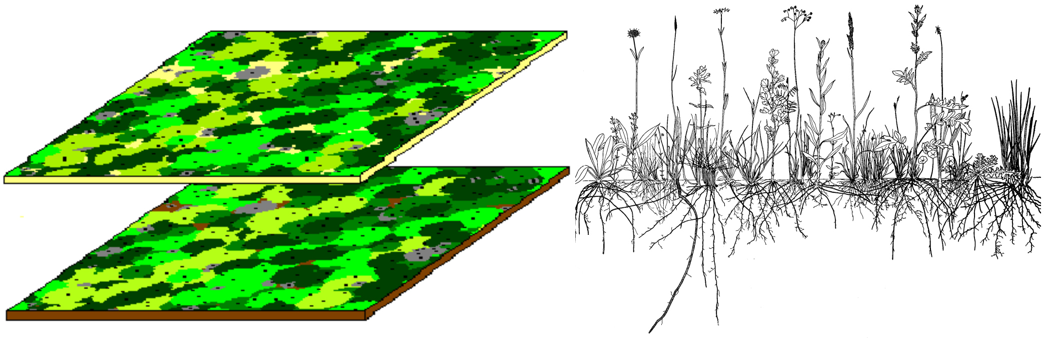
Diplomarbeit

Modelling coexistence of plant functional types in grassland communities – the role of above- and below-ground competition



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Titelgrafik

Links:	Grafische Ausgabe des Grasland-Modells, ober- und unterirdische „Zones-of-Influence“ der Pflanzenindividuen
Rechts:	Wurzelprofil des *Molinietum balticum*, aus Fukarek, F. (1961). Die Vegetation des Darß und ihre Geschichte, VEB Gustav Fischer Verlag, Jena.

Contents

Zusammenfassung

Für artenreiche Pflanzengemeinschaften ist immer noch ungeklärt, welche Mechanismen und Prozesse die Entstehung und Erhaltung einer hohen Diversität ermöglichen. Basierend auf mathematischen Modellen und auf Computersimulationen bietet die theoretische Ökologie eine Vielzahl von Erklärungsansätzen für die Koexistenz von Pflanzenarten auf verschiedenen räumlichen und zeitlichen Skalen. Durch die stark vereinfachenden Annahmen im Hinblick auf biotische Interaktionen und die oftmals monokausalen Erklärungsansätze bisheriger Modelle, sind Rückschlüsse auf reale Ökosysteme dennoch oft kaum möglich.

Mit dem Ziel, Mechanismen der Koexistenz besser zu verstehen, wurden im Rahmen der hier vorgelegten Diplomarbeit die Auswirkungen lokaler Konkurrenzmechanismen und Umweltbedingungen für die funktionelle Diversität in gemäßigten Grasland-Ökosystemen untersucht.

Zu diesem Zweck wurde ein individuen-basiertes, räumlich-explizites Simulationsmodell entwickelt, dass den Lebenszyklus von Pflanzenindividuen beschreibt. Anstelle von tatsächlichen Pflanzenarten werden 72 Pflanzentypen (PFTs) verwendet, die durch unterschiedliche Ausprägungen ihrer funktionellen Eigenschaften charakterisiert sind. Für eine detaillierte Beschreibung der Interaktion zwischen Pflanzenindividuen wurde der „Zone-of-Influence“ Ansatz übernommen: Jede Pflanze wird im Raum durch eine kreisförmige Fläche repräsentiert. Nur innerhalb dieser Fläche bezieht die Pflanze Ressourcen und interagiert mit benachbarten Individuen. Im Gegensatz zu den meisten früheren Ansätzen wird im Modell zwischen asymmetrischer Spross- und symmetrischer Wurzelkonkurrenz unterschieden. Die Unterscheidung Asymmetrie/Symmetrie bezieht sich dabei auf die Konkurrenzfähigkeit von Pflanzen relativ zu ihrer Größe bzw. Höhe. Umweltfaktoren, die im Modell das Wachstum der Pflanzen beeinflussen, sind das Angebot an oberirdischen (Licht) und unterirdischen Ressourcen (Nährstoffe, Wasser), sowie zwei Arten von Störungen: Beweidung und die Bildung kleinskaliger, vegetationsfreier Patches. Mit Hilfe des Modells wurde die Vegetationsdynamik einer Fläche von 1,29 x 1,29 m für 100 Jahre simuliert, um gezielt die Auswirkungen der genannten Mechanismen und Faktoren für die funktionelle Diversität der Graslandgemeinschaft zu untersuchen.

In Simulationen ohne Differenzierung zwischen intra- und interspezifischer Konkurrenz koexistierten maximal 11 PFTs. Unter Berücksichtigung von Nischendifferenzierung in der Ressourcenkonkurrenz stieg die Diversität bis auf maximal 22 PFTs. Dieses Maximum der Diversität wurde für hohe oberirdische und mittlere unterirdische Ressourcenverfügbarkeit gefunden. In den Szenarien ohne Störung zeigte sich ein unimodaler Zusammenhang zwischen unterirdischer Ressourcenverfügbarkeit und Diversität. Als Reaktion auf Beweidung ergaben sich zwei unterschiedliche Muster: Bei vorherrschender unterirdischer Ressourcenlimitierung sagte das Modell einen Rückgang der Diversität mit steigendem Beweidungsdruck voraus. Im Gegensatz dazu resultierte ein unimodaler Zusammenhang bei gleicher Verfügbarkeit der Ressourcen oder bei geringerer Verfügbarkeit oberirdischer Ressourcen. Die Bildung vegetationsfreier Patches führte zu keinem klaren positiven Effekt auf die Diversität. Dieses Ergebnis begründet sich durch die Annahme, dass es keine feste Konkurrenzhierarchie zwischen PFTs gibt, sowie die fehlende Limitierung in der Ausbreitung konkurrenzstarker PFTs.

Wie sich zeigte, ist die Asymmetrie der Konkurrenz zwischen Pflanzen verschiedener Größen und Wuchsformen eine entscheidender Faktor für die Diversität im untersuchten System. Stark asymmetrische (oberirdische) Konkurrenz begünstigt schnellen Ausschluss konkurrenzschwacher Arten, während symmetrische (unterirdische) Konkurrenz Unterschiede in der Fitness von PFTs bzw. Individuen reduziert. Dadurch wird Konkurrenzausschluss verlangsamt und Diversität entsprechend erhöht. Eine geringe Asymmetrie der Konkurrenz insgesamt kann nun einerseits durch vorherrschende Nährstoff-/Wasserlimitierung und andererseits durch eine Verringerung oberirdischer Konkurrenz, z.B. durch Beweidung, verursacht werden.

Neben der Verringerung von Asymmetrie führt Nischendifferenzierung in der Konkurrenz um Ressourcen zu einer deutlichen Erhöhung der Diversität. Folglich unterstützen die Modellergebnisse die Hypothese, dass Nischendifferenzierung auch in Pflanzengemeinschaften ein wichtiger Faktor für den Erhalt der lokalen Diversität ist. Daraus abgeleitet unterstreicht diese Studie den weiterer Forschungsbedarf für ein besseres Verständnis welche Unterschiede zwischen Pflanzenarten deren Koexistenz ermöglichen.

Insgesamt wurde deutlich, dass eine detaillierte Betrachtung der Interaktion von Pflanzen auf Individueneben unerlässlich ist, um die Wechselwirkungen zwischen Umweltbedingungen und Biodiversität besser zu verstehen.

Abstract

For species rich plant communities the question, which mechanisms and processes generate and maintain diversity, remains still unresolved. Based on mathematical models or computer simulations, ecological theory offers a variety of explanations for coexistence of plant species on different spatial and temporal scales. Nevertheless, the possibility to draw conclusions about real ecosystems has been often limited due to oversimplifications with respect to biotic interactions and monocausal approaches of previous ecological models.

In this thesis, the effects of local competitive mechanisms and environmental conditions on plant functional diversity in grassland ecosystems were investigated, in order to gain a more detailed understanding of the mechanisms of species coexistence.

For this purpose an individual-based, spatially-explicit simulation model was developed that describes the life cycle of plant individuals including their interaction with other plants. Instead of real species 72 plant functional types (PFTs) were used. These were characterised by different attributes of their functional traits.

In order to model individual interactions in detail, the “zone-of-influence” approach was adopted. Accordingly, each plant is represented in space by a circular area. The plant acquires resources and competes with neighbouring individuals within this area only. In contrast to most previous approaches, size-asymmetrical shoot competition and size-symmetrical root competition were explicitly distinguished. Environmental factors influencing plant growth in the model are the availability of above-ground (light) and below-ground (nutrients, water) resources, as well as two types of disturbance, namely grazing and gap formation. With the model the vegetation dynamics on a patch of 1.29 x 1.29 m size were simulated for a time span of 100 years, to study the effects of the mechanisms and factors mentioned on the functional diversity of the grassland community.

In simulations without differentiation of intra- and interspecific competition at maximum 11 PFTs coexisted. Including the assumption of resource niche separation increased diversity up to 22 coexisting PFTs. This maximum of diversity was found for high above-ground and intermediate below-ground resource availability. In scenarios

without disturbance a hump-shaped relation between below-ground resource availability and diversity emerged. As response to grazing two different pattern were produced. In the case of prevailing below-ground resource limitation the model predicted a decrease of diversity with increasing grazing pressure. In contrast a hump-shaped pattern was found for equal resource availabilities in both layers as well as for lower above-ground resource supply. Gap formation did not yield a clear positive effect on diversity. This result is caused by the assumption that there is no fixed competitive hierarchy between PFTs as well as the lack of recruitment limitation of competitive superior PFTs.

It was shown that competitive size asymmetry is a key factor of diversity in the system under consideration. Size-asymmetric (above-ground) competition favoured competitive exclusion of inferior PFTs, while size-symmetric (below-ground) competition reduces fitness differences between species or individuals respectively. Therefore, competitive exclusion is slowed down and diversity increases. A low degree of competitive size asymmetry can be explained by predominant nutrient/water limitation on the one hand and by the reduction of above-ground competition, e.g. by grazing, on the other hand.

Besides the reduction of size asymmetry, niche separation with respect to resource competition remarkably increased diversity. In this way the model results provide support for the hypothesis that resource niche separation is an important mechanism of local diversity maintenance in plant communities. Therefore this study stresses the need for further research revealing the differences between plant species that allow their coexistence.

In general it became clear that it is necessary to consider interactions between plant individuals in detail, in order to gain a more detailed understanding of the interactions between environmental conditions and diversity.

1 Introduction

Understanding the mechanisms of species coexistence is a key issue in community ecology (Tilman, 1997; Chesson, 2000a,b; Jeltsch et al., 2000; Amarasekare, 2003). In particular for species rich plant communities, e.g. grasslands ecosystems, the question, which factors and processes facilitate coexistence and maintain diversity, still remains unresolved (Silvertown, 2004; Hubbell, 2005). Coexistence of animal species is often explained by separation of their "trophic niche", as they are able to specialize on certain plant species or plant parts as their food source. In contrast, all plants require a common set of resources, e.g. light, CO_2, water, nitrogen, mineral nutrients, and thus their fundamental niches overlap substantially. Following classical ecological theory, competition should therefore be strong within plant communities and favour the exclusion of species (Chase and Leibold, 2003; Silvertown, 2004). Field studies and manipulative experiments confirmed that competition for limiting resources is a general mechanism in natural plant communities (reviewed in Aarssen and Epp, 1990; Goldberg and Barton, 1992; Gurevitch et al., 1992). Obviously, there must be processes and factors that counteract the reduction of diversity by competitive exclusion, but their identification or even quantification for species-rich plant communities remains one of the fundamental challenges in basic ecology.

Current ecological theory provides a large variety of explanations for coexistence and diversity maintenance on different spatial scales. The spectrum ranges from theories based on trade-offs to the concept of neutral competition. In the first case, coexistence is explained by differences between species, which allow coexistence due to niche separation (e.g. Levins and Culver, 1971; Tilman, 1994; Rees et al., 2001; Kneitel and Chase, 2004). In the second case, diversity is considered as a dynamic equilibrium resulting from stochastic extinction, immigration and speciation processes (Bell, 2000, 2001; Hubbell, 2001). This variety of potential explanations for diversity contrasts the lack of understanding claimed above and apparently there is a mismatch between numerous theories and their application for the understanding of diversity maintenance within real plant communities (Amarasekare, 2003). Over the last decades, theoretical progress in the field of competitive coexistence has been largely based on mathematical models and computer simulations. These have proved to be a valuable tool to explore general mechanisms of species coexistence, though the simplicity and generality that is typical of many modelling approaches, has likely contributed to the gap between theory and its application.

One important reason for the limited comparability of theoretical and field studies is caused by the generation and maintenance of diversity by processes acting on different spatial scales. The recently established metacommunity framework proposes that diversity within a community of interacting populations (local or α-diversity) is often maintained by seed input from other communities (Leibold et al., 2004). Therefore high regional (β) diversity and the resulting source-sink dynamics between sites might be more important for local diversity than interactions and environmental factors within the local community itself. Based on the idea of metacommunity processes, models tend to explain local diversity in a limited area by immigration from a regional species pool (Huston and DeAngelis, 1994; Loreau and Mouquet, 1999; Esther et al., submitted). But if regional dynamics are not considered explicitly, the explanation for diversity is just transferred to a scale outside of the model domain, or as stated by Chesson (2000b, pg. 344): “Thus, nothing is learned about diversity maintenance beginning with the assumption that migration rates into local areas are constant.” For grassland ecosystems there is no general answer to the question, if species diversity is limited more by local competitive interactions and or by propagule availability from the regional species pool (Turnbull et al., 2000; Vandvik and Goldberg, 2006). Instead, the effect of seed immigration varies with local habitat conditions, e.g. productivity (Foster, 2001).

Previous modelling studies claimed that disturbance is a main factor structuring communities and facilitating coexistence (Schippers et al., 2001; Cousins et al., 2003; Johst and Drechsler, 2003; Kahmen, 2003; Roxburgh et al., 2004; Johst and Huth, 2005). Nevertheless, the term “disturbance” refers to a whole set of mechanisms that affect plants differently and a general concept is still missing (van der Maarel, 1993; Grime, 2001; White and Jentsch, 2001; Shea et al., 2004). The positive effect of livestock grazing on diversity, which has been a common form of land use in semi-natural grasslands, was demonstrated in both, empirical (Olff and Ritchie, 1998; Watkinson and Ormerod, 2001) as well as modelling studies (e.g. Cousins et al., 2003). In contrast to other forms of disturbance, grazing by large herbivores affects plants only partly and can act selectively towards plant traits (Schwinning and Parsons, 1999; Bullock et al., 2001; Díaz et al., 2001). Nevertheless, even in small scale grassland models, disturbance is often represented as removal of whole plants and formation of bare gaps, ignoring the question whether different types of disturbance cause differentiated effects on diversity (e.g. Colasanti et al., 2001; Schippers et al., 2001; Kahmen, 2003).

Another environmental factor often used to explain species diversity, is spatial heterogeneity. Following Chesson (2000b) and Amarasekare (2003) species can coexist in heterogeneous environments, if their competitive abilities respond differently to the changing environmental variable. In landscape models, this covariance between environment and competition is often included in the model assumptions and thus easily allows spatial niche separation and coexistence (Levine and Rees, 2002; Plotnick and Gardner, 2002). For the understanding of real plant communities systems it would be much more comprehensive to model the response of species to environment based on their functional traits (Lavorel and Garnier, 2002). In this way the change of competitive hierarchy in space would not be assumed a priori but would rather emerge from species interactions with environment and with each other. Most of our theoretical knowledge about spatial coexistence has been derived from patch occupancy models (Amarasekare, 2003). In this framework, the scale of spatial heterogeneity (between grid cells) is always larger and separated from the scale of interaction between species (within grid cells). Therefore these models are not able to explore the effects of heterogeneity on the same spatial scale as competitive interactions.

All models dealing with coexistence, implicitly or explicitly include the assumption that competition is one major determinant of diversity. Nevertheless, interactions between species or individuals are often modelled highly simplified, although different mechanisms of competition can cause differences in community structure. In non-spatial models, competitive pressure is usually linked to global population density, ignoring that sessile organisms compete locally and that spatial structure generated by the distribution of interacting individuals only, can change the outcome of competition even in homogeneous environment (Weiner and Conte, 1981; Stoll and Weiner, 2000; Law et al., 2003). Spatially-explicit cellular models widely assume either a constant dominance hierarchy between species (e.g. Tilman, 1994), or a lottery competition, where competition for empty patches is influenced by local abundance (Jeltsch et al., 1996, 1998; Schippers et al., 2001; Esther et al., submitted). Several studies showed that both assumptions lead do different results with regard to coexistence (e.g. Yu and Wilson, 2001; Levine and Rees, 2002).

In plant population ecology, the effects of local competitive mechanisms have been addressed in more detail in modelling as well as in empirical studies. In particular the distinction between size asymmetry and size symmetry of competition is a main factor explaining size variation (Weiner, 1990; Bonan, 1991; Weiner et al., 2001) or biomass-density relationships within even aged plant monocultures (Stoll et al., 2002). In this study, competition is called size-symmetric if competitive ability is proportional to individual size and size-asymmetric if larger plants receive a disproportionally higher share of resources relative to their size (Weiner et al., 2001). The term size-asymmetric competition between individuals must not be mixed up with the meaning of asymmetric competition between species as it is used in patch occupancy models. There, competitive asymmetry means that competitive superior species negatively affect inferior competitors, while the latter do not affect superior competitors at all.

With respect to the question of competitive size asymmetry Schwinning and Weiner (1998) provide theoretical reasoning that competition for light is size-asymmetric as light is “pre-emptable” by higher individuals due to the unidirectional supply of light, while competition for nutrients and water is size-symmetric. These findings were confirmed empirically by Berntson and Wayne (2000), who studied nitrogen uptake and light interception of birch seedlings. Despite the long and intensive debate about the role and importance of above- and below-ground competition (reviewed in Craine, 2005; Grime, 2007; Tilman, 2007), differentiation in competitive modes for different resources has been rarely included in community models. Two examples where root and shoot competition are explicitly modelled are presented by Colasanti et al. (2001) and Lehsten and Kleyer (2007), but both studies focus more on plant strategies under different environmental conditions than on the implications of shoot and root competition for species coexistence.

The possibility to draw conclusions about real systems based upon model results, is not only limited by the simplification of processes, but arguably even more by the fact that most modelling studies focussed on the effect of one factor or mechanism only. In real systems it is much more likely that the interaction of different factors and processes determines diversity rather than a single dominating mechanism. Despite this inevitable fact and despite the huge variety of mechanisms that have been explored in isolation, effects of interacting processes on diversity have been rarely studied with models (but compare Plotnick and Gardner, 2002).

Therefore, a modelling approach is needed, that allows including different environmental drivers at the same time and that explicitly links plant traits, which should be measurable in the field, to the response at the community level (Reineking et al., 2006). From our point of view, only the individual-based approach meets these requirements. In contrast to “classical” ecological models (as reviewed by Chesson, 2000b), this approach describes mechanisms at the level of the individual. Therefore it remains conceptually simple and properties of the community directly emerge from processes and interactions at the individual scale. Due to the high flexibility of the individual-based framework different environmental factors, e.g. disturbance and spatial heterogeneity, can be easily included (Grimm, 1999; Jeltsch and Moloney, 2002; Grimm and Railsback, 2005; Reineking et al., 2006).

In this study we focus on local diversity within temperate grassland communities, which are among the most diverse plant communities with up to 40 species per m^2 (Silvertown, 2004). In order to improve the mechanistic understanding of species coexistence and diversity maintenance within these ecosystems, we developed an individual-based simulation model, explicitly addressing the shortcomings of previous models described above. On purpose, seed immigration was excluded as potential explanation for diversity, because we only model local dynamics and feedbacks between local and regional scale are outside of the scope of this study.

Instead of describing a specific grassland site in detail, we intend to capture general processes and properties of these communities. Therefore, we use plant functional types (PFTs) instead of real species, as this approach allows the inclusion of enough detail to be comparable to measured data, but is yet transferable and general enough to allow conclusions for several grassland systems (Gitay and Noble, 1997; Díaz et al., 2002; Lavorel and Garnier, 2002; Jeltsch et al., 2008). Similar to previous studies, in our approach all PFTs comprise a common set of functional traits but are differentiated by their attributes for these traits (Colasanti et al., 2001; Schippers et al., 2001; Lehsten and Kleyer, 2007). Thus, one PFT can represent one or several plant species with similar trait features. As this study is primarily focussed on the question of diversity and trait composition at different environmental conditions , the traits chosen and included in the model belong predominantly to the “functional response” group (Lavorel and Garnier, 2002). In this way, trade-offs that potentially allow coexistence of PFTs, and the response of plant individuals to environment can be conveniently described based on trait attributes.

With regard to previous simplifications of species interaction, we explicitly include size-asymmetric above-ground and size-symmetric below-ground competition. Both are modelled adopting the “zone-of-influence” (ZOI) approach (Bonan, 1991, 1993; Weiner et al., 2001), which includes the key elements that were proposed as a minimal standard for individual-based modelling of plant interactions by Berger et al. (2002).

In particular, the approach implicitly includes changing competitive abilities of individuals during their life cycle, in contrast to more simplistic models mentioned above (Amarasekare, 2003; Law et al., 2003). In addition to trade-offs and the distinction of shoot- and root competition, we included two different methods to consider niche separation between PFTs with respect to resource requirements.

In our model, environment is characterised by resource supply and disturbance regime. According to the description of shoot and root competition, availability of above-ground resource (light) is considered independently from below-ground resource (water, nutrients). For the latter, we tested the effects of homogeneous vs. heterogeneous spatial distributions In contrast to other studies, two different types of disturbance, grazing and gap formation, are considered in our model. Grazing is considered as a process that affects plants only partly and acts selectively towards plant traits, while creation of gaps causes instantaneous removal of plants and creates space for establishment of other individuals. Both types can be varied in intensity and frequency independently.

We used the individual-based model to conduct simulation experiments for different environmental conditions with respect to resource availability and disturbance in order to address the following questions:

(i) What are the effects of varying above- and below-ground resource availabilities one size asymmetry of competition and on grassland diversity?

(ii) What are the effects of grazing and gap formation on grassland diversity?

(iii) How do the effects of both disturbance types interact with resource availability and spatial heterogeneity of resource supply?

(iv) Which level of grassland diversity can be explained by local mechanism only?

(v) What are the most important drivers and mechanisms of diversity maintenance at the local scale?

2 Methods

2.1 Model description

2.1.1 Purpose

The model is designed to evaluate the relative importance of competitive mechanisms and local environmental factors for maintenance of plant functional trait diversity in isolated grassland communities. Interaction between individuals is modelled in detail, incorporating size asymmetric above-ground and size symmetric below-ground competition. Furthermore, different concepts of niche separation between plant types are tested. Abiotic factors that are investigated, include disturbances, resource availability and spatial heterogeneity of resource supply. Instead of plant species, plant functional types (PFTs) are used. In this way the model is not limited to a specific site, but is able to provide general understanding for maintenance of local diversity in temperate grassland communities.

2.1.2 State variables and scales

The model explicitly simulates the life cycle of individual plants, including their interaction with other individuals. The state of each plant is characterised by its position in space, its age, the size of three plant compartments, viz. shoot, root and reproductive mass, as well as an indicator for resource stress exposure. Besides, each individual belongs to a certain PFT with specific parameters (see Tab. 3). Seeds are considered as individual entities and described by the state variables position, age and mass, as well.

