PLANT TRAIT RESPONSES TO GRASSLAND MANAGEMENT AND SUCCESSION

DISSERTATION ZUR ERLANGUNG DES DOKTORGRADES DER
NATURWISSENSCHAFTEN (DR. RER. NAT.)
DER NATURWISSENSCHAFTLICHEN FAKULTÄT III –
BIOLOGIE UND VORKLINISCHE MEDIZIN DER UNIVERSITÄT REGENSBURG

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REGENSBURG
JUNI 2003

Veröffentlichung:

Kahmen, S. (2004) Plant trait responses to grassland management and succession. *Dissertationes Botanicae* **382**, pp. 123.

Promotionsgesuch eingereicht am 18. Juni 2003

Mündliche Prüfung am 10. Oktober 2003

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Chapter 1

General Introduction

Grassland management and succession

Semi-natural grasslands with their specific flora and fauna are of high conservation value in Central Europe. They became threatened when intensification of agricultural practice increased in the middle of the last century. From this time on, semi-natural grasslands have been fertilised, afforested or, alternatively, been abandoned owing to their low agricultural productivity (Poschlod & Schumacher 1998, WallisDeVries et al. 2002). A major goal of nature conservation is to ensure the protection and maintenance of these semi-natural grasslands and their unique floristic and faunistic diversity by conservation management. Aiming to find the best management, i.e. optimal maintenance of the species composition at the lowest cost possible, several studies on management treatments have been started in the last decades (e.g. Schreiber 1977, Krüsi 1981, Schmidt 1981, Kapfer 1988, Bakker 1989, Bobbink & Willems 1993, Huhta & Rautio 1998, Huhta et al. 2001, Fischer & Wipf 2002). Most of these studies investigated the impact of management-induced shifts in fertility on changes in species composition. Due to different environmental conditions and species sets, however, the transfer of conservation knowledge between sites or regions remains difficult.

When management ceases and a site is abandoned, grassland succession leads to the establishment of shrubs and trees until the site is entirely covered by forest. The course of succession, however, differs greatly among sites. Species composition, environmental conditions, but also site characteristics like the history of a site, determine the succession process to a large extent, thus preventing the generation of one general, unifying theory (Clements 1916, Margalef 1963, Odum 1969, Connell & Slatyer 1977, Miles 1987, Pickett et al. 1987, Glenn-Lewin & van der Maarel 1992).

Without such a theory, predictions of the effects of grassland management or abandonment for the purpose of nature conservation require individual studies for each region and grassland type. As this approach is both unaffordable and time consuming, conservationists have been forced to explore other methods of assessment. In recent years, there has been a growing interest in the role of biological characteristics of plants (plant functional traits) for vegetation changes induced by management or succession (Hodgson 1990, Briemle & Schreiber 1994, Olff et al. 1994, Hobbs 1997, Prach et al. 1997, Poschlod et al. 1998, Dupré & Diekmann 2001, Pywell et al. 2003). Focusing on plant functional traits instead of species is promising since more general processes can be exposed. This thesis investigates plant functional trait responses to grassland management and succession in order to identify regulating mechanisms.

Plant functional traits

Plant functional trait responses to ecosystem processes are of increasing interest in plant ecology (Gitay & Noble 1997, Lavorel et al. 1997, Grime 2001). Plant traits are biological characteristics like morphological or regenerative features. These features may determine whether a plant species is able to establish, survive or increase in abundance under specific environmental conditions or processes like disturbance, land use, climate change, fire etc. A plant trait that is sensitive to an environmental factor is defined as functional. As a consequence, plant functional traits are biological characteristics of plant species that respond to environmental conditions or processes in an ecosystem (Keddy 1992b, Kelly 1996, Gitay & Noble 1997, Lavorel et al. 1997). The benefit of knowing about the relationship between plant functional traits and specific processes is twofold. Firstly, by interpreting trait responses ecologists gain a better understanding of the mechanisms underlying the processes. Secondly, examining traits instead of species is useful for predictive purposes. Predictions based on species responses to a specific process are of a limited validity because most sites differ with respect to the species set and these differences increase with increasing spatial scale. In contrast to that, trait responses are more general, and sites with different environmental conditions or different species sets are thus rendered comparable. In a valuable study, Díaz et al. (2001) found similar trait responses to grazing for two geographic regions with completely different floras (Argentina and Israel).

Functional groups versus functional traits

There is a great variety of studies on functional trait responses (e.g. Boutin & Keddy 1993, Kelly 1996, Noble & Gitay 1996, Skarpe 1996, Thompson et al. 1996, Díaz & Marcelo 1997, Kleyer 1999, Lavorel et al. 1999b, Leishman 1999, Díaz et al. 2001, Thompson et al. 2001, Pywell et al. 2003). This has led to an equally great variety of methods used in plant functional trait analyses. According to their methodology, studies may, however, be broadly grouped into two categories, as they either focus on single plant traits or plant groups.

Lavorel et al. (1997) as well as Gitay & Noble (1997) gave an overview of the approaches to identifying plant groups, functional types sensu Lavorel et al. (1997) and response groups sensu Gitay & Noble (1997). Based on a set of common plant traits, plant functional types are defined as non-phylogenetic groups of species that exhibit similar responses to ecosystem processes (Kelly 1996, Gitay & Noble 1997, Lavorel et al. 1997). Reducing the high amount of species to some plant functional types is appealing for comparative as well as for predictive reasons. Unfortunately, plant functional types are highly context-specific so that a set of specific types has to be defined for each process. Although a lot of studies identified similar plant functional types that respond to grazing (Díaz et al. 1992, Lavorel et al. 1998, Hadar et al. 1999, Landsberg et al. 1999, Lavorel et al. 1999a, Sternberg et al. 2000), until now each study has used its own specific types. Gitay & Noble (1997) devised four criteria for plant functional types, namely *uniqueness*, *repeatability*, *congruency* and *convergence* but these criteria are seldom met.

In the temperate zone, widely applied functional concepts comprise the life form groups of Raunkiaer (1934) and the CSR-strategy scheme proposed by Grime (1974).

'Life form' classifies plants with respect to the location of the regeneration buds as strategy to survive cold winters (Raunkiaer 1934). It encapsulates sets of correlated traits relating to plant persistence and architecture. The CSR strategy scheme uses resource availability and disturbance as two orthogonal dimensions for plant classification. Both concepts help to identify important ecological processes and to predict vegetation responses under various conditions. However, considering processes that exhibit a low variability (e.g. grassland management) rather than steep environmental gradients, 'life form' alone is too broad a classification by which to describe and predict vegetation changes (Kelly 1996, Semenova & van der Maarel 2000). Even though the CSR strategies are better able to capture more subtle forms of variation, in most studies a number of processes are still not represented (Wilson & Lee 2000, Pywell et al. 2003, Moog et al. submitted). Especially along narrow gradients or in more subtly contrasted ranges of environmental conditions, broad classifications lead to a loss of information unique to particular traits. In these cases it may be necessary to study several single trait responses (Lavorel & Garnier 2002, Pywell et al. 2003).

In conclusion, I suggest that analysing single trait performance is appropriate in order to identify mechanisms and to get a better understanding of the processes concerned. It is not possible, however, to extrapolate from single trait responses to species responses merely by combining the trait performances. Consequently, a classification of the plants is needed for predictive purposes. The classification should be an optimal compromise reflecting the trade-off between generality and explanatory power. Paying tribute to the explanatory power in this thesis, I analyse single trait responses to identify traits sensitive to the processes concerned. Sensitive traits are combined in trait syndromes in a subsequent analysis using a simulation model.

Phylogenetic constraints

Much of the interspecific variation of plant functional traits is associated with phylogeny. Since all species have a common ancestor at some point in their evolutionary history, there will always be some degree of ancestral similarity among the species. Analysing plant functional traits in relation to environmental conditions may raise the problem that ”common ancestry, not adaptation” is responsible for similar trait responses (Silvertown & Dodd 1997). Silvertown & Dodd (1997) stated that related species are pseudoreplications rather than independent samples. In statistical evaluations, this fact would result in an overestimation of the degrees of freedom. Attempting to identify purely ecological relationships it would be necessary to extract the variation associated with phylogeny preliminary to any multi-species analysis (Kelly 1996). Analysing phylogenetically independent contrasts (PIC) is a common method to extract phylogenetic variation by using taxonomic relationships if no information on phylogeny is available (Kelly 1996, Silvertown & Dodd 1997, Eriksson & Jakobsson 1998). This method concentrates on those branches of the phylogenetic tree that demonstrate changes of traits or trait combinations.

However, the use of phylogenetically independent contrasts is discussed controversially (Westoby et al. 1997). Much of the variation in functional traits is expected to be correlated both with phylogeny and ecology and these two aspects should not be treated as mutually exclusive interpretations of variation (Leishman et al. 1995). In ecological terms, the maintenance of a trait is as meaningful as the change. The abundance of a trait is constrained by ecological conditions since in each generation the trait has to be maintained by diaspores establishing in some habitats but failing in others (Westoby et al. 1997). Trait abundances are thus rather ecologically than phylogenetically constrained. Following Westoby et al. (1997), the use of phylogenetically independent contrasts is correct for testing correlated evolutionary changes but incorrect for analyses of ecological outcomes. In their opinion, species are independent samples and unless treated as such, the degrees of freedom will in fact be underestimated.

As the objective of this thesis is to investigate the ecological relationship between functional traits and grassland management, I refrain from considering phylogenetically independent contrasts.

Thesis outline

This thesis is part of the cooperative project MOSAIK funded by the German Federal Ministry of Education and Research under FKZ 01 LN 0007. The objective of the project is to test the impact of management on semi-natural grasslands. In Central Europe, these grasslands are threatened by intensification, afforestation or abandonment. Nature conservation aims to maintain them and the MOSAIK-project examines two management alternatives (grazing at low intensities and ploughing) for the conservation of biodiversity. Since management effects on the faunistic and floristic composition become measurable after decades rather than after the three-year time frame of the project, MOSAIK focuses on predicting the treatment effects.

This thesis considers vegetation dynamics caused by grassland management in contrast to abandonment. Aiming to identify regulating mechanisms I investigate plant functional trait responses to management and abandonment. Traits found to be sensitive may be further employed for predictive purposes. The thesis implements three different approaches to investigate functional traits in relation to grassland management.

In the first approach (chapters 2 to 5), I conduct analyses of plant functional trait responses using vegetation data of the ”Fallow Experiments in Baden Württemberg” which were initiated by Prof. K.F. Schreiber (Münster) in 1975. This long-term experiment compares different management treatments and abandonment at 14 study sites. I analysed the performance of several plant functional traits in relation to grassland management and abandonment. This represents an indirect approach since plant functional trait responses are deduced from vegetation data. A trait list of the species of the ”Fallow Experiments” is attached in Appendix B. In an extensive analysis including all study sites, Chapter 2 (PLANT FUNCTIONAL TRAIT RESPONSES TO GRASSLAND SUCCESSION OVER 25 YEARS) investigates the processes of abandonment. Focusing on one study site, chapter 3 (CONSERVATION MANAGEMENT OF CALCAREOUS GRASSLANDS. CHANGES IN PLANT SPECIES COMPOSITION AND FUNCTIONAL TRAITS OVER 25 YEARS) compares different treatments and abandonment over a period of 25 years. Subsequently, chapter 4 (EFFECTS OF GRASSLAND MANAGEMENT ON PLANT FUNCTIONAL TRAIT COMPOSITION) once again considers all 14 study sites. This chapter focuses on the present state of the sites, investigating various traits in relation to 25 years of management treatment. A comparison of different techniques of analyses is discussed in chapter 5 (COMPARISON OF UNIVARIATE AND MULTIVARIATE ANALYSIS OF PLANT TRAIT RESPONSES TO MANAGEMENT TREATMENTS).

In the second approach (chapter 6), I test for the effects of functional traits on the outcomes of vegetation dynamics. In contrast to the first approach, the relationship between plant functional traits and management is investigated directly by experimental testing. Chapter 6 (DOES GERMINATION SUCCESS DIFFER REGARDING THE TRAITS SEED MASS AND GERMINATION SEASON? EXPERIMENTAL TESTING OF PLANT FUNCTIONAL TRAIT RESPONSES TO GRAZING, MOWING AND SUCCESSION) concerns the link between functional traits relevant to germination and germination success with respect to management and abandonment. The experiment was conducted on a semi-natural grassland in the Müritz National Park.

Leaving field surveys behind, the third approach uses a mechanistic simulation model to investigate relations between functional traits and management. Here, functional traits are combined in trait syndromes. In chapter 7 (EVALUATION OF PLANT TRAIT RESPONSES TO DIFFERENT GRAZING INTENSITIES USING A MECHANISTIC, SPATIALLY EXPLICIT SIMULATION MODEL) I systematically analyse the effects of functional traits on vegetation dynamics along a grazing gradient from no grazing (abandonment) to high grazing pressure.

Chapter 2

Plant functional trait responses to grassland succession over 25 years

Abstract

Describing, understanding and predicting succession processes is still an important task in plant ecology and nature conservation since many grasslands and arable fields have been abandoned in Europe in the last decades. So far, however, ecologists have not been able to establish one general, unifying theory for successionally induced changes in species composition. In fact, the course of succession seems to be unique for each site and year. In this study, we focused on the analysis of plant functional traits in order to detect general trends in trait responses to succession which would prove independent of site characteristics. We studied permanent plot series of 14 grassland sites in Southwest Germany that had been abandoned for 25 years. Species composition as well as the course of succession varied significantly among the grasslands.

Response to succession was analysed for the following traits: ‘plant height’, ‘canopy structure’, ‘specific leaf area’ (SLA), ‘storage organ’, ‘vegetative spread’, ‘plant persistence’, ‘seed bank longevity’, ‘start of flowering’, ‘duration of flowering’ and ‘seed mass’. We compared a univariate with a multivariate approach. In the univariate approach, attributes of each trait were analysed separately employing GLM whereas in the multivariate approach all traits were handled together in NMS. Both analyses indicated similar trait responses to succession. There was a significant increase in the proportion of species characterised by the following attributes: plant height >0.6 m, leaves distributed regularly along the stem, vegetative spread >100 mm, start of flowering later than May, duration of flowering 1-2 months and seeds of either low or high mass.

Introduction

In the last decades, the scientific interest in succession processes has been encouraged by policy constraints in Europe. Since the middle of the 20th century, many semi-natural grasslands have been removed from agricultural use and have been abandoned. Additionally, the Common Agricultural Policy of the European Union has supported the abandonment of arable land by the set-aside scheme since 1988.

Successional vegetation dynamics represent the process of species replacement over time (Pickett et al. 1987). Ecologists have developed numerous theories and typologies to describe successionally induced changes in plant species composition (Clements 1916, Margalef 1963, Odum 1969, Connell & Slatyer 1977, Pickett et al. 1987). Differences in species composition, site characteristics or climate, however, lead to multiple pathways of succession that prevent the generation of one general, unifying theory (Miles 1987, Glenn-Lewin & van der Maarel 1992). In contrast to that, using plant functional traits instead of species might help identify general processes of succession. Functional traits are biological characteristics of plant species that respond to the dominant processes in an ecosystem (Keddy 1992b, Kelly 1996, Gitay & Noble 1997, Lavorel et al. 1997). Several previous studies have already identified functional responses to processes like climate change (Skarpe 1996, Díaz & Marcelo 1997), disturbance (McIntyre et al. 1995, Lavorel et al. 1999b) or land use (Briemle & Schreiber 1994, Landsberg et al. 1999, Díaz et al. 2001, Dupré & Diekmann 2001, Köhler 2001, Kahmen et al. 2002). The advantage of dealing with traits instead of species is that different vegetation types or even floras may be compared with respect to a specific process and general trends may be exposed (Díaz et al. 2001). Thus, we are able to predict vegetation dynamics using our knowledge of functional trait responses (Noble & Gitay 1996, Roberts 1996b, Campbell et al. 1999, Kleyer 1999, Pausas 1999, Díaz et al. 2001). Furthermore, functional trait responses provides an insight into the mechanisms underlying succession. It improves our understanding of succession processes and provides the basis for thorough experimental studies on the mechanisms involved.

