-	-	-	-	-	2.5	0.1	-	-	0.01
Creeping plants																												
Agrostis stolonifera	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2.5	10	10	2.5	2.5	-	-	-	-	-	-	0.17
Galium saxatile	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.03
Hieracium pilosella (A)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.02
Medicago lupulina	-	-	-	0.2	2.5	-	-	-	-	-	-	-	-	-	-	-	2.5	10	10	2.5	2.5	-	-	-	-	-	-	0.06
Poa trivialis (A)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.2	-	2.5	2.5	-	-	-	-	-	-	-	-	-	0.09
Potentilla anserina	-	-	-	-	2.5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.01
Prunella vulgaris (A)	-	-	-	0.2	2.5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.02
Ranunculus repens (x)	-	-	-	-	2.5	2.5	-	-	-	0.2	-	-	3	3	0.2	0.1	2.5	2.5	2.5	2.5	2.5	2.5	-	2.5	0.1	0.1	0.1	0.57
Stellaria graminea (x)	2.5	-	-	-	2.5	-	-	-	-	-	2.5	-	3	3	0.2	-	2.5	2.5	2.5	2.5	2.5	2.5	2.5	2.5	2.5	2.5	2.5	0.64
Trifolium repens (A)	20	1	10	10	20	37.5	15	15	2	10	10	-	7.5	5	-	0.2	-	-	-	-	-	-	-	-	2.5	-	-	0.61
Veronica serpyllifolia (A)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.01
Climbing plants																												
Galium mollugo agg. (A)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	20	20	10	2.5	2.5	2.5	2.5	2.5	2.5	7.5	20	20	2.5	0.37
Lathyrus pratensis (A)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2.5	2.5	-	2.5	2.5	2.5	2.5	2.5	-	2.5	0.1	0.2	-	0.34
Vicia angustifolium (x)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.04
Vicia cracca (A)	-	-	-	-	2.5	-	-	-	-	-	-	-	-	0.1	2.5	2.5	2.5	2.5	2.5	2.5	2.5	2.5	2.5	2.5	10	2.5	2.5	0.79
Vicia sepium (A)	-	-	-	-	2.5	-	-	-	-	-	-	-	-	-	0.2	0.2	2.5	2.5	2.5	2.5	2.5		2.5	2.5	-	2.5	2.5	0.35
Veronica chamaedrys *(x)	-	5	-	-	2.5	0.2	-	-	-	-	2.5	-	3	0.1	2.5	10	2.5	2.5	-	2.5	2.5	2.5	2.5	2.5	2.5	-	0.2	0.87
Rosette plants																												
Bellis perennis (A)	-	1	1	0.2	2.5	0.2	5	5	2.5	-	-	-	3	1	-	-	-	-	-	-	-	-	-	-	-	-	-	0.09
Cirsium vulgare *(A)	-	-	-	0.2	0.2	-	-	-	2.5	-	-	-	-	-	-	-	0.2	-	-	-	-	-	-	-	-	-	-	0.09
Hypochoeris radicata (A)	2.5	1	-	-	-	2.5	1	-	-	-	2.5	-	3	-	-	0.1	-	-	-	-	-	-	-	-	-	-	-	0.38
Leontodon autumnalis (A)	2.5	5	1	2.5	2.5	2.5	10	5	0.2	-	-	-	-	-	-	0.1	2.5	-	-	2.5	2.5	-	-	-	-	-	-	0.39
Leontodon hispidus (A)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.01
Odontites vulgaris *(A)	-	-	1	-	0.2	-	10	10	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.03
Plantago lanceolata (A)	2.5	5	-	2.5	2.5	2.5	5	5	2.5	2.5	2.5	-	7.5	7.5	-	2.5	2.5	2.5	2.5	2.5	2.5	-	2.5	2.5	2.5	2.5	2.5	0.89
Plantago major	-	-	-	-	2.5	-	-	-	2.5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.02
Taraxacum officinalis (x)	2.5	-	1	2.5	2.5	2.5	-	-	0.2	-	-	-	5	5	-	0.2	.2	2.5	2.5	2.5	2.5	-	-	2.5	2.5	2.5	0.2	0.53
Erect forbs																												
Achillea millefolium (A)	2.5	1	5	2.5	2.5	2.5	1	-	2.5	2.5	10	-	1.5	-	-	0.1	2.5	2.5	2.5	2.5	2.5	-	-	2.5	0.2	0.2	0.2	0.73
Aegopodium podagraria	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2.5	-	-	-	0.01
Anthriscus sylvestris (A)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.02