Plant growth and competition are modelled using the “zone-of-influence” (ZOI) approach (Schwinning and Weiner, 1998; Weiner et al., 2001). Accordingly, each plant is represented in space by a circular area, referred to as ZOI in the following. Within this area the individual can take up resources. In case of overlapping ZOIs of neighbouring plants, the individuals compete for resources solely in the area of overlap. In contrast to earlier ZOI models (e.g. Weiner et al., 2001), in our approach

Table 1. State variables for all biological and spatial entities.

State variable	Unit	Description
Plants		
M_{shoot}	mg	vegetative shoot mass (leaf + stem)
M_{root}	mg	root mass
M_{repro}	mg	reproductive mass (flowers, seeds)
W_{stress}	weeks	duration of resource stress exposure
AGE	weeks	
PFT ID	-	identification number for plant functional type
Seeds		
M_{seed}	mg	seed mass
AGE	years	time of dormancy
Cells		
ARES	units/cm^2	above-ground resource availability
BRES	units/cm^2	below-ground resource availability

plant growth and interaction is modelled at two layers, one above and one below ground. Therefore, for each plant, shoot and root zones with independent diameters are derived.

The number of plants that can overlap is theoretically unlimited and in order to simplify spatial calculations of resource competition, these are transferred to a grid of discrete cells. As cell size and hence the smallest scale of plant interaction 1 cm^2 is used. The state of each single cell is defined by separate above-ground and below-ground resource availabilities. Defining resource supply individually for each cell offers the possibility to include environmental heterogeneity in space conveniently.

Simulations were usually performed with a grid size of 129 cm x 129 cm and periodic boundary conditions in order to avoid edge effects. An overview of state variables for all biological and spatial entities is given in Tab. 1. In addition the position of all entities on the 2D-grid is specified by x,y-coordinates. In order to facilitate readability, coordinates were not included in the table. The names of state variables are written in capital letters to distinguish them from model parameters in the following.

2.1.3 Process overview and scheduling

All processes are modelled at a time step of one week and a vegetation period of 30 weeks per year is assumed (Lehsten and Kleyer, 2007). In the initial state there are no plants on the patch but 10 seeds of each PFT are randomly distributed over the grid. To assure equal initial population sizes for all PFTs, the germination probabilities of these seeds are set to 1 irrespective of PFT-specific parameters. The dynamics of the grassland community are simulated for a time span of 100 years.

The flowchart (Fig. 1) shows all processes incorporated in the model and the scheduling of their execution. Within each week the processes "resource competition" and "establishment" are executed for each cell, while "plant growth", "seed dispersal" and "plant mortality" are calculated for each plant. "Seed mortality" and "winter dieback" are only modelled once a year after the end of the vegetation period.

The simulation model is implemented in C++ using the application development system Borland Builder 6.0.

2.1.4 Process descriptions

Resource uptake and competition

Plants acquire and compete for resources in those areas defined as their above- and below-ground ZOI. To relate shoot and root mass to the corresponding ZOI area, we adopt an allometric relation introduced by Weiner et al. (2001). Besides shoot mass, above-ground ZOI area ($\mathrm{A}_{\mathrm{shoot}}$) also depends on the leaf fraction of the shoot, as only leaves contribute to light interception (see section 2.2). The meaning and values of all parameters used in the following are provided in Tab. 2 and Tab. 3 respectively.

$$\mathrm{A}_{\mathrm{shoot}} = c_{shoot} \cdot (f_{leaf} \cdot \mathrm{M}_{\mathrm{shoot}})^{2/3} \tag{1}$$

$$\mathrm{A}_{\mathrm{root}} = c_{root} \cdot \mathrm{M}_{\mathrm{root}}{}^{2/3} \tag{2}$$

The circular areas of shoot and root ZOI are projected onto a grid of discrete cells. If the distance between the central point of a cell and the central point of a plant is smaller than the respective ZOI radius, this cell is covered by the plant. The projection is executed independently for above- and below-ground ZOIs, therefore a plant can cover different numbers of cells at both layers. Thus, each cell contains the information by which plant individuals it is overlapped above as well as below ground and resource uptake and competition can be calculated cell-wise.

With regard to the availability of above- and below-ground resources in each cell, we assume that both remain unchanged of plant uptake and are completely governed by environmental conditions given by ARES and BRES. Instead of modelling the influence of plants on their environment by local resource depletion explicitly, the ZOI approach implicitly includes the effect of plants on resource availability for other plants. According to Lehsten and Kleyer (2007) the "zone-of-influence" of one plant

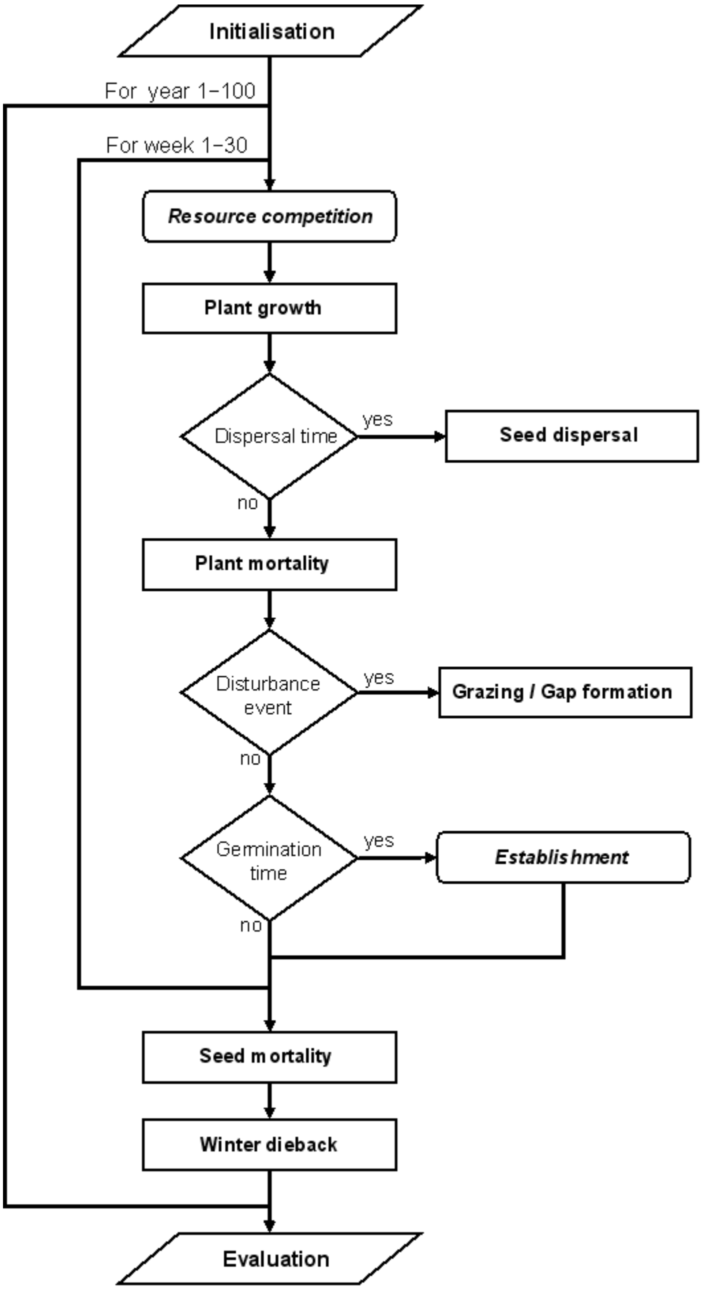

Figure 1. Process scheduling within the grassland model. Processes printed in italics in boxes with rounded corners are evaluated for each cell. Upright bold font indicates processes that are evaluated for all plant/seed individuals. Each process is evaluated for all entities (plants, seeds, grid cells), before the simulation proceeds to the next process.

represents an area of depleted resources for other individuals.

For the resource uptake (Δres) of each plant at the cell scale, we assume that it depends on the relative competitive effect of the plant in focus (β_i) and the competitive effect of all plants that cover the respective cell. Resource uptake for plant i from a given cell which is covered by n plants is calculated at both layers as:

$$\Delta res_i = \frac{\beta_i}{\sum_{j=1}^{n} \beta_j} \cdot \mathrm{RES}, \tag{3}$$

where RES is the resource concentration (above- or below-ground) in the cell.

Following Schwinning and Weiner (1998) and Berntson and Wayne (2000), there is strong evidence for size asymmetry of competition for light, as this resource is "pre-emtable" and higher individuals are able to shade smaller ones. Therefore, we assume that the relative competitive effect for above-ground resource is a function of shoot size given by parameters f_{leaf} and $\mathrm{M}_{\mathrm{shoot}}$. In contrast, competition for below-ground resource is considered as size-symmetric and the below-ground competitive effect of a plant is thus independent of root mass. In both layers the competitive effect of an individual is proportional to maximum resource utilization per unit shoot or root area (Δres_{max}) and is calculated as:

$$\beta_{above} = \Delta res_{max} \cdot \frac{1}{f_{leaf}} \cdot M_{shoot}, \tag{4}$$

$$\beta_{below} = \Delta res_{max}. \tag{5}$$

In this way below-ground competition corresponds to the case of perfect size symmetry according to the nomenclature of Schwinning and Weiner (1998), as all plants receive the same amount of below-ground resource per unit ZOI area. Above-ground competition refers to the case of partial size asymmetry in contrast to the studies of Weiner et al. (2001); Stoll et al. (2002), who compared perfect size symmetry with complete asymmetry. In the latter case the larger plant receives all of the contested resource.

Classical theory of species coexistence suggests that niche separation is a necessary prerequisite to maintain diversity, as it increases intraspecific and decreases interspecific negative interactions relative towards each other (Chesson, 2000b; Chase and Leibold, 2003; Silvertown, 2004). Therefore, we tested two alternative methods to include niche separation with respect to resource competition between individuals of different PFTs. In the first method the relative competitive effect of one individual within a cell depends one the number of plants that belong to the same PFT (n_{PFT}) and cover the same cell.

$$\beta_{i.pft} = \beta_i \cdot \frac{1}{\sqrt{n_{pft}}}, \tag{6}$$

where β_i is the competitive effect of the individual without the influence of other individuals (Eq. 4 or Eq. 5). This case represents a situation where the influence of two individuals of PFT A towards an individual of PFT B is less than twice the influence of one individual of PFT A. Eq. 6 is used for above- as well as for below-ground competition.

In the second method the fraction of total below-ground resource (BRES) that is available for all plants ($\mathrm{BRES}_{\mathrm{available}}$) in a grid cell, is a function of the number of different PFTs (N_{PFT}) that are present in this cell.

$$\mathrm{BRES}_{\mathrm{available}} = \frac{N_{PFT}}{1 + N_{PFT}} \cdot \mathrm{BRES}. \tag{7}$$

Therefore, if only individuals of one PFT are present, they can only access 50% of the total below-ground resource availability. Eq. 7 reflects a situation where different PFTs exploit different fractions of total below-ground resource.

Plant growth

For each time step (= 1 week) the growth routine calculates the increment of the three plant compartments shoot mass, root mass and reproductive mass. While shoot and root growth is possible over the entire vegetation period, growth of reproductive biomass is limited for all PFTs to the time between week 16 and week 20. Plant growth exclusively depends on the resource uptake of the current time step and is limited by the minimum uptake of above- and below-ground resource (Lehsten and Kleyer, 2007). The resource type that is taken up in excess can not be stored and is lost. Instead we assume that all plant individuals are able to show plasticity in their shoot/root-ratio as reaction to different uptake of above- and below-ground resource. Therefore, resource allocation is modelled according to optimal allocation theory and a higher fraction of resources is allocated to the plant compartment that currently harvests the limiting resource (Weiner, 2004; Shipley and Meziane, 2002).

For the described resource partitioning the model of Johnson (1985) is adopted.

Accordingly, the fraction of resource allocated to shoot growth is calculated as:

$$\alpha_{shoot} = \frac{\Delta bres}{\Delta bres + \Delta ares}, \tag{8}$$

where $\Delta ares$ and $\Delta bres$ are the uptake of above- and below-ground resources respectively. With the partitioning parameter (α_{shoot}) the amount of resources allocated to shoot and root is then determined as:

$$\begin{aligned} \Delta res_{shoot} &= \alpha_{shoot} \cdot \min(\Delta ares\, , \, \Delta bres), & (9) \\ \Delta res_{root} &= (1 - \alpha_{shoot}) \cdot \min(\Delta ares\, , \, \Delta bres). & (10) \end{aligned}$$

In extreme situations, if the uptake one resource type was zero, all resource would be allocated to the compartment that harvests this resource. If uptake is equal for both resource types, 50% of resources will be allocated to shoot as well as root growth.

In the absence of competition plants show sigmoidal growth of biomass (Hunt, 1982). Therefore, we adopt the logistic growth equation presented by Weiner et al. (2001) for shoot and for root growth. The growth term of this equation is proportional to resource uptake, while the loss term is proportional to biomass squared. In addition to the model of Weiner et al. (2001), we introduce a limit for plant growth, assuming that there is a maximum amount of resource per unit shoot/root area (Δres_{max}) that can be converted to biomass within one time step. For both growth limitation is determined in the same way:

$$\begin{aligned} \Delta res_{shoot} &= \min\left(\Delta res_{shoot}\, , \, \mathrm{A_{shoot}} \cdot \Delta res_{max}\right), & (11) \\ \Delta res_{root} &= \min\left(\Delta res_{root}\, , \, \mathrm{A_{root}} \cdot \Delta res_{max}\right). & (12) \end{aligned}$$

The growth of one plant compartment does not directly depend on the mass of the other compartment, but as described above, shoot and root growth are coupled by resource allocation. For each time step, the mass increment of shoot and root is thus calculated as:

$$\begin{aligned} \Delta \mathrm{M_{shoot}} &= g \cdot \left(\Delta res_{shoot} - c_{shoot} \cdot f_{leaf} \cdot \Delta res_{max} \cdot \frac{\mathrm{M^2_{shoot}}}{m_{max}^{4/3}} \right), & (13) \\ \Delta \mathrm{M_{root}} &= g \cdot \left(\Delta res_{root} - c_{root} \cdot \Delta res_{max} \cdot \frac{\mathrm{M^2_{root}}}{m_{max}^{4/3}} \right). & (14) \end{aligned}$$

The growth coefficient g is a conversion rate between resource units and biomass. Shoot and root do not differ with respect to their maximum resource utilization per unit ZOI area (Δres_{max}) and their maximal mass (m_{max}). Negative growth is not allowed and plants will not change their shoot or root mass, if Eq. 13 or 14 produce negative results.

During the period of reproduction a constant proportion of resource uptake (α_{repro}) is allocated to growth of reproductive mass before root-shoot-allocation is considered. The mass increment of reproductive mass is calculated as:

$$\Delta \mathrm{M}_{\mathrm{repro}} = g \cdot \alpha_{repro} \cdot \min(\Delta aRes, \Delta bRes). \tag{15}$$

For the conversion between resource and biomass the same parameter value (g) as for vegetative growth is used. The maximal reproductive mass that a plant can produce is limited to 5% of shoot mass (Schippers et al., 2001; Kahmen, 2003). No resource is allocated to reproductive growth if the maximum value has already been reached.

Seed dispersal

Differences in seeding time are not considered here and all plants disperse their seeds in the same week of the year (see Tab. 2). The seed number that each plant has produced, is determined dividing the individual reproductive mass by PFT-specific seed mass (Schippers et al., 2001; Lehsten and Kleyer, 2007). Direction and distance of dispersal are randomly chosen for each seed. The direction is drawn from a uniform distribution and for the distance a log-normal dispersal kernel is assumed (Nathan and Muller-Landau, 2000; Stoyan and Wagner, 2001). Seeds can not get lost by dispersal to coordinates outside of the grid. Otherwise on the small scale investigated here, plants that grow close to the edges would face a disadvantage because of high seed loss. To avoid this edge effect, analogous to competition, a periodic boundary condition is used for seed dispersal.

Seed mortality

Survival and mortality of seeds in the seed bank is simulated at a yearly time step. Factors for seed mortality like granivory, pathogens or unfavourable conditions are not modelled explicitly, but are lumped into a yearly survival probability of 0.5. If a seed reaches its maximum age (age_{max}), without germinating or dying at random it is removed from the seed bank.

Establishment

Germination and seedling establishment is allowed during 4 weeks in spring and 4 weeks in autumn (Tab. 2) (Kahmen, 2003). The PFTs used here do not differ in their timing of germination. Seedling recruitment is modelled according to Schippers et al. (2001) and can be divided into two consecutive processes: (i) Seed germination and (ii) seedling competition. Germination is only allowed in grid cells that are not covered by any plant in the above-ground layer. In uncovered cells, seeds germinate and are converted to seedlings with a PFT-specific probability (Tab. 3). All seeds that do not germinate remain in the seed bank until they die or until the next season of germination.

In each cell only a single plant is allowed to establish. Seedling competition is modelled as weighted lottery, using seed mass as measure of competitive ability between seedlings (Schippers et al., 2001). The seedling that is chosen for establishment is converted to a plant with a shoot and root mass equal to seed mass. All the other seedlings within the cell die and are removed from the grid.

Plant mortality

In the model plants can die because of resource stress or due to unspecified stochastic “background” mortality. Without resource stress for all plants a weekly mortality rate of 0.007 is assumed, which is derived from the annual survival probability of 0.8 used by Schippers et al. (2001) and the assumption of equal mortality rates during all weeks of the vegetation period. Therefore, plants’ average longevity is about 5 years, about 10% of the individuals live for more than 10 years and less than 1% for more than 20 years.

In addition to this stochastic “background” mortality, the probability of death during the vegetation period is increased by resource stress. If a plant does not compete with neighbours and there are enough resources available from environment, optimal uptake is calculated as:

$$\Delta aRes_{opt} = 2 \cdot \mathrm{A}_{\mathrm{shoot}} \cdot \Delta res_{max}, \tag{16}$$

$$\Delta bRes_{opt} = 2 \cdot \mathrm{A}_{\mathrm{root}} \cdot \Delta res_{max}. \tag{17}$$

The factor 2 has to be used because 50% of the resource taken up by one plant compartment is allocated to the other one. We define that a plant suffers resource stress, if the current uptake for above-ground or below-ground resource is less than a fixed fraction of the optimum uptake ($thr_{stress} \cdot \Delta res_{max}$). For each individual, consecutive weeks with exposure to resource stress are counted ($\mathrm{W}_{\mathrm{stress}}$). The current probability of death increases proportionally to the duration of resource stress exposure.

$$p_{mort} = \frac{\mathrm{W}_{\mathrm{stress}}}{surv_{max}} \tag{18}$$

The maximum number of weeks that a plant can survive under stress exposure is thus given by the PFT-specific parameter $surv_{max}$. Plants are able to recover from resource stress. If their uptake is more than thr_{stress} times the optimum, $\mathrm{W}_{\mathrm{stress}}$ is decreased by one step, but is limited to the interval $[0, surv_{max}]$.

In case a plant dies, it does not grow and reproduce any more, but it still suppresses establishment within its above-ground ZOI cells. We assume that dead plants do not take up nutrients, but that they are still able to shade other plants. Therefore, dead plants are considered in competition for above-ground, but not for below-ground resources. Each week shoot and root mass of all dead plants is reduced by 50% and they are removed from the grid completely, as soon as their total mass decreases below 10 mg, i.e. a plant with the mass of 10 000 mg at time of death is removed after 10 weeks.

Grazing and gap formation

Two different types of disturbance are considered in the model: (i) Grazing, modelled as partial removal of above-ground biomass. (ii) Formation of bare gaps, e.g. by trampling. The frequencies of grazing and gap formation are given independently as constant incidence probabilities within one week (p_{graz} , p_{dist}).

Grazing is a process that acts selectively towards trait attributes (see section 2.2). For each plant the susceptibility to grazing (s_{graz}) is calculated as a function of shoot geometry and PFT-specific palatability.

$$s_{graz} = \mathrm{M}_{\mathrm{shoot}} \cdot \frac{palat}{f_{leaf}} \tag{19}$$

This susceptibility is converted into a probability to be grazed for each plant, dividing by the maximum susceptibility of all plants:

$$p_{graz} = \frac{s_{graz}}{\max([s_{graz}]_{i=1}^{n})}, \tag{20}$$

where n is the number of living plants in the patch. All plants are checked for grazing in random order. In case a plant is grazed, 50% of its shoot mass and its complete reproductive mass are removed. The random choice of plants is repeated without replacement, until a fixed proportion (f_{graz}) of the above-ground biomass on the whole grid has been removed. When all plants have been checked for grazing once, but the required amount of mass has not been removed yet, grazing probabilities for all individuals are calculated once more with Eq. 20 and the whole procedure is repeated, until the required mass has been removed or until a residual biomass is reached that is considered as ungrazable. This fraction is set to 15 g/m^2 following Schwinning and Parsons (1999). In this way it is possible that a plant individual is grazed never or several times during one week with a grazing event.

In contrast, gap formation is not selective towards plant traits, but the effects are spatially correlated. Intensity of gap formation is specified by a fraction of the grid area that is affected each year (f_{year}) and the fraction of area that is effected in one event (f_{event}) following the approach of Plotnick and Gardner (2002). Accordingly, the probability of a disturbance event for one week is calculated as:

$$p_{gap} = \frac{f_{year}}{f_{event} \cdot 30}. \tag{21}$$

The area affected in one event is divided into circular gaps with the radius of 10 cm, which are randomly distributed on the grid. All plants, whose central point is located within a gap are immediately and completely removed from the grid. Besides stochastic grazing and disturbance events, every year at the end of the vegetation period the above-ground mass of all plants is deterministically reduced to 50% representing vegetation dieback in winter (Lehsten and Kleyer, 2007).

2.2 Plant traits and PFT parametrisation

The PFTs that are used in the model differ in their attributes for 11 plant functional traits (Tab. 2). These are grouped into five trait syndromes based on well documented trade-offs and trait correlations . The traits we chose, comprise a subset of the “common core list of plant traits”, proposed by Weiher et al. (1999).

Table 2. PFT parameters

Symbol	Description	Unit	Value
Vegetative traits			
f_{leaf}	fraction of leaf mass per shoot mass	mg/mg	*
c_{shoot}	above-ground ZOI area per leaf mas	cm^2/mg	*
c_{root}	below-ground ZOI area per root mass	cm^2/mg	1.0
g	conversion rate resource to biomass	mg/resource unit	0.2
Δres_{max}	maximal resource utilization per time step and ZOI area (equal for shoot and root)	resource units/cm^2	*
thr_{stress}	threshold of Δres_{max} for resource stress	-	0.2
$surv_{max}$	maximal survival time during resource stress	weeks	*
m_{max}	maximal mass (equal for shoot and root)	mg	*
$palat$	palatability - susceptibility towards grazing	-	*
Generative traits			
m_{seed}	seed mass	mg	*
$mean_{disp}$	mean of dispersal distance	cm	*
std_{disp}	standard deviation of dispersal distance	cm	*
$dorm$	maximum seed longevity	years	*
p_{germ}	germination probability	-	*
t_{disp}	time of seed dispersal	week of the year	21
t_{germ}	time of seed germination	week of the year	1–4 , 21–25

* PFT-specific values, see Table 3

The growth form of a plant can be characterised by the ratio between leaf mass and total shoot mass (f_{leaf}), instead of using categorical types as “rosette” or “semi-rosette”, following the suggestion of Poschlod et al. (2000). Plants with a low f_{leaf} use more biomass to build up support tissue (e.g. stems) instead of leave mass. Therefore this trait includes a trade-off between plant height and leaf area. Plants with a high f_{leaf} are inferior competitors for light at the cell scale (implemented in Eq. 4), but without competition their relative growth rate is higher, because they use a high fraction of their above-ground mass for resource acquisition (Eq. 1). Three growth forms are considered here, with 50%, 75% and 100% of leave mass.