In this study different grassland communities in Southwest Germany are analysed with respect to vegetation dynamics induced by succession over 25 years of abandonment. Vegetation dynamics are studied using vegetation relevés of permanent plots. Permanent plot observations are crucial to study the mechanisms of species replacement during succession (Austin 1981, Brown 1992, Bakker et al. 1996a, Herben 1996, Bakker et al. 2002b). While chronosequences are sometimes considered a useful alternative (e.g. Foster & Tilman 2000), they cannot replace permanent plot observations, as specific site characteristics, like the history of a site, determine the succession process to a large extent (Pickett et al. 2001). Bakker et al. (1996a) summarised the relevance of permanent plot observations as follows: they help to separate trends and fluctuations in species composition, to extrapolate beyond time range and to other sites, to predict vegetation changes for future combinations of environmental factors and to test ecological models. For these reasons, long-term observations as presented here are of major scientific interest (e.g. Bornkamm 1981, Schmidt 1981, Bakker 1989, Prach et al. 1997, Chytrý et al. 2001, Deng 2001, Köhler 2001).

In our study we concentrate on functional trait analyses, as species composition differs strongly among the grassland communities. Our aim is to expose general trends and relationships of functional trait responses to succession. We thus consider plant traits that are 'ecologically meaningful' with respect to grassland succession (McIntyre et al. 1999, Weiher et al. 1999, Poschlod et al. 2000b). Since functional trait analyses aim at finding responses which are transferable to sites with different species sets, we focus on traits which are easy to measure. On the basis of functional trait responses we discuss which mechanisms may rule succession. Furthermore, we indicate a method to parameterise the rate and direction of changes in trait composition in the course of succession.

Methods

Study sites

The ”Fallow Experiments in Baden-Württemberg” were initiated by K.F. Schreiber in 1975. He selected 14 study sites of different types of semi-natural grassland that were threatened by abandonment (e.g. Schiefer 1981, Schreiber 1997b). These grasslands are located in Southwest Germany. They were formerly used as meadows or pastures at low intensities. The study sites are characterised in Table 2.1.

Table 2.1 Characterisation of the 14 study sites. Altitude (m a.s.l.), precipitation (mm/year), mean annual temperature (°C), geology and Ellenberg (1992) indicator values of pH and nitrogen (N), calculated from the vegetation relevés in 1976. Vegetation types are taken from Schiefer (1981), nomenclature of vegetation types according to Rennwald (2000).

no	study site	m a.s.l.	mm/year	°C	geology	pH	N	initial vegetation
1	Bernau	1100	1800	5.5	sandstone	2.2	2.9	Festuco-Genistelletum sagittalis Issler 1929
2	Ettenheim	290	900	8.5	sandstone	6.5	5.8	Arrhenatheretum elatioris BRAUN 1915
3	Fischweiher	220	950	8.5	raw warp	4.3	3.9	Angelico-Cirsietum oleracei Tx. 1937
4	Fröhnd	840	1800	6	gneiss	3.3	2.4	Festuco-Genistelletum sagittalis Issler 1929
5	Hepsisau	560	900	8	limestone	6.9	6.2	Arrhenatheretum elatioris BRAUN 1915
6	Mambach	550	1400	8	granite	4.5	3.6	Lolio perennis-Cynosuretum cristati Tx. 1937
7	Melchingen	810	900	6	limestone	6.5	5.6	Arrhenatheretum elatioris BRAUN 1915
8	Oberstetten	380	700	9	limestone	7.7	4.1	Arrhenatheretum elatioris BRAUN 1915
9	Plättig	740	1900	6.5	granite	4.4	4.5	Geranio sylvatici-Chaerophyllum hirsuti Kästner 1938
10	Rangendingen	460	750	8	gypsum	7.2	3.4	Brometum Scherrer 1925
11	Schönau	730	1600	7	granite	4.5	2.6	Arrhenatheretum elatioris BRAUN 1915
12	Schopfloch	730	1000	7	limestone	5.4	5.0	Lolio perennis-Cynosuretum cristati Tx. 1937
13	St Johann	760	1000	6.5	limestone	7.3	2.5	Gentiano-Koelerietum pyramidatae Knapp ex Bornkamm 1960
14	Todtmoos	1060	1800	5.5	gneiss	3.0	2.4	Festuco-Genistelletum sagittalis Issler 1929

Field methods

In 1975, one field of about 0.5 ha was fenced and abandoned on each of the 14 study sites. Since then, the course of succession has been documented by vegetation relevés in one permanent plot of 25 m² on each field. Vegetation relevés have been conducted periodically so that the data analysis is based on a period of 25 years. The percentage cover values have been estimated on a fine scale following Schmidt et al. (1974). In contrast to Kahmen et al. (2002) who compared management treatments and abandonment of one site, this study considers 14 sites as replications and focused on the process of abandonment. Comprising only one plot of 25 m² per succession field, the experimental design established in 1975 unfortunately did not reflect the spatial variability within the sites (Schreiber 1997b, Moog et al. 2002). Still, this does not diminish the high scientific value of this long-term observation on different habitats with diverse succession series.

Data analysis

Course of succession

To characterise the course of succession of the 14 study sites we concentrated on the years 1976, 1980, 1985, 1991, 1994, and 2000. For each of these six years, vegetation relevés of all plots were available. To document the rate of succession for each study site, the invasion of shrub and tree species was presented by summing up the cover values of the woody species of the permanent plots. The sums were transformed into natural logarithms for better presentation. For each of the entire sites, the respective proportion covered by woody species in 2000 was additionally calculated from unpublished maps of K.F. Schreiber. In order to detect relationships between the cover of woody species of the entire sites and site characteristics we conducted Spearman correlations with the following site characteristics (Table 2.1): altitude, precipitation, mean temperature and Ellenberg indicator values for pH and nitrogen (Ellenberg et al. 1992). The indicator values were weighted averages of the plots in 1976 to characterise the sites at the start of the experiment.

Plant functional traits

Plant functional trait analysis was performed in order to detect general trends in trait promotion and inhibition during succession. We selected ten traits with two or three attributes each that were supposed to respond to grassland succession (Table 2.2). Due to the different species sets we focused on traits which were easy to measure. Attribute classes were large to allow for trait plasticity (Dyer et al. 2001). Each plant species was graded for each trait according to the attributes. The traits were ‘plant height’, ‘canopy structure’, ‘specific leaf area’ (SLA), ‘vegetative spread’, ‘storage organ’, ‘plant persistence’, ‘seed bank longevity’, ‘start of flowering’, ‘duration of flowering’ and ‘seed mass’.

The trait ‘canopy structure’ discriminated between species bearing leaves close to the ground (leaves basal) and species with leaves distributed along the stem (leafy). The first group included rosette, semi-rosette, tussock as well as prostrate species (see Poschlod et al. 1996). The classification of ‘SLA’ was done with respect to habitats that differ in their fertility since SLA is positively related to resource richness (Westoby 1998, Wilson et al. 1999). For classification, we selected the character species of deciduous woodland (Querco-Fagetea), fertile grassland (Molinio-Arrhenatheretea) and grassland poor in nutrients (Festuco-Brometea) in Central Europe following Ellenberg et al. (1992). The mean SLA of these character species was 29 (1.8 SE) for Querco-Fagetea, 23 (1.0 SE) for Molinio-Arrhenatheretea, and 19.8 (0.9 SE) for Festuco-Brometea, resulting in three classes of SLA: <20, 20-25 and >25. We classified ‘plant persistence’ by combining life cycle (Ellenberg et al. 1992) and clonality (Klimeš et al. 1997) distinguishing between annuals and biennials, perennials without clonal growth and perennials with clonal growth. ‘Seed bank longevity’ was determined using the database of Thompson et al. (1997) complemented by data of Kiefer (1998). At least three records per species were needed for the calculation of the longevity index. Species were classified as persistent 1) if the longevity index was ≥ 0.3 or 2) if the class ‘long-term persistent’ was recorded at least 3 times or in more than 20% of all records. In total, 239 species were included in the study.

Table 2.2 Plant Functional Traits. Trait description, data sources, missing values. For detailed trait description see text. CLOPLA1 is the database of Klimeš (1997) and the numbers refer to types of clonal growth. Data source: 1 (Grime et al. 1988) 2 (Hunt & Cornelissen 1997) 3 (Klimeš et al. 1997) 4 (own measurements) 5 (Rothmaler 1994) 6 (Thompson et al. 1997). 239 species in total.

trait	attribute	description	data source	missing values
plant height	< 0.3 m	maximal plant height	5	-
	0.3-0.6 m			
	> 0.6 m			
canopy structure	leaves basal	main part of phytomass near the ground	5	-
	leafy	main part of phytomass along the stem		
SLA (specific leaf area)	< 20		4	58 (24%)
	20-25		2	
	> 25			
storage organ	no storage organ		5	-
	storage organ			
vegetative spread	< 100 mm	CLOPLA1 (1,2,4,6,7,9,12,13,15-19)	3	-
	≥ 100 mm	CLOPLA1 (3,5,8,10,11,14)		
plant persistence	annual, biennial		5	-
	perennial, not clonal	CLOPLA1 (1,2,4,12,16-19)	3	
	perennial, clonal	CLOPLA1 (3,5-11,13-15)		
seed bank longevity	transient	longevity index < 0.3	6	31 (13%)
	persistent	longevity index ≥ 0.3 or class 'long term persistence' more than 3 times or more than 20% of all records		
start of flowering	May and earlier		5	-
	after May			
duration of flowering	1-2 months		5	-
	≥ 3 months			
seed mass	< 0.5 mg		4	20 (8%)
	0.5-2 mg		1	
	> 2 mg			

Trait analysis

Trait development over the 25 years of abandonment was mapped for six dates regarding the relative abundance of the attributes per trait. Mean values and standard errors of the 14 sites were presented.

In order to expose clear trends in trait development, we subsequently restricted our analyses to those species that consistently changed abundance within one plot during succession. The following criteria were established:

1. species appeared from 1976 to 2000
2. species disappeared from 1976 to 2000
3. species monotonously increased or decreased in abundance between 1976 and 2000, effecting a difference in percentage cover value of more than 5%.

All species that did not fulfil at least one of these criteria were excluded from further analyses. Additionally, we concentrated on the relative species number of the attributes per trait. In average, 50% of the initial number of species per plot were still included.

Aiming to parameterise attribute response to succession, we compared a univariate with a multivariate trait analysis. Various ecologists recommend multivariate methods for trait analyses since traits may be related or interact (e.g. Díaz & Marcelo 1997, Landsberg et al. 1999, Lavorel et al. 1999b, Pillar 1999) and intercorrelations remain hidden in univariate analyses.

As a univariate technique, we established linear models (GLM). For every attribute we separately calculated linear regressions of the relative attribute abundances using time as continuous explanatory variable and sites as grouping variable. The grouping variable accounted for the differences among the study sites. The time series of each attribute and plot were tested for autocorrelations using autocorrelation diagrams of SPSS 10.0. As the coefficients of autocorrelation were rather low, we were able to rule out autocorrelations for all of the attributes. It was thus possible to use linear regressions despite the analysis of time series. GLM was done in GENSTAT 5-4.1.

We chose an indirect ordination method as a multivariate technique. We expected to find a time-axis in the ordination diagram by analysing all traits and sites together for the sampling dates 1976 and 2000. Since the multivariate distribution of the trait data was not known, we chose Nonmetric Multidimensional Scaling (NMS) as an indirect ordination method without underlying model of variable distribution. NMS was run in PCORD 4.21 with the following configuration: Euclidean distance, two dimensions, best solution of 500 runs, stability criterion = 0.0005, random starting configuration.

After the calculation, the ordination diagram was rotated so that the first axis pointed in direction of the time gradient. Subsequently, site parameters were correlated with both axes. These were the time gradient (1976 and 2000), percentage cover of woody species of the plots and the entire sites (Figure 2.1) and the site characteristics presented in Table 2.1. Additionally, the attribute proportions of all traits were correlated with the time-axis (axis 1). The variance of the data set which was represented by the two axes was calculated by correlating the Euclidean distances of the plots in the original space with those of the ordination space.

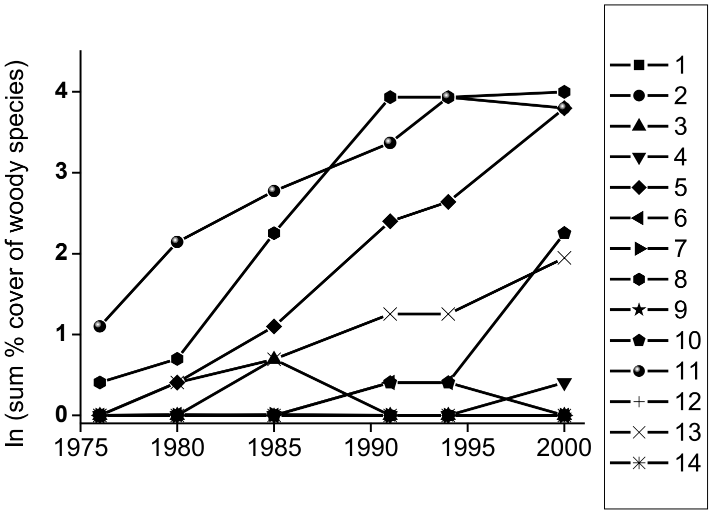
Finally, we compared trait responses to succession between multivariate and univariate analysis by correlating the correlation coefficients of the NMS-time-axis with the regression coefficients of the linear models. For these calculations, Pearson coefficients were employed in SPSS 10.0.

Results

Course of succession

Invasion of woody species (trees and shrubs) differed significantly among the study sites (Figure 2.1). The majority of the 14 plots showed no (eight plots) or minor (three plots) growth of woody species after 25 years of abandonment. Only three plots had developed a relatively high cover of woody species (amounting to 50%). Regarding the entire sites instead of the plots, up to 99% had been covered by woody species in Hepsisau (Table in Figure 2.1). The Spearman correlation coefficients with the site characteristics were as follows: altitude $r=-0.36$ *n.s.*, precipitation $r=-0.53$, $p<0.1$, mean temperature $r=0.47$, $p<0.1$, pH indicator value $r=0.3$ *n.s.* and nitrogen indicator value $r=0.47$, $p<0.1$, (N=14).

After abandonment, the number of species (median) decreased from 33 (1976), 30 (1980), 32 (1985), 28 (1991), 29 (1994) to 27 species per plot in 2000.



	plot	field
Bernau	-	24%
Ettenheim	-	42%
Fischweiher	-	21%
Fröhnd	0.5%	32%
Hepsisau	44%	99%
Mambach	-	75%
Melchingen	-	41%
Oberstetten	54%	91%
Plättig	-	-
Rangendingen	9%	28%
Schönau	44%	86%
Schopfloch	-	12%
St Johann	6%	23%
Todtmoos	-	11%

Figure 2.1 Total percentage cover of shrub and tree species of the permanent plots of the 14 study sites at six sampling dates from 1976 to 2000. Percentage cover is transformed to natural logarithm. Cover percentages of woody species in 2000 (not transformed) are given in the table at the right side of the figure for the permanent plots as well as for the entire succession fields in 2000.

Trait analysis

Figure 2.2 shows the average relative attribute abundance for each trait during the 25 years of succession. Results of the linear models were summarised in Table 2.3 for every attribute. Highly significant regression models were built for all attributes. Regression coefficients did not differ significantly from zero for attributes of the traits 'SLA', 'storage organ', 'plant persistence' and 'seed bank longevity'.