Table A-4 a (continued)

Current number	1	2	3°	4	5	6	7°	8°	9	10	11	12°	13°	14°	15	16	17	18	19	20	21	22	23	24°	25	26	27	
Campanula rotundifolia (x)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.03
Capsella bursa-pastoris	0.2	-	-	-	-	-	-	-	0.2	-	-	-	-	-	-	-	-	-	-	-	-		-	-	-	-	-	0.03
Carum carvi (A)	-	-	-	-	-	-	-	-	-	-	2.5	-	-	-	-	-	2.5	2.5	-	-	2.5	-	2.5	-	-	-	-	0.21
Centaurea jacea agg. (A)	-	-	-	-	-	-	-	-	-	-	-	-	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.04
Chrysanthemum leucanthemum (A)	-	-	-	-	-	-	-	-	-	-	0.2	-	3	3	-	-	-	-	-	-	-	-	-	2.5	-	-	-	0.27
Cirsium palustre (A)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2.5	-	-	2.5	-	-	-	2.5	0.1	-	-	0.04
Crepis capillaris (A)	-	-	-	-		-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2.5	-	-	-	0.04
Euphrasia officinalis agg. (A)	-	-	-	-	2.5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.09
Galeopsis tetrahit	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.02
Heracleum sphondylium (A)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2.5	-	-	-	-	-	-	-	2.5	-	-	-	0.06
Hypericum maculatum	2.5	-	-	-	-	-	-	-	-	-	2.5	-	-	0.1	0.2	10	2.5	2.5	2.5	2.5	2.5	-	2.5	2.5	2.5	2.5	2.5	0.66
Hypericum perforatum	-	5	-	-	-	-	1	1	-	-	-	-	-	-	-	0.2	-	-	-	-	-	-	-	-	-	-	-	0.11
Knautia arvensis (A)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.07
Malva moschata (A)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.2	2.5	2.5	-	-	-	-	-	-	-	0.14
Meum athamanticum	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.03
Pimpinella saxifraga	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2.5	-	-	2.5	-	-	2.5	-	-	-	0.26
Ranunculus acris (A)	2.5	-	-	-	-	-	-	-	-	-	2.5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.20
Ranunculus bulbosus	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.04
Ranunculus nemorosus agg. (x)	-	-	-	-	-	-		-	-	-	-	-	-	-	-	0.1	-	-	-	-	-	-	-	-	-	-	-	0.02
Rhinanthus minor (A)	-	-	-	-	-	-	-	-	-	-	2.5	-	3	5	-	-	-	-	-	-	-	-	-	2.5	-	-	-	0.30
Rumex acetosa (A)	-	-	-	-	-	-	-	-	-	-	2.5	-	3	3	2.5	0.2	2.5	2.5	2.5	2.5	2.5	2.5	2.5	7.5	20	20	10	0.76
Rumex obtusifolius	0.2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2.5	-	-	-	0.03
Senecio jacobaea (A)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.04
Tragopogon pratensis agg. (A)	-	-	-	-	-	-	-	-	-	-	-	-	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.02
Trifolium dubium (A)	-	-	-	2.5	2.5	2.5	-	-	-	-	0.2	-	3	5	-	-	-	-	-	-	-	-	-	-	-	-	-	0.29
Others																												
Aphanes arvensis	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.01
Carduus nutans	-	-	-	0.2	-	-	-	-	-	-	-			-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.01
Euphorbia cyparissias	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2.5	-	-	-	-	-	2.5	-	2.5	-	-	-	0.08
Geranium dissectum	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.01
Geranium pusillum	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.01
Gnaphalium sylvaticum	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.06
Linaria vulgare	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.2	2.5	-	-	2.5	-	-	-	-	-	-	0.11
Matricaria chamomilla	-	-	-	-	-	-	-	-	2.5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.01
Reseda luteola	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.01
Scleranthus annuus	-	-	-	-	-	-	-	-	0.2	-	-	-	-	-	-	-		-	-	-	-	-	-	-	-	-	-	0.01
Sisymbrium officinale	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		-	-	-	-	-	-	-	-	-	-	-	0.01
Spergularia rubra	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.01
Verbascum nigrum	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2.5	-	-	-	-	-	-	-	-	-	-	-	-	0.08
Vicia tetrasperma	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.02