Maximum plant mass is the second trait that describes plant geometry and is positively related to actual plant mass, because it decreases the loss term of the growth equation for shoot and root mass (Eq. 13, 14). Thus, complete information on shoot size and geometry is given by $\mathrm{M}_{\mathrm{shoot}}$ together with f_{leaf}. In the case of size-asymmetric competition, both values influence the competitive effect of a plant at the cell scale (Eq. 4). According to empirical evidence that higher plants respond negatively to grazing (Díaz et al., 2001; Dorrough et al., 2004), individual susceptibility to grazing is modelled as a function of f_{leaf} and $\mathrm{M}_{\mathrm{shoot}}$ (Eq. 19).

Eriksson and Jakobsson (1998) report a correlation between plant mass and seed mass within a semi-natural grassland community in Sweden. Therefore maximum plant mass and individual seed mass are combined within a trait syndrome in our parametrisation. The well-documented trade-off between seed size and seed number is included in our model in a straightforward way. PFTs with higher seed mass produce less seeds from the same amount of reproductive mass (Schippers et al., 2001; Leishman, 2001; Westoby et al., 2002). The disadvantage of low seed number is balanced by higher recruitment success of large seedlings (Jakobsson and Eriksson, 2000). In our model, the advantage of large seeds is incorporated in the weighted lottery of seedling competition and in a higher initial mass of plants that germinated from large seeds. Parameter values for maximum plant mass and seed mass do not correspond to specific species (Tab. 3), but they are taken from the range found in a temperate grassland community (Eriksson and Jakobsson, 1998). Although the relationship between seed mass and dispersal distance is less clear (Leishman et al., 2000), a negative correlation is assumed here, which should be valid at least for wind-dispersed seeds (Jongejans and Schippers, 1999). The mean dispersal distance of 10 cm for large seeds is adopted from Schippers et al. (2001) while the value for small seeds was chosen in order to allow dispersal over the whole grid. For simplicity, equal values are used for mean and standard deviation of the dispersal kernel assuming a higher variance for dispersal distances of smaller seeds.

The response of plants to different resource conditions is distinguished into two classes reflecting the trade-off between competitive ability and stress tolerance (Grime, 1977, 2001). The "competitor" strategy is characterised by a high growth rate in resource-rich environment, which is given here as the maximum resource utilization per shoot/root area (Δres_{max}), but a low longevity under resource stress conditions, specified by $surv_{max}$. The contrasting attributes of lower potential growth rate, but higher longevity during resource stress exposure are assigned to the "stress-tolerant" strategy. Resource units in our mode do not directly correspond to any measurable quantity, because we do not focus on a specific community, but are rather interested in relative differences between resource-rich vs. resource-poor environment. Therefore, the parameter values related to resource uptake and conversion to biomass (g, Δres_{max}) were not derived from real data but were estimated. PFT specific values are distinguished by factor 2 to assure sufficient difference between PFTs (Tab. 3).

We considered two strategies of response to grazing: (i) Grazing tolerance by fast regrowth of removed biomass and (ii) grazing avoidance by low palatability through defence structures or secondary compounds (Bullock et al., 2001; Adler et al., 2004). In our model the relationship between leaf mass and leaf area is given by the parameter c_{shoot} (Eq. 1). This parameter is functional analogue to specific leaf area (SLA), which was proposed by Westoby (1998) as a key trait to characterise plant strategies. High SLA is related to high efficiency of light interception and fast growth, while leaves with low SLA show higher longevity, structural strength or high allocation to defensive compounds (Reich et al., 1997; Westoby et al., 2002). Accordingly, a high c_{shoot} value for grazing tolerance vs. a low value for grazing avoidance is used here. The positive effect of defence compounds is expressed as a low palatability. Thus, a low individual probability of being grazed counteracts the disadvantage of low c_{shoot} (Eq. 19). Despite the functional equivalence, measured SLA values can not be interpreted as c_{shoot} directly, because the total leaf area of a real plant does not necessarily correspond to the ZOI area as it is used in our model. Therefore values for c_{shoot} and $palat$ were estimated.

Similar to previous models (Schippers et al., 2001; Kahmen, 2003; Lehsten and Kleyer, 2007) for seed dormancy only two categories, dormant and non-dormant seeds, are considered. While all seeds have the same survival probability for each year, their maximum longevity is different. Non-dormant seeds can only survive for one

Table 3. Trait syndromes and parameter values

Trait/ trait syndrome	Trait parameters			
Growth form	f_{leaf}			
Rosette	1.0			
Intermediate	0.75			
Erect	0.5			
Maximum plant size	m_{max}	m_{seed}	$mean_{disp}$	std_{disp}
Large	10000 mg	1 mg	0.1 m	0.1 m
Medium	5000 mg	0.5 mg	0.25 m	0.25 m
Small	2500 mg	0.1 mg	0.5 m	0.5 m
Resource response	Δres_{max}	$surv_{max}$		
Competitor	50	2 weeks		
Stress tolerator	25	4 weeks		
Grazing response	$palat$	c_{shoot}		
Tolerator	1	1		
Avoider	0.3	0.75		
Dormancy	$dorm$	p_{germ}		
Dormant	5 years	0.1		
Non-dormant	1 year	0.3		

year, so they may either germinate directly after dispersal or in spring of the next year. Dormant seeds can survive for up to 5 years in the soil seed bank, but high seed longevity is counterbalanced by a lower germination probability within one year (Schippers et al., 2001). Parameter values for germination probabilities were derived by Kahmen (2003) based on a review of seed sowing experiments (see references therein).

The parameter values for all trait attributes are presented in Tab. 3. Based on these five traits and trait syndromes, we defined 72 PFTs, corresponding to all possible combinations of trait attributes. All 72 PFTs are used within the simulations of grassland patch dynamics, described in the following section.

2.3 Design and analysis of simulation experiments

Simulation experiments were conducted with three different versions of the model. All of them describe competitive interactions at the individual scale only, but they differ in their assumptions for competition between individuals of the same PFT (conspecifics) or between individuals of different PFTs (heterospecifics). Version 1 is the standard model and does not consider any differences between intra- and interspecific competition (Eq. 4 and 5). In version 2, the relative competitive effect of an individual for above- as well as below-ground competition decreases with the number of conspecifics in the same cell (Eq. 6). In contrast, in version 3 it is assumed that PFTs access different fractions of the total below-ground resource concentration and therefore the resource concentration, which is available to the plants is a function of the number of PFTs that are present in one cell (Eq. 7).

2.3.1 Simulations of cohort growth

In a first step we conducted simulations with cohorts of one PFT only, in order to test whether realistic patterns emerge from plant interactions within the model. During cohort development plant growth and resource competition lead to density-dependent mortality. This process of self-thinning has been studied intensively in field as well as in theoretical studies (Yoda et al., 1963; White and Harper, 1970; Enquist et al., 1998; Stoll et al., 2002) and is therefore useful to test the plausibility of plant population models (Colasanti and Hunt, 1997; Berger et al., 2002). Here, we analysed self-thinning for cohorts at five different initial densities (200, 500, 1000, 2000, 5000 individuals) and for a full factorial design of 2 x 2 above- and below-ground resource levels (50, 100 units per cm^2). In the initial state individuals were randomly distributed within the grid and cohort development was simulated for one year. The single PFT used for these simulation experiments, was parametrized with a rosette growth form, large maximum plant mass and a competitive, grazing-tolerant, non-dormant strategy (for parameter values see Table 3).

Within populations, size variation is another pattern that emerges from competitive interactions and is particularly influenced by competitive size asymmetry (Weiner et al., 2001). This effect was tested with the same PFT and the same factorial set of resource distributions as self-thinning, but at two densities only (200, 2000 individuals). In order to assure comparability with the model of Weiner et al. (2001), plant mortality was deactivated for these simulations. Otherwise the death of competitive inferior individuals counteracts the emergence of size variation within the cohort and the effects of density and resource combination would be hidden.

Furthermore, Weiner et al. (2001) as well as Stoll et al. (2002) compared the effects of perfectly size-symmetric to completely size-asymmetric competition. Therefore, all simulations for self-thinning and size variation were conducted twice: (i) With partial size asymmetry of above-ground competition, using Eq. 4; (ii) with complete size asymmetry, i.e. the individual with the highest competitive effect (Eq. 4) acquired all resource from the area of overlap. Below-ground competition was considered as size symmetric in both cases. Only model version 1 was applied here, because versions 2 and 3 consider differences between intra- and interspecific competition, which are not relevant if only one PFT used. All scenarios for density, resource combination and competitive asymmetry were replicated 20 times.

2.3.2 Simulations of community dynamics

Community composition, structure can be driven by interactions between individuals as well as by environmental conditions. Simulations of community dynamics were performed in order to reveal the influence of both factors on diversity and trait composition. As explained above, the mode of competitive interactions differs between model versions and all three model versions were applied for community simulations. Environmental conditions investigated here, include above- and below-ground resource availability, two types of disturbance (grazing and gap formation) at varying frequencies and intensities and the effect of spatial heterogenous vs. homogeneous distribution of below-ground resource.

Community dynamics were modelled with the full set of 72 PFTs, derived as combinations of the trait values in Table 3. A spatial extent of 129 cm x 129 cm and 100 years of simulation time were used. All scenarios described in the following, were replicated 20 times with each of the three model versions.

Effect of resource availability

We tested the effects of different above- and below-ground resource availabilities in the absence of disturbance and for spatially homogeneous below-ground resource distribution. A factorial design of two above-ground (50, 100) times six below-ground resource levels (20, 40, 50, 60, 80, 100) was used.

Effect of grazing

The influence of grazing on community structure and diversity was also explored with a 2 x 2 design of resource levels (50, 100). At first, only the frequency of grazing, given as grazing probability per week (p_{graz}), was varied over a gradient with 10 levels (0, 0.05, 0.1, 0.15, 0.2, 0.3, 0.4, 0.5, 0.7, 0.9), but grazing intensity for a single event (f_{graz}) was kept constant at 0.5, i.e. at maximum 50% of total above-ground biomass could be removed in one week. In a second step, two more levels for f_{graz} (0.25, 0.75) were combined with a subset of five grazing probabilities (0.05, 0.1, 0.2, 0.4, 0.7) in order to reveal effects of different grazing intensities.

Effect of gap formation

The disturbance regime of gap formation is specified by two parameters: The fraction of grid area that is disturbed during one year (f_{area}) and the fraction of the grid that is disturbed during one event (f_{event}). The probability that a gap formation event occurs in a week is given by Eq. 21. Here, we used five levels for f_{area} (0.1, 0.2, 0.5, 1.0, 2.0) times two levels for f_{event} (0.1, 0.5). The first parameter can be higher than 1.0, because the sum of the area affected during all weeks of one year, may be higher than the total grid area. This does not necessarily mean, that the whole grid is cleared at one point in time, but that the same gap might be disturbed and recolonized several times during one year. Analogous to grazing, these 10 combinations (2 x 5) for intensity of gap formation were applied to 4 different resource combinations with the levels 50 and 100 for both resource types.

Effect of spatial heterogeneity

To include spatial heterogeneity, we used fractal maps for below-ground resource availability. To generate these maps, we applied the well-documented and tested "midpoint displacement algorithm", which produces square fractal maps with the side length of $2^n + 1$ cells (Saupe, 1988; Körner and Jeltsch, 2008). Here $n = 7$ is used to produce maps of 129 x 129 grid cells. The algorithm requires only two parameters: The variance associated with the displacement of points (σ) and the Hurst Factor (H), which measures the spatial autocorrelation between points. The fractal dimension (D) of the map can estimated as $D \approx 3.0 - H$ (Plotnick and Gardner, 2002). Here two values for H (0.2, 0.8) were applied and displacement variance was kept constant at $\sigma = 15$. Linear transformation was used to produce resource maps with a specified mean of below-ground resource availability and a coefficient of variation of 0.25. Examples for landscapes are shown in Fig. 2.

In order to allow conclusions about the interacting effects of spatial heterogeneity in combination with other environmental factors, the same simulation experiments that were used to reveal effects of resource levels and grazing were repeated with heterogeneous below-ground resource distribution. The design with 2 x 5 resource levels but without disturbance was combined with two degrees of spatial heterogeneity (H=0.2, 0.8). Furthermore, these two levels of heterogeneity were combined with a subset of 5 grazing probabilities (0, 0.1, 0.15, 0.2, 0.5) and 2 x 2 resource levels (50, 100).

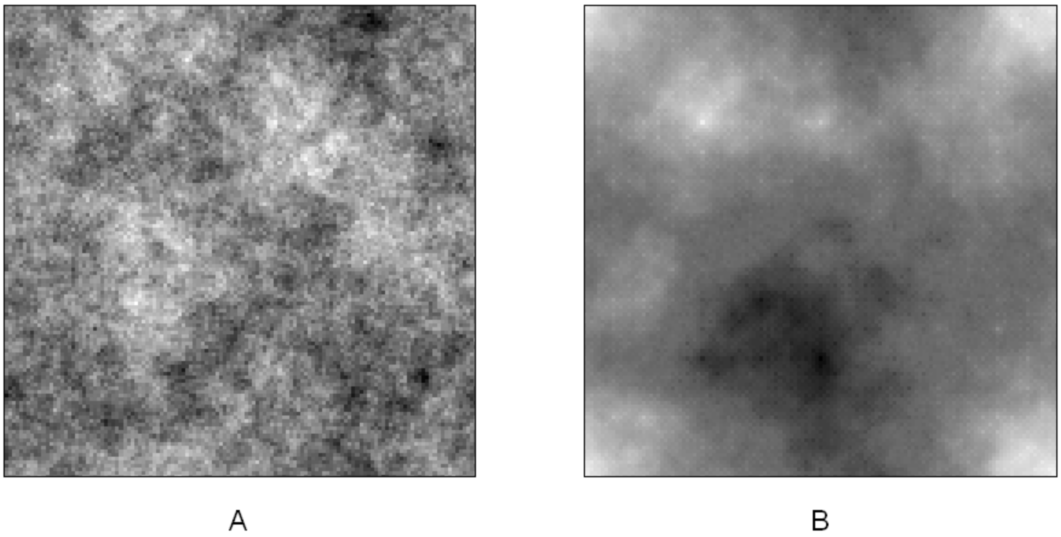

Figure 2. Examples for fractal maps of 129 x 129 cm, used as below-ground resource availability. Grey levels corresponds to resource availabilities between 0 (white) and 100 (black) units per cm^2. Both maps have a mean resource availability of 50 and a standard deviation of 12.5 units per cm^2, but they differ in their spatial auto-correlation. A: $H = 0.2$. B: $H = 0.8$.

2.3.3 Analysis of community features and trait composition

The diversity that emerged in each simulated scenario was quantified in two different ways. First, we recorded the number of PFTs that coexisted over the simulation time of 100 years. Second, we calculated the Shannon-Diversity-Index, as the number of PFTs does not contain any information about evenness or dominance among the abundances of PFTs in the community.

$$\text{Shannon-Diversity} = -\sum_{PFT=1}^{72} p_i \cdot \ln p_i \tag{22}$$

where p_i is the relative abundance of individuals of PFT i.

To characterise the community in further details, we recorded the number of living individuals, total biomass, total above- and below-ground mass. Sizes of mass pools were calculated as the sum of total plant, shoot or root mass of all living plants, respectively. All community features, except the number of surviving PFTs, were evaluated each year before seed germination in autumn (week 20). To derive measures of one model run, these annual values were averaged over the last 25 years of total simulation time.

For the description of plant strategies and community structure the distribution of attributes for functional traits was analysed, instead of dealing with "population sizes" of 72 PFTs. According to the evaluation of community features, individual numbers were counted each year in week 20 and the mean value of the last 25 years was calculated. For all five functional traits (Tab. 3) the attribute distribution was analysed with multinomial models (Venables and Ripley, 2002). These estimate the probability that a randomly chosen plant shows a particular trait attribute at certain environmental conditions (Reineking et al., 2006).

All statistical analyses we conducted with **R** for Windows Version 2.6.1 (R Development Core Team, 2007). Multinomial models were fitted with the function `multinom` from the package `nnet` (Venables and Ripley, 2002).

3 Results

3.1 Cohort development

Simulations with a single PFT and activated resource stress mortality reproduced realistic self-thinning trajectories with a section of a linear relationship between the logarithms of mean plant mass and population density (Fig. 3). A linear regression model of the form $\log(mean\ mass) = a + b \cdot \log(density)$ was fitted to the simulation results in order to estimate the slopes of self-thinning trajectories. For the case of partially size-asymmetric above-ground competition in all resource scenarios a slope close to -1.5 emerged (Fig. 3A, B). Therefore, only results for the “extreme” resource scenarios with different levels of above-ground resource (ARES) and below-ground resource (BRES) are shown. In contrast, for complete size asymmetry of above-ground competition the self-thinning slope depended on the resource scenario (Fig. 3C, D). Equal resource levels (not shown) or lower above-ground resource, yielded slope values between -0.9 and -1.0 (Fig. 3C). For the scenario ARES 100/BRES 50 a significantly steeper slope of -1.22 was estimated (Fig. 3D). Furthermore, scenarios with ARES equal to or lower than BRES showed more concave curvature and less linearity. Therefore slope values were more dependent one the data points used for regression. At the end of the simulation time for the same resource combination the number of surviving individuals was generally higher with partially than with completely size.asymmetric above-ground competition.

In simulations without resource stress mortality mean plant mass showed logistic trajectories as expected from growth equations (Eq. 13, 14), but growth rate as well as equilibrium mass clearly depend on resource levels and plant density (Fig. 4A, D). Obviously, the tenfold change of density had a stronger effect than the twofold change of resource levels. For each density, highest average plant mass was reached for ARES 100/BRES 100. In scenarios with at least one low resource level, average individual mass was maximal for ARES 100/BRES 50 and minimal for ARES 50/ BRES 50. Variation between these three resource combinations changed with density as well as with competitive asymmetry. With the assumption of partial size

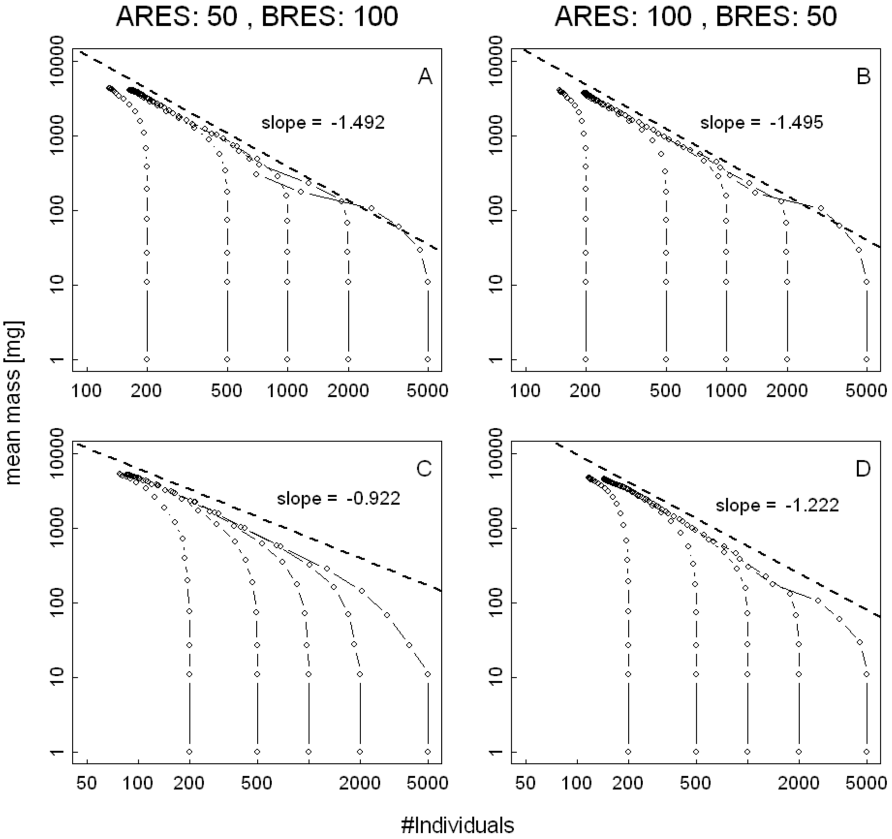

Figure 3. Self-thinning trajectories with one PFT for different initial densities and different resource combinations. Cohort growth was simulated for 30 weeks. Size-symmetric below-ground competition was used in all scenarios. For above-ground competition either partial size asymmetry (A, B) or complete size asymmetry (C, D) was assumed. Self-thinning slopes were derived by linear regression with log-transformed data for densities 1000, 2000, 5000 and $t \geq 10$ weeks.

asymmetry for above-ground competition there was little variation in average mass (Fig. 4A), while for complete size asymmetry variation was high for low density, but was strongly reduced at high density (Fig. 4D). For the same resource combination, average equilibrium mass was generally higher with partially size-asymmetric above-ground competition.

Size variation, measured as coefficient of variation (CV) of individual masses, not only responded to a change in density but also to a change between above-ground and below-ground resource availability. Variation increased rapidly during the exponential phase of plant growth, but when mean plant mass approached its equilibrium, size variation decreased for partial size asymmetry but converged to a maximum for complete size asymmetry. At high density, size variation was significantly higher with completely size-asymmetrical above-ground competition for all resource scenarios (Fig. 4B, D). This was also true for low density, but there the difference described was less pronounced (Fig. 4C, E). For both cases of competitive asymmetry the highest variation occurred for ARES 50/BRES 100 and the lowest for ARES 100/BRES 50, but again this effect was more prominent for high than for low density. For equal levels of resource availabilities, size variation was intermediate at the end of the simulation time, but showed a more rapid increase for ARES 100/BRES 100 than in any other scenario. Surprisingly, at the end of the simulation time, size variation was slightly higher at low density for resource levels 100/100 and 100/50 in the case of partially size-asymmetric above-ground competition (Fig. 4B, C).

3.2 Grassland patch diversity

3.2.1 Effect of resource availability

Simulations with different above- and below-ground resource levels revealed a unimodal relationship between diversity and below-ground resource availability for the same level of above-ground resource availability (Fig. 5). Maximum diversity was reached for intermediate to high BRES and ARES=100 resource units per cm^2. This patterns was observed for all model versions, but the scenario with highest diversity clearly differed between the three versions.