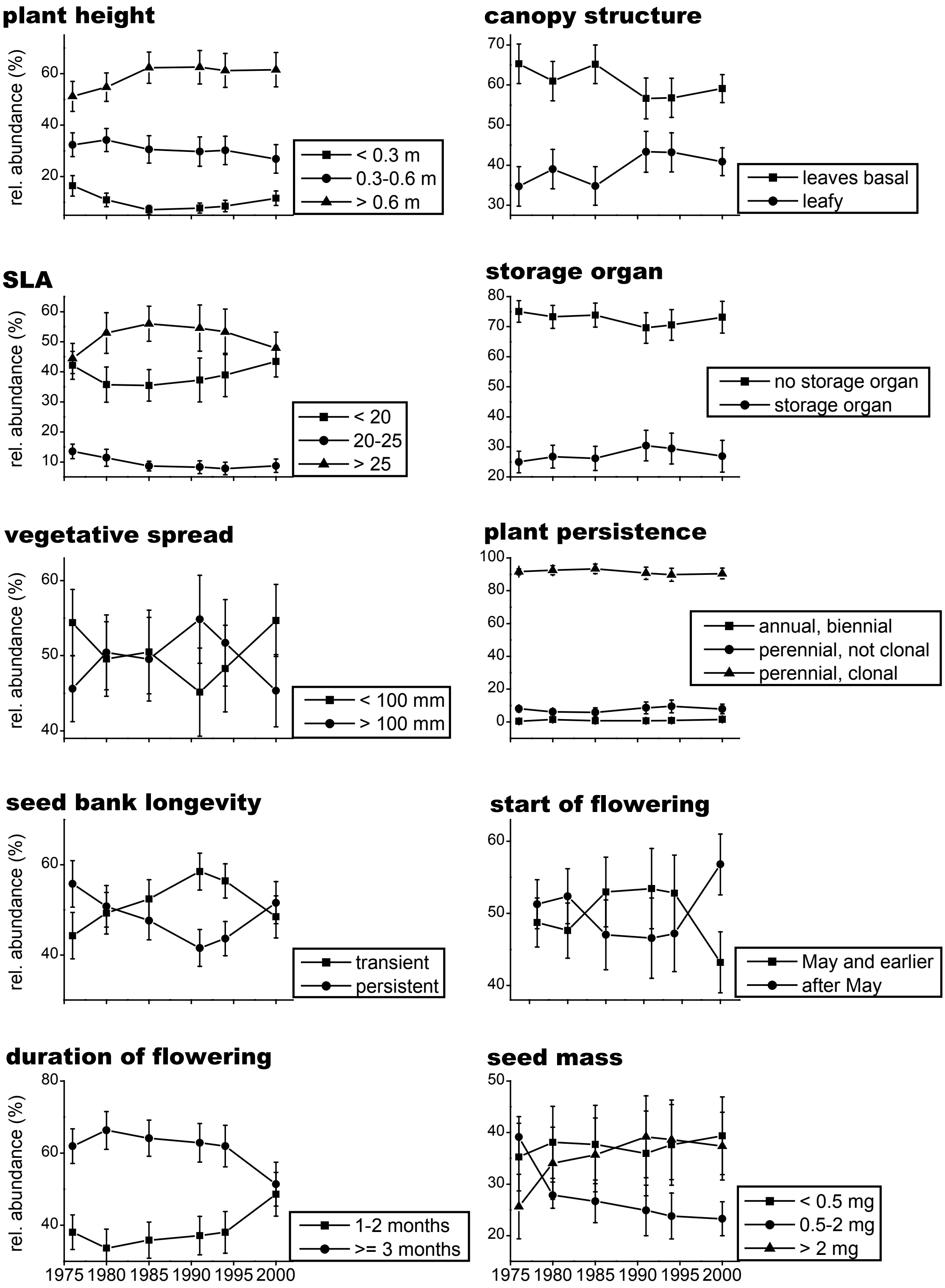


Figure 2.2 Changes in plant trait composition with time of succession. Attributes are presented with respect to relative abundance per trait for six sampling dates including all species. Mean values and standard errors are given for the 14 sites.

Table 2.3 General linear modelling (GLM) of the changes in trait composition in relation to time of succession. Linear regressions for every attribute with respect to the relative number of species per trait. Only those species that change abundance consistently during succession are included. Time is the continuous and sites are the grouping variables. b=regression coefficient, N=84, df=69.

*** p<0.001, ** p<0.01, * p <0.05, *n.s.* not significant

trait	attribute	R²	F	b
plant height	< 0.3 m	86.0	37.4 ***	-0.23 ***
	0.3-0.6 m	61.7	10.6 ***	-0.67 ***
	> 0.6 m	87.6	42.9 ***	0.89 ***
canopy structure	leaves basal	55.6	8.4 ***	-1.02 ***
	leafy	55.6	8.4 ***	1.02 ***
SLA	< 20	76.1	19.9 ***	0.03 *n.s.*
	20-25	52.6	7.6 ***	-0.22 *
	> 25	71.8	16.1 ***	0.19 *n.s.*
storage organ	no storage organ	49.9	6.9 ***	0.09 *n.s.*
	storage organ	49.9	6.9 ***	-0.09 *n.s.*
vegetative spread	< 100 mm	78.2	22.3 ***	-0.41 ***
	≥ 100 mm	78.2	22.3 ***	0.41 ***
plant persistence	annual, biennial	60.2	10.0 ***	0.25 **
	perennial, not clonal	72.0	16.2 ***	-0.08 *n.s.*
	perennial, clonal	81.2	26.6 ***	-0.17 *n.s.*
seed bank longevity	transient	64.0	11.5 ***	0.18 *n.s.*
	persistent	64.0	11.5 ***	-0.18 *n.s.*
start of flowering	May and earlier	78.1	22.2 ***	-0.67 ***
	after May	78.1	22.2 ***	0.67 ***
duration of flowering	1-2 months	57.5	9.0 ***	0.59 ***
	≥ 3 months	57.5	9.0 ***	-0.59 ***
seed mass	< 0.5 mg	70.9	15.5 ***	0.36 *
	0.5-2 mg	61.9	10.6 ***	-0.84 ***
	> 2 mg	79.9	24.6 ***	0.48 ***

The ordination diagram of the multivariate trait analysis (NMS) is presented in Figure 2.3. The diagram was rotated so that axis 1 points in the direction of temporal changes in trait composition between 1976 and 2000 (NMS-time-axis). Pearson correlation coefficients between both axes and the site parameters are represented by the length and direction of the arrows in Figure 2.3. Apart from the time gradient, axis 1 was highly correlated with the cover of woody species of the entire sites. Axis 1 represented about 20% of the variance in the data set whereas most of the variance was represented by axis 2 (53%). The pH indicator value in 1976, the mean temperature and the cover of woody species in the plots positively correlated with axis 2. A strong negative correlation was observed with the mean precipitation.

The correlation coefficients of the time-axis and the attribute proportions are listed in Table 2.4 for all attributes. Comparing the two analyses, most attributes exhibited consistent changes during succession. The regression coefficients of GLM and the correlation coefficients of NMS were significantly correlated (r=0.95, N=14, p<0.001). The changes during succession are described by the algebraic sign of change in Table 2.4. Figure 2.2, which shows the time series of the relative abundance per trait for all species as well as the results of GLM and NMS are described in the following.

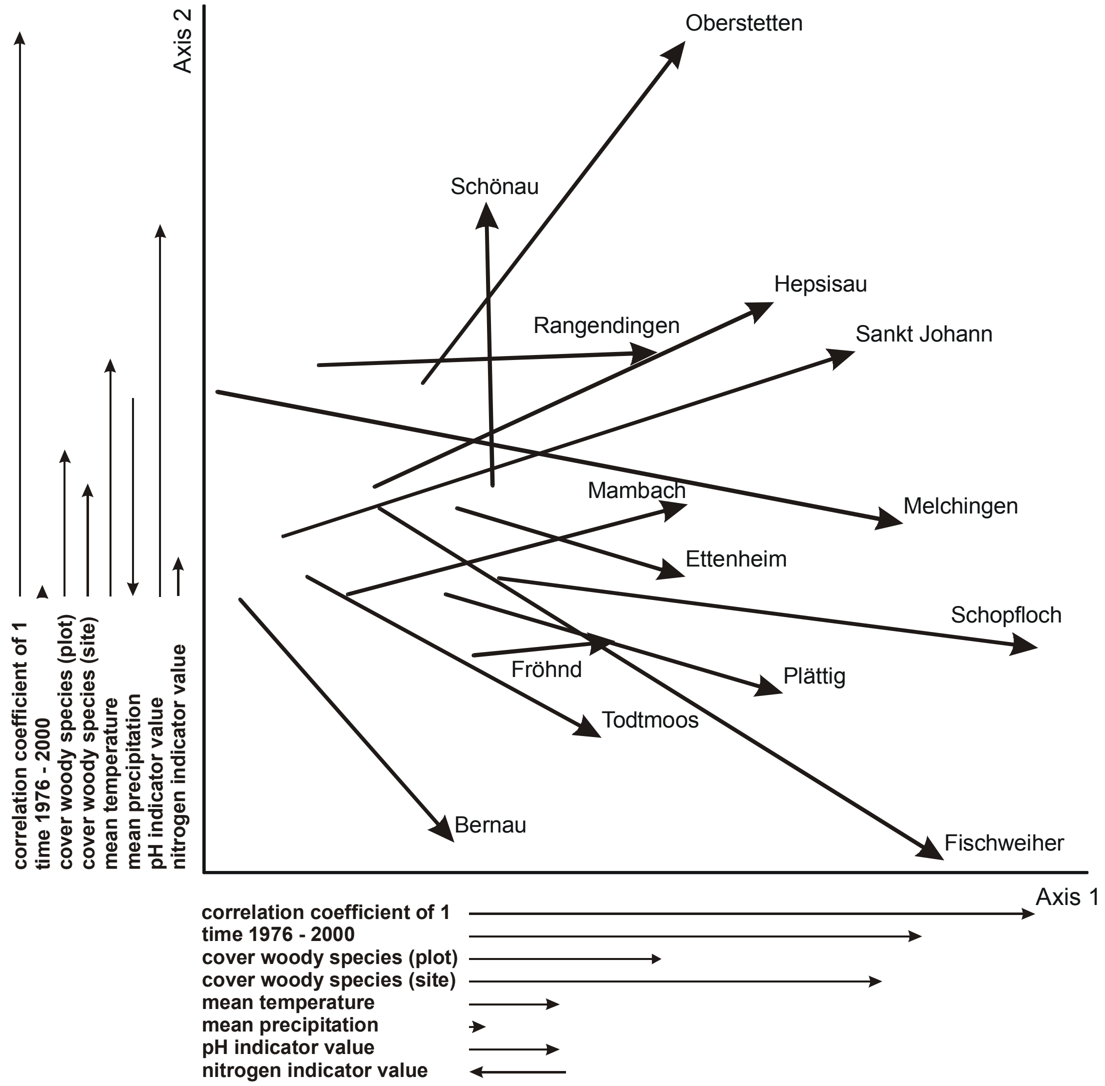


Figure 2.3 Ordination diagram of Nonmetric Multidimensional Scaling (NMS) of all traits and sites for the sampling dates 1976 and 2000 (N=28). Attribute proportions per trait related to the number of species. Only those species that changed abundance consistently during succession were included. The diagram was rotated in direction of the time gradient, arrows represent the plots in 1976 and 2000 of one site each. Pearson correlation coefficients of site parameters with the NMS axes are visualised by the length and direction of the arrows. The first arrow gives the length of r=1 for calibration. The time parameter and the cover of woody species changed from 1976 to 2000 whereas the site characteristics were the same per site. PH and nitrogen indicator values were calculated after Ellenberg et al. (1992) for the plots in 1976 to represent the conditions at the start of the experiment. NMS configuration: Euclidean distance, 2 dimensions, best solution of 500 runs, stability criterion = 0.0005, random starting configuration. Variance represented by Axis 1 = 20% and Axis 2 = 53%.

Table 2.4 Comparison of two approaches to parameterise changes in trait composition over 25 years of succession. (a) Regression coefficients of GLM for each attribute (Table 2.3), (b) Pearson correlation coefficients between attribute proportions and the NMS-time-axis (Figure 2.3). The sign of change is marked for attributes that exhibit consistent changes in both approaches, + increase, - decrease. The regression coefficients of GLM and the correlation coefficients of the NMS are significantly related (r=0.94*). Only those species that change abundance consistently during succession are included.**

trait	attribute	change	GLM regression coefficient	NMS correlation coefficient
plant height	< 0.3 m	-	-0.23	-0.44
	0.3-0.6 m	-	-0.67	-0.59
	> 0.6 m	+	0.89	0.65
canopy structure	leaves basal	-	-1.02	-0.70
	leafy	+	1.02	0.70
SLA	< 20		0.03	-0.13
	20-25	-	-0.22	-0.24
	> 25	+	0.19	0.34
storage organ	no storage organ		0.09	-0.04
	storage organ		-0.09	0.04
vegetative spread	< 100 mm	-	-0.41	-0.39
	≥ 100 mm	+	0.41	0.39
plant persistence	annual, biennial	+	0.25	0.32
	perennial, not clonal		-0.08	0.11
	perennial, clonal	-	-0.17	-0.24
seed bank longevity	transient		0.18	-0.10
	persistent		-0.18	0.10
start of flowering	May and earlier	-	-0.67	-0.56
	after May	+	0.67	0.56
duration of flowering	1-2 months	+	0.59	0.44
	≥ 3 months	-	-0.59	-0.44
seed mass	< 0.5 mg	+	0.36	0.26
	0.5-2 mg	-	-0.84	-0.73
	> 2 mg	+	0.48	0.24

With time of succession, the trait 'plant height' changed with tall species (> 0.6 m) increasing in number and abundance at the expense of species smaller than 0.6 m. During succession species with leaves distributed regularly along the stem were highly favoured at the expense of species with leaves growing close to the ground (Table 2.4), although the species characterised by the latter attribute preserved a high relative abundance (Figure 2.2). The trait 'SLA' showed a slight increase in species characterised by high SLA but this response was not significant. After abandonment, there was no obvious change with respect to 'storage organs' but species that may spread vegetatively for more than 100 mm per year did significantly increase in relative number at the expense of species with no or sparse vegetative spread. Regarding the relative abundances of all species, however, this pattern was not obvious because attribute abundances changed repeatedly and there was a high variance among the plots (Figure 2.2). The trait ‘plant persistence’ showed an increase in annual and biennial species whereas the perennials did not respond significantly to succession. Trait response of ‘seed bank longevity’ differed between univariate and multivariate analyses and no significant changes during succession could be observed in regression analysis (also see Figure 2.2). Species which started flowering in May or earlier declined in relative number in contrast to species flowering later in the season. This trend, however, was not reflected in their relative abundance. The number of species characterised by a short flowering period (1-2 months) increased at the expense of species with a flowering period of longer than 2 months. Species with both, low and high seed mass increased in relative number and abundance whereas species with medium seed mass (0.5-2 mg) decreased.

Discussion

Course of succession

The course of succession differed markedly among the 14 study sites as woody species appeared only on some plots during the 25 years of abandonment (Figure 2.1). However, regarding the entire sites (Table in Figure 2.1) all sites except Plättig were partly covered by woody species. This shows that the permanent plots often did not satisfactorily represent the sites.

Still, colonisation of woody species was relatively slow, although the succession fields were fenced to avoid every kind of grazing, even game biting. All sites were close to seed sources of woody species, so that differences in tree invasion could not be attributed to seed limitation. Furthermore, we did not find a relation between the fertility of the sites in 1976 and the cover of woody species although invasibility was found to be related to fertility by Thompson et al. (2001). Generally, the establishment of woody species was higher with increasing temperature and decreasing precipitation and soil reaction. These relationships confirm observations of Schreiber (1997) who found various tree seedlings indicating that germination happened frequently during the 25 years of the study. The majority of the seedlings, however, died from late spring frosts and a thick litter layer (Schreiber, personal communication).

Changes in trait composition

Using NMS ordination, 73% of the pattern of trait composition in 1976 and 2000 were represented in two dimensions. The diagram (Figure 2.3) shows that axis 2, which represented 53% of the structure in the trait dataset, was strongly correlated with site characteristics like the pH indicator value, mean temperature and precipitation. To a large extent we may thus attribute trait composition to site characteristics. Furthermore, the cover of woody species in the plots increased along axis 2, which must be attributed to the sites Schönau and Oberstetten. Apart from the relation with site characteristics, 20% of the variance of the trait dataset was represented by the time gradient, expressed by axis 1. In this study, we concentrated on this time gradient in order to discuss general changes in trait composition which are caused by succession. The time axis correlated positively with the cover of woody species of the entire sites. Surely, the increasing woodiness of the sites influenced the trait composition of the plots even if there were no trees or shrubs on the plots themselves.

Most attributes responded significantly to succession (Figure 2.2, Table 2.4). Until 1976, trait composition of the grasslands was determined by regular mowing or grazing. Beginning with the time of abandonment, the conditions of regular agricultural use were replaced by the process of succession.

Nutrient storage capacity is a useful strategy if a plant may withdraw a high amount of its nutrients at the end of the vegetation period. As long as biomass is regularly removed by mowing or grazing, the capacity for nutrient storage is less important than after abandonment or if management measures are conducted at the end of the vegetation period (see e.g. Köhler 2001). In this study, the trait 'storage organ' did not exhibit a significant response during succession (Table 2.4). As described above, the sites differed strongly with respect to establishment of woody species. An additional subdivision of the sites into those with significant growth of trees (group 1: sites 5, 8, 11) and those without significant growth of trees (group 2: remaining sites) yields a more differentiated view of trait responses to succession. Table 2.5 shows general linear models conducted separately for each group. For group 2 (no significant growth of trees) abandonment did not lead to an increase in the number of species with storage capacity as expected from theory. Management intensity before the start of the experiment had generally been low which might explain the missing response after abandonment. In contrast, group 1 with highly shaded plots exhibited an increase in the number of species without nutrient storage organs. Under shading, light rather than nutrients was a limited resource so that probably storage capacities were of minor importance.