Table A-4 b: Recently changed land use

Former biotope type	FC													FC	FC				
Former land use	**Ext. past**													**Ext. past**	**Ext. past**				
Years since land use change	**4**													**4**	**4**				
Current biotope type	**FC-f**													**LC**	**(GT)**				
Current land use	**Fallow**													**Int. past**	**ext. pasture + mowing**				
Editor	**H**	**H**	**H**	**H**	**H**	**H**	**H**	**S**	**S**	**S**	**S**	**S**	**S**	**H**	**H**	**H**	**H**	**H**	**H**
Current number	**28**	**29**	**30**	**31**	**32**	**33**	**34**	**35°**	**36°**	**37°**	**38°**	**39°**	**40°**	**41**	**42**	**43**	**44**	**45**	**46**
Year	**2008**	**2008**	**2008**	**2008**	**2008**	**2008**	**2008**	**2009**	**2009**	**2009**	**2009**	**2009**	**2009**	**2008**	**2008**	**2008**	**2008**	**2008**	**2008**
Single species																			
Arrhenatherum elatius	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Cynosurus cristatus	0.2	-	0.2	-	2.5	-	-	5	5	-	1	1	10	10	0.2	-	-	0.2	-
Dactylis glomerata	2.5	10	10	2.5	2.5	2.5	2.5	20	25	20	25	10	25	2.5	2.5	2.5	2.5	2.5	0.2
Festuca nigrescens	20	20	20	20	20	10	20	40	40	35	40	35	30	10	37.5	37.5	37.5	20	20
Lolium perenne (AC-V_2)	-	-	-	-	-	-	-	-	-	-	-	-	1	10	-	-	-	-	-
Holcus lanatus	2.5	-	0.2	2.5	2.5	2.5	2.5	5	10	30	5	20	5	2.5	2.5	2.5	10	10	2.5
Cirsium arvense	-	-	-	-	-	-	-	-	-	-	-	-	-	2.5	-	-	-	-	-
Tufted plants																			
Agropyron repens	-	-	-	-	2.5	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Agrostis tenuis	2.5	2.5	2.5	2.5	2.5	2.5	2.5	25	25	20	25	15	15	2.5	2.5	2.5	2.5	2.5	2.5
Alchemilla spec.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Alopecurus pratensis	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Anthoxanthum odoratum	0.2	-	-	-	-	-	-	10	5	5	5	1	-	-	2.5	2.5	2.5	2.5	2.5
Bromus hordeaceus	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Cerastium fontanum	2.5	2.5	2.5	2.5	2.5	-	-	1	1	1	1	-	-	2.5	2.5	-	-	-	2.5
Deschampsia flexuosa	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Festuca pratensis	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Festuca tenuifolia	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Galium verum	2.5	2.5	2.5	2.5	-	2.5	2.5	5	1	1	1	1	-	2.5	2.5	2.5	-	2.5	2.5
Holcus mollis	-	-	-	-	-	10	-	-	-	-	-	-	-	-	-	-	-	-	-
Lotus corniculatus	2.5	2.5	2.5	2.5	2.5	2.5	2.5	1	1	1	1	1	-	2.5	2.5	2.5	2.5	2.5	2.5
Luzula campestre	-	-	-	-	-	0.2	-	-	-	-	-	-	-	-	-	-	-	-	-
Luzula multiflora	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Phleum pratense	2.5	2.5	0.2	2.5	-	-	-	1	1	1	1	-	-	-	-	-	2.5	2.5	0.2
Poa pratensis agg.	-	-	-	-	2.5	-	2.5	-	-	-	-	1	-	-	2.5	2.5	2.5	2.5	2.5
Potentilla erecta	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Rumex acetosella agg.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Trifolium pratense	0.2	-	2.5	-	2.5	0.2	-	5	5	5	5	1	-	10	-	-	-	-	-
Trisetum flavescens	2.5	2.5	2.5	2.5	-	-	-	-	-	-	-	-	-	2.5	0.2	2.5	2.5	2.5	0.2
Veronica arvensis	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Viola canina	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Viola tricolor	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

Table A-4 b (continued)