Comparing maximum diversity between different model versions showed that version 2 yielded the highest and version 1 the lowest diversity, but obviously there was no simple additive interaction between resource combination and model version. For

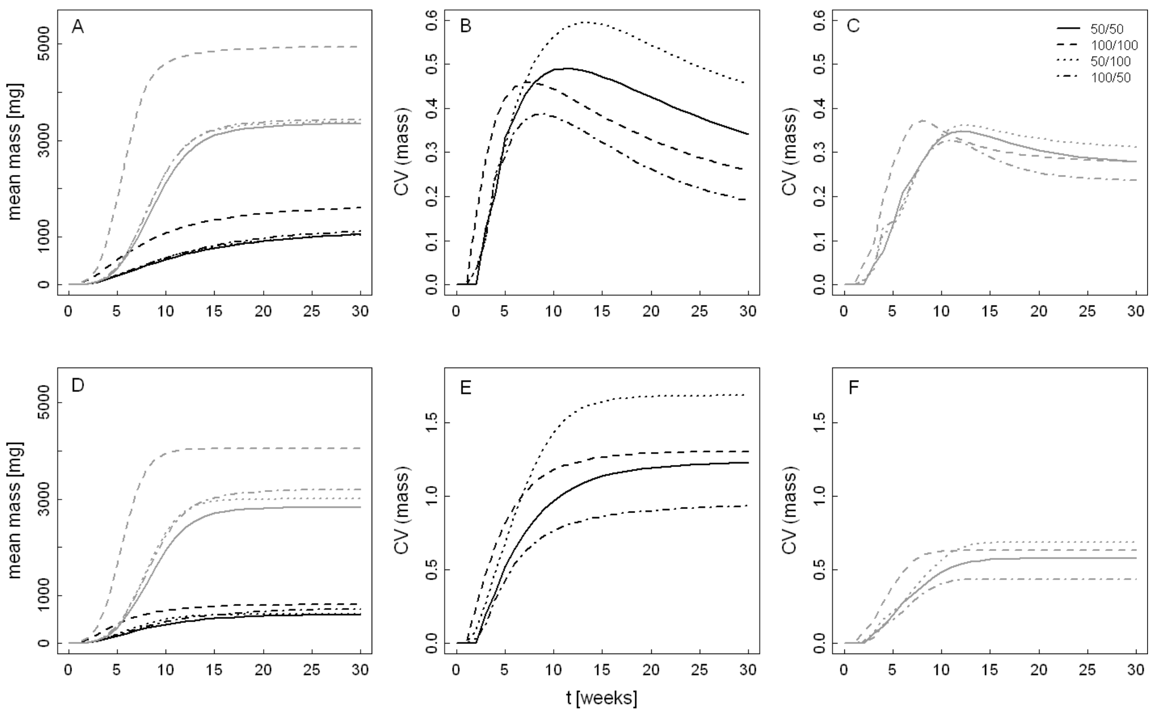

Figure 4. Mean plant mass and size variation of a cohort with a single PFT for different densities (black lines: 2000 individuals; grey lines: 200 individuals) and different resource levels (indicated by line type). Size variation is measured as coefficient of variation (CV) of individual masses. For above-ground competition either partial size asymmetry (A, B, C) or complete size asymmetry (D, E, F) was assumed. Mortality was deactivated in the underlying simulations.

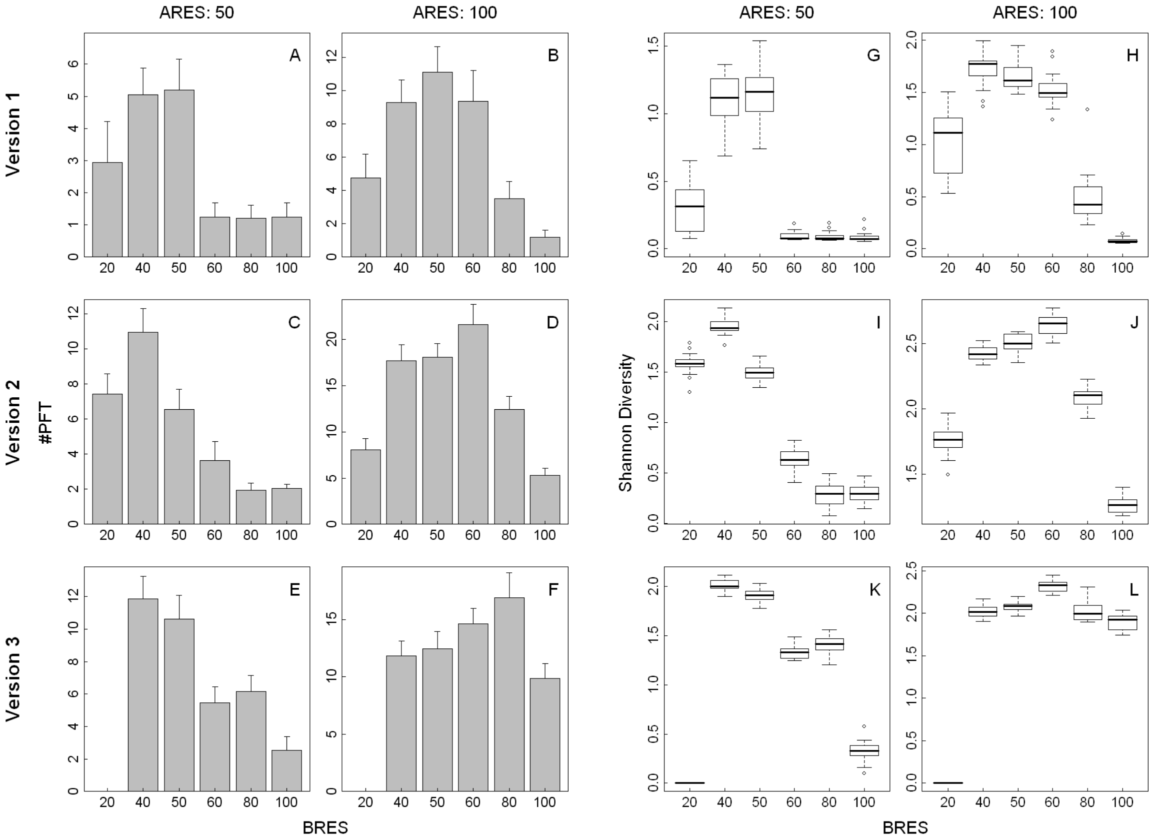

Figure 5. Number of PFTs that coexisted for 100 years and Shannon-Diversity for different resource levels. Bars with errors show mean and standard deviation of PFT number of 20 replicates. Boxplots represent mean values over the last 25 simulation years of 20 replicates. Subplots for the same above-ground resource level (ARES) are arranged in columns, subplots for the same model version in rows.

version 1 diversity peaked at BRES=50 for both above-ground resource levels, but decreased sharply with further increase of BRES. At a high level of ARES, this abrupt decrease occurs at higher level of BRES (Fig. 5A, B, G, H). In contrast, version 2 showed a peak at BRES=40 if ARES was low and at BRES=60 if ARES was high (Fig. 5C, D). In version 3 no PFT could exist at BRES=20. At ARES=100 maximum diversity was reached even at a higher level for BRES than in version 2 (Fig. 5E, F).

The results for both measures of community diversity, number of surviving PFTs and Shannon-Diversity, closely coincided, but for version 3 at ARES=100, an increase in BRES from 80 to 100 results in a change of number of PFTs but not of Shannon-Diversity (Fig. 5F, L).

3.2.2 Effect of grazing

The effect of different grazing frequencies on diversity clearly depended on resource combination and two general pattern could be distinguished (Fig. 6). Either there was a unimodal, hump-shaped relationship with a peak of diversity at low to intermediate grazing probabilities, or diversity decreased with increasing grazing probability. All model versions consistently predicted a unimodal relation if ARES was lower (Fig. 6B, F, J) and a negative relation if ARES was higher than BRES (Fig. 6C, G, K). For the scenario ARES 50/BRES 50, model version 2 showed a clear peak at intermediate grazing probabilities, while for versions 1 and 3 highest diversity was already reached at comparably low grazing probabilities. At equal, but high resource levels (ARES 100/BRES 100), diversity peaked at intermediate grazing levels for versions 1 and 2, but at low grazing levels for version 3.

Although the response of diversity to grazing probability was similar for the model versions, the levels of diversity were obviously different. In accordance with the results for resource variation (see section 3.2.1), the maximum of diversity across all resource scenarios increased in the order version 1, version 3, version 2. Besides the generally lower diversity in version 1 the increase of grazing probability in the scenario ARES 100/BRES 50 resulted in a sharp decrease of diversity compared to a more gradual decrease in versions 2 and 3.

Remarkably, although there was a positive effect of grazing on diversity for most resource scenarios at least for version 1 and 2 maximum of diversity was observed without grazing at ARES 100/BRES 50. In version 3 the maximum was found at ARES 100/BRES 100 and low grazing probability. Still, this value was lower than the highest value in version 2 without grazing.

Due to the close coincidence between mean number of PFTs and median Shannon-Diversity, boxplots of Shannon-Diversity are not shown here, but given in the appendix. In addition to the response of mean diversity to grazing and resource combination they revealed that variability between replicates can be very high, in particular in model version 1 at intermediate grazing probabilities (Fig. A.1).

Results for different grazing intensities during one grazing event are only shown for resource scenarios where positive effects of grazing on diversity occurred (Fig. 7). In model version 1 lower or higher fractions of above-ground biomass removal did not yield a higher maximum diversity. At ARES 50/BRES 50 low grazing intensity allowed a relatively high diversity at intermediate grazing probabilities (Fig. 7A). Furthermore, there was the trend that higher grazing intensity increases diversity at low grazing

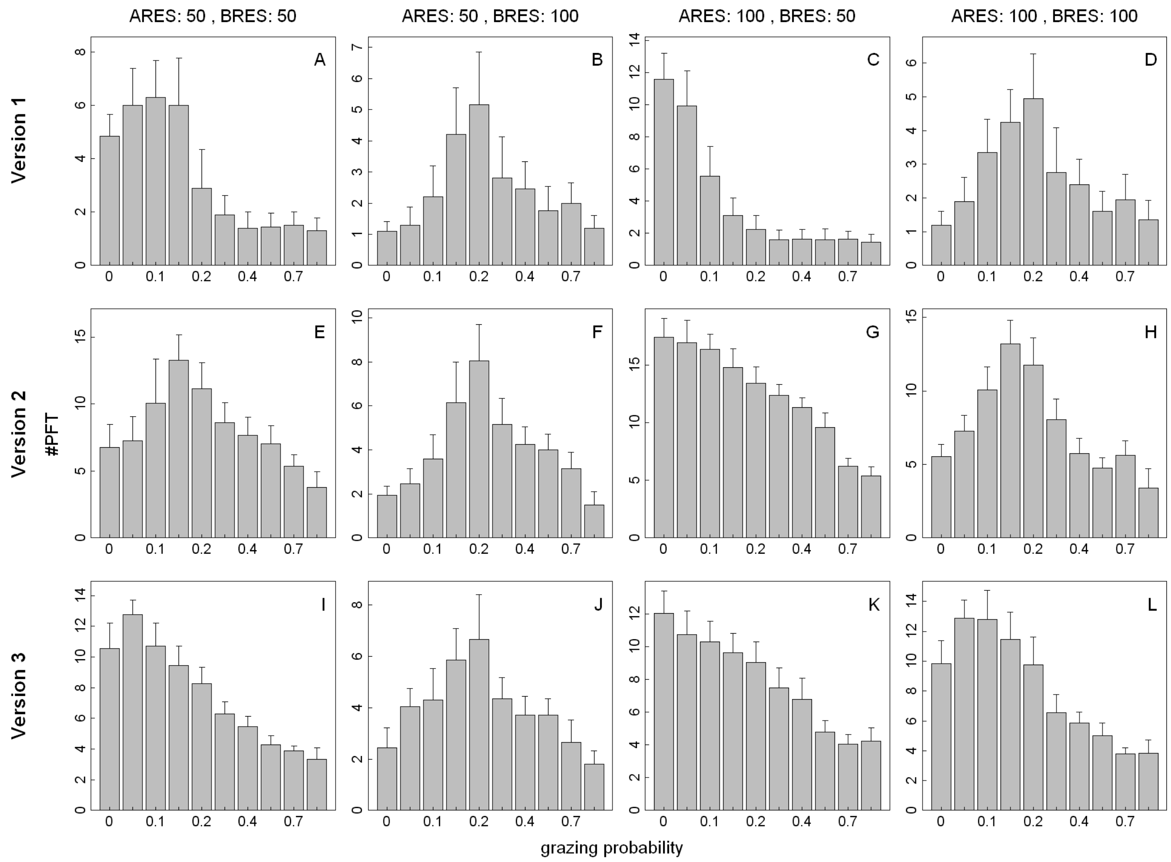

Figure 6. Number of PFTs that coexisted for 100 years along a gradient of grazing probability. Bars and errors represent mean and standard deviation of 20 replicates. Subplots for the same above-ground (ARES) and below-ground (BRES) resource combination are arranged in columns, subplots for the same model version in rows.

probabilities and vice versa.

In model version 2 increasing grazing intensity produced a significantly higher maximum of diversity at intermediate grazing probabilities in resource scenarios where ARES equalled BRES (Fig. 7D, F). The effect of grazing intensity was generally low in version 3.

3.2.3 Effect of gap formation

In contrast to grazing, disturbance by gap formation did not result in clear positive effects on diversity. For scenarios with low levels of both resource types, increasing disturbance intensity reduced diversity in all model versions, but this effect was relatively week in version 3 (Fig. 8A, E, I). If ARES was lower than BRES diversity was very low throughout all model versions. In version 1 only one PFT survived, therefore disturbance could not reduce diversity any more. In version 2 coexistence of two PFTs occurred independently of disturbance intensity and in version 3 diversity tended to decrease with increasing disturbance intensity in (Fig. 8B, F, J). For the resource combination ARES 100/BRES 50, diversity responded negatively to gap formation in model version 1 and 3, but the number of coexisting PFTs was reduced more rapidly in version 1 than in version 3 (Fig. 8C, K). Only in model version 2 low to intermediate disturbance intensities increased diversity compared to scenarios without grazing, but this positive effect disappeared at high disturbance intensity (Fig. 6G, Fig. 8G). Still, the negative effect at intensive gap formation was surprisingly small compared to version 1. For equally high resource levels the number of PFTs showed no significant response besides a weak negative effect at high disturbance intensities in version 3 (Fig. 8D, H, L). Differences in the fraction of area that was disturbed in one event had no clear effect at all.

3.2.4 Effect of spatial heterogeneity

Introducing heterogeneity in the spatial distribution of below-ground resource led to consistent effects on diversity comparing model versions, but to remarkably different effects comparing resource combinations. In general, heterogeneity increased diversity, but this positive effect was not significant in most scenarios. However, for ARES 50/BRES 60 diversity increased considerably in all model versions and in version 2 this effect also appeared for ARES 50/BRES 50 (Fig. 9A, C, E). In version 3 heterogeneity allowed the survival of 4–5 PFTs, even if the spatial average of BRES

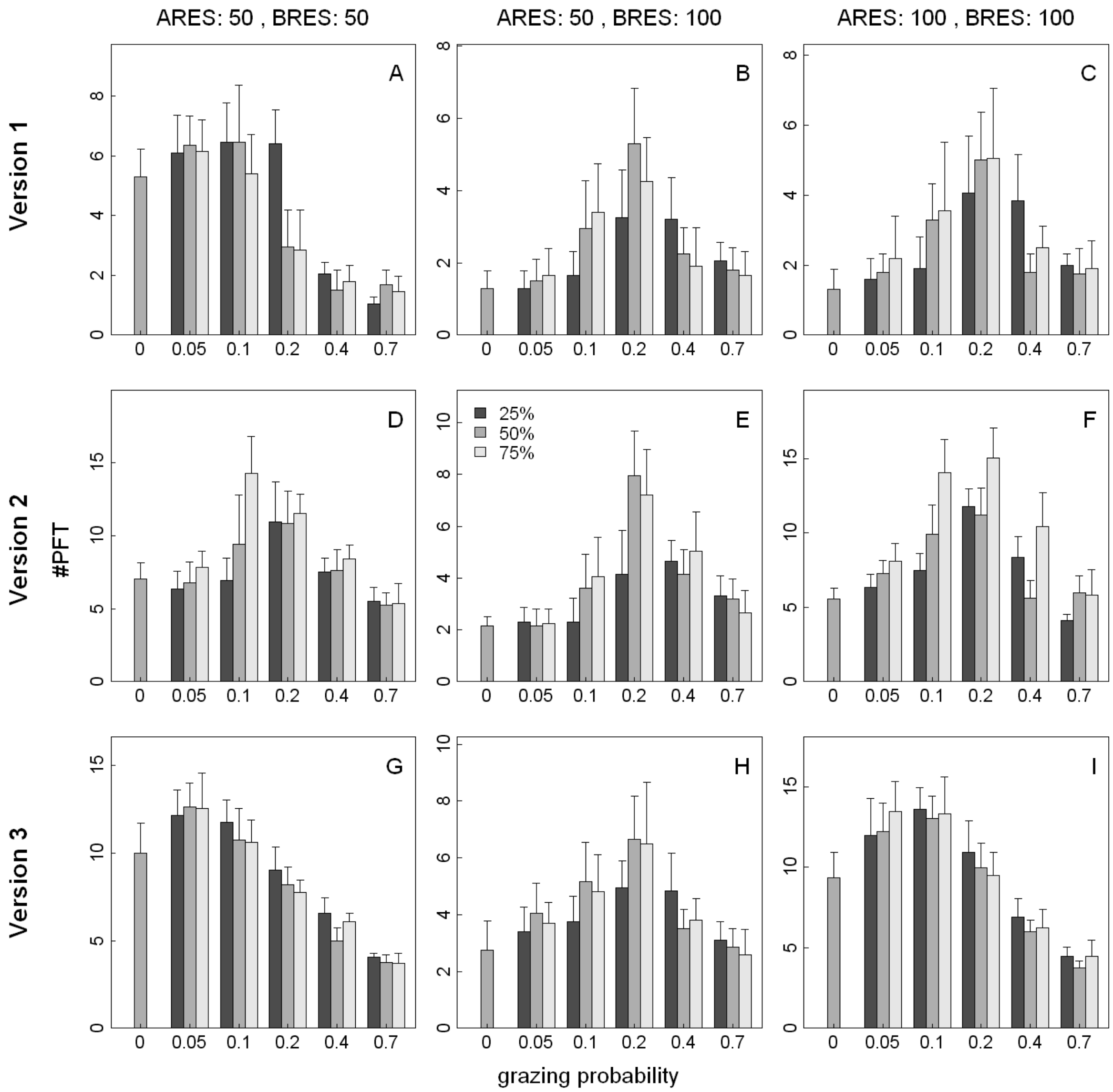

Figure 7. Number of PFTs that coexisted for 100 years along a gradient of grazing probability and different fractions of above-ground biomass removal during a single grazing event.

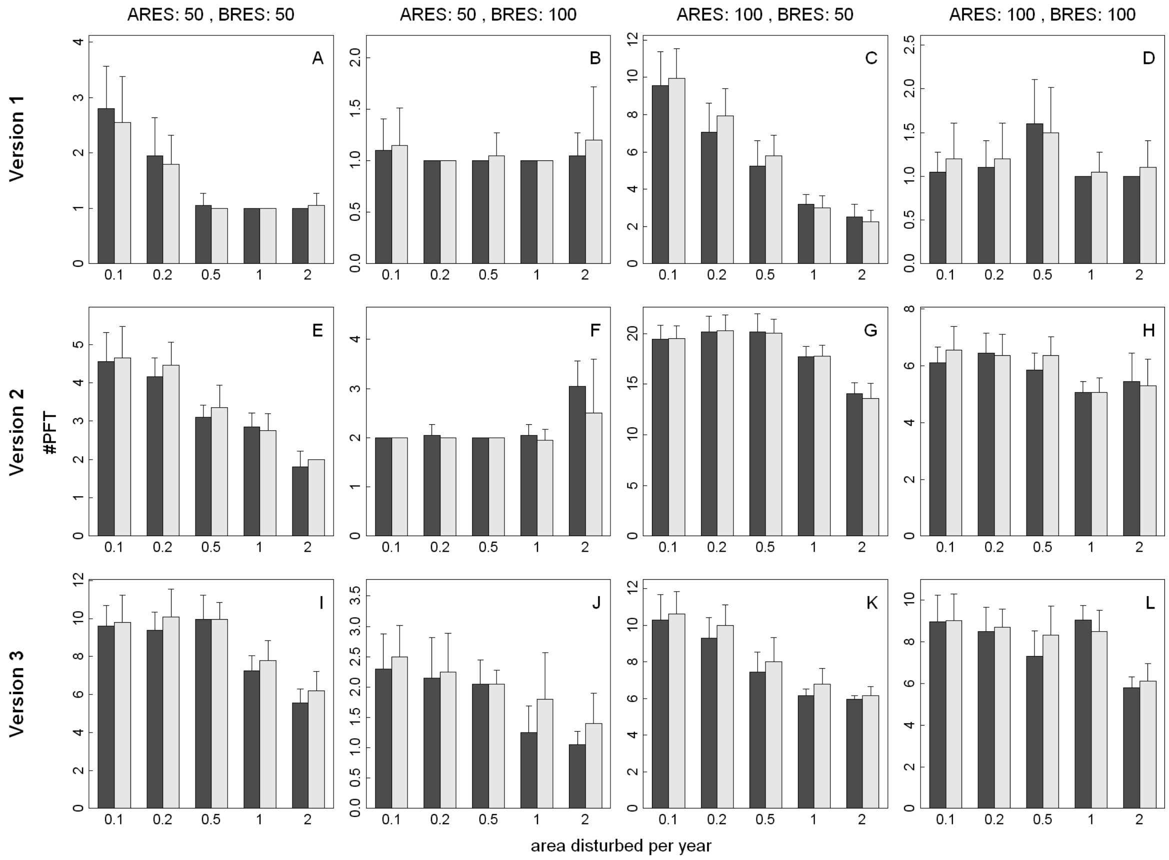

Figure 8. Number of PFTs that coexisted for 100 years for different intensities of gap formation. The area disturbed per year is given as fraction of total grid area. In one disturbance event either 10% (dark grey bars) or 50% (light grey bars) of the grid area were affected and therefore the number of events per year differed. Gaps were circular with a radius of 10 cm. For one event the number of gaps was determined dividing the total area disturbed by the area of one gap.

equalled 20 resource units per cm^2. Though, spatial heterogeneity could not increase the overall maximum of diversity found in version 2 at ARES 100/BRES 60 with the coexistence of 21–22 PFTs (Fig. 9D).

Below-ground spatial heterogeneity combined with grazing scenarios did not alter the general pattern described above. Unimodal or negative responses to increasing grazing probability were preserved for all resource combinations and model versions (Fig. 10). Again, heterogeneity had a strong effect in some scenarios, while in other ones the effect was negligible. This result indicates remarkable interactions between grazing frequency, resource combination and spatial heterogeneity.

Without grazing, heterogeneity did not increase diversity in version 1, but for equal resource levels and intermediate grazing a positive effect occurred (Fig. 10A, D). The same result was found for version 2, but here the positive effect was weak for ARES 100/ BRES 100 and strong for ARES 50/BRES 50. In the latter case diversity increased due to heterogeneity even without grazing (Fig. 10E). A different response was observed in version 3. There, for ARES 50/BRES 50 no effect occurred at all, but for ARES 50/BRES 100 diversity is increased by heterogeneity, with intermediate as well as without grazing (Fig. 10I, J).

The effect of different degrees of spatial autocorrelation, expressed as Hurst-Factor (H) was generally low for the variation of resource levels as well as for the variation of grazing probability, but diversity tended to be slightly higher for higher spatial autocorrelation ($H = 0.8$) and thus larger patches of similar resource availability (compare section 2.3.2, Fig. 2).

3.2.5 Comparison of environmental factors

Previous sections were focussed on the effects of a specific factor or process on community diversity, namely grazing, gap formation and spatial heterogeneity. In the following, the effects of these factors are compared with each other and with the control scenario that did neither incorporate any type of disturbance nor spatial heterogeneity. For this analysis only the maximum values of diversity observed with grazing (Fig. 7), gap formation (Fig. 8) and spatial heterogeneity (Fig. 10) were compared. The exact combination of environmental parameters (i.e. frequency and intensity of grazing/gap formation or degree of spatial autocorrelation) that yielded the maximum of diversity was not considered here.