Similarly, grazing or mowing promotes species that concentrate their leaves near the ground so that the biomass is preserved despite agricultural usage (Harper 1977, Hadar et al. 1999, Lavorel et al. 1999b). Without biomass removal, the plant height increases with tall species out-competing small species in the competition for light. This may result in higher competitiveness of species with leafy stems compared to species whose leaves are accumulated near the ground (Table 2.4) (Gaudet & Keddy 1988).

The trait 'SLA' did not respond significantly to succession. Representing the relative growth rate of a species, SLA is positively related to resource richness (Westoby 1998, Wilson et al. 1999). After abandonment, the priority of retaining captured resources is lower than during agricultural use. Therefore, species with high SLA should increase due to the relative increase in resources after abandonment. However, SLA is related to fertility only in unshaded habitats. In heavy shade, light rather than nutrients represents the limiting resource so that slow-growing species may also exhibit high values of SLA to catch a maximum of light (Wilson et al. 1999). We consequently restricted our analyses to the sites without significant growth of woody species and thus without heavy shading and indeed, we observed an increase in the number of species with high SLA values (Table 2.5, group 2).

The two traits related to persistence, viz. 'seed bank longevity' and 'plant persistence', did not respond consistently to succession. Regarding the relative abundance of all species (Figure 2.2), those with a persistent seed bank decreased in the first 15 years but recovered afterwards. Concentrating on the plots with a clear increase in woody species, the decrease in species with a persistent seed bank was significant (Table 2.5, group 1). A persistent seed bank is rendered less important in late successional vegetation in which major disturbances are uncommon and outlasting adverse conditions as seeds in the soil does not represent a useful strategy for plants (Fenner 1987, Poschlod et al. 1991, Poschlod et al. 1998, Thompson et al. 1998, Hyatt & Casper 2000).

Table 2.5 General linear modelling (GLM) of the changes in trait composition in relation to time of succession analysing the sites with significant growth of woody species (group 1, sites 5, 8, 11) and those without (group 2, remaining sites) separately. Linear regressions for every attribute with respect to the relative number of species, time is the continuous and sites are the grouping variables, b=regression coefficient. Only those species that change abundance consistently during succession are included. Group 1: N=18, df=14. Group 2: N=66, df=54.
*** $p<0.001$, ** $p<0.01$, * $p<0.05$, *n.s.* not significant

		group 1 (significant growth of woody species)			group 2 (low growth of woody species)		
trait	**attribute**	**R^2**	**F**	**b**	**R^2**	**F**	**b**
plant height	< 0.3 m	64.8	11.4 ***	-0.01 *n.s.*	85.9	36.9 ***	-0.29 ***
	0.3-0.6 m	79.3	22.7 ***	-1.20 ***	58.7	9.4 ***	-0.51 ***
	> 0.6 m	79.4	22.9 ***	1.25 ***	86.5	39.0 ***	0.80 ***
canopy structure	leaves basal	6.0	1.4 *n.s.*	-0.67 *n.s.*	63.7	11.4 ***	-1.11 ***
	leafy	6.0	1.4 *n.s.*	0.67 *n.s.*	63.7	11.4 ***	1.11 ***
SLA	< 20	81.3	25.7 ***	0.09 *n.s.*	72.8	16.9 ***	0.01 *n.s.*
	20-25	73.3	16.6 ***	0.26 *n.s.*	53.3	7.8 ***	-0.35 **
	> 25	67.1	12.6 ***	-0.35 *n.s.*	74.4	18.2 ***	0.34 *
storage organ	no storage organ	51.4	7.0 **	0.55 *	53.8	7.9 ***	-0.04 *n.s.*
	storage organ	51.4	7.0 **	-0.55 *	53.8	7.9 ***	0.04 *n.s.*
vegetative spread	< 100 mm	84.2	31.3 ***	0.06 *n.s.*	72.5	16.6 ***	-0.54 ***
	≥ 100 mm	84.2	31.3 ***	-0.06 *n.s.*	72.5	16.6 ***	0.54 ***
plant persistence	annual, biennial	78.4	21.6 ***	0.34 *	49.0	6.7 ***	0.22 **
	perennial, not clonal		0.3 *n.s.*	0.11 *n.s.*	69.0	14.1 ***	-0.11 *n.s.*
	perennial, clonal	62.8	10.6 ***	-0.36 *n.s.*	76.4	20.1 ***	-0.12 *n.s.*
seed bank longevity	transient	71.8	15.4 ***	1.08 ***	66.3	12.6 ***	-0.07 *n.s.*
	persistent	71.8	15.4 ***	-1.08 ***	66.3	12.6 ***	0.07 *n.s.*
start of flowering	May and earlier	no model			80.3	25.1 ***	-0.77 ***
	after May	no model			80.3	25.1 ***	0.77 ***
duration of flowering	1-2 months	79.0	22.3 ***	1.20 ***	52.0	7.4 ***	0.42 **
	≥ 3 months	79.0	22.3 ***	-1.20 ***	52.0	7.4 ***	-0.42 **
seed mass	< 0.5 mg	82.8	28.3 ***	-0.55 ***	66.8	12.9 ***	0.61 ***
	0.5-2 mg	61.2	9.9 ***	-0.81 ***	60.6	10.1 ***	-0.84 ***
	> 2 mg	83.2	29.1 ***	1.36 ***	73.4	17.3 ***	0.24 *

The increase of annuals and biennials is slight but significant and indicates better conditions for seedling recruitment during succession. After abandonment, accumulation of litter generally depresses seedling recruitment (Schütz 2000). On the other hand, light conditions in the shadowed lower strata are impaired by growing tree species. This leads to small gaps of bare soil which generally enhance seedling recruitment (summarised in Schütz 2000, Turnbull et al. 2000, Zobel et al. 2000). Accordingly, we observed a higher increase in annuals and biennials at the sites which contained woody species than at the sites at which these were absent (Table 2.5, group 1). After abandonment, however, colonisation and propagation mainly happens by vegetative means (Van der Valk 1992, Jensen & Schrautzer 1999). As vegetative reproduction is also dominant in grasslands (Eriksson & Jakobsson 1998) there was no increase in clonal species after abandonment. Instead, we found an increase in species with long spacers which must be attributed to the plots that lacked a significant cover of woody species (Table 2.5). Similarly, Prach et al. (1994) observed an increase in species with extended vegetative spread in succession series after 10 years. We may thus conclude that a dense vegetation and litter layer might have promoted long vegetative spread (see also Köhler 2001).

The traits 'duration of flowering' and 'start of flowering' of the generative life cycle are thought to be related to phenological constraints (Poschlod et al. 2000a). Mowing or grazing in June or July promotes those species that have finished seed production by the time the site is used agriculturally. After abandonment, seed production is not time-limited any more which explains the increase in late flowering species (Table 2.4). Similarly, Köhler (2001) found late-flowering species to outnumber early-flowering ones on plots of a calcareous grassland that had been abandoned for 20 years, and Hadar et al. (1999) observed a positive response of early flowering species to grazing. Another strategy for successful seed production under agricultural use is to extend the flowering period, so that seeds may ripen before or after land use by grazing or mowing. The increase in species characterised by a short flowering period at the expense of those exhibiting a long flowering period is in accordance with this theory. The increase was particularly pronounced at sites characterised by a significant growth of woody species (Table 2.5).

Late successional species have often been shown to have heavier seeds than early successional ones (Salisbury 1942, Fenner 1987, Leishman 1999). In the tall and shadowed late successional vegetation, seeds require a greater amount of nutrient reserves for successful germination and establishment. In this study, we found an increase of species characterised by heavy seeds. The increase is especially significant when analyses are restricted to sites which exhibit a high cover of tree species (Table 2.5, group 1). The remaining sites, however, showed an unexpected promotion of small-seeded species (Table 2.5, group 2). Reader (1993) as well as Eriksson and Eriksson (1997) found that small-seeded species are favoured by gaps of bare soil for seedling emergence. These gaps, however, are typical of the sites characterised by a significant abundance of trees (group 1) and thus do not serve to explain the increase in small-seeded species in group 2. Another possible explanation is that small seeds profited less from gaps than from the abandoned vegetation functioning as protection against physical hazards (Ryser 1990). Furthermore, seed predation, which is more severe for large than for smaller seeds, might increase after abandonment (Reader 1993, Bonser & Reader 1998).

Attribute parameters

Beyond the ecological interpretation of trait responses, we were interested in parameterising the rate of attribute changes. Due to a high correlation between their respective coefficients, the univariate linear models (regression coefficients) and the multivariate ordination NMS (correlation coefficients) revealed approximately the same parameters for attribute changes. As the two approaches differed fundamentally, this was not to be expected. In the multivariate ordination NMS all traits were included whereas in the linear models each attribute was analysed separately. Furthermore, only two dates (1976 and 2000) were analysed in NMS whereas six dates were included in the linear models. Last but not least, their concepts differ substantially. Linear modelling constitutes a statistical approach which serves to identify and predict linear relationships, in this case of attribute changes with respect to duration of succession. In contrast to that, the ordination NMS is a descriptive approach employed to detect similarities, in this case between plots with regard to trait composition, without an underlying model. Subsequently, we looked for a time-axis describing the temporal gradient. Since both approaches resulted in similar outcomes, we prefer linear modelling to multivariate ordination. Whereas the outcome of ordination analysis strongly depends on the traits included, linear modelling is highly flexible with respect to adding or deleting traits, because each attribute is analysed separately. Furthermore, statistical testing provides information on the significance of attribute changes during succession.

Chapter 3

Conservation management of calcareous grasslands. Changes in plant species composition and response of plant functional traits during 25 years

Abstract

Five management treatments have been applied to a calcareous grassland since 1974 to study their efficiency in maintaining high diversity of grassland species. The treatments were: continuing sheep grazing, mowing, mulching, burning and leaving fallow (unmanaged). After 25 years of management, the treatments mowing and mulching resulted in a species composition similar to that from grazing by sheep. Thus, mowing and mulching can be useful management alternatives to grazing. In contrast, both burning and leaving fallow considerably changed the species composition. The changes were similar in both treatments and neither can be recommended for management purposes. We also evaluated eight traits with assumed sensitivity to the treatments (life form, life cycle, growth form, runners, lateral spread, fecundity, seed mass, germination season). In 1999, all traits except life cycle were found to respond to the different treatments. Trait response is discussed in detail.

Introduction

Over the last few decades, calcareous grasslands have become rare habitats in Europe owing to their low agricultural productivity (Willems 1990, Van Dijk 1991). Nowadays, they are threatened by abandonment, afforestation, and intensive land use practices which include fertilization. A major goal of nature conservation is to ensure the protection and the maintenance of these grasslands and their unique floristic and faunistic diversity.

Several management experiments on the maintenance of calcareous grasslands in Europe have been conducted as an alternative to the traditional land use practice of sheep grazing (e.g. Schreiber 1977, Bakker 1989, Bobbink & Willems 1993). Still, long term studies of management treatments are rare, even when taking surveys of different terrestrial ecosystems into account (e.g. Krüsi 1981, Schmidt 1981, Kapfer 1988). Most of these studies investigated the impact of management-induced shifts in nutrient conditions on changes in species composition. In recent years, there has been a growing interest in the role of biological characteristics of plants for vegetation changes induced by management (Hobbs 1997). Hodgson (1990) demonstrated the significance of plant characteristics for identifying ecological processes in conservation management of calcareous grasslands. Briemle & Schreiber (1994) studied the effect of management treatments on life form and growth form of plants. Olff et al. (1994) observed changing germination strategies over 25 years of succession in grassland after the cessation of fertilizer application and Poschlod et al. (1998) found that dispersal and seedbank features are crucial for both the maintenance and restoration of calcareous grasslands.

In a functional approach we identify plant characteristics that respond to the dominant ecosystem processes (Keddy 1992a, Kelly 1996, Gitay & Noble 1997). These characteristics are called functional traits. Functional traits must be selected in consideration of the types of responses that are likely to be relevant (Hobbs 1997). They can then be used in models of vegetation changes, predicting shifts in their relative abundance (Noble & Gitay 1996, Thompson et al. 1996, Lavorel et al. 1997, Kleyer 1999). The recent interest in functional characterisation of plants is due to the advantage that predictions can be made without having to resort to the impracticable course of describing the natural history of every singe plant species in a region (Thompson et al. 1996, Campbell et al. 1999). Several previous studies had already addressed the response of functional traits to processes such as disturbance or climatic change and have led to a classification of species into plant functional groups (McIntyre et al. 1995, Noble & Gitay 1996, Díaz & Marcelo 1997, Díaz et al. 1998, Lavorel et al. 1999b).

In the study presented here, we investigate the effects of different management treatments on the species composition of a calcareous grassland. The aim is to assess the efficiency of the treatments for the maintenance of this plant community and to identify functional traits responding to the treatments. In a first step we analysed the development of species composition caused by the treatments. Changes in the community were compared using an ordination method. We then tested eight plant functional traits for their sensitivity to the treatments. We studied morphological as well as regenerative traits, since previous studies had shown that the correlations between the two sets of traits were rather weak (Grime et al. 1988, Leishman &

Westoby 1992). However, both sets may comprise functional associations between plant traits and vegetation dynamics (Díaz et al. 1992, Leishman et al. 1995, Hobbs 1997, Weiher et al. 1998, Lavorel et al. 1999b).

Methods

Study site

In 1974 the project “Fallow experiments in Baden-Württemberg” was initiated by the third author to study the suitability of different management practices for maintaining the characteristic floristic composition of semi-natural grasslands, and to investigate the extent and course of succession of these grasslands (see e.g. Schreiber 1977, Schiefer 1981, Schreiber 1997b). Fourteen study sites in Southwest Germany were chosen, representing different types of grassland threatened by abandonment.

This paper focuses on one study site known as ”St Johann”, a species rich calcareous grassland of high conservation value. The site is situated on the western flank of the Swabian Alb on Upper Jurassic bedrock (760 m a.s.l.). The site is documented to have been continually used for sheep grazing since at least 1955. The vegetation is classified as Gentiano-Koelerietum (Schiefer 1981).

Table 3.1 Description of the management treatments.

management treatment	regime	time of treatment
grazing	sheep grazing twice a year in low intensity	early and late summer
mowing	cutting once a year with removal of hay crop	August
mulching	cutting once a year, leaving finely chopped hay on site	August
burning	burning once a year	winter
leaving fallow	unmanaged, abandoned grassland (succession)	no treatment

At the top end of a slope (5 % inclination) an exclosure of about 1 ha was set up. This area was sub-divided into four distinct strips, each strip being subjected to one of four treatments, namely mowing, mulching, burning, and leaving fallow (Table 3.1). As the area grazed by sheep was adjacent to the exclosure, this reference treatment experienced the same altitude and gradient.

As we restricted our analysis to the St Johann study site, there are no replications of the treatments. Although this reduces the significance of the results, they still yield substantial insight into the long-term effects of management treatments on vegetation dynamics, which are exceptional, since long-term studies of management treatments are rare.

Field methods

Vegetation dynamics were examined in one permanent plot of 25 m² for all five treatments. Vegetation relevés were carried out according to Schmidt et al. (1974) enabling the detection of even slight changes in species composition (Table 3.2).

Since the beginning of the project in 1975 vegetation relevés have been carried out at regular intervals, providing a study series of 25 years for analysis. The development of the species composition of the herbaceous layer under different management treatments was analysed. Vegetation relevés of the plots in 1975 and 1999 are listed in Appendix A. The nomenclature follows Rothmaler (1999).

Table 3.2 Scale of the percentage cover values according to Schmidt et al. (1974) and their respective rank values.

cover (%)	0.1	0.5	1	2	3	4	5	6	7	8	9	10	15	20	25	30	35	40	45	50	60	70	80	90	100
rank value	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25

Data analysis

Community development under the different treatments during 25 years of management was investigated in a detrended correspondence analysis (DCA). The DCA was run with percentage cover data in PCOrd 4.0. From each treatment we used relevés at approximately every fifth year, starting in 1975. The first two axes of the DCA are presented in the ordination diagram (Figure 3.1).