Current number	28	29	30	31	32	33	34	35°	36°	37°	38°	39°	40°	41	42	43	44	45	46
Creeping plants																			
Agrostis stolonifera	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Galium saxatile	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Hieracium pilosella	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Poa trivialis	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Potentilla anserina	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Ranunculus repens	-	-	-	-	-	2.5	2.5	1	1	1	1	-	-	-	2.5	2.5	0.2	2.5	-
Stellaria graminea	2.5	-	2.5	2.5	2.5	2.5	2.5	1	1	1	1	-	1	2.5	2.5	2.5	2.5	2.5	2.5
Trifolium repens	-	0.2	2.5	-	2.5	2.5	-	1	1	1	1	-	-	20	10	2.5	10	2.5	10
Veronica serpyllifolia	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Climbing plants																			
Galium mollugo agg.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Lathyrus pratensis	2.5	-	-	-	-	-	-	-	-	-	-	-	-	-	2.5	2.5	0.2	-	-
Vicia angustifolium	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Vicia cracca	2.5	2.5	2.5	-	-	-	2.5	-	-	-	1	1	5	-	2.5	10	2.5	2.5	10
Vicia sepium	-	-	-	-	-	-	2.5	1	1	-	-	-	-	-	2.5	-	-	-	-
Veronica chamaedrys	-	2.5	2.5	2.5	-	2.5	2.5	1	1	1	1	-	-	-	2.5	2.5	2.5	2.5	2.5
Rosette plants																			
Bellis perennis	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Cirsium vulgare	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.2	-
Hypochoeris radicata	2.5	2.5	-	2.5	2.5	0.2	-	-	-	-	-	1	-	2.5	-	-	-	-	-
Leontodon autumnalis	-	2.5	2.5	-	-	2.5	-	7.5	1	5	1	-	1	2.5	2.5	2.5	2.5	-	-
Leontodon hispidus	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Odontites vulgaris	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-
Plantago lanceolata	2.5	2.5	2.5	2.5	2.5	2.5	2.5	10	5	5	5	5	-	2.5	2.5	2.5	2.5	2.5	2.5
Plantago major	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Taraxacum officinalis	0.2	0.2	2.5	2.5	2.5	2.5	-	-	-	1	1	-	1	2.5	2.5	-	2.5	-	2.5
Erect forbs																			
Achillea millefolium	10	2.5	2.5	2.5	2.5	0.2	0.2	1	1	1	1			2.5	2.5	2.5	2.5	2.5	2.5
Aegopodium podagraria	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Anthriscus sylvestris	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Campanula rotundifolia	-	-	-	-	-	-	-	1	1	-	-	-	-	-	-	-	-	-	-
Capsella bursa-pastoris	-	-	-	-	-	-	-	-	-	-	-	-	-	0.2	-	-	-	-	-
Carum carvi	2.5	2.5	2.5	2.5	-	2.5	-	-	-	-	-	-	-	-	-	-	-	-	-
Centaurea jacea agg.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Chry. leucanthemum	-	-	-	-	2.5	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Cirsium palustre	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Crepis capillaris	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Euphrasia officinalis agg.	2.5	2.5	-	2.5	2.5	0.2	-	-	-	-	-	-	-	-	-	-	-	-	-
Galeopsis tetrahit	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Heracleum sphondylium	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Hypericum maculatum	2.5	2.5	-	-	2.5	2.5	-	-	-	-	-	-	-	2.5	10	-	-	2.5	2.5

Table A-4 b (continued)

Current number	28	29	30	31	32	33	34	35°	36°	37°	38°	39°	40°	41	42	43	44	45	46
Hypericum perforatum	-	-	-	-	-	2.5	-	1	1	1	5	5	-	-	-	-	-	-	-
Knautia arvensis	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-
Malva moschata	-	-	-	-	-	-	-	1	-	-	1	-	-	-	-	-	-	-	-
Meum athamanticum	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Pimpinella saxifraga	2.5	2.5	2.5	2.5	-	0.2	-	10	1	-	1	1	-	-	-	-	-	-	-
Ranunculus acris	-	-	-	-	-	2.5	-	-	-	-	-	-	-	2.5	-	-	-	-	-
Ranunculus bulbosus	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Ranunculus nemorosus agg.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Rhinanthus minor	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Rumex acetosa	2.5	-	-	-	2.5	2.5	-	-	-	-	-	-	-	-	2.5	2.5	2.5	0.2	2.5
Rumex obtusifolius	-	-	-	-	-	-	-	-	-	-	1	-	-	0.2	-	-	-	-	-
Senecio jacobaea	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Tragopogon pratensis agg.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Trifolium dubium	-	-	-	-	0.2	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Others																			
Aphanes arvensis	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Euphorbia cyparissias	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Geranium dissectum	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Geranium pusillum	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Gnaphalium sylvaticum	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Matricaria chamomilla	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Reseda luteola	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Scleranthus annuus	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Sisymbrium officinale	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Spergularia rubra	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Verbascum nigrum	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Vicia tetrasperma	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

Table A-5: Observed trees in fallow grasslands (current numbers 47-82). Abbreviations for authors as in Table A-4.