The comparison between different resource combinations revealed, that the scenario ARES 100/BRES 50 differed remarkably from all the other resource combinations

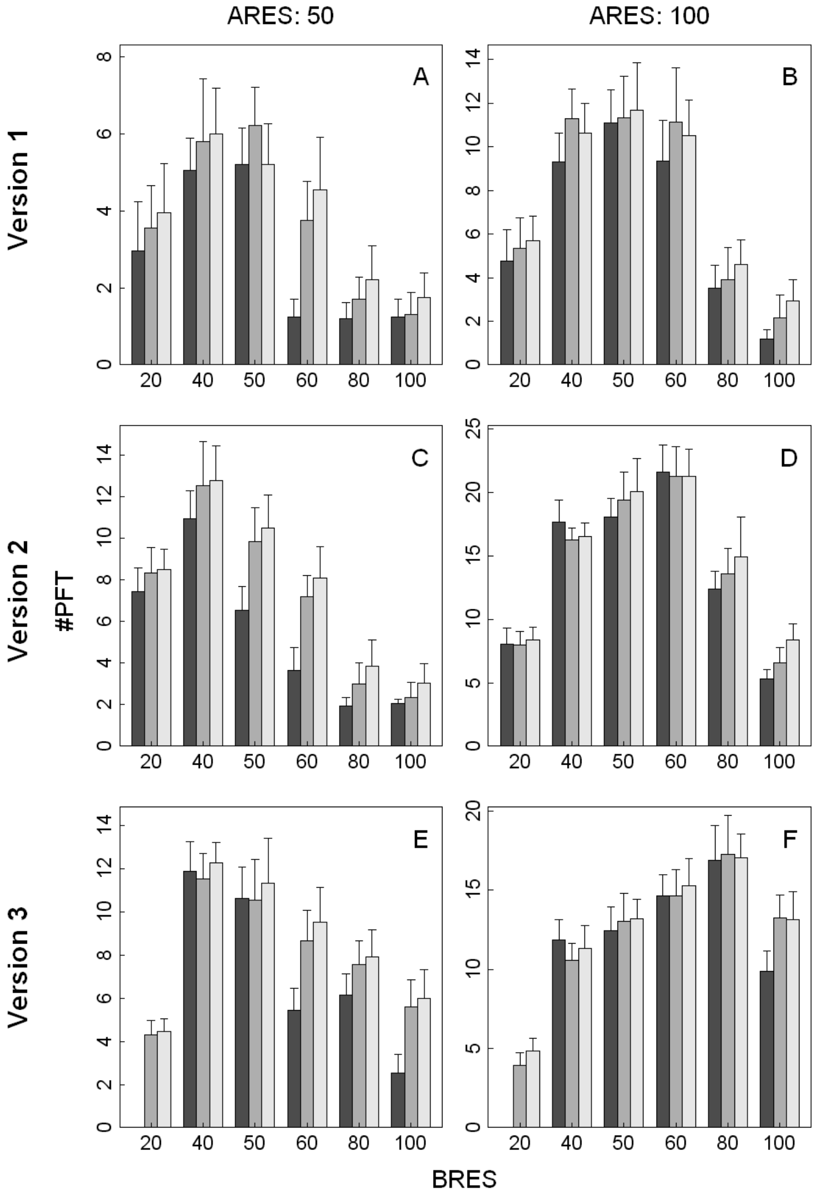

Figure 9. Number of PFTs that coexisted for 100 years for different resource combinations and different degrees of below-ground resource heterogeneity: homogeneous (darkgrey), Hurst Factor 0.2 (grey), Hurst Factor 0.8 (lightgrey)

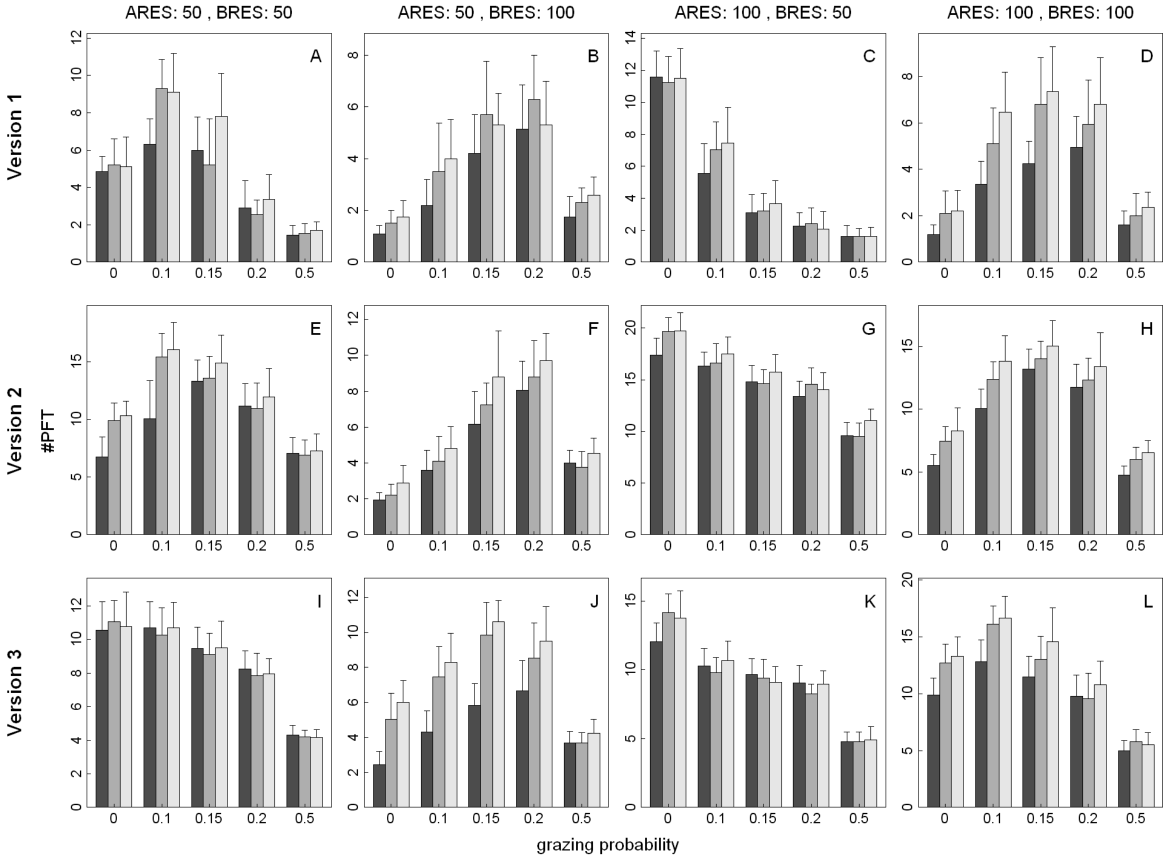

Figure 10. Number of PFTs that coexisted for 100 years for different grazing probabilities and different degrees of below-ground resource heterogeneity: homogeneous (darkgrey), Hurst-Factor 0.2 (grey), Hurst-Factor 0.8 (lightgrey)

with regard to diversity itself as well as the response of diversity towards disturbance and heterogeneity (Fig. 11C). Grazing had no positive effect at all, gap formation led to contrasting results in different model versions and heterogeneity caused only minor effects. Nevertheless, diversity was comparably high throughout all model versions, irrespective of disturbance and heterogeneity. The highest number of coexisting PFTs was found in version 2 and lower, but similar numbers in versions 1 and 3. For model versions 1 and 2 the maximum overall diversity was found with this resource combination. In contrast, in model version 3 diversity was maximised with grazing as well as heterogeneity for the resource combination ARES 100/BRES 100.

In all the other resource scenarios, where ARES equalled or was less than BRES, grazing produced a clear positive response of diversity , but the magnitude of the increase mediated by grazing differed with resource combination and model version (Fig. 11A, B, D). In versions 1 and 3 the effect, measured as difference in the number of coexisting PFTs, was relatively low for ARES 50/BRES 50 (about 1–2 PFTs) (Fig. 11A) and higher for BRES 100 (about 4–5 PFTs) (Fig. 11B, D). In model version 2 diversity strongly increased in all three resource scenarios but the largest effect (approx. 9 PFTs) was also found for ARES 100/BRES 100 (Fig. 11D).

In comparison to grazing, gap formation produced completely contrasting results. Diversity decreased in most scenarios relatively to the control. A significant but weak positive effect was only found for ARES 100/BRES 50 with model version 2 (Fig. 11C).

Heterogeneity without any disturbance did not cause major effects on diversity. Compared to the control scenario an increase of circa 3 PFTs occurred in model version 2 for ARES 50/BRES 50 (Fig. 11A) and in model version 3 for BRES 100 (Fig. 11B, D). For the same scenarios, the joint effect of grazing and below-ground resource heterogeneity yielded an additional increase in diversity. Furthermore this positive interaction of grazing and heterogeneity was found in model version 1 for ARES 50 (Fig. 11A, C).

In general, for the same disturbance regime, but for different resource combinations diversity was lowest for ARES 50/BRES 100, intermediate for equal above- and below-ground resource availabilities and maximal for ARES 100/BRES 50, as mentioned above.

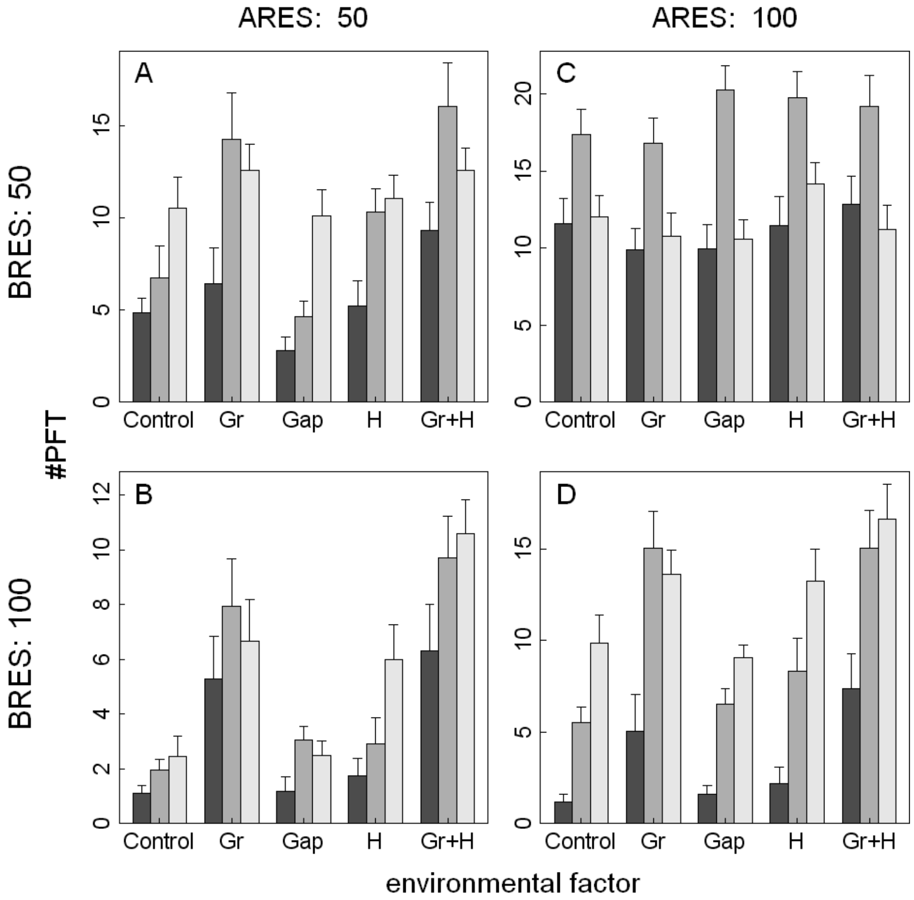

Figure 11. Maximum number of PFTs that coexisted for 100 years for different environmental factors. Control: no disturbance and homogeneous resource distribution; Gr: grazing; Gap: gap formation; H: heterogeneous below-ground resource distribution; Gr+H: grazing and spatial resource heterogeneity. Results for model versions are distinguished by bar colours: version 1 (dark grey); version 2 (grey); version 3 (light grey).

3.3 Community features

Of course, diversity is only one characteristic of a community in an isolated area. In addition to measures of diversity, we evaluated the number of living plant individuals and their standing biomass on the patch. The latter was distinguished in shoot, root and total biomass and calculated as the sum over shoot, root or total masses of all living individuals, respectively. In this section, only results for scenarios with varying resource combinations and without disturbance or heterogeneity are shown. The corresponding data for grazing scenarios are provided in the appendix (Fig. A.6, A.7).

Community biomass did not show a simple positive response to increasing belowground resource availability. For a low level of ARES, total biomass increased from low to intermediate BRES but remained at a high level or even gradually decreased with a further increase of BRES. In versions 1 and 2 a peak of biomass was found at BRES=40, but in version 3 at BRES=60. In all model versions root was higher than shoot biomass at low BRES and vice versa at high BRES. The point where both compartments showed equal biomass consistently coincided with the resource level of maximum total biomass. Obviously the decrease of total biomass predominantly results from a decrease of root biomass, while shoot biomass remained constant or gradually increased in versions 1 and 2. In version 3, the biomass of both plant compartments slightly decreased (Fig. 12A, C, E).

For a high level of ARES, total biomass increased over the whole range of BRES in versions 1 and 2. Again, shoot and root biomass responded differently. The latter approached a constant maximum at BRES=50, while shoot biomass increased continuously. The resource level where shoot became higher than root biomass was found at higher level of BRES than in scenarios with low ARES (Fig. 12B, D). In contrast, total biomass peaked at BRES 80 in version 3 and shoot was higher then root biomass, over the whole gradient, though the difference between both decreased with increasing BRES (Fig. 12F). Remarkably, maximum total biomass at low ARES was higher in version 3 than in versions 1 and 2, but the opposite result was found for high ARES.

With regard to individual number, model versions 1 and 2 again showed very similar response. At low ARES two ranges with relatively constant values occurred. There were 350–400 individuals in the patch up to BRES=40 and approx. 200 individuals for higher values of BRES (Fig. 12G, I). At high ARES a hump-shaped pattern emerged for both versions with a peak at BRES=50 (Fig. 12H, J). Of course in version 3 no

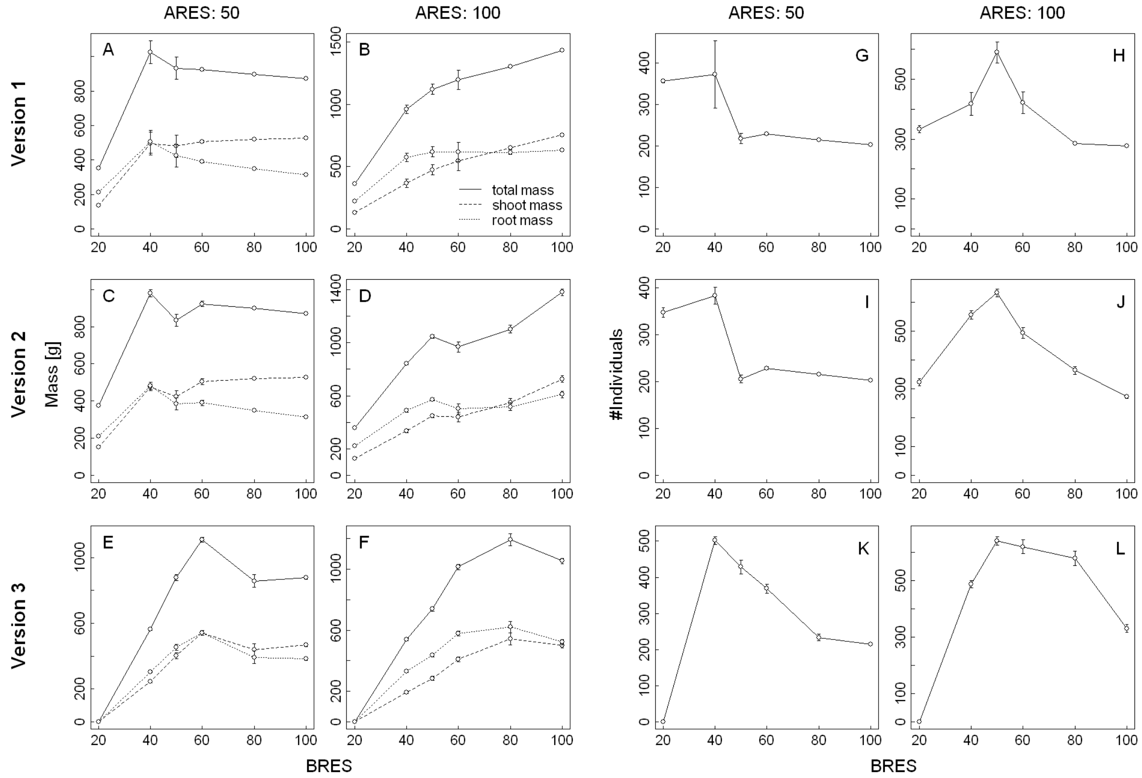

Figure 12. Biomass (above-ground, below-ground and total) and individual numbers for different resource combinations. Data was averaged over the last 25 simulation years. Points and error bars show mean and standard deviation of 20 replicates.

individuals survived at BRES=20. For higher values, there was a negative relation between individual number and BRES if ARES was low and a hump-shaped response, similar to the other versions, if ARES was high. Nevertheless, in the latter case, high individual numbers were found across a broader range than in versions 1 and 2 (Fig. 12K, L).

3.4 Trait composition

In order to gain a better understanding of the diversity pattern presented above, it is useful to identify which PFTs were able to coexist at certain conditions. In this approach PFTs were derived as combinations from a set of plant functional trait attributes and therefore it is possible to describe community composition with respect to the attributes of each trait, instead of analysing the abundances of 72 PFTs. The attribute distribution of all five traits or trait syndromes (see Tab. 3), was analysed with multinomial models (see section 2.3.3). Only results for scenarios with varying grazing frequencies are shown here, while the analogous analysis for trait response to varying resource combinations in the absence of disturbance is provided in the appendix (Fig. A.8).

Maximum plant size

With respect to the trait syndrome of maximum plant size, in the following the terms small, medium and large are used to refer to plants with small, medium and large *maximum* individual size, respectively. In model versions 1 and 2 large plants dominated without grazing, but with increasing grazing probability there was an abrupt shift to small plants (Fig. 13). Only in the scenario with ARES 100/ BRES 50 small plants dominated even without grazing, but all size classes could coexist there. The main difference between these two model versions occurred in the scenario with ARES 100/BRES 100. There, PFTs with medium size were more successful at low to intermediate grazing probabilities in version 2. Furthermore the range for coexistence of small and medium types was broader at ARES 100/BRES 50. The results for model version 3 coincided with the other versions for ARES 50/ BRES 100 and ARES 100/BRES 50, but differed remarkably for equal above- and below-ground resource availabilities. Similar to ARES 100/BRES 50, coexistence of several types was possible and small PFTs were present or even dominant in scenarios without grazing. With increasing grazing probability large and medium PFTs disappeared already at low grazing frequencies.

Growth form

The response of growth form attributes to grazing differed much more between the model versions than the attribute distributions of maximum plant size. In general intensive grazing favoured PFTs with rosettes growth form at all resource combinations, but the results for low and intermediate grazing probability differed considerably (Fig. 14). In version 1 all height classes were almost equally abundant without grazing, if both resources were supplied at a low level. For ARES<BRES, PFTs with erect growth form were dominant, but still all three classes were present. Coexistence of PFTs from all classes also occurred if ARES>BRES, but here already a low increase of grazing probability led to dominance of rosette types. Erect growth forms dominated in the absence of grazing if both resource levels were high and here coexistence of all types was observed at intermediate grazing probabilities. In version 2 these pattern

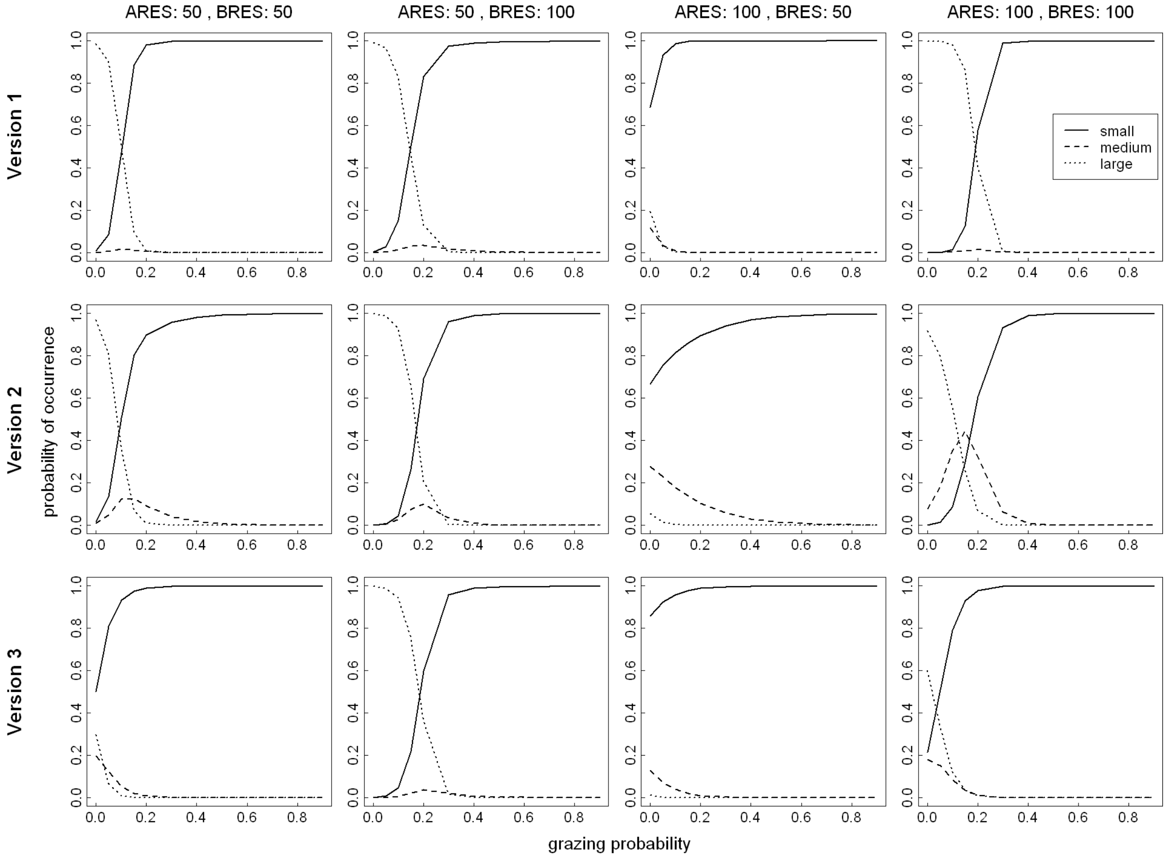

Figure 13. Probability of occurrence for trait attributes of maximum plant size along a gradient of grazing probability. The trait composition of each replicate was averaged over the last 25 simulation years. Multinomial models were fitted to mean values of 20 replicates.