For the functional analysis we pre-selected plant functional traits with regard to their assumed sensitivity to the management treatments (see Thompson et al. 1996, Lavorel et al. 1999b). We considered ‘life form’, ‘life cycle’, ‘growth form’, ‘runners’, ‘lateral spread’, ‘fecundity’, ‘seed mass’ and ‘germination season’. All traits consisted of two to five attributes each (Table 3.3). With this set of traits we included morphological and regenerative characteristics of the plants’ life histories. We classified the growth forms following Ellenberg & Müller-Dombois (1967) distinguishing between tussock-forming plants (caespitosa), plants with rosettes and stems without leaves (rosulata), plants with leaves evenly spread along the stem (scaposa), and plants with rosettes and leafy stems (semi-rosulata). Plants with runners were divided into those with stolons (runners above ground) and those with rhizomes (runners below ground).

Using χ^2-statistics we tested for associations between traits and treatments in contingency tables (Table 3.4). We listed the abundance of every attribute for every treatment. Since species occurrence differed only little among the treatments but species abundance revealed large differences, we weighted the species by their specific cover values instead of presence/absence data. In order to avoid over-weighting of dominant species, we took the rank cover values instead of the original percentage data of the cover scale (Table 3.2). χ^2-tests were performed for every trait to test for random distribution of attributes among the treatments. Those traits that differed in their distribution between the treatments were expected to respond to the treatments. The standardized residuals (st. res.) indicated that attributes occurred in statistically different abundances ($p < 0.05$) among the treatments ($-2.0 <$ st. res. < 2.0, see Bühl & Zöfel 2000, p.187). Analyses were performed using SPSS 9.0.

The analysis of temporal variation and development of the trait composition was restricted to the six sampling years that had been selected for the DCA (Figure 3.2). We focused on those traits that responded to the management treatments in 1999. In contrast to the contingency tables, species were now weighted by their specific percentage cover values to reflect the actual species composition. Figure 3.2 shows the proportion of the attributes for each trait.

Table 3.3 List of functional traits and their attributes.

trait	attributes	code	data source
life form (*sensu* Raunkiaer 1934)	chamaephyte	1	Grime et al. 1988
	geophyte	2	Kleyer 1995
	hemicryptophyte	3	Poschlod et al. 1996
	phanerophyte	4	
	therophyte	5	
life cycle	annual/biennial	1	Grime et al. 1988, Kleyer 1995
	perennial	2	Poschlod et al. 1996
growth form	tussock	1	Poschlod et al. 1996
	rosette	2	
	leafy stem	3	
	rosette and leafy stem	4	
runners	no runners	1	Poschlod et al. 1996
	stolons (above ground)	2	
	rhizomes (below ground)	3	
lateral spread	no	1	Grime et al. 1988, Kleyer 1995
	< 250 mm	2	
	> 250 mm	3	
fecundity (no. seeds per shoot)	< 1000	1	Grime et al. 1988, Kleyer 1995
	> 1000	2	
seed mass	< 0.5 mg	1	Grime et al. 1988, Kleyer 1995
	0.5-2 mg	2	Poschlod et al. 1996
	> 2 mg	3	Bonn & Poschlod 1998
germination season	autumn	1	Kleyer 1995
	spring	2	Eriksson & Eriksson 1997
	all year round	3	

Results

Vegetation ordination

The detrended component analysis (DCA) revealed differences in the development of species composition due to management treatment (Figure 3.1). The first two axes of the DCA reached eigenvalues of 0.3 and 0.1, respectively. The 1975 plots are all close together at the bottom right quadrant of the diagram. By 1999, the plots are widely separated with the grazed plot at the right-hand side, the burnt and the fallow plot at the left-hand side, and the mown and mulched plot in an intermediate position.

For all treatments, species composition continued to change significantly throughout this period.

Unlike all the other treatments, the plot grazed by sheep (1) exhibited a clockwise curve on the ordination diagram ending to the right end of axis 1. This could be largely attributed to an increase in rosette species such as *Hieracium pilosella* and *Scabiosa columbaria* as well as to *Thymus pulegioides* (Appendix). All other treatments caused a +/- unidirectional trend in the development of vegetation during the 25 years of the project. The species composition of the mown (2) and the mulched plot (3) shifted mainly along axis 2. Until 1994, the species composition of the mown plot resembled that of the grazed plot. The species compositions of both the burnt (4) and the fallow plot (5) shifted in the opposite direction to that of the grazed plot and were mainly characterised by an increase in dominance of *Brachypodium pinnatum* (Appendix A).

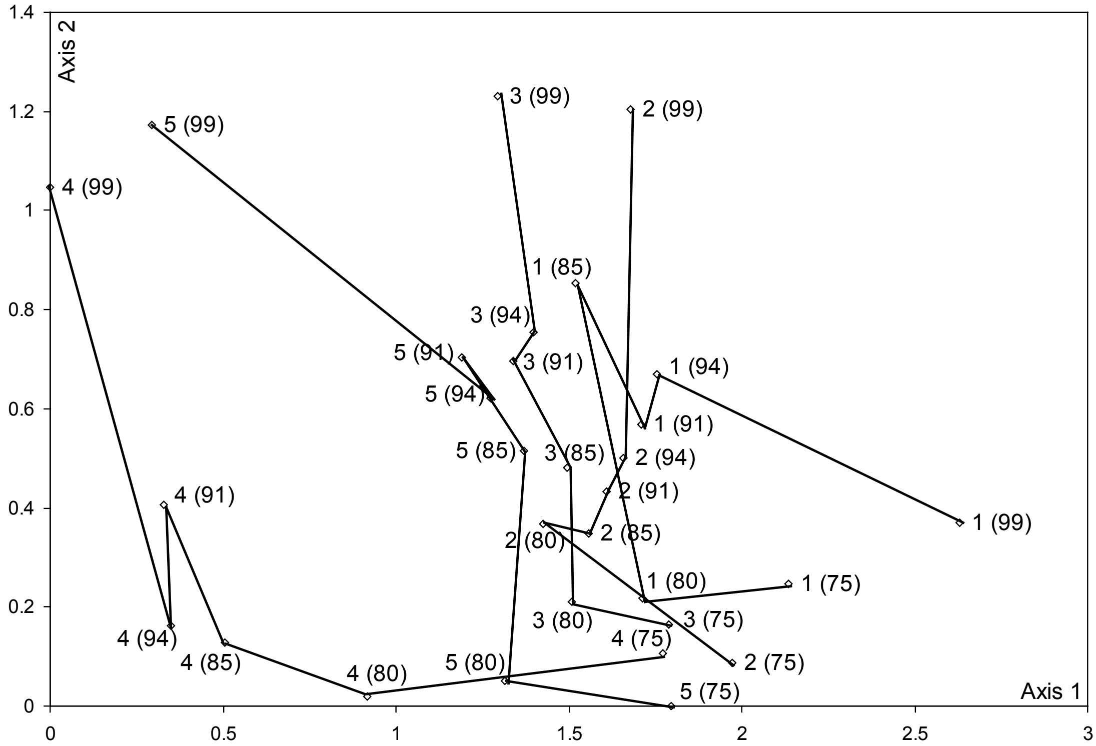


Figure 3.1 Development of species composition under five different management treatments from 1975 to 1999 presented in an ordination diagram of a DCA. Total number of species = 84. Eigenvalues: Axis 1 = 0.3; Axis 2 = 0.1. Treatments: 1 = grazing, 2 = mowing, 3 = mulching, 4 = burning, 5 = leaving fallow. Years are given in parentheses.

Response of plant functional traits to management

The results of the functional analysis are presented in Figure 3.2 (species abundance weighted by their specific percentage cover values) and in Table 3.4 (species abundance weighted by their rank cover values). Figure 3.2(a-f) shows that at the start of the management in 1975 the attributes of all traits were similarly distributed at all five plots. Within the first five years, the abundances of the attributes changed slightly under the different treatments followed by a period of relative stability until 1994. Between 1994 and 1999, however, trait composition changed significantly, which is in line with the development of the species composition demonstrated in the ordination diagram (Figure 3.1). Contingency table analysis of the 1999 data revealed that the attributes of all traits except 'life cycle' differed significantly between the five management treatments (Table 3.4).

Phanerophytes and therophytes were excluded from the analysis of the trait 'life form', as these attributes were not frequent enough for statistical testing. Geophytes occurred in the burnt and the fallow plot more frequently than statistically expected (Table 3.4). Figure 3.2a shows that the increase in geophytes at the burnt plot started right at the beginning of the management, whereas at the fallow plot, geophytes increased as late as between 1994 and 1999. The trait 'life cycle' exhibited no significant differences between the treatments. Regardless of the treatment, most of the species were perennials. With respect to the 'growth forms', there were significantly more rosette-forming species in the grazed plot than expected (Table 3.4). The increase in rosette species occurred mainly in the last few years (Figure 3.2b). As regards the development of the attributes in the fallow plot, we find a steady increase in tussock-forming species displacing rosette species. The trait 'runners' divided the treatments into three distinct groups, each of which was characterised by a different pattern: burning and fallow, mowing and mulching, and grazing (Table 3.4). Species with rhizomes dominated in the burnt and fallow plots over species without runners or with stolons. In the burnt plot, this trend can be noted right from the beginning of the management, but in the fallow plot it started as late as 1994 (Figure 3.2c). Grazing supported species with stolons in the last few years.

The 1999 results for the trait 'lateral spread' showed grouping patterns largely identical with that of runners. Relatively fewer species exhibited lateral spread at the mown and mulched plots, which is consistent with the higher abundance of species without stolons in these plots. The treatments grazing, burning, and leaving fallow expressed a tendency towards species with long runners (Figure 3.2d). 'Fecundity' showed different abundances among the treatments in 1999 but no distinct pattern. 'Seed mass' differed between the treatments in 1999, with significantly fewer seeds of large weight in the grazed plot. An overall trend from light to medium seeds became evident during the 25 years, except for the grazed plot (Figure 3.2e). In 1999, 'germination season' revealed a differentiation between the treatments burning and the fallow as opposed to the remaining three plots. The burnt and fallow plot had relatively more species germinating in spring, whereas species germinating in autumn or all year round were most frequent in the other plots (Table 3.4). The similarity between the burnt and the fallow plot developed in recent years (Figure 3.2f).

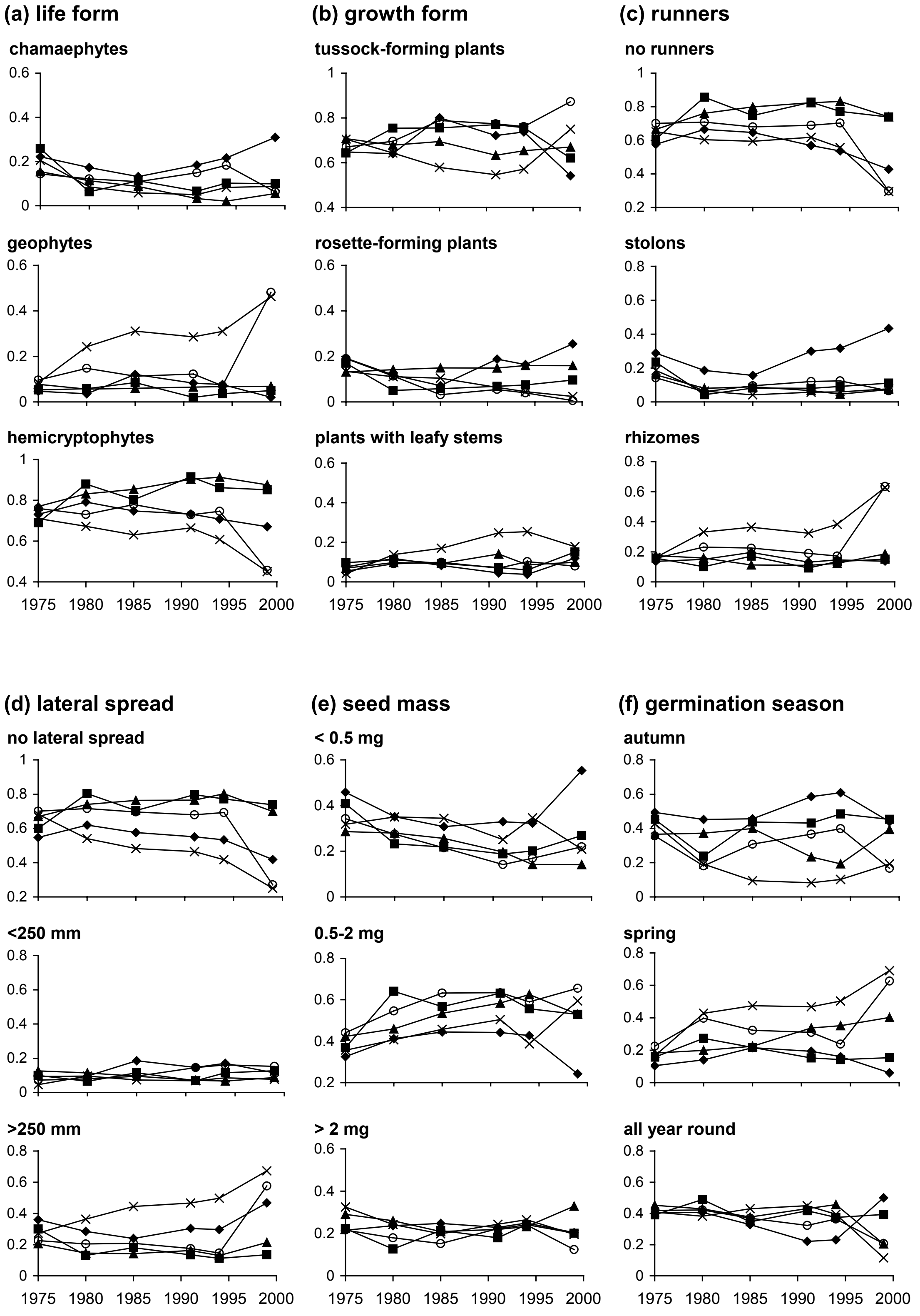


Figure 3.2 Proportion of the attributes of the traits life form (a), growth form (b), runners (c), lateral spread (d), seed mass (e), and germination season (f) in the vegetation plots from 1975 to 1999 for the five management treatments. Species are weighted by their percentage cover values. The life forms 'phanerophytes' and 'therophytes' were excluded from analysis due to too little abundance. Number of species = 84.

Table 3.4 Contingency tables of attributes within each trait and treatments. Cell abundances are species numbers weighted by their specific rank cover values from vegetation relevés in 1999[a].

	life form***			life cycle *n.s.*		growth form***				runners ***			lateral spread***			fecundity*		seed mass*			germination season***		
	χ^2 41.5, df 8			χ^2 3.0, df 4		χ^2 46.1, df 12				χ^2 58.6, df 8			χ^2 37.1, df 8			χ^2 11.2, df 8		χ^2 18.2, df 8			χ^2 47.9, df 8		
	chamaephytes	geophytes	hemicryptophytes	annual/biennial	perennial	tussock	rosette	leafy stem	rosette and leafy stem	no	stolons (above ground)	rhizomes (below ground)	no	< 250 mm	> 250 mm	< 1000 seeds	> 1000 seeds	< 0.5 mg	0.5-2 mg	> 2 mg	autumn	spring	year round
grazing	32^a	5^a	125^a	4^a	164^a	75^a	40^b	30^a	18^a	98^a	42^b	28^c	92^a	27^a	49^a	111^a	33^a	67^a	59^a	39^c	42^a	10^c	51^b
mowing	34^a	13^a	186^a	3^a	245^a	124^a	28^a	53^a	39^a	167^a	35^a	46^c	165^b	41^a	42^c	145^a	52^a	76^a	69^a	85^a	70^a	27^a	67^a
mulching	13^a	11^a	115^a	2^a	141^a	80^a	17^a	24^a	17^a	93^a	17^a	33^a	83^a	25^a	35^a	102^a	21^a	31^a	56^a	47^a	53^a	29^a	24^c
burning	17^a	22^b	96^a	2^a	136^a	74^a	8^a	33^a	15^a	71^a	14^a	53^b	65^a	19^a	54^b	81^a	35^a	36^a	50^a	46^a	37^a	40^b	25^a
fallow	13^a	23^b	76^a	0^a	119^a	80^a	3^c	23^a	13^a	53^c	14^a	52^b	48^c	25^a	46^b	91^a	15^a	37^a	30^a	43^a	27^a	31^b	30^a

[a] Pearson ^{2}-test was applied for testing for differences across the treatments. Significant deviations ($p<0.05$) of cells from the expected values within the traits are represented by letters: a - no deviation, b - positive deviation, c negative deviation. The life forms 'phanerophytes' and 'therophytes' were excluded from analysis due to too little abundance. Number of species = 74, percentage of valid abundances: runners, lateral spread, life cycle = 100%; growth form = 97.5%;
life form = 95.7%; seed mass = 93.5%; fecundity = 84.1%; germination season = 69.0%.