Current No.	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	35	36	80	81	37	82
Year	08	08	08	08	08	08	08	08	08	08	08	08	08	08	08	08	08	08	08	08	08	08	08	08	08	08	08	08	08	08	08	08	08	09	09	09	09	09	09
Author	K	K	K	K	K	K	K	K	K	K	K	K	K	K	K	K	K	K	K	K	K	K	K	K	K	K	K	K	K	K	K	K	K	S	S	S	S	S	S
Area [m²]	634	833	397	37	35	118	386	182	25	38	24	28	36	25	134	143	48	139	623	767	826	2855	2055	2508	626	2791	5482	2533	1702	4223	3231	2344	578	11905	12070	1616	2013	16802	2624
	Fallow grassland																																						
Cytisus scoparius																																							
< 0,2m	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	3	-	-	1	1	4	-	-	-	-	-	1	-	-	2	n.d.	n.d.	n.d.	n.d.	n.d.
0,2m-0,5m	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	71	1	15	21	35	11	23	11	11	-	46	64	17	9	53	n.d.	n.d.	n.d.	n.d.	n.d.
0,5m-1m	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	14	20	-	2	50	188	59	25	37	19	-	116	386	16	23	132	n.d.	n.d.	n.d.	n.d.	n.d.
1m-2m	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	21	16	-	2	10	33	3	9	3	5	-	36	125	4	8	42	n.d.	n.d.	n.d.	n.d.	n.d.
>2m	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	n.d.	n.d.	n.d.	n.d.	n.d.
Sum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	1	36	110	1	19	82	257	77	57	51	35	0	198	576	37	40	230					
Sum /m²	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.1	0.1	0	0.01	0.04	0.1	0.1	0.02	0.01	0.01	0	0.05	0.18	0.02	0.1	0.019					
Acer pseudoplatanus																																							
< 0,2m	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
0,2m-0,5m	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
0,5m-1m	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
1m-2m	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
>2m	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Betula pendula																																							
< 0,2m	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	6	-	-	-	-	-	-	-	-	-	-
0,2m-0,5m	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
0,5m-1m	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
1m-2m	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
>2m	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Fagus sylvatica																																							
< 0,2m	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
0,2m-0,5m	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
0,5m-1m	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
1m-2m	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
>2m	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Frangula alnus																																							
< 0,2m	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
0,2m-0,5m	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
0,5m-1m	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
1m-2m	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
>2m	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Malus sylvestris																																							
< 0,2m	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
0,2m-0,5m	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
0,5m-1m	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
1m-2m	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
>2m	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Picea abies																																							
< 0,2m	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
0,2m-0,5m	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
0,5m-1m	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
1m-2m	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
>2m	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

Table A-5 (continued):

Current No.	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	35	36	80	81	37	82
Fallow grassland																																							
Pinus spec.																																							
< 0.2m	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	11	-	-	-	-	-	-	-	-	-	-
0.2m-0.5m	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-
0.5m-1m	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
1m-2m	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
>2m	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Populus tremula																																							
< 0.2m	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-
0.2m-0.5m	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
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Prunus avium																																							
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Quercus petraea																																							
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Quercus robur																																							
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0.2m-0.5m	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
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Salix spec.																																							
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0.2m-0.5m	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
0.5m-1m	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
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Sorbus aucuparia																																							
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0.2m-0.5m	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
0.5m-1m	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
1m-2m	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
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Sum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	22	0	0	0	0	0	0	0	0	0	0
Sum /m²	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.01	0	0	0	0	0	0	0	0	0	0

Table A-6: Observed trees in fallow grasslands (current numbers 38-111). Abbreviations for authors as in Table A-4.