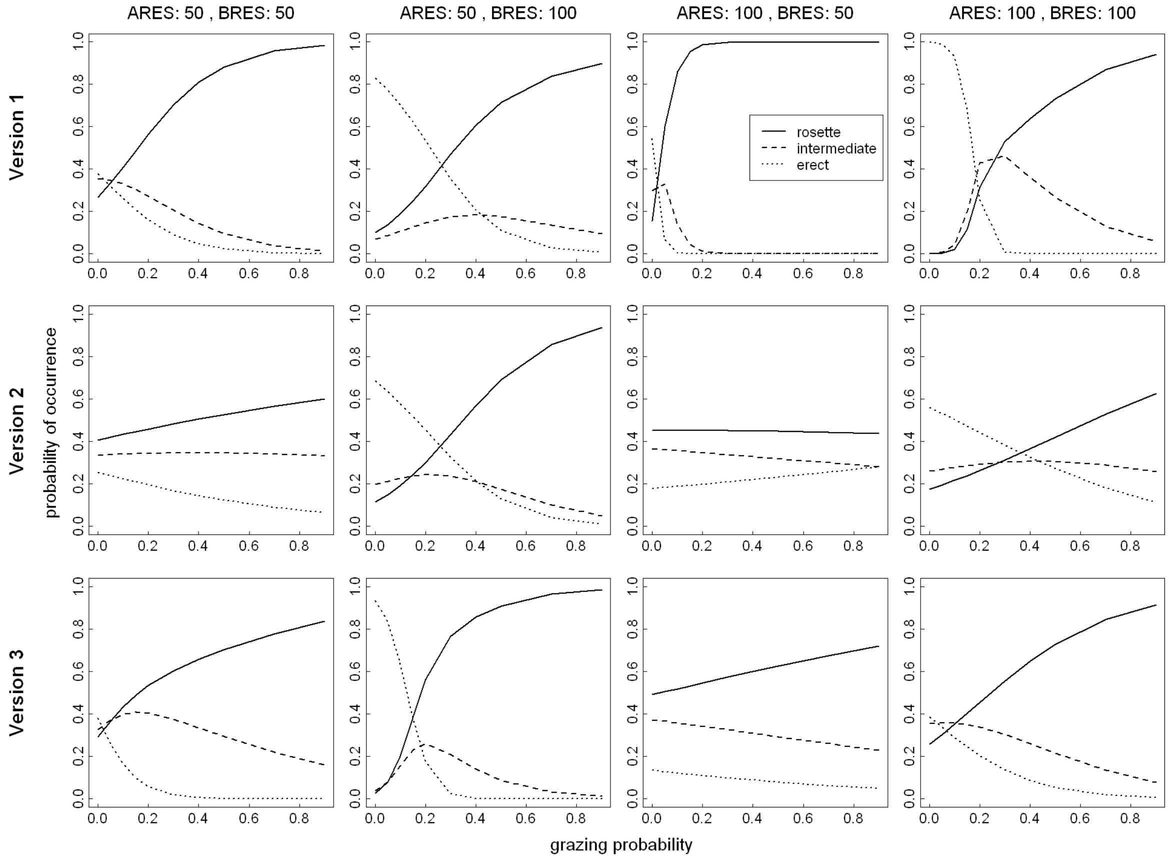

Figure 14. Probability of occurrence for trait attributes of growth form along a gradient of grazing probability. The trait composition of each replicate was averaged over the last 25 simulation years. Multinomial models were fitted to mean values of 20 replicates.

differ remarkably and there coexistence of all three height classes is likely all over the grazing gradient for all resource scenarios, except for ARES 50/BRES 100. In the case of strong below ground limitation (ARES 100/BRES 50) the abundances of trait attributes were even almost constant.

In model version 3 for ARES 50/BRES 100 the dominance of erect PFTs at low and of rosettes PFTs at high grazing probability was increased compared to version 1. In contrast, for ARES 100/BRES 50 the strong dominance of rosettes PFTs disappeared and coexistence of two or three attribute classes was much more likely than in version 1, but less likely then in version 2. For equal but high resource supply at both layers, the results for version 3 were again intermediate compared to the other model versions. Without grazing all growth forms could coexist, but with increasing grazing probability rosettes became dominant.

Resource response

For most resource scenarios the distribution of trait attributes characterizing resource response changed with grazing probability, although the resource availability itself did not change. In model version 1, PFTs with the competitor strategy dominated at low grazing probability, but stress-tolerates were more abundant or displaced competitors with increasing grazing. This change in dominance occurred at very low grazing probabilities for ARES 50/BRES 50 for intermediate at ARES 50/BRES 100 and at severe grazing for ARES 100/BRES 100. Thereby the range of coexistence was relatively wide for ARES 50/BRES 100. In the scenario with strong below-ground limitation (ARES 100/ BRES 50) competitors never survived all over the grazing gradient (Fig. 15). Model version 2 showed almost identical results, except for the scenario ARES 50/BRES 50. There, without grazing competitors and stress-tolerators were equally abundant. For the same resource scenario competitor PFTs disappeared completely in model version 3. Another difference in contrast to the other model versions occurred for ARES 100/BRES 100. For these conditions the range for coexistence was broader and equal probabilities of occurrence for both strategies were found at lower grazing probability than in versions 1 and 2.

Grazing response

The attributes of grazing response were similarly distributed for all resource conditions in version 1. Without grazing the tolerator strategy dominated and usually excluded the avoider strategy (Fig. 16). Only for ARES 100/BRES 50 coexistence between both strategies was possible without grazing. For a grazing probability of 0.3 or higher only the avoider strategy could persist. In general the “niche overlap”, i.e. the range of grazing probability, where individuals with both attributes survived was very narrow. In model version 2 coexistence of both types without grazing was also possible for equal levels of above- and below-ground resource. Furthermore for ARES 100/BRES 50 abundances were much more equal and the range for coexistence was much broader than in model version 1. In contrast to the other traits, here the pattern for the versions 2 and 3 were almost identical.

Dormancy

Dormancy of seeds was the trait with the least response to varying grazing and resource conditions. In model version 1 the non-dormant strategy dominated and only at high

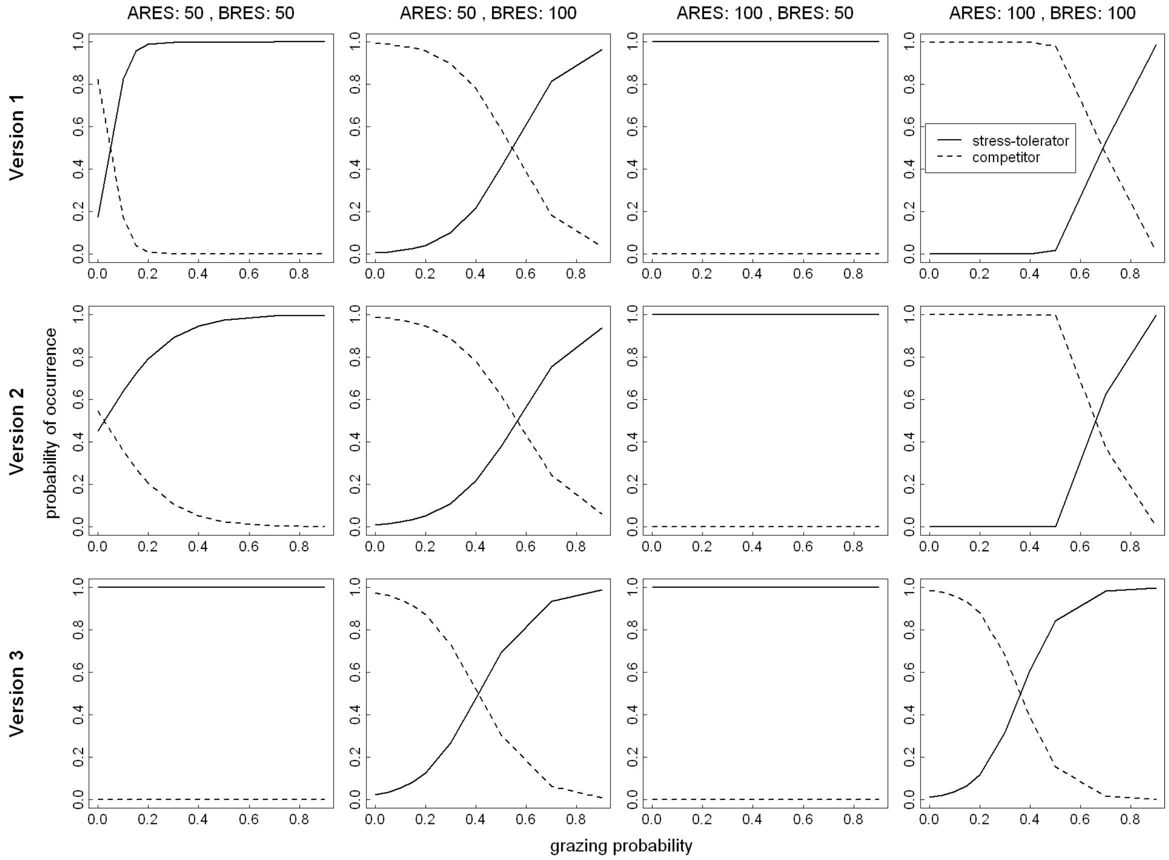

Figure 15. Probability of occurrence for trait attributes of resource response along a gradient of grazing probability. The trait composition of each replicate was averaged over the last 25 simulation years. Multinomial models were fitted to mean values of 20 replicates.

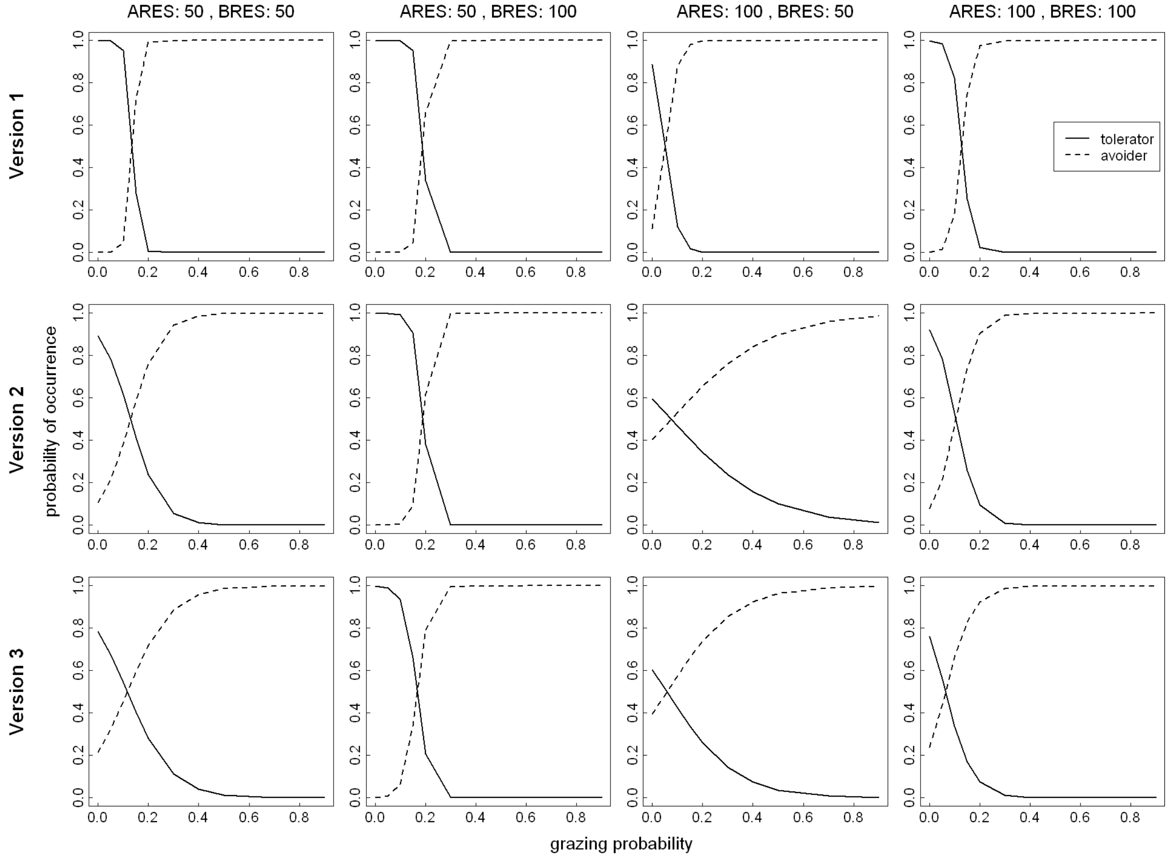

Figure 16. Probability of occurrence for trait attributes of grazing response along a gradient of grazing probability. The trait composition of each replicate was averaged over the last 25 simulation years. Multinomial models were fitted to mean values of 20 replicates.

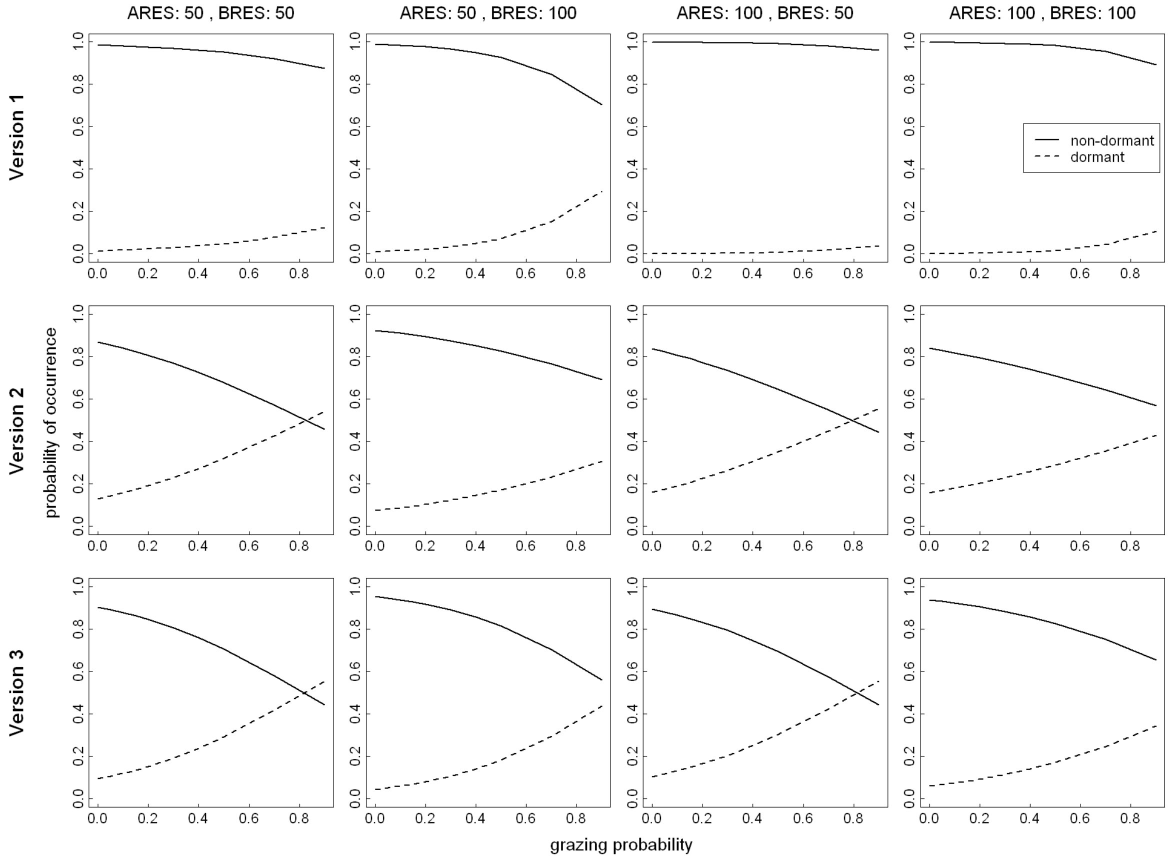

Figure 17. Probability of occurrence for trait attributes of dormancy strategy along a gradient of grazing probability. The trait composition of each replicate was averaged over the last 25 simulation years. Multinomial models were fitted to mean values of 20 replicates.

grazing probabilities individuals with dormant seeds survived. This effect was most pronounced for ARES 50/BRES 100 and weakest for ARES 100/BRES 50. In model version 2, coexistence of dormant and non-dormant PFTs occurred all over the grazing gradient and the probability of occurrence for PFTs with dormant seeds increased with increasing grazing probability. For scenarios with BRES=50, abundances of both strategies were almost equal at maximum grazing frequency. Again, the results for model version 3 coincide more with version 2 than with version 1.

4 Discussion

In this study, we investigated the role of competitive mechanisms and local environmental factors for plant functional trait diversity in temperate grassland communities. For this purpose, we developed a stochastic, spatially-explicit and individual-based simulation model. Individual interactions were modelled in detail, taking into consideration size asymmetric above-ground as well as size symmetric below-ground competition. In order to account for differentiated effects of intra- and interspecific interactions, two distinct concepts of resource niche separation were included in the model.

Besides competitive interactions, we explored the role of environmental factors for grassland diversity. Two types of disturbance, grazing and gap formation, were considered at several levels of frequency and intensity. The effects of disturbance were studied for different resource scenarios, including spatially homogeneous and heterogeneous resource distributions, in order to reveal interactions between the effects of disturbance and resource supply on diversity. Seed input was ignored on purpose, as we explicitly focus on local mechanisms of diversity maintenance in this study.

Community dynamics of a grassland patch of 129 x 129 cm size, were simulated for 100 years at weekly time steps. Simulations started with bare soil and 10 randomly distributed seeds per 72 PFTs.

Without differences between intraspecific and interspecific competition at maximum 11 PFTs coexisted over the simulation time, corresponding to a Shannon-Diversity of 1.6. Including the assumption that effects of resource competition are higher between individuals of the same PFT than between individuals of different PFTs (model version 2), diversity increased up to 22 PFTs or Shannon-Diversity of 2.7 respectively. This overall maximum of diversity was found for a scenario with high above-ground and intermediate below-ground resource availability as well as the incorporation of resource niche separation between PFTs. Neither disturbance nor spatial heterogeneity were activated in the scenario that maximised diversity.

4.1 Cohort development

4.1.1 Self-thinning

The long debate about the shape and the slope of self-thinning trajectories within plant populations started with the study of Yoda et al. (1963), who proposed a linear relation between the logarithms of average plant mass and stand density with a slope of $-3/2$. This value was derived based on experimental data and a simple geometrical model. Subsequent research questioned the generality of this "self-thinning-law" and provided empirical evidence for shallower slope values (Weller, 1987; Zeide, 1987; Weller, 1989; Lonsdale, 1990). In close agreement with these studies, Enquist et al. (1998) and West et al. (1999) derived a value of $-4/3$ by taking into consideration allometric scaling of resource use and metabolic rates rather than pure plant geometry.

With regard to the implications of plant interactions on self-thinning, Stoll et al. (2002) used a ZOI model to demonstrate the influence of competitive size asymmetry on biomass-density relationships. Our approach goes one step further by coupling two resource layers with different degrees of competitive size asymmetry. In the case of partially size-asymmetric above-ground competition (below-ground competition was size-symmetric in all scenarios) the self- thinning slope that emerged in our model, was remarkably robust against changes in resource levels and close to the "classical" value of $-3/2$.

The geometrical derivation of this value is build on the premise that plant area is proportional to the square, while plant mass is proportional to the cube of plant radius (compare Zeide, 1987; Colasanti and Hunt, 1997). At least for each single layer this assumption is fulfilled in our model, because it is implicitly included in the allometric equation used to relate shoot and root mass to the corresponding ZOI area (Eq. 1, 2). In addition, the "$-3/2$ power law" includes two more assumptions: (i) Plant growth and self-thinning maintain complete canopy closure; (ii) All plants of a species or PFT are geometrically similar in shape during all stages of their development and irrespective of environmental conditions (Yoda et al., 1963; Zeide, 1987). While the latter was clearly true in our model as long as only one PFT was used, we found by visual inspection (Grimm, 2002) that the assumption of complete canopy closure was fulfilled at high initial density, but was violated at low density and especially with increasing size asymmetry.

Complete size asymmetry of above-ground competition resulted in significantly shallower self-thinning slopes and stronger non-linearity of the relationship between log(*mean mass*) and log(*individual number*). Strong asymmetry causes high mortality rates of plants that remain smaller due to high local crowding and thus self-thinning proceeds more rapidly (Stoll et al., 2002). Furthermore, the slope value depended on resource levels. Lower above-ground resource availability produced extremely shallow, while lower below-ground resource availability yielded intermediate values of self-thinning slopes. Obviously, shifting resource limitation is able to alter the size asymmetry of competition, which in turn determines the progress of self-thinning.

Remarkably, the different results for partially and completely size-asymmetric competition reveal that even in the case of lower below-ground resource availability, above-ground competition can not be neglected. In agreement to our results, increasing density-dependent mortality and shallower self-thinning slopes with increasing competitive size asymmetry were analytically derived by Adler (1996) and experimentally confirmed by Stoll et al. (2002).

Our simulations of cohort development were intended as a model test, rather than a contribution to the ongoing debate about self-thinning. Nevertheless, the approach is not only able to reproduce realistic self-thinning trajectories, but adds another view on slope values and shapes of self-thinning trajectories. We argue that there is no single, “real” self-thinning slope, because variability including $-3/2$ as well as $-4/3$ can easily arise due to different degrees of competitive asymmetry in plant populations.

4.1.2 Size variation

With the same ZOI model used by Stoll et al. (2002) to simulate self-thinning, Weiner et al. (2001) studied size variation in plant populations for different densities, spatial pattern and degrees of competitive size asymmetry. Our two layer ZOI model is able to reproduce their results and confirmed the increase of size variation with increasing density as well as with increasing competitive asymmetry.

In contrast to the self-thinning slope, size variation was not only influenced by the change between partially and completely size-asymmetric above-ground competition, but in both cases resource combinations showed a significant effect. The lowest size variation emerged for lower below-ground resource availability and vice versa. This result is consistent with our argumentation above, that predominant below-ground limitation reduces the overall size asymmetry of competition.

In contrast to Weiner et al. (2001) we followed cohort development not only over the exponential phase of plant growth, but until individuals have reached their equilibrium mass for the particular resource and neighbourhood conditions. For partial size asymmetry, size variation increased in the beginning, but gradually decreased when plant growth turned towards a logistic trajectory instead of an exponential one. This reduction of variation is possible, because smaller, competitive inferior plants still gain resources from the areas of overlap with their superior neighbours and therefore they can “catch up”, as soon as superior competitors converge towards their maximum mass. Although competition starts earlier and is more intensive at high density, size variation can be similar at the end of the year for different densities. At low density, some individuals will experience strong competition while others will grow almost unaffected by neighbours due to the spatially random arrangement of individuals. At high density, all individuals will experience spatially variable but still relatively severe competition.

In the case of completely size-asymmetric competition inferior individuals do not receive any resource from areas of overlap and are therefore not able to close up to their larger neighbours. Consequently, size variation converges towards a maximum but can not decrease during cohort development and size variation is consistently higher at high density.

For the analysis of size variation, mortality of plants was ignored in order to allow a comparison between our results and the study of Weiner et al. (2001), but as mentioned there, density-dependent mortality or self-thinning respectively, alters size variation. During the process of self-thinning, smaller, competitive inferior individuals die, leaving behind survivors that are more similar in size. In case that model results should be compared to data, it would be necessary to know whether dead individuals were included in plant size distributions or not. With respect to modelling in the ZOI framework, more detailed knowledge would be needed, about the relationship between competitive pressure and mortality rate.

4.2 Grassland patch diversity

4.2.1 Effect of resource availability

In the search for general principles in ecology, the relationship between ecosystem productivity and diversity has been discussed controversially for several decades (Grime, 1973; Huston, 1979; Tilman, 1987; Mittelbach et al., 2001; Tilman et al., 2001). Although no general pattern could be identified, Mittelbach et al. (2001) found in an extensive meta-analysis that for vascular plant communities the hump-shaped relation is the most common one at local to landscape scale.

Our model reproduced a hump-shaped response of PFT number and diversity to increasing below-ground resource availability given a constant above-ground resource supply. According to (Mittelbach et al., 2001), standing biomass is the most widely used indirect measure for productivity in studies at the small scale, but in our simulations, we did not find a simple positive response of total biomass to increasing below-ground resource (Fig. 12) and thus no general hump-shaped relation between biomass and diversity.