*** p<0.001, * p<0.05, *n.s.* not significant

Discussion

Vegetation ordination

In each of the three treatment groups of mulching and mowing, burning and leaving fallow, and grazing, species composition exhibited a distinct pattern of change. The significant changes in species composition under all treatments between 1994 and 1999 indicate that management still affects vegetation dynamics after 20 years, thus stressing the importance of long term surveys. Surprisingly, species composition of the grazed plot changed significantly during the 25 years of the project, although grazing had been the land use practice long before the start of the project. These substantial vegetation dynamics may be due to small scale disturbances by livestock and re-colonisation events typical of grazed sites (Noy-Meir et al. 1989, Bullock et al. 1995). The similarity between the mown and the mulched plot was probably due to being cut at the same time of year; it is noteworthy that removing or leaving the vegetation made only a minor difference to the sward composition.

Neitzke (1991) reported that burning in early winter resulted in a specific species composition different from all other treatments. However, the vegetation analyses conducted here demonstrated clear similarities to the herbaceous layer of the fallow plot. The vegetation of both, the burnt and fallow plots, was commonly characterised by a significant increase in *Brachypodium pinnatum*. Low-growing species, such as *Asperula cynanchica*, *Cerastium holosteoides* and *Hieracium pilosella*, disappeared. Similar findings have been documented by Bobbink & Willems (1987) of a chalk grassland in The Netherlands.

Response of plant functional traits to management

Grazing

Since grazing was the land-use practice prior to the start of the project, the high variability of trait response to this treatment is rather remarkable (Figure 3.2). This demonstrates that grazing leads not only to variation in species composition (Figure 3.1), but also to variation in trait composition. Grazing obviously favoured rosette species when compared to the other treatments, which is in line with the finding of Noy-Meir et al. (1989). Stolons also permit species to effectively colonise bare ground micro-sites (Stöcklin 1992) which could explain the high abundance of species such as *Thymus pulegioides* and *Hieracium pilosella*. The relatively higher proportion of plants with small seeds is in accordance with studies of Reader (1993), Leishman et al. (1995) and Eriksson & Eriksson (1997) who found that disturbance in grasslands enhanced seedling recruitment in small-seeded species to a stronger extent than in large-seeded species. As in our study, Eriksson and Eriksson (1997) observed increased germination in autumn if the grassland has been disturbed, while Lavorel et al. (1999b) showed that seasonality of germination was the regeneration-trait most strongly associated with species response to disturbance.

Mowing and mulching

Both treatments preserved the trait composition that had been established prior to the beginning of the project. They did not show any temporal variation, except for an increase in hemicryptophytes which started immediately after the beginning of the management. Since the cutting regimes lead to a dense vegetation, seedling recruitment is thought to be rare (McIntyre et al. 1995, Eriksson & Eriksson 1997) which may explain the lack of response in fecundity and germination.

Burning and fallow

At the beginning of the project, burning immediately favoured attributes different from the other three treatments, whereas trait composition of the fallow plot remained initially similar to them. In recent years, the trait composition of the herbaceous layer of the fallow plot changed abruptly, which may be due to advanced succession and the establishment of woody species. However, it seems likely that the mechanisms affecting trait composition in the fallow plot differ from those at the burning plot. Both treatments favoured geophytes with long rhizomes (see also Briemle & Schreiber 1994). Burning in early winter removed the litter and the above-ground biomass to a great extent (Schreiber 1997a), but the buds of the geophytes were not affected, so these plants could sprout easily in spring. On the other hand, seedlings emerging in autumn would suffer heavily from burning in winter. Thus, mainly spring-germinating species, i.e. after the fire treatment, such as *Brachypodium pinnatum*, *Hypericum perforatum* and *Trifolium repens*, might successfully recruit from seedlings. However, since these species also spread vegetatively, we cannot determine the relative importance of the two sets of traits.

In contrast to the burning treatment, the fallow led to an accumulation of litter and the vegetation became a dense sward (Schreiber 1997b). Thus the increase of geophytes on the fallow plot was possibly due to the fact that they can utilise the nutrients stored in rhizomes or bulbs to grow through the dense litter in spring (Bobbink & Willems 1987, Schreiber 1987). Hemicryptophytes, however, were under-represented in the fallow plot despite the fact that they may also store nutrients in the base of their shoots (Schreiber 1987).

Plant functional traits

The differences among the treatments were less significant for the generative traits and ‘life cycle’ than for the morphological traits and ‘life form’. Since most species of calcareous grasslands are long-lived perennials with clonal growth (Hutchings & Booth 1996a), generative reproduction is probably not a dominant process in vegetation dynamics (Thórhallsdóttir 1990). However, seedling recruitment is supposed to be a rare but general event that influences both species diversity and the rejuvenation of populations (Thompson et al. 1996, Eriksson & Eriksson 1997). Rusch (1988, in Rusch & van der Maarel 1992) revealed that regeneration by seed is important for various species of limestone grasslands on Öland, Sweden. In our study, new species invaded each of the treated plots between 1975 and 1999, and, since some of them do not show clonal growth, we expect them to be established by seeds (e.g. *Carpinus betulus*, *Primula veris*, *Salvia pratensis*, *Taraxacum officinale*, see Appendix A). Therefore, generative traits may respond to management treatments as well as morphological traits, but rare events like seedling recruitment were insufficiently accounted for in this analysis.

Conclusions

Evaluating the different management treatments for the nutrient-poor calcareous grassland from a conservation point of view, mowing and mulching in August seem to provide useful management alternatives to low-intensity grazing. Vegetation dynamics is higher if a spot is grazed rather than mown or mulched and more species may re(colonise) by seeds. However, species composition remains similar regardless whether the plot is subjected to mowing, mulching or low-intensity grazing. The similarity of mowing and mulching is particularly interesting for conservation management, because mulching is considerably less expensive than mowing, since the hay remains on the site and does not have to be removed. Regular burning is not recommended, since species composition would shift to a variant that very much resembles the herbaceous layer of the fallow.

Chapter 4

Effects of grassland management on plant functional trait composition

Abstract

Semi-natural grasslands are threatened in Central Europe by intense fertilisation, afforestation or abandonment due to changes in agricultural practice during the last decades. Nature conservation seeks to maintain these grasslands by management. The study presented here investigated the effects of different management treatments on grassland vegetation of various vegetation types. The treatments were low-intensity grazing, mulching once and twice a year and burning in winter. We investigated plant functional trait responses to the treatments aiming to identify dominant or differentiating processes of the treatments ruling trait responses. We hypothesised that the processes ‘selective removal of the phytomass by grazing’, ‘small scale soil disturbances’, ‘treatment frequency’, ‘nutrient conditions’, ‘vertical defoliation’ and ‘timing of the treatment’ are associated with the plant functional traits ‘life form’, ‘plant height’, ‘canopy structure’, ‘specific leaf area’, ‘storage organs’, ‘lateral spread’, ‘plant persistence’, ‘seed bank longevity’, ‘start of flowering’, ‘duration of flowering’ and ‘seed mass’.

All treatments maintained grassland vegetation by regular phytomass removal with hemicryptophytes and perennials with clonal growth being dominant. Grazing encouraged the life forms chamaephyte and phanerophyte by selective removal of the phytomass as well as species with small seeds and seeds with a persistent seed bank by soil disturbances. The mulching treatments were especially characterised by dominance of ground-layer species through regular vertical defoliation close to the ground. Burning in winter benefited species with storage capacities for nutrient withdraw. The traits ‘plant height’ and ‘SLA’, associated with treatment frequency and nutrient conditions, as well as the phenological traits ‘start and duration of flowering’, associated with the timing of the treatments, did not respond differently among the treatments.

Introduction

Semi-natural grasslands with their specific flora and fauna are of high conservation value in Central Europe. They became threatened when intensification of agricultural practice increased in the middle of the last century. From this time on semi-natural grasslands have been fertilised, afforested or they have been abandoned (Poschlod & Schumacher 1998, WallisDeVries et al. 2002). One major task in European nature conservation is the maintenance of these semi-natural grasslands by management. Aiming to find the best management, i.e. optimal maintenance of the species composition by low costs, several studies on management treatments have been started in the last decades (Schiefer 1981, Schmidt 1981, Bakker 1989, Huhta & Rautio 1998, Huhta et al. 2001, Fischer & Wipf 2002). However, the transfer of conservation knowledge between sites or regions remains difficult due to different site characteristics and different species sets. Thus, individual studies of management treatments for each region and grassland type would be required which is neither realisable nor worthwhile.

One way to obtain general results is the plant functional trait approach which became popular in the last years. Plant functional traits are biological characteristics of plant species that respond to the dominant processes in an ecosystem (Keddy 1992b, Kelly 1996, Gitay & Noble 1997, Lavorel et al. 1997). The advantage of dealing with traits instead of species is that different vegetation types or even floras may be compared and general trends may be exposed (Díaz et al. 2001). Functional trait responses give hints to the mechanisms of the processes like e.g. management treatments (Thompson et al. 1996, Gillison & Carpenter 1997, Díaz et al. 1999, Bullock et al. 2001) and a profound understanding of these mechanisms is a precondition for predicting management induced vegetation changes (Bakker et al. 1996a, Noble & Gitay 1996, Roberts 1996a, b, Campbell et al. 1999, Kleyer 1999, Pausas 1999).

Several previous studies had already addressed functional responses to management, most of them to grazing pressure (e.g. Briemle & Schreiber 1994, Lavorel et al. 1999b, Bullock et al. 2001, Dupré & Diekmann 2001, Köhler 2001). There are some general findings in trait responses to grazing from temperate (Díaz et al. 1992, McIntyre et al. 1995, Lavorel et al. 1999a, Bullock et al. 2001, Dupré & Diekmann 2001), Mediterranean (Noy-Meir et al. 1989, Hadar et al. 1999, Sternberg et al. 2000) and arid grasslands (Landsberg et al. 1999), suggesting that differential defoliation and soil disturbances are the main processes conditioning trait responses. Differential defoliation on the vertical gradient implies an increase in small or ground-layer species. Short lived species are encouraged by soil disturbances. Díaz et al. (2001) identified similar plant traits being associated with positive responses to grazing comparing grasslands of Argentina and Israel. These are small plant height and small leaf size, both related to grazing avoidance and high SLA related to grazing tolerance (resistance and resilience, respectively, in the sense of MacGillivray et al. 1995). The generality of these trait responses among ecosystems is of high scientific value, yet for more specific studies we need subtle differentiated trait responses.

In the study presented here we change from the global level to Central Europe. We investigate the effect of management treatments aiming to maintain temperate semi-natural grasslands. Hence, further processes are becoming important (discussed e.g. in Bullock et al. 2001). We hypothesise the following processes being dominant and/or differentiating among the treatments: ‘removal of the phytomass’, ‘selective removal by grazing’, ‘small scale soil disturbances’, ‘treatment frequency’, ‘nutrient conditions’, ‘vertical defoliation’ and ‘timing of the treatment’. The main tasks of this paper are:

1. We aim to compare the management treatments with respect to trait responses (comparative approach). By including semi-natural grasslands of different vegetation types of a region, we test for generalisation.

2. We aim to identify absolute trait responses. Thus in a second analysis, we analyse trait responses of each treatment independent of the remaining treatments (deviation approach).

Methods

Study sites and treatments

The “Fallow Experiments in Baden-Württemberg” were initiated by K.F. Schreiber in 1975. The objective of the experiment was to evaluate different management treatments with respect to their suitability for maintaining the characteristic floristic composition of semi-natural grasslands. He selected 14 study sites of different types of semi-natural grassland that were threatened by abandonment (e.g. Schiefer 1981, Schreiber 1997b). The study sites are located in Southwest Germany. They were formerly used as meadows or pastures at low intensities. The study sites are characterised in Table 4.1.

Each study site was split in fields, being subjected to one of the management treatments which were applied continuously since 1975. Additionally, one field was being abandoned for comparison reasons. The succession series were analysed in Kahmen & Poschlod (in press). The present study focused on management, namely on the treatments grazing, mulching twice a year (mulching-2), mulching once a year (mulching-1), and burning once a year (Table 4.1). Grazing took place by sheep or cattle at low intensities two or three times a year. At the mulching treatment, the crop was cut and chopped into small pieces. The chopped hay was left on the site. Mulching-2 was conducted in June and August, mulching-1 in August. The burning treatment took place in winter after the growing season. The treatments were established once per site.

Since 1975, plant species composition has been documented by vegetation relevés in one permanent plot of 25 m² per treatment and site. Percentage cover values have been estimated on a fine scale following Schmidt et al. (1974). Studies of treatment effects on species composition were published elsewhere (e.g. Schiefer 1981, Schreiber 1997b, 2001, Kahmen et al. 2002, Moog et al. 2002). In contrast to Kahmen et al. (2002), this study included all 14 sites of the experiment so that more general trends could be exposed. There were nine replications of grazing, mulching-2 and mulching-1, respectively, and six replications of burning (Table 4.1). In this study, we analysed the vegetation relevés in 2000, after 25 years of management treatment.

Table 4.1 Characterisation of the 14 study sites and respective management treatments. G: grazing with sheep and/or cattle two to three times a year, M-2: mulching twice a year in June and August, M-1: mulching once a year in August, B: burning once a year in winter. Altitude (m a.s.l), precipitation (mm/year), geology and vegetation type from Schiefer (1981), nomenclature of vegetation types according to Rennwald (2000).

study site	G		M-2	M-1	B	m a.s.l.	mm/year	geology	initial vegetation
Bernau	x	cattle	x	x	x	1100	1800	sandstone	Festuco-Genistelletum sagittalis Issler 1929
Ettenheim			x	x	x	290	900	sandstone	Arrhenatheretum elatioris BRAUN 1915
Fischweiher			x	x	x	220	950	raw warp	Angelico-Cirsietum oleracei Tx. 1937
Fröhnd	x	cattle				840	1800	gneiss	Festuco-Genistelletum sagittalis Issler 1929
Hepsisau	x	sheep	x	x		560	900	limestone	Arrhenatheretum elatioris BRAUN 1915
Mambach I	x	sheep, cattle				550	1400	granite	Lolio perennis-Cynosuretum cristati Tx. 1937
Mambach II	x	sheep, cattle				550	1400	granite	Lolio perennis-Cynosuretum cristati Tx. 1937
Melchingen			x	x		810	900	limestone	Arrhenatheretum elatioris BRAUN 1915
Oberstetten			x	x	x	380	700	limestone	Arrhenatheretum elatioris BRAUN 1915
Plättig			x	x		740	1900	granite	Geranio sylvatici-Chaerophyllum hirsuti Kästner 1938
Rangendingen			x	x	x	460	750	gypsum	Brometum Scherrer 1925
Schönau	x	sheep, cattle				730	1600	granite	Arrhenatheretum elatioris BRAUN 1915
Schopfloch	x	sheep				730	1000	limestone	Lolio perennis-Cynosuretum cristati Tx. 1937
St. Johann	x	sheep	x	x	x	760	1000	limestone	Gentiano-Koelerietum pyramidatae Knapp ex Bornkamm 1960
Todtmoos	x	cattle				1060	1800	gneiss	Festuco-Genistelletum sagittalis Issler 1929

Plant Functional Traits

We selected eleven plant functional traits (Table 4.2) that were supposed to be 'ecologically meaningful' with regard to the studied management treatments (McIntyre et al. 1999, Weiher et al. 1999, Poschlod et al. 2000b). Since we aimed at finding responses which are transferable to sites with different species sets, we focused on traits which are easy to measure. Attribute classes were large to allow for trait plasticity (see Dyer et al. 2001). The traits were 'life form', 'plant height', 'canopy structure', 'specific leaf area' (SLA), 'storage organ', 'vegetative spread', 'plant persistence', 'seed bank longevity', 'start of flowering', 'duration of flowering' and 'seed mass'. Each plant species was graded for each trait according to the attributes listed in Table 4.2.