Current No.	38	83	84	85	86	87	88	89	90	91	92	93	94	95	96	97	98	99	100	101	102	103	104	105	106	107	108	109	110	111
Year	09	08	08	08	08	09	09	09	09	09	09	09	09	08	08	08	10	10	10	10	10	10	10	10	10	10	10	10	10	10
Author	S	H	H	H	H	E	S	S	S	S	S	S	S	K	K	H	vW	vW	vW	K	K	K	K	K	K	K	K	K	K	K
Area [m²]	22649	36	24	560	1040	4620	18311	24398	700	11841	316	8819	222	100	100	1220	25	25	25	100	100	100	100	100	100	100	100	100	100	100
Fallow grassland																														
Cytisus scoparius																														
< 0,2m	-	-	-	-	-	-	-	1	2	-	-	-	-	6	1	2	-	-	-	9	-	-	-	-	-	-	-	-	-	-
0,2m-0,5m	-	-	-	-	-	19	21	6	24	24	13	8	19	2	1	22	-	-	-	-	-	-	-	-	-	6	-	-	-	-
0,5m-1m	-	-	-	-	-	14	26	4	9	25	9	8	4	2	-	23	-	-	-	-	-	-	-	-	-	-	-	-	-	-
1m-2m	-	-	-	-	-	8	1	-	-	-	1	-	-	-	-	4	-	-	-	-	-	-	-	-	-	-	-	-	-	-
>2m	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Sum	0	0	0	0	0	41	48	11	35	49	23	16	23	10	2	51	0	0	0	9	0	0	0	0	0	6	0	0	0	0
Sum /m²	0	0	0	0	0	0.01	0.003	5E-04	0.1	0.004	0.1	0	0.1	0.1	0	0.04	0	0	0	0.1	0	0	0	0	0	0.1	0	0	0	0
Acer pseudoplatanus																														
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0,2m-0,5m	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
0,5m-1m	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
1m-2m	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
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Betula pendula																														
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0,2m-0,5m	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
0,5m-1m	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
1m-2m	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
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Fagus sylvatica																														
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0,5m-1m	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
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Frangula alnus																														
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0,5m-1m	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
1m-2m	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
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Malus sylvestris																														
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0,2m-0,5m	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
0,5m-1m	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
1m-2m	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
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Picea abies																														
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Table A-6 (continued):

Current No.	38	83	84	85	86	87	88	89	90	91	92	93	94	95	96	97	98	99	100	101	102	103	104	105	106	107	108	109	110	111
Fallow grassland																														
Pinus spec.																														
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0,2m-0,5m	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
0,5m-1m	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
1m-2m	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
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Populus tremula																														
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0,2m-0,5m	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
0,5m-1m	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
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Prunus avium																														
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0,5m-1m	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
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Quercus petraea																														
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Quercus robur																														
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0,2m-0,5m	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
0,5m-1m	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
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Salix spec.																														
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0,2m-0,5m		-	-	-	-	2	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
0,5m-1m		-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
1m-2m		-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
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Sorbus aucuparia																														
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0,2m-0,5m	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
0,5m-1m	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
1m-2m	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
>2m	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Sum	0	0	0	0	0	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sum /m²	0	0	0	0	0	0	5E-05	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Table A-7: Observed trees on disturbed ground and in *Cytisus scoparius* shrubberies. Abbreviations for authors as in Table A-4.