However, resource availability within the ZOI area is directly linked to plant growth in our approach (Eq. 10, 14). Therefore, below-ground resource concentration is more closely related to the definition of productivity, as mass increment per time and area, than standing biomass (compare Mittelbach et al., 2001). Taking this into consideration, we argue that our findings provide support for the hump-shaped relationship between productivity and diversity commonly found in plant communities.

Across all model versions, diversity was higher in scenarios where below-ground was lower than above-ground resource availability and plant growth was thus predominantly limited by below-ground resource uptake. Furthermore, the peak of diversity occurred at a lower level of below-ground resource, given a lower above-ground resource supply. Both results suggest that on the one hand increasing productivity, due to increasing below-ground resource, allows survival and coexistence of more PFTs, but on the other hand an increasing importance of size-asymmetric (above-ground) competition favours competitive exclusion and reduces diversity.

The introduction of niche separation in model versions 2 and 3 clearly increased community diversity. While in version 2 interspecific competitive effects are explicitly reduced relative to intraspecific effects (Eq. 6), in version 3 only the amount of available below-ground resource is changed as a function of the number of PFTs that cover a cell (Eq. 7). Above we argued that low below-ground resource availability is able to facilitate coexistence, because of reduced size asymmetry of competition. Nevertheless, the reduction of below-ground resource alone is not able to explain the increase of diversity between model versions 1 and 3, as the maximum of diversity observed in version 3 is significantly higher than in version 1. The assumption included in model version 3 effectively translates into higher resource stress of individuals that compete with conspecifics compared to individuals that compete with heterospecifics (compare section 2.1.4, pg. 18). In addition to the decrease of below-ground resource availability, this relative difference between intraspecific and interspecific competition is responsible for the higher diversity in model version 3.

4.2.2 Effect of grazing

Two different effects of varying grazing frequencies and intensities were found in our simulations. For most resource combinations a hump-shaped relation emerged, but for predominant below-ground limitation diversity responded negatively to grazing. Both pattern have been known previously and were conceptually unified in the dynamic equilibrium model of Huston (1979, 2004), which predicts a unimodal response of diversity to grazing for intermediate population growth rates and a negative response in case of low growth rates. Indeed, both types of grazing response were found in grasslands, but even across a wider range of terrestrial and aquatic ecosystems (reviewed by Olff and Ritchie, 1998; Proulx and Mazumder, 1998). These studies provided support for the reversed effect of grazing in nutrient-poor vs. nutrient-rich environments.

In the context of the dynamic equilibrium hypothesis, the positive effect of grazing on diversity has been explained by its negative effect on dominant species. Even if grazing was not selective towards plant species or traits, repeated reductions of biomass or abundance of all species could prevent the exclusion of competitive inferior species, because a competitive equilibrium would be never reached (Huston, 1979). In reality, grazing is often selective towards plant traits related to high growth rates and high competitive ability, e.g. high specific leaf area (SLA), large plant size and height (Olff and Ritchie, 1998; Lavorel et al., 1999; Bullock et al., 2001; Díaz et al., 2001; Westoby et al., 2002). Selective grazing can act as a buffering mechanism preventing the dominance of superior competitors and the exclusion of competitive inferior plant types or species respectively (Jeltsch et al., 2000).

Although the pattern we identified correspond to Huston's concept, his explanation does not completely apply in our case. Of course, a reduction of below-ground resource availability causes a decline of individual was well population growth rates, but in the case of low resource availabilities in both layers, Huston's model predicts a negative response to grazing, while we found a hump-shaped relation. Besides, grazing does not reduce population density directly in our model, but rather reduces above-ground biomass of individuals.

Therefore, we argue that grazing does not facilitate coexistence in grassland systems because it reduces competition in general, but rather because it reduces the effect of above-ground relative to below-ground competition. The shift from dominant light to nutrient competition mediated by grazing was previously supported by Olff and

Ritchie (1998). Our model provides a mechanistic test for this hypothesis and offers the more detailed explanation that grazing reduces size asymmetry of competition and in this way facilitates coexistence.

With respect to trait responses towards grazing, our simulation results are in line with empirical studies. Increasing grazing pressure favours PFTs with small maximum size, a rosette growth form and low palatability (Lavorel et al., 1999; Díaz et al., 2001; Kahmen, 2003; Kahmen and Poschlod, 2004).

Remarkably, also the attributes of the trait-syndrome “resource response” change with increasing grazing frequency. As explained above, this trait syndrome includes a trade-off between growth rate at high resource levels and mortality rate at low resource levels (compare section 2.2). In the case of low size asymmetry of competition, due to predominant below-ground resource limitation, only “stress-tolerant” PFTs occurred, as the disadvantage of low growth rate was obviously outweighed by low mortality at these environmental conditions. Taking this into consideration, the change from “competitor” to “stress-tolerator” strategy with increasing grazing frequency in the other resource scenarios supports our conclusion, that grazing alters the degree of competitive size asymmetry.

4.2.3 Effect of gap formation

In contrast to previous modelling studies, disturbance, implemented as small scale gap formation in both vegetation layers, did not yield a clear positive effect on diversity in our simulations (compare Schippers et al., 2001; Plotnick and Gardner, 2002; Kahmen, 2003; Johst and Drechsler, 2003; Johst and Huth, 2005). The facilitation of coexistence by gap formation, has been commonly explained based on a trade-off between competitive and colonization ability (Levins and Culver, 1971; Tilman, 1994; Amarasekare, 2003). Bare gaps provide new space for establishment and in case of a competition-colonization trade-off individuals of competitive inferior species reach open sites faster and can therefore escape competitive exclusion by recruitment in these gaps.

In our approach the competition-colonization trade-off is included in the trait syndrome for maximum plant size. PFTs that can grow larger are superior competitors, but PFTs with small maximum size have smaller seeds and therefore higher fecundity as well as a higher mean dispersal distance (section 2.2, Tab. 3). However, gap formation in combination with the competition-colonization trade-off did not increase diversity in our model for two different reasons:

(i) Patch occupancy models, which predicted coexistence mediated by the competition-colonization trade-off, include the assumption of a fixed competitive hierarchy in the sense that superior competitors always can displace inferior ones in occupied cells, irrespective of the life stage of competing individuals, while inferior competitors do not have any effect on superior ones (Tilman, 1994). This assumption is not fulfilled in our model, as germination within the above-ground ZOI of established individuals is not allowed for any PFT and established individuals have higher competitive effects on seedlings at least in the case of size-asymmetric competition due to higher shoot mass of adult plants. Furthermore, even for partially size-asymmetric competition resource uptake of all competing individuals is reduced and therefore competitive inferior individuals do have at least a small negative effect on superior ones. Several studies showed that the competition-colonization trade-off can not explain coexistence if a lottery competition is used (Yu and Wilson, 2001; Kisdi and Geritz, 2003) or if only partial competitive asymmetry is assumed (Levine and Rees, 2002).

(ii) Even though there is distance-limited dispersal in our model, mean and variance of the dispersal kernels used, are relatively high compared to the small spatial extent of 1.29 x 1.29 m (compare Tab. 3). Therefore, seeds of abundant PFTs are easily dispersed all over the patch, irrespective of seed weight. Due to this reason gaps are not able to provide safe sites for recruitment of inferior competitors, as there is not sufficient recruitment limitation of superior competitors (Tilman, 1997; Turnbull et al., 2000; Potthoff et al., 2006).

Nevertheless, even if our parameter values for fecundity, germination rates and dispersal distances do not correspond to real species, they are adopted from a range that is realistic within temperate grassland communities (Eriksson and Jakobsson, 1998; Kahmen, 2003; Kahmen and Poschlod, 2004). Likewise the assumption of a fixed dominance hierarchy between species is obviously unrealistic for competition between individuals, as seedlings will not be able to displace established adults. Therefore, we conclude that the competition-colonization trade-off in combination with gap formation is unlikely to be an important *local* mechanism of diversity maintenance in the system under consideration.

Schippers et al. (2001) investigated plant strategies in disturbed grassland habitats based on three plant functional traits. They applied a lottery system for seedling competition and therefore they did not find coexistence due to a competition-colonization trade-off, according to the argumentation above. Instead, PFTs with non-dormant and dormant seeds coexisted at low to intermediate disturbance intensity and PFTs with dormant seeds dominated at intensive disturbance.

In our case, dominance of PFTs with dormant seeds was never observed and coexistence between both strategies occurred primarily in versions 2 and 3 or at very high grazing frequency. Apparently, in our model coexistence between dormant and non-dormant PFTs is not satisfactory explained by the trade-off between seed longevity and annual germination rate, but rather caused by the incorporation of resource niche separation in model versions 2 and 3. The reason between the different results of Schippers' and our model is explained by a different timing of seed germination. In Schippers' approach there was a fixed order of disturbance and germination processes within the year. Dormant seeds were allowed to germinate directly after a disturbance event, before non-dormant seeds were dispersed and could germinate. Thus, seedlings with the dormant strategy could avoid the competition with non-dormant ones in time. In our model disturbance events can occur over the whole vegetation period, but even more important germination in autumn is scheduled after seed dispersal of all PFTs and therefore seedlings with different strategies can not avoid the lottery competition with each other. Obviously in this case a higher annual germination probability is the superior strategy.

Correspondingly to the competition-colonization trade-off that only facilitates coexistence if there is spatial separation of intra- and interspecific, strategies of dormancy vs. non-dormancy are not able to coexist per se, but only if temporal separation is possible (Amarasekare, 2003; Roxburgh et al., 2004).

4.2.4 Effect of spatial heterogeneity

The introduction of below-ground resource heterogeneity did not produce a consistent response of diversity. For particular combinations of resource availability and grazing frequencies the number of coexisting PFTs increased remarkably, but for other environmental conditions only minor or no effects occurred at all.

In scenarios with resource variation but without grazing, we found a clear positive effect at low above-ground and intermediate below-ground resource availability (Fig. 9). For these conditions diversity increased, because spatial heterogeneity enhanced coexistence of PFTs with different trait attributes of “resource response” compared to homogeneous resource distribution.

In the case of activated grazing, the effects of resource heterogeneity could not be explained by the response of one single trait and besides “resource response”, the attribute distributions of maximum plant size and growth form were also changed.

Interactions between grazing frequency, resource availability and spatial distribution arise, because all three factors influence the degree of competitive symmetry.

Overall, the effect of heterogeneity was relatively small and was not able to maintain higher diversity than the factors discussed before. In contrast to other studies, we considered heterogeneity on a scale smaller or equal to the spatial range of competitive interactions between individuals. In models where spatial heterogeneity was identified as main mechanism of diversity maintenance, environmental differences between patches were assumed, while competition was only considered within patches (Plotnick and Gardner, 2002; Levine and Rees, 2002).

4.3 Synthesis and conclusions

In our approach all environmental factors investigated could potentially influence diversity. Furthermore, different factors produced interactive, rather than simple additive effects. Despite these numerous potential drivers of grassland diversity, we found that coexistence of PFTs in our model system can be mainly explained based on two mechanisms only. On the one hand diversity increased with decreasing competitive size asymmetry, on the other hand separation of resource niches between PFTs enhanced coexistence.

Size symmetry of competitive interactions results from predominant root competition, but it does not matter whether the latter is caused by prevailing nutrient/water limitation or the reduction of shoot competition due to the removal of above-ground biomass, e.g. by grazing. With increasing importance of below-ground competition, plant attributes as shoot height and shoot mass become negligible with respect to competitive effects of plants on each other. In the case that competitive effects are considered per unit of ZOI area, even root mass can be neglected. This is the reason why PFTs with different attributes of growth form and maximum size coexisted in scenarios with dominant below-ground limitation or with intermediate grazing.

In addition to reduced size asymmetry of competition, resource niche separation between PFTs remarkably increased diversity, caused by the relative decrease of interspecific compared to intraspecific competition. With respect to resource competition, this shift was implemented a priori in the rules for competitive interactions at the individual scale, but obviously these assumptions effectively translate into a different structure at the community scale.

Theories of competitive coexistence suggest that life history trade-offs are able to produce spatial or temporal separation of intra- vs. interspecific competition and thus may enable coexistence. However, we did not find these effects in our model and obviously they depend on the characteristics of the system and the plant species or types under investigation. Therefore, trade-offs between species, expressed as contrasting trait attributes, can not be interpreted as niche separation in general, but rather their potential to allow niche separation and coexistence has to be considered in detail.

Following the framework described by Chesson (2000b), diversity can be maintained by two different types of mechanisms: "Equalizing mechanisms" reduce differences in fitness between individuals or species, while "stabilizing mechanisms" increase the negative effect of intraspecific relative to interspecific interactions. Both mechanisms identified to be responsible for grassland diversity in our approach can be interpreted accordingly. Size-symmetric competition can be clearly classified as "equalizing mechanism", while the separation between intra- and interspecific resource competition explicitly included in model version 2 and 3 offers the potential for stabilizing effects. Indeed, large positive effects of resource niche separation were observed for scenarios with either strong below-ground limitation or reduction of above-ground competition by grazing. These results completely correspond to a statement of Chesson (2000b, pg. 347): "In the absence of the stabilizing term, equalizing mechanisms can, at best, slow competitive exclusion; but in the presence of stabilizing mechanisms, equalizing mechanisms may enable coexistence."

In general, our study shows that size asymmetry of competition does not only structure populations, but has important implications for the key question of diversity maintenance. Considering the interaction between above- and below-ground competition and their particular features sheds new light on patterns of diversity as the reversed effect of grazing in nutrient-poor vs. nutrient-rich habitats as well as the relationship between diversity and productivity. We conclude that a more detailed knowledge about mechanisms of interaction at the individual scale will improve our understanding of species diversity and its response to environmental drivers.

4.4 Prospects

We showed that it is possible to explain diversity pattern at the small scale by local conditions and processes only. On purpose we did not consider seed immigration as an explanation for diversity maintenance, as there is still an ongoing debate about the role of recruitment limitation and its relation to environmental conditions within grassland ecosystems (Turnbull et al., 2000; Foster, 2001; Vandvik and Goldberg, 2006). Nevertheless, our model concept theoretically allows coupling the dynamics of several patches via seed exchange. In this way processes could be studied at the scale of metacommunities (Leibold et al., 2004) and interactions between local and regional processes as well as the effects of environmental heterogeneity on a scale between patches could be explored.

We suggested that grassland diversity is primarily maintained by size symmetry of competition on the one hand and resource niche separation one the other hand. While the requirement of low size asymmetry can be explained by prevailing below-ground competition, we a priori assumed niche separation at the individual scale without defining a particular mechanism. But of course trade-offs between species related to resource uptake and utilization are a prerequisite for the hypothesized niche separation. Therefore we subscribe the conclusion of Silvertown (2004), who expressed a strong need for further and more sophisticated research in order to identify axis of niche separation within plant communities and thus gain a better understanding for mechanisms of coexistence.

In the scope of this study, our model results have been tested against general pattern, which have been observed in several studies, rather than against quantitative data for a particular system (Grimm et al., 1996, 2005). In further applications, model parameters for plant traits as well as for environmental conditions could be derived from measured data and our hypothesis could be validated with community data of specific sites.

Especially in combination with real data, the concept of plant functional traits offers further potential. In this study we primarily focussed on the response of trait diversity to environmental conditions and we only briefly addressed the relationship between productivity and diversity. Nevertheless, functional traits related to species effects on ecosystem functioning could be easily incorporated (see Lavorel and Garnier, 2002). In this way the model could be extended in order to address the questions how environmental drivers influence ecosystem functions, e.g. the flow of energy and matter or the resilience of grassland ecosystems against large scale disturbances, and how these functions are related to diversity.

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A Appendix

A.1 Shannon-Diversity

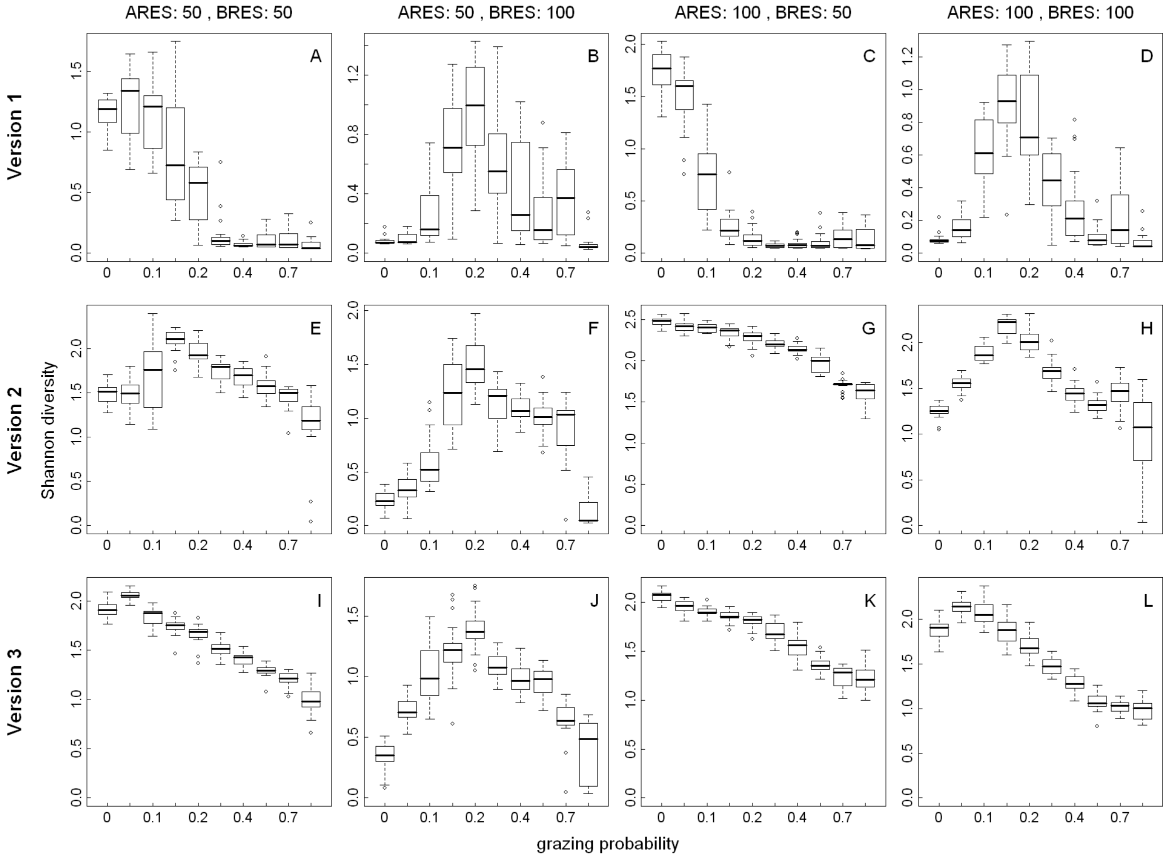


Figure A.1. Shannon-Diversity along a gradient of grazing probability. Boxplots represent mean values over the last 25 simulation years of 20 replicates. Subplots for the same above-ground (ARES) and below-ground (BRES) resource distribution are arranged in columns, subplots for the same model version in rows.

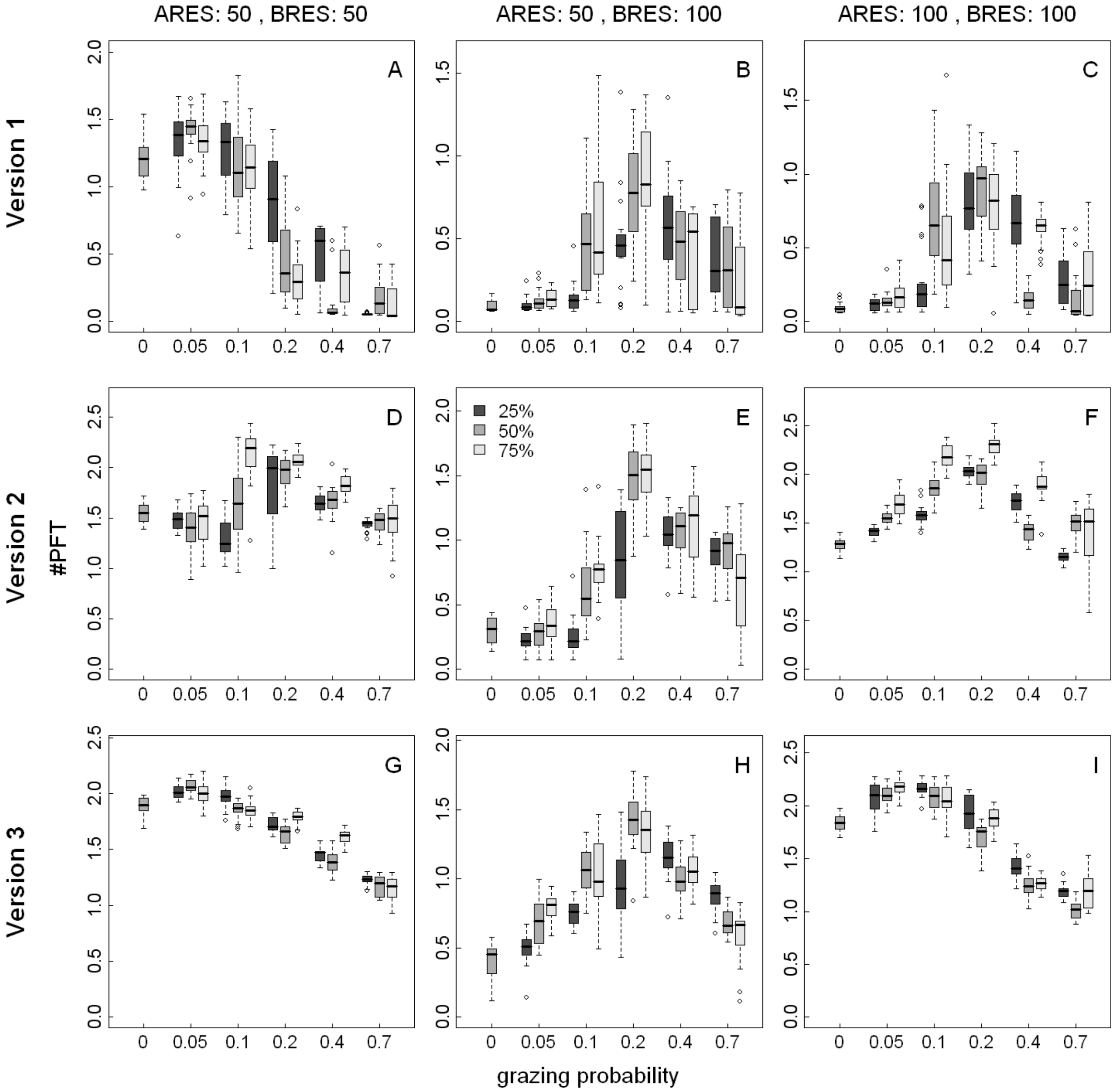


Figure A.2. Shannon-Diversity along a gradient of grazing probability and different fractions of biomass removal during a single grazing event.