The trait 'life form' is an integrative trait comprising plant species strategies to survive cold winters (Raunkiaer 1934). 'Life form' is partly represented by other traits like 'plant height', 'storage organs' and 'plant persistence'. We still employed 'life form' to take account for woodiness (chamaephytes and phanerophytes) and to give a superior impression of responses to management. Since each trait is analysed separately in the analyses of this study, there is no conflict with correlated traits. The trait 'canopy structure' discriminated between ground-layer species (leaves basal) and species with leaves distributed along the stem (leafy). The first group included rosette, semi-rosette, tussock as well as prostrate species (see Poschlod et al. 1996). The classification of 'SLA' was done with respect to habitats that differ in their fertility since SLA is positively related to resource richness (Westoby 1998, Wilson et al. 1999). For classification, we selected the character species of deciduous woodland (Querco-Fagetea), fertile grassland (Molinio-Arrhenatheretea) and grassland poor in nutrients (Festuco-Brometea) in Central Europe following Ellenberg et al. (1992). The mean SLA of these character species was 29 (1.8 SE) for Querco-Fagetea, 23 (1.0 SE) for Molinio-Arrhenatheretea, and 19.8 (0.9 SE) for Festuco-Brometea, resulting in three classes of SLA: <20, 20-25 and >25.

Table 4.2 Plant functional traits. Attribute description, data sources, missing values. Trait description in detail see text. CLOPLA1 is the database of Klimeš (1997) and the numbers refer to types of clonal growth used in this database (http://www.butbn.cas.cz/klimes/). Data source: 1 (Ellenberg et al. 1992) 2 (Grime et al. 1988) 3 (Hunt & Cornelissen 1997) 4 (Klimeš et al. 1997) 5 (own measurements) 6 (Rothmaler 1994) 7 (Thompson et al. 1997). 212 species in total.

trait	attribute	description	data source	missing values
life form (*sensu* Raunkiaer 1934)	therophyte geophyte hemicryptophyte chamaephyte phanerophyte	main life form	1	-
plant height	< 0.3 m 0.3-0.6 m > 0.6 m	maximal plant height	6	-
canopy structure	leaves basal	main part of phytomass near the ground	6	-
	leafy	main part of phytomass along the stem		
SLA (specific leaf area)	< 20 20-25 > 25		5 2	46 (22%)
storage organ	no storage organ storage organ		6	-
vegetative spread	< 100 mm	CLOPLA1 (1,2,4,6,7,9,12,13,15-19)	4	-
	≥ 100 mm	CLOPLA1 (3,5,8,10,11,14)		
plant persistence	annual, biennial		6	-
	perennial, not clonal	CLOPLA1 (1,2,4,12,16-19)	4	
	perennial, clonal	CLOPLA1 (3,5-11,13-15)		
seed bank longevity	transient	longevity index < 0.3	7	29 (14%)
	persistent	longevity index ≥ 0.3 or class 'long term persistence' more than 3 times or more than 20% of all records		
start of flowering	May and earlier after May		6	-
duration of flowering	1-2 months ≥ 3 months		6	-
seed mass	< 0.5 mg 0.5-2 mg > 2 mg		5 2	15 (7%)

We classified 'plant persistence' by combining life cycle (Rothmaler 1994) and the feature for clonal growth (Klimeš et al. 1997) distinguishing between annuals and biennials, perennials without clonal growth, and perennials with clonal growth. 'Seed bank longevity' was determined using the database of Thompson et al. (1997) complemented by data of Kiefer (1998). At least three records per species were needed for the calculation of the longevity index. Species were classified as persistent 1) if the longevity index was ≥ 0.3 or 2) if the class 'long-term persistent' was recorded at least 3 times or in more than 20% of all records. In total, 212 species were included in the study.

Data analysis

We tested the correlation between attribute abundances and fertility of the sites for each treatment separately. As presented in Table 4.1, we investigated different types of semi-natural grasslands on various geology leading to different soil fertility. Since the experimental design was not balanced we excluded those traits whose attribute abundances were strongly related to the fertility. The fertility was determined by weighted averages of the Ellenberg indicator values for nitrogen (Ellenberg et al. 1992) for each site and treatment (Figure 4.1). Correlations between attribute abundances and nutrition status were calculated for each attribute using Spearman rank correlation coefficient.

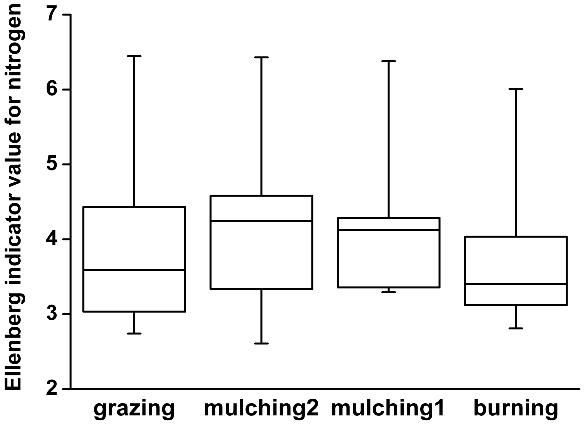


Figure 4.1 Ellenberg indicator value for nitrogen for the treatments grazing (N=9), mulching-2 (N=9), mulching-1 (N=9) and burning (N=6), determined by weighted averages per site and treatment using the respective vegetation relevés. Boxplots.

In the comparative approach, we compared the management treatments with regard to their relative attribute distribution. First, the relative abundance (percentage cover) of the attributes per trait was determined for each plot. We took relative data to reduce differences among the sites. Considering the relative abundance we could identify the attributes leading to dominance in the vegetation.

Next, we summed the percentage cover values of all plots per treatment. With these data, we again determined the relative abundance of the attributes per trait for each treatment. These attribute proportions were listed in cross tables with treatments and attributes for each trait separately. Using χ^2-statistics, we tested for non-random attribute distribution among the treatments. The life form ‘phanerophyte’ was excluded form the analysis as it was not frequent enough for statistical testing.

In the deviation approach, we analysed attribute responses for each management treatment separately without relating them to the remaining treatments. We tested for each trait and treatment if the observed attribute distribution differed from a ‘null model distribution’ which was received from the species pool. This means that the attribute distribution concerning the abundance was compared with the attribute distribution concerning the species occurring at all study sites. Likewise the comparative approach, we summed the percentage covers of all plots per treatment and calculated attribute proportions per trait and treatment. The attribute proportions of the species pool were again determined for each treatment separately, summarising all species that occurred in the plots of one treatment. For each trait, deviations of the null model distribution were analysed using χ^2-statistics. Residuals (observed minus expected values) per attribute and treatment indicated the magnitude and direction of the deviation. They were standardised through division by the expected values each. This approach identified the attributes favouring dominance of species out of the species pool. All analyses were done in SPSS 10.0.

Results

None of the traits except ‘plant height’ were significantly related to the nutrient status ($p<0.01$, correction for multiple correlations). Considering ‘plant height’, we found a negative relationship between small plants (<0.3 m) and a positive relationship between plants >0.6 m and the nutrient status for all treatments, respectively.

Figure 4.2 pictures for each trait the mean relative abundance per attribute, comparing the four treatments grazing, mulching-2, mulching-1 and burning. The standard errors were documented as a measure for variance among the sites. Additionally, the results of the χ^2-tests (cross tables, comparative approach) were presented in the same figure for each trait. Non-randomly attribute distributions are described below.

Table 4.3 presents the χ^2-statistics of the deviation approach. The standardised residuals indicate for each attribute the deviation of the treatment induced attribute distributions from the null model distribution per trait and treatment. Most traits exhibited high similarities in the deviation of attribute distributions among the treatments. Grazing showed significant responses for seven traits, mulching-1 for five and mulching-2 as well as burning for four traits.

Regarding the trait ‘life form’, therophytes increased in relative abundance after burning (Figure 4.2). The abundance of geophytes was higher in the mulching-1 and burning treatment than after grazing and mulching-2 but only burning showed a clear promotion of geophytes out of the species pool (Table 4.3). Chamaephytes were significantly benefited by grazing whereas grazing favoured phanerophytes only in comparison to the other treatments (Figure 4.2, Table 4.3). ‘Plant height’ was equally distributed among the treatments with more tall species (>0.6 m) in the mulching-1 and burning treatment in comparison to grazing or mulching-2 (Figure 4.2). A positive deviation of tall plants with respect to the species pool was also observed for grazing and mulching-2 (Table 4.3).

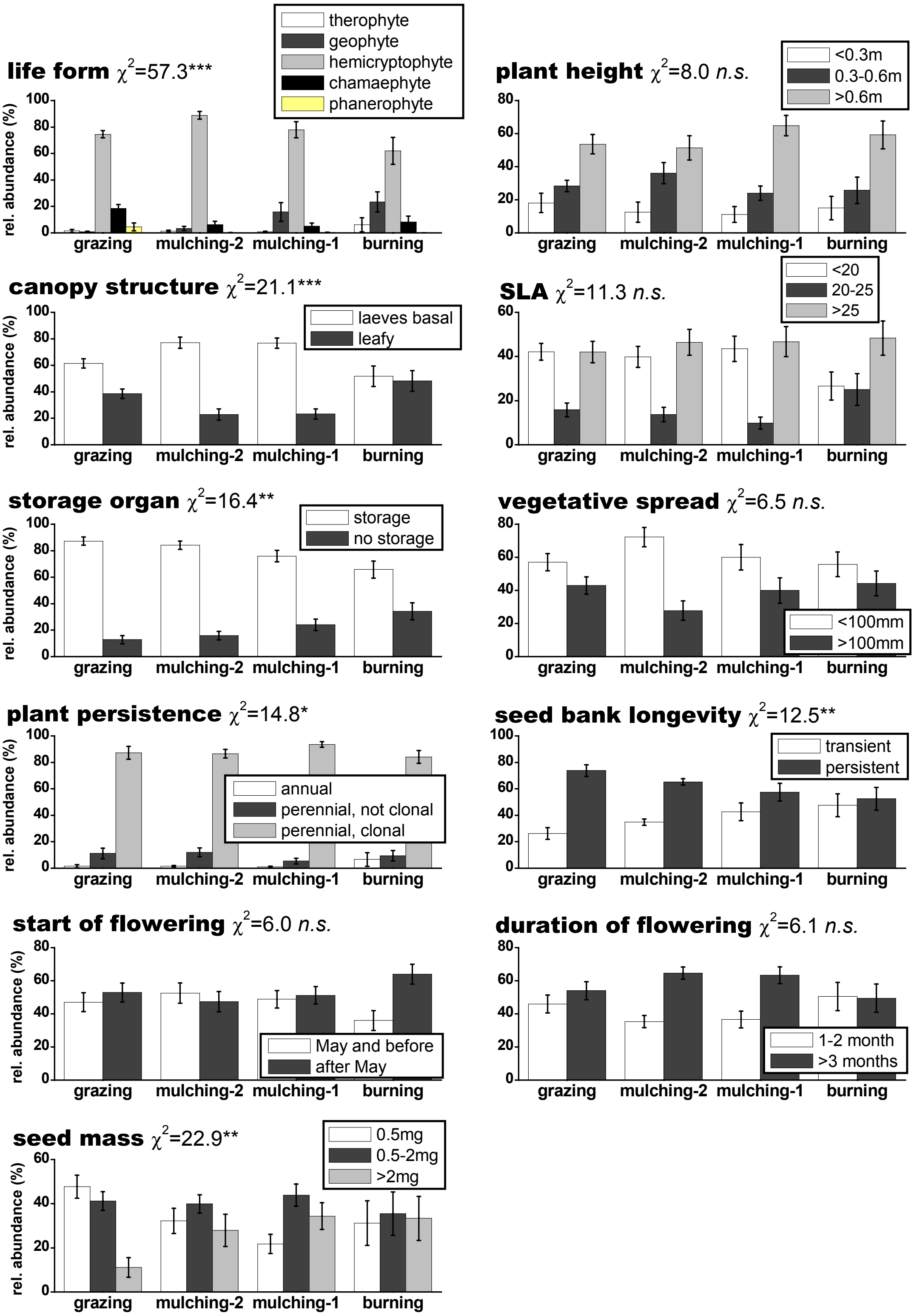


Figure 4.2 Relative species abundance of the attributes per trait. Mean and standard errors for each treatment with N(grazing, mulching-2, mulching-1) = 9 and N(burning) = 6. χ^2-statistics testing for associations between treatments and traits regarding attribute proportions per trait of the total abundance for each treatment. *** $p<0.001$, ** $p<0.01$, * $p<0.05$, *n.s.* not significant

Table 4.3 χ^2-statistics testing for significant deviations of treatment induced attribute proportions (abundances) from attribute proportions of the species pool for each trait and treatment (null model). Deviations of the total percentage cover versus the total number of species per trait and treatments are presented by standardised residuals.
*** p<0.001, ** p<0.01, * p<0.05, *n.s.* not significant

		grazing		**mulching-2**		**mulching-1**		**burning**	
		χ^2	st. res.	χ^2	st. res.	χ^2	st. res.	χ^2	st. res
life form	therophyte	12.5 *	-1.6	17.6 **	-3.0	11.1 *	-2.0	27.4 ***	0.0
	geophyte		-1.8		-1.8		2.3		4.9
	hemicryptophyte		0.6		2.0		0.1		-1.7
	chamaephyte		2.1		0.0		-0.4		0.0
	phanerophyte		-1.3		-1.2		-1.2		0.0
plant height	< 0.3 m	9.4 **	-1.1	11.7 **	-2.4	20.8 ***	-2.2	8.5 *	-1.0
	0.3-0.6 m		-1.6		-0.3		-2.0		-1.7
	> 0.6 m		2.4		2.5		3.5		2.1
canopy structure	leaves basal	4.8 *	1.5	19.6 ***	3.0	21.2 ***	3.2	0.6 *n.s.*	0.6
	leafy		-1.6		-3.3		-3.4		-0.5
SLA	< 20	2.2 *n.s.*	1.2	3.0 *n.s.*	0.4	5.3 *n.s.*	1.3	3.6 *n.s.*	-1.5
	20-25		-0.7		-1.5		-1.9		0.9
	> 25		-0.6		0.7		0.0		0.8
storage organ	no storage organ	3.1 *n.s.*	0.8	6.3 *	1.3	2.3 *n.s.*	0.8	0.2 *n.s.*	-0.2
	storage organ		-1.6		-2.2		-1.3		0.4
vegetative spread	< 100 mm	3.2 *n.s.*	-1.0	0.5 *n.s.*	0.4	1.6 *n.s.*	-0.7	8.5 **	-1.7
	> 100 mm		1.5		-0.6		1.0		2.4
plant persistence	annuel, biennial	6.2 *	-1.6	11.2 **	-2.8	16.1 ***	-2.5	1.0 *n.s.*	-0.3
	perennial, not clonal		-1.4		-1.0		-2.5		-0.8
	perennial, clonal		1.2		1.6		1.9		0.4
seed bank longevity	transient	9.2 **	-2.3	2.4 *n.s.*	-1.2	0.4 *n.s.*	0.5	1.7 *n.s.*	1.0
	persistent		2.0		1.0		-0.4		-0.9
start of flowering	May and earlier	1.7 *n.s.*	-0.9	0.6 *n.s.*	-0.5	0.4 *n.s.*	-0.4	3.3 *n.s.*	-1.3
	after May		1.0		0.6		0.4		1.2
duration of flowering	1-2 months	5.3	1.9	3.0 *n.s.*	1.5	1.3 *n.s.*	1.0	20.6 ***	3.8
	≥ 3 months		-1.4		-1.0		-0.6		-2.5
seed mass	< 0.5 mg	17.3 ***	2.6	0.5 *n.s.*	0.4	1.2 *n.s.*	-0.9	2.1 *n.s.*	0.1
	0.5-2 mg		0.4		0.1		0.5		-1.0
	> 2 mg		-3.2		-0.5		0.2		1.1

Both mulching treatments were similar regarding ‘canopy structure’ (Figure 4.2, Table 4.3), showing a significantly higher abundance of species that have most of their leaves close to the ground in comparison to grazing and burning. Concerning ‘specific leaf area’ (SLA) we found no significant differences in attribute distribution among the treatments. There was a slightly higher abundance of species with SLA >20 after burning (Figure 4.2). The trait ‘storage organ’ showed differences among the treatments with a relatively higher abundance of species with storage organs after burning (Figure 4.2). Furthermore, we found fewer plants with storage organs than expected after mulching-2 (Table 4.3). A significant promotion of plants with vegetative spread >100 mm was exposed by burning (Table 4.3). Regarding the trait ‘plant persistence’ we found a relatively higher abundance of annuals and biennials after burning and of perennials without clonal growth after grazing and mulching-2 (Figure 4.2). Analysing trait responses for each treatment separately, however, we observed a trend towards perennials with clonal growth for each treatment (Table 4.3). From grazing to mulching-2, mulching-1 and burning, species with a persistent seed bank decreased significantly in abundance (Figure 4.2). Additionally, grazing exhibited a positive deviation of plants with a persistent seed bank in relation to the species pool (Table 4.3). The phenological traits ‘start of flowering’ and ‘duration of flowering’ showed no significant differences in attribute distribution among the treatments although we observed a higher abundance of species flowering after May and with a short flowering period after burning (Figure 4.2). This promotion of species characterised by a short flowering period was significant in the deviation approach (Table 4.3). Concerning ‘seed mass’, small seeded species were favoured by grazing at the expense of large seeded species (Figure 4.2, Table 4.3).