Current No.	112	113	114	115	116	117	118	119	120	121	122	123	124	125	126	127	128	129	130	131	132	133	134	135	136	137	138	139	140	141	142	143	144	145	146	147	148	149	150	151	152	153	154
Year	09	10	10	10	10	08	10	10	10	10	10	10	10	10	10	08	10	10	10	10	10	10	10	10	10	10	10	10	10	10	10	10	10	10	10	10	10	10	10	10	10	10	10
Author	S	vW	vW	vW	S	H	vW	vW	vW	vW	vW	vW	vW	vW	vW	H	K	K	K	K	K	K	K	K	K	K	K	K	K	K	K	K	K	K	K	K	K	K	K	K	K	K	K
Area [m²]	434	25	25	25	25	248	25	25	25	25	25	25	25	25	25	112	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100
	disturbed ground															Cytisus scoparius shrubbery																											
Cytisus scoparius																																											
< 0,2m	-	2	-	-	28	10	15	1	2	n.d.	-	-	-	-	-	n.d.	-	2	3	41	14	0	16	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
0,2m-0,5m	-	6	6	1	-	55	32	35	34	n.d.	-	-	-	-	5	n.d.	2	1	6	12	30	16	11	2	-	4	-	-	-	3	-	1	-	-	1	-	-	-	-	-	-	-	-
0,5m-1m	-	3	5	1	-	50	9	24	21	n.d.	-	-	1	-	8	n.d.	1	-	23	30	26	12	14	1	-	34	-	-	-	4	1	3	1	6	2	8	-	1	-	-	5	-	-
1m-2m	-	1	3	-	-	18	-	3	4	n.d.	-	-	2	1	-	n.d.	31	50	19	22	2	25	52	-	63	4	37	60	49	-	6	11	4	17	5	42	51	13	-	63	11	42	-
>2m	-	-	-	-	-	-	-	-	-	n.d.	-	-	-	-	-	n.d.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	47	-	-	-	60
Sum	0	12	14	2	28	133	56	63	61		0	0	3	1	13		34	53	51	105	72	53	93	6	63	42	37	60	49	7	7	15	5	23	8	50	51	14	47	63	16	42	60
Sum /m²	0	0.5	0.6	0.1	1.1	0.5	2.2	2.5	2.4		0	0	0.1	0	0.5		0.3	0.5	0.5	1.1	0.7	0.5	0.9	0.1	0.6	0.4	0.4	0.6	0.5	0.1	0.1	0.2	0.1	0.2	0.1	0.5	0.5	0.1	0.5	0.6	0.2	0.4	0.6
Acer pseudoplatanus																																											
< 0.2m	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
0.2m-0.5m	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
0.5m-1m	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
1m-2m	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
>2m	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Betula pendula																																											
< 0.2m	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
0.2m-0.5m	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	39	3	44	67	40	1	3	3	1	13	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0.5m-1m	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	0	0	1	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1m-2m	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
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Fagus sylvatica																																											
< 0.2m	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
0.2m-0.5m	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
0.5m-1m	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
1m-2m	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
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Frangula alnus																																											
< 0.2m	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
0.2m-0.5m	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
0.5m-1m	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
1m-2m	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
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Malus sylvestris																																											
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0.2m-0.5m	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
0.5m-1m	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
1m-2m	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
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Picea abies																																											
< 0.2m	-	-	-	-	344	1	18	9	4	-	1	-	-	-	-	-	-	50	-	-	1	-	-	118	3	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
0.2m-0.5m	-	-	-	-	-	2	8	21	10	-	1	-	-	-	-	25	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
0.5m-1m	-	-	-	-	-	-	2	2	1	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
1m-2m	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	11	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
>2m	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

Table A-7 (continued)

Current No.	112	113	114	115	116	117	118	119	120	121	122	123	124	125	126	127	128	129	130	131	132	133	134	135	136	137	138	139	140	141	142	143	144	145	146	147	148	149	150	151	152	153	154
	disturbed ground															Cytisus scoparius shrubbery																											
Pinus spec.																																											
< 0.2m	1	-	-	-	-	6	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
0.2m-0.5m	-	-	-	-	-	1	-	-	1	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
0.5m-1m	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
1m-2m	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
>2m	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Populus tremula																																											
< 0.2m	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	5	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
0.2m-0.5m	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
0.5m-1m	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
1m-2m	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
>2m	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Prunus avium																																											
< 0.2m	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
0.2m-0.5m	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
0.5m-1m	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
1m-2m	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
>2m	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Quercus petraea																																											
< 0.2m	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
0.2m-0.5m	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
0.5m-1m	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
1m-2m	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
>2m	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Quercus robur																																											
< 0.2m	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
0.2m-0.5m	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
0.5m-1m	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
1m-2m	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
>2m	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Salix spec.																																											
< 0.2m	1	-	-	-	-	1	-	-	1	-	-	1	-	-	-	-	10	-	13	11	1	2	1	3	-	4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
0.2m-0.5m	-	-	-	-	-	11	-	-	-	-	-	-	-	-	-	-	-	-	3	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
0.5m-1m	-	-	-	-	-	-	-	-	-	-	-	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
1m-2m	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
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Sorbus aucuparia																																											
< 0.2m	-	-	-	-	-	6	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
0.2m-0.5m	-	-	-	-	-	1	-	-	1	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
0.5m-1m	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
1m-2m	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
>2m	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Sum	3	0	0	0	344	29	28	32	20	0	2	4	1	0	0	41	53	53	65	80	45	3	4	126	5	19	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sum /m²	0	0	0	0	14	0.1	1.1	1.3	0.8	0	0.1	0.2	0	0	0	0.4	0.5	0.5	0.7	0.8	0.5	0	0	1.3	0.1	0.2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Table A-8: Observed trees in *Rubus* spec. and *Prunus spinosa* shrubberies. Abbreviations for authors as in Table A-4.