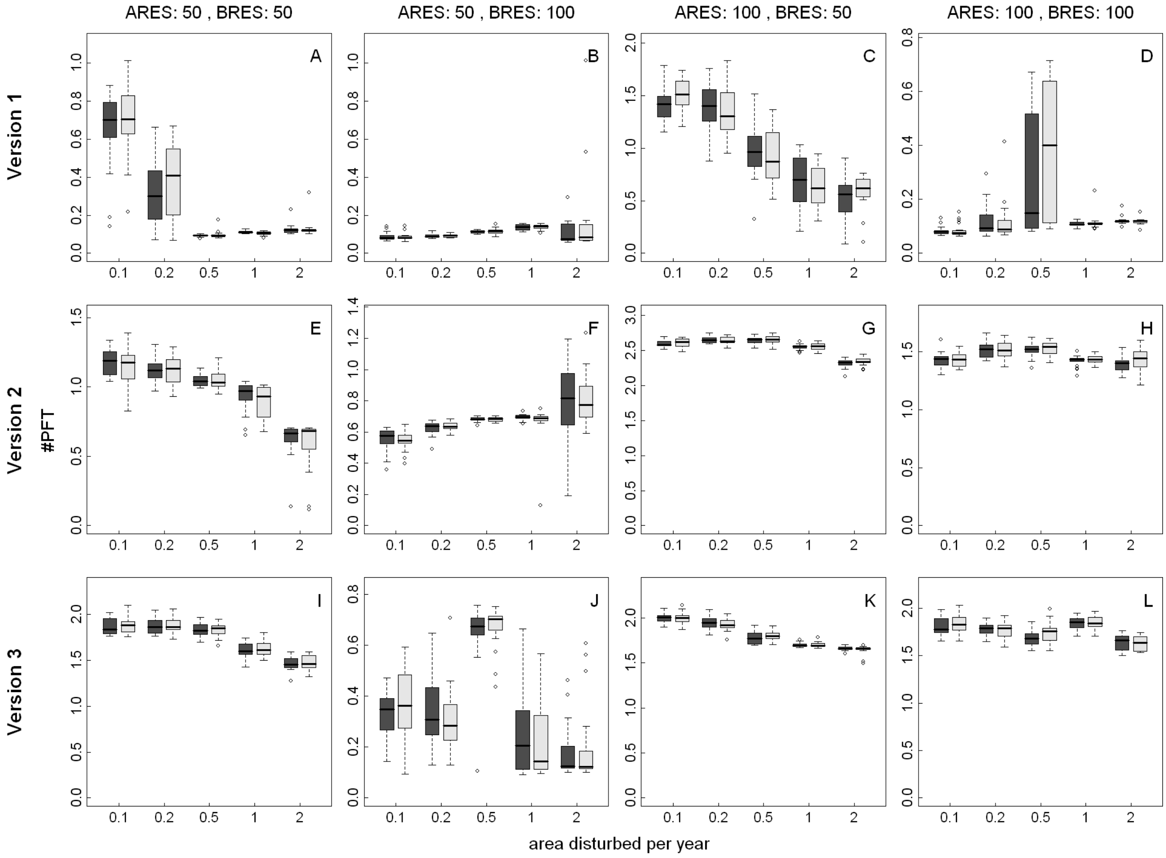


Figure A.3. Shannon-Diversity for different intensities of gap formation. The area disturbed per year is given as fraction of the grid area. In one disturbance event either 10% (dark grey bars) or 50% (light grey) of the grid area were affected. Gap disturbances were circular with a radius of 10 cm. For one event the number of gaps was determined dividing the total area disturbed by the area of one gap.

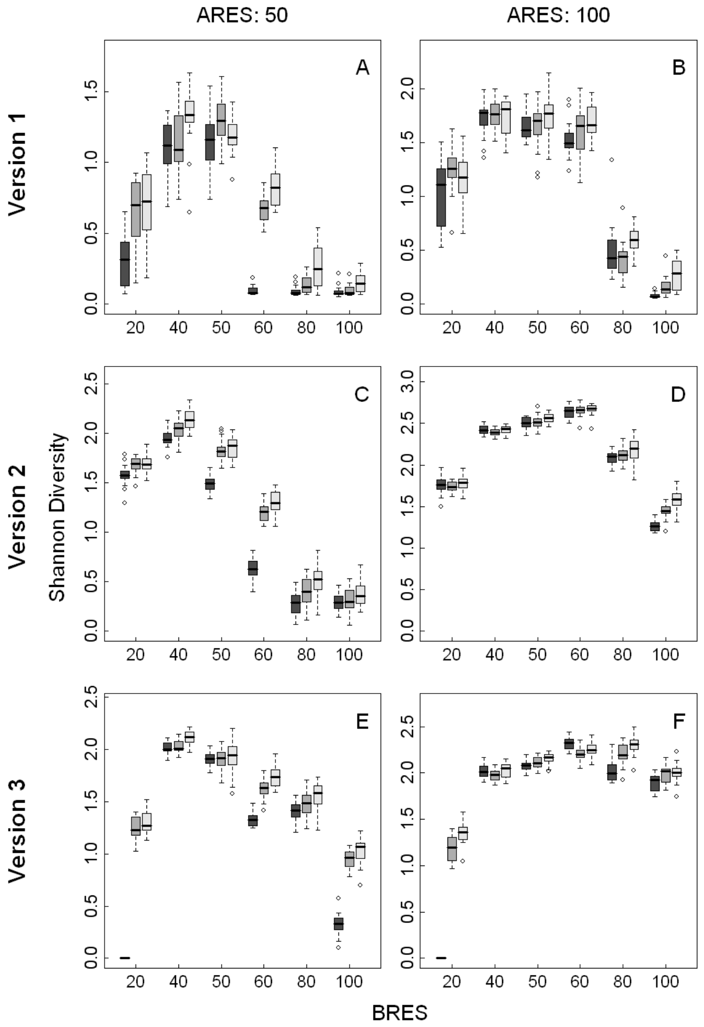


Figure A.4. Shannon-Diversity at different resource combinations and different degrees of below ground resource fragmentation: homogeneous (darkgrey), Hurst Factor 0.2 (grey), Hurst Factor 0.8 (lightgrey)

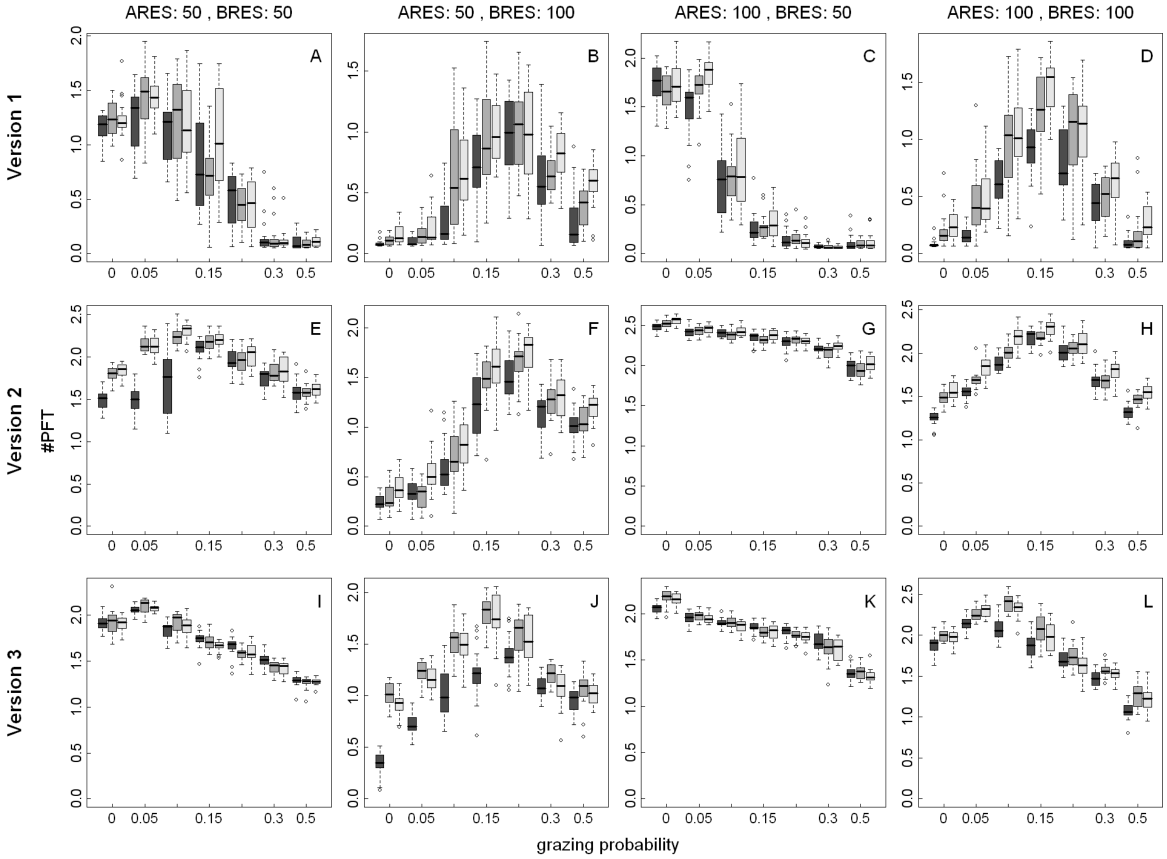


Figure A.5. Shannon-Diversity for different grazing probabilities and different degrees of below ground resource fragmentation: homogeneous (darkgrey), Hurst Factor 0.2 (grey), Hurst Factor 0.8 (lightgrey)

A.2 Community data

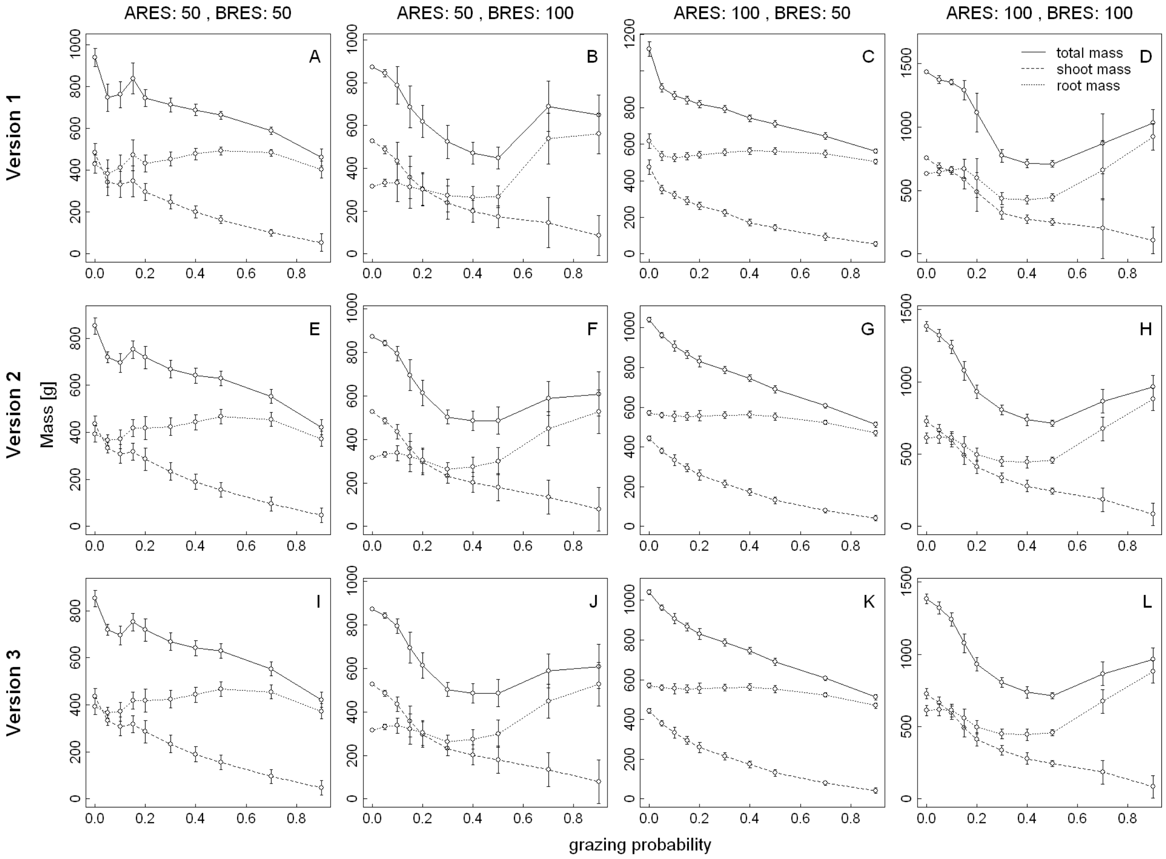


Figure A.6. Biomass (above-ground, below-ground and total) along a gradient of grazing probability. Data was averaged over the last 25 simulation years. Points and error bars show mean and standard deviation of 20 replicates.

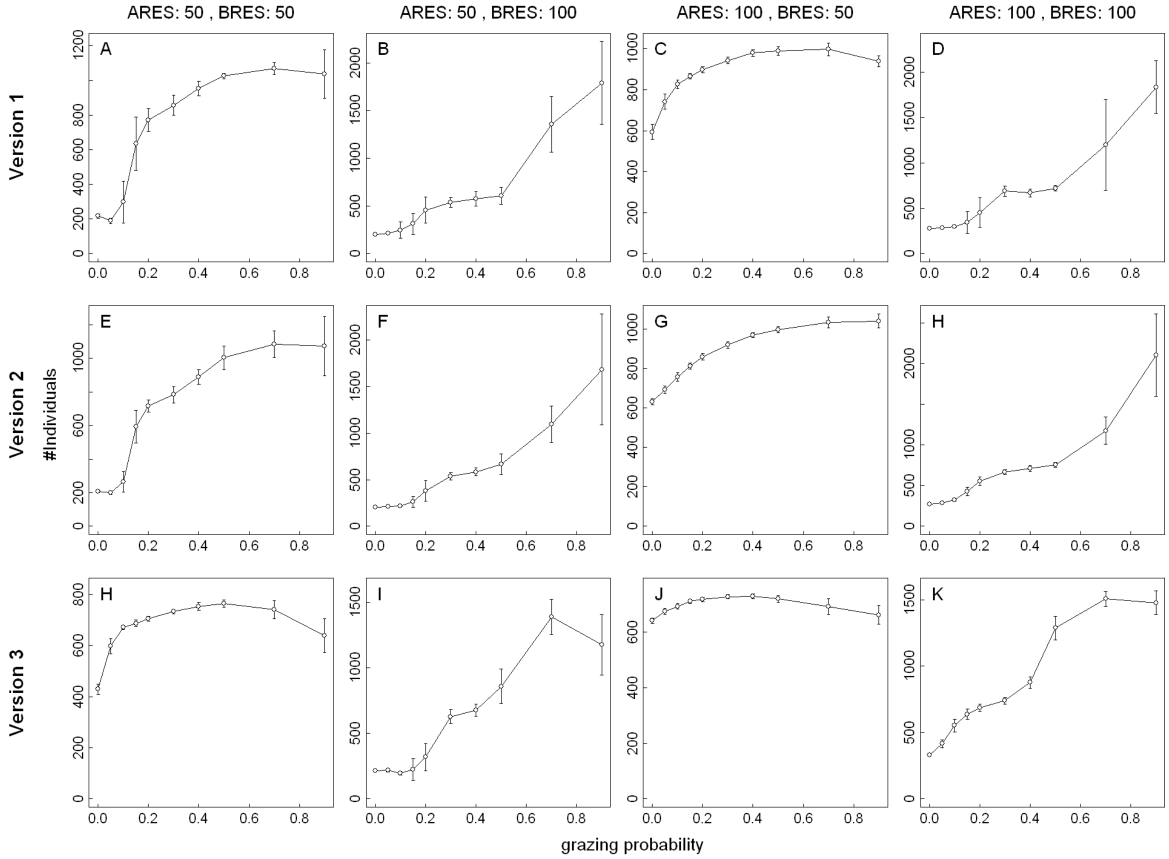
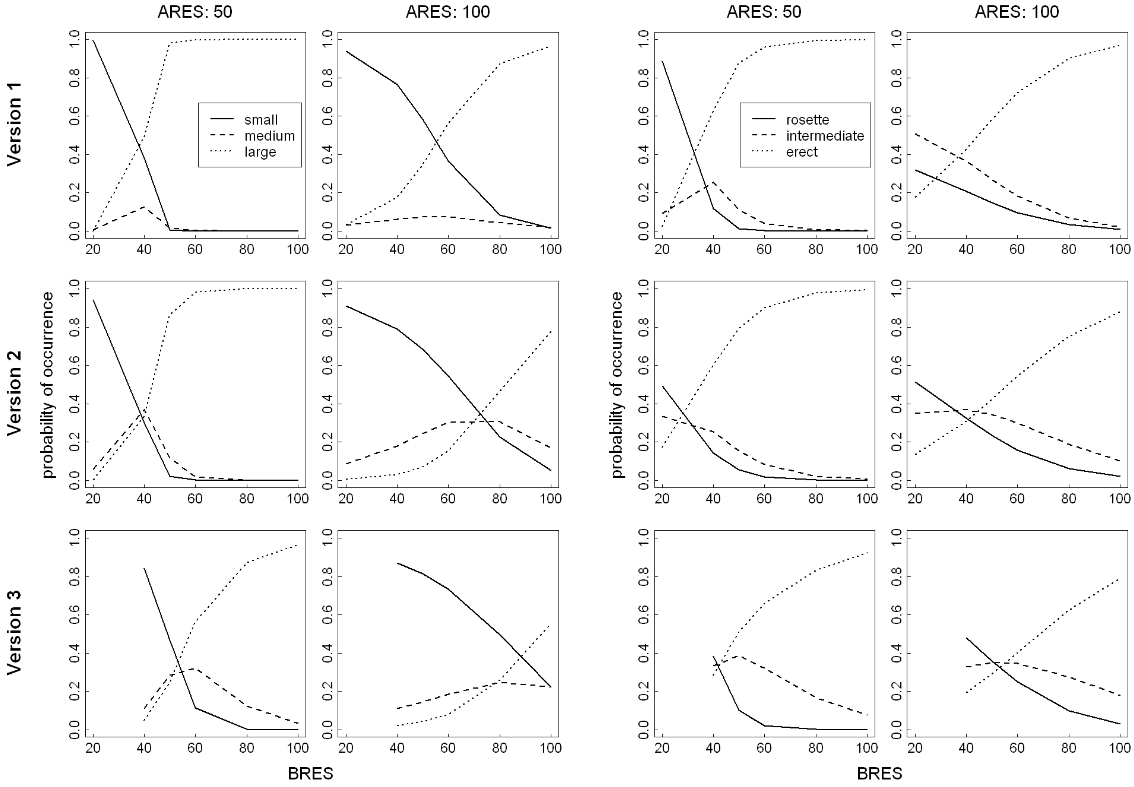


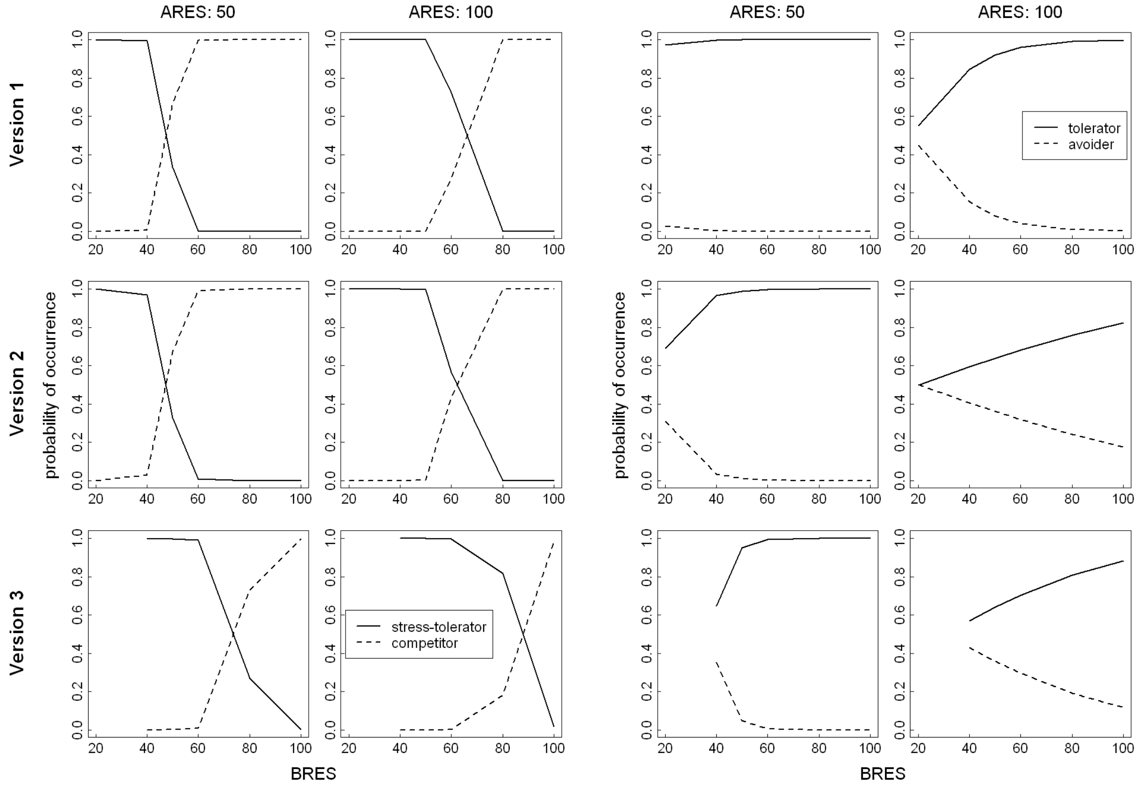
Figure A.7. Total individual numbers along a gradient of grazing probability. Data was averaged over the last 25 simulation years. Points and error bars show mean and standard deviation of 20 replicates.

A.3 Trait data



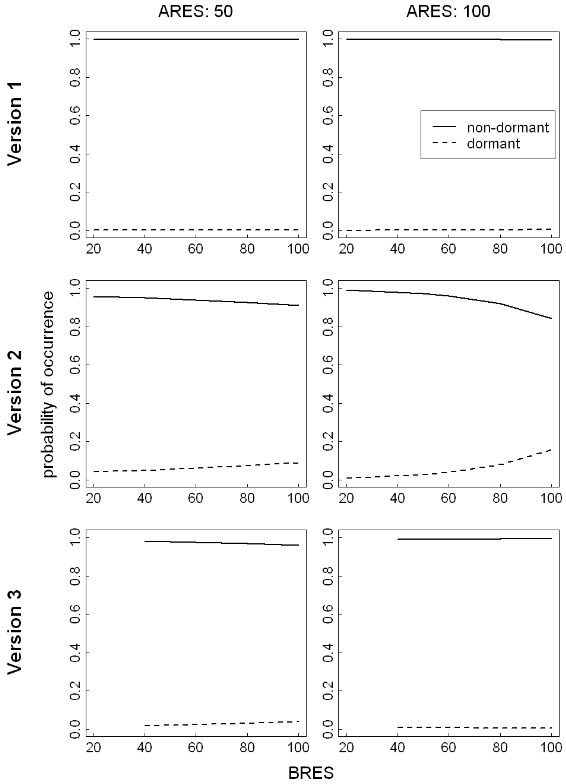
(a) Maximum plant mass **(b)** Growth form

Figure A.8. Probability of occurrence for trait attributes for different resource combinations. The trait composition of each replicate was averaged over the last 25 simulation years. Multinomial models were fitted to mean values of 20 replicates.



(c) Resource response **(d)** Grazing response

Figure A.8. Probability of occurrence for trait attributes for different resource combinations. The trait composition of each replicate was averaged over the last 25 simulation years. Multinomial models were fitted to mean values of 20 replicates.



(e) Dormancy

Figure A.8. Probability of occurrence for trait attributes for different resource combinations. The trait composition of each replicate was averaged over the last 25 simulation years. Multinomial models were fitted to mean values of 20 replicates.

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Eidesstattliche Erklärung

Hiermit versichere ich, die vorgelegte Diplomarbeit selbständig verfasst und ausschließlich die angegebenen Hilfsmittel und Quellen benutzt haben. Zitate aus anderen Arbeiten wurden unter Angabe der entsprechenden Referenz als solche gekennzeichnet.

Potsdam, 24. Januar 2008

Felix May