Current No.	155	156	157	158	159	160	161	162	163	164	165	166	167	168	169	170	171	172	173	174	175	176	177	178	179	180	181
Year	10	10	10	10	10	10	10	10	10	10	08	10	10	10	10	10	10	10	10	10	10	10	10	10	10	10	10
Author	K	K	K	K	K	K	K	K	K	K	H	K	K	K	K	K	K	K	K	K	K	K	K	K	K	K	K
Area [m²]	100	100	100	100	100	100	100	100	100	100	600	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100
	Rubus spec. shrubbery																	Prunus spinosa shrubbery									
Cytisus scoparius																											
< 0,2m	-	-	17	2	-	-	-	-	4	1	n.d.	1	-	-	-	1	-	-	-	-	-	-	-	-	2	-	-
0,2m-0,5m	-	-	17	2	-	-	-	-	4	1	n.d.	1	-	-	-	1	-	-	-	-	-	-	-	-	1	-	-
0,5m-1m	-	2	-	14	3	40	-	1	1	3	n.d.	2	-	3	1	4	3	-	-	5	-	-	-	-	-	-	-
1m-2m	-	60	-	-	22	4	20	3	10	4	n.d.	9	6	28	27	6	5	-	-	24	8	8	5	-	-	-	-
>2m	43	-	-	-	-	-	-	-	-	-	n.d.	-	-	-	-	-	-	-	-	0	0	0	0	-	-	2	-
Sum	43	62	34	18	25	44	20	4	19	9		13	6	31	28	12	8	0	0	29	8	8	5	0	3	2	0
Sum /m²	0.4	0.6	0.3	0.2	0.3	0.4	0.2	0	0.2	0.1		0.1	0.1	0.3	0.3	0.1	0.1	0	0	0.3	0.1	0.1	0.1	0	0	0	0
Acer pseudoplatanus																											
< 0.2m	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
0.2m-0.5m	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
0.5m-1m	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
1m-2m	-	-	-	-	-	-	-	1	1	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-
>2m	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	1	-	-	1	-	-	-
Betula pendula																											
< 0.2m	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
0.2m-0.5m	-	-	4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
0.5m-1m	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
1m-2m	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
>2m	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	-	-	-	-	-	-	-	-	-	-	-	1
Fagus sylvatica																											
< 0.2m	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
0.2m-0.5m	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	4	2	4
0.5m-1m	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	1	-	3
1m-2m	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
>2m	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Frangula alnus																											
< 0.2m	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
0.2m-0.5m	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	6
0.5m-1m	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-
1m-2m	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
>2m	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Malus sylvestris																											
< 0.2m	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
0.2m-0.5m	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
0.5m-1m	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
1m-2m	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
>2m	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-
Picea abies																											
< 0.2m	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
0.2m-0.5m	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
0.5m-1m	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
1m-2m	-	-	-	-	-	-	-	-	-	-	6	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
>2m	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

Table A-8 (continued).

Current No.	155	156	157	158	159	160	161	162	163	164	165	166	167	168	169	170	171	172	173	174	175	176	177	178	179	180	181
	Rubus spec. shrubbery																	Prunus spinosa shrubbery									
Pinus spec.																											
< 0.2m	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
0.2m-0.5m	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
0.5m-1m	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
1m-2m	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
>2m	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Populus tremula																											
< 0.2m	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
0.2m-0.5m	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
0.5m-1m	-	-	-	-	-	5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
1m-2m	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
>2m	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	4
Prunus avium																											
< 0.2m	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
0.2m-0.5m	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
0.5m-1m	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
1m-2m	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
>2m	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-
Quercus petraea																											
< 0.2m	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-
0.2m-0.5m	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-
0.5m-1m	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
1m-2m	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
>2m	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Quercus robur																											
< 0.2m	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-
0.2m-0.5m	-	-	-	-	-	-	-	-	2	1	-	-	-	1	-	1	-	-	-	1	-	-	-	-	-	-	-
0.5m-1m	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
1m-2m	-	-	-	-	-	-	1	-	2	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-
>2m	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Salix spec.																											
< 0.2m	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
0.2m-0.5m	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-
0.5m-1m	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
1m-2m	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
>2m	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-
Sorbus aucuparia																											
< 0.2m	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
0.2m-0.5m	2	-	2	-	-	-	-	-	1	-	1	2	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-
0.5m-1m	-	-	-	-	-	-	-	-	7	1	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-
1m-2m	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
>2m	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Sum	2	0	7	0	1	11	1	1	16	2	12	5	0	2	2	2	0	0	5	1	3	2	1	1	7	4	18
Sum/m²	0	0	0.1	0	0	0.1	0	0	0.2	0	0	0.1	0	0	0	0	0	0	0.1	0	0	0	0	0	0.1	0	0.2

Curriculum Vitae

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