Discussion

Trait responses differed relatively little among the management treatments (Figure 4.2). Likewise, deviations in attribute distribution from the species pool data were often similar among the treatments (Table 4.3). These similarities did not surprise since all treatments have been applied to maintain grassland ecosystems. Still, there were several processes found to discriminate among the treatments. In the following, we describe the hypothesised processes of the treatments and discuss the mechanisms ruling trait responses. Figure 4.3 gives an overview of the hypotheses and expected trait responses.

(a) All four treatments grazing, mulching-2, mulching-1 and burning have been applied to maintain grassland ecosystems. They all remove the above-ground vegetation regularly but leave at least a part of the phytomass at the sites. As generally expected, hemicryptophytes were the dominant life form equally in all treatments and most perennials had the feature for clonal growth (Ellenberg 1996).

(b) Growth of phanerophytes should be prevented by management, still we observed a relative promotion of phanerophytes as well as of chamaephytes by grazing. Both life forms are unpalatable to life-stock due to their woody stems so that their increase may be explained by the selective removal by grazers. Selective grazing is especially high at low grazing pressure as it was the case in this experiment. A promotion of chamaephytes by grazing was also observed by (Dupré & Diekmann 2001) but in contrast to their study, we found no positive response to grazing of therophytes or annuals/biennials.

(c) Small scale soil disturbances through trampling are typical for grazed sites and they generally favour seedling recruitment which is a rare event in dense grassland vegetation (summarised in Schütz 2000, Turnbull et al. 2000, Zobel et al. 2000). This should lead to an increase in therophytes or annuals as found e.g. by Noy-Meir et al. (1989) and McIntyre et al. (1995). In contrast, this study revealed comparatively more therophytes and annuals/biennials after burning, caused possibly by the lots of anthills at all burned sites or by too strong and deep burning leading to deletion of the above ground phytomass which enhances overall germination (Schreiber 1997a).

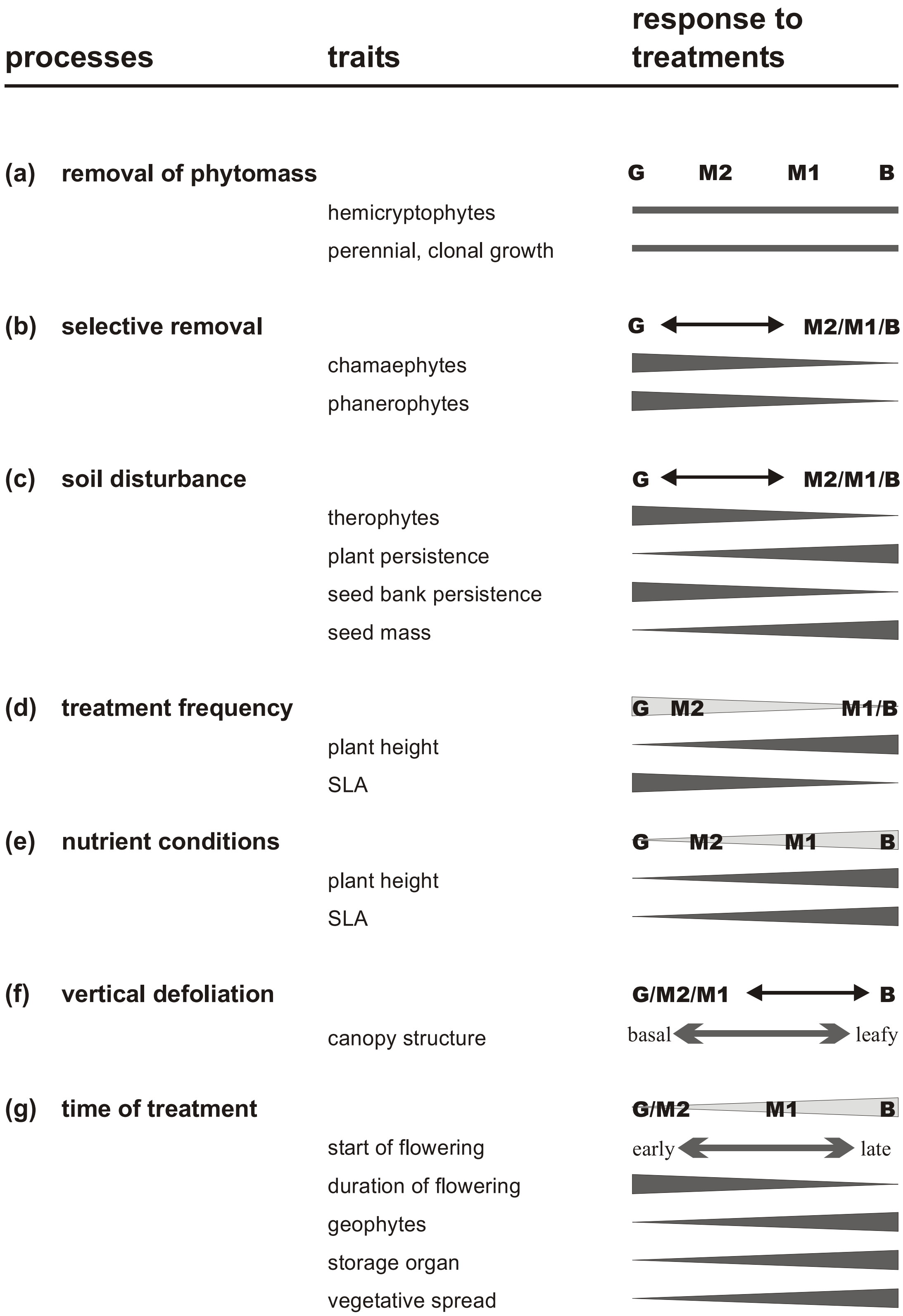


Figure 4.3 Dominant and differentiating processes of the management treatments grazing (G), mulching in June and August (M2), mulching in August (M1) and burning in winter (B). Differences among the treatments regarding the processes as well as the hypothesised plant trait responses are indicated by arrows and discussed in the text, list of traits see Table 4.2.

Contrary to the general finding that relatively few grassland species form persistent seed banks (Bakker et al. 1996b, Hutchings & Booth 1996b, Kalamees & Zobel 1997, Davies & Waite 1998, Bekker et al. 2000), we observed a higher frequency of species with a persistent than with a transient seed bank for all treatments (Figure 4.2). Our classification criteria emphasised records of 'long term persistence' in the database of Thompson et al. (1997) which may explain this pattern. Still, we found a relative and absolute promotion of species with a persistent seed bank by grazing (Figure 4.2, Table 4.3). The soil disturbances through grazers occurred at random so that permanent seed supply through a persistent seed bank could be a competitive strategy as also observed e.g. by Lavorel et al. (1999b) and partly by Dupré and Diekmann (2001). Furthermore, grazing seemed to benefit small seeded species which is in accordance with theory since Reader (1993) and Eriksson and Eriksson (1997) found experimentally that seedling recruitment of small seeds is benefited by small scale soil disturbances. However, since seed bank persistence is negatively correlated with seed size (Thompson et al. 1993, Hodkinson et al. 1998) we may not identify the dominant mechanism here.

(d) Grazing as well as mulching-2 have been applied at least two times a year whereas mulching-1 and burning happened once a year. The higher treatment frequency by grazing and mulching-2 should lead to a shift towards smaller plants since low growing plants lose less biomass than tall growing plants. Köhler (2001) as well as Ryser et al. (1995) found such a tendency towards smaller plants comparing mowing at different frequencies and grazing pressure is generally correlated with a reduction in plant size (Noy-Meir et al. 1989, Díaz et al. 1992, Sternberg et al. 2000, Díaz et al. 2001, Dupré & Diekmann 2001). In this study, however, the distribution of 'plant height' did not differ among the treatments and tall plants were more frequent than expected for all treatments. Additionally, we found the trait 'plant height' being strongly correlated with the nutrition status of the sites so that site differences might dominate treatment effects. Since the experimental design was not balanced among the sites, we cannot state treatment induced trait response for 'plant height' here.

Suggesting higher growth rate as a mechanism of grazing tolerance by frequent grazing, we could expect a promotion of high SLA species at the grazing treatment since growth rate is positively related to SLA (MacGillivray et al. 1995, Westoby 1998, Wilson et al. 1999). Accordingly, Díaz et al. (2001) found SLA being related to species that show a positive grazing response. This study, however, did not reveal a significant response of SLA to any of the treatments. Testing the LHS-concept of Westoby (1998) on partly the same study sites, Moog et al. (submitted) found a trend to higher mean SLA after grazing and mulching in comparison to succession plots but also independent of treatment frequencies.

(e) Nutrient conditions have not been measured directly in the field, but Schreiber (2001) stated an increase in fertility from grazing, mulching-2 and mulching-1 to burning referring to biomass measurements. Grazing led to a slight nutrient decline at the sites. At the mulching treatments, the chopped hay remained on the site, but it decomposed quickly so that no litter accumulated. In the climate of Southwest Germany mulching generally leads to a reduction in nutrients which is different to mulching experiments in The Netherlands (Bakker 1989, Bakker et al. 2002a). Nutrient loss was higher after mulching twice a year than mulching once a year. Burning in winter resulted neither in nutrient loss nor in nutrient enrichment.

With increasing fertility the competition for light increases (Campbell & Grime 1992). Thus, the relative increase in nutrients from grazing, mulching to burning should have resulted in higher plants towards the latter treatments. Another trait responding on changing nutrient conditions is SLA. Representing the relative growth rate of a species, SLA is positively related to fertility (Westoby 1998, Wilson et al. 1999). In this study, however, the differences in SLA were low among the treatments with just a minor shift towards SLA >20 at the burning treatment. As demonstrated in Figure 4.1, between-site variation in nutrient conditions was higher than between treatment variation so that responses to nutrient conditions were blurred. Furthermore, the two contrasting effects of treatment frequency and nutrition conditions on SLA (see Figure 4.3) may account for the missing trait response of SLA.

(f) Surprisingly, grazing showed a lower proportion of species accumulating most leaves close to the ground than the mulching treatments. This is inconsistent to most studies on grazing impact where the promotion of rosette and other ground-layer species is a major response to grazing (Noy-Meir et al. 1989, Díaz et al. 1992, McIntyre et al. 1995, Hadar et al. 1999, Sternberg et al. 2000, Dupré & Diekmann 2001). Indeed, regular cutting surely enhance ground-layer species, too. Furthermore, we counted grasses with a tussock growth form to the attribute ‘basal leaves’ and grasses were benefited by hay making and mulching (e.g. Berlin et al. 2000, Huhta et al. 2001, Schreiber 2001, Kahmen et al. 2002). Probably, the differential defoliation on the vertical gradient by mulching was more intense than by low-intensity grazing. Burning, on the other site, was characterised by vegetation deletion down near the ground and approximately ¾ of the litter layer was being destroyed which explains the relative increase in plants with a leafy canopy structure.

(g) The timing of the treatment is relevant regarding the phenology of seed production (Poschlod et al. 2000a). If the first phytomass removal occurred in summer, seeds should be matured before the treatment. A further strategy for the production of matured seeds despite phytomass removal is to prolong the flowering period to find a phenological niche before or after the treatment. In this study, neither ‘start of flowering’ nor ‘duration of flowering’ showed significant differences in attribute distribution among the treatments. Solely, we observed the treatment burning favouring plants that have a short flowering period in relation to the species pool (Table 4.3). This might be a consequence of the timing of burning after the vegetation period in winter since prolonging of the flowering period to find time between the phytomass removal was not required. Comparing the treatments, we found a relative, but not significant, promotion of plants that start flowering after May when burned (Figure 4.2). Similarly, Köhler (2001) found less early flowering species after burning on a calcareous grassland and explained this by the nearly total removal of the above ground phytomass through the fire in winter. Surprisingly, we did not find early flowering species being encouraged by mulching twice a year in comparison to mulching in August so that seed production could have finished before the first cutting at the end of June. Comparing mowing in July with mowing in October, Köhler (2001) revealed a relatively higher abundance of early flowering species in the first treatment. The low response of both phenological traits in this study was probably due to the small treatment fields. Seeds from the neighboured treatments as well as from the surrounding vegetation might be exchanged by dispersal so that the phenological niche is weak.

Another consequence of burning in winter is that plants may have withdrawn their nutrients by time of the treatment. These nutrients remain at the plants during burning and support the established plants so that species with nutrient storage capacity in the ground are favoured. This mechanism may explain the promotion of geophytes and the existence of storage organs after burning (Figure 4.2). Furthermore, species increased in abundances that invest in extended vegetative expansion (Table 4.3). Similarly, Köhler (2001) observed a strong enhancement of plants with fast vegetative spread as well as with below-ground storage capacity after the burning treatment in a calcareous grassland.

Conclusion

The objective of this study was to reveal the mechanisms ruling trait responses to the treatments. The comparative approach helped to differentiate among the treatments whereas the deviation approach indicated absolute trait responses. We could identify some of the hypothesised processes and it was possible to differentiate among the treatments. Some processes, however, remained unclear like e.g. trait responses to treatment induced differences in fertility. As discussed before, between site variation in nutrient conditions was higher than between treatment variation. Including sites of different vegetation types helped to find trait responses that are general with respect to environmental conditions. However, several processes are only significant when concentrating on one vegetation type as done e.g. by Bullock et al. (2001), Köhler (2001) and Kahmen et al. (2002). Thus there is a trade-off between generalisation and differentiation.

Aiming to identify trait responses to a treatment for predictive purposes we stress the importance of generalisation. If these general trait responses have not enough explanatory power to distinguish among treatments on a specific site it could be reasonable to focus on one vegetation type.

Chapter 5

Comparison of univariate and multivariate analysis of plant trait responses to management treatments

Abstract

Using plant traits for analysing and predicting vegetation responses to specific processes has become popular in plant ecology. There is a huge variety of objectives for studying plant trait responses and as huge is the variety of different approaches.

In this paper a univariate and a multivariate method are compared. In order to analyse plant trait responses to management treatments eleven categorical plant traits with two to five attributes each were considered. In the univariate analysis, each trait was tested separately for relationships between attribute distribution and treatments using contingency tables and χ^2-statistics. In the multivariate analysis, all traits were considered together using the ordination technique NMS.

The univariate and the multivariate analysis showed similar trait responses to the management treatments. The differences between the two methods were attributed to associations among the traits since these associations were considered in the multivariate but not in the univariate analysis. An example are the correlated traits ‘seed mass’ and ‘seed bank longevity’. Univariate analyses alone could not distinguish if both traits responded independently of each other. Instead, the ordination results gave hints that ‘seed mass’ responses dominated ‘seed bank’ responses.

Concluding from this study, the univariate approach is reasonable when each trait is of ecological interest. Additional multivariate analyses help interpreting trait responses with respect to correlated traits, yet at the expense of information of every single trait. When using multivariate analyses alone, the traits must be selected carefully because correlated traits significantly influence the ordination outcome.

Introduction

Research on plant functional trait responses has become popular in plant ecology in the last decade. Plant functional traits are biological characteristics of plants that respond to the dominant processes in an ecosystem (Keddy 1992b, Kelly 1996, Gitay & Noble 1997, Lavorel et al. 1997). By identifying trait responses to specific processes, like e.g. climate change, disturbance or management, we can hypothesise the mechanisms of these processes. Following, functional trait analyses help for a better understanding of the mechanisms in ecosystems. Furthermore, different vegetation types or even floras can be compared to identify general mechanisms. These two features support the application of functional trait responses for predictive purposes.

There is a great variety of studies of functional trait responses (e.g. Boutin & Keddy 1993, Kelly 1996, Noble & Gitay 1996, Skarpe 1996, Thompson et al. 1996, Díaz & Marcelo 1997, Kleyer 1999, Lavorel et al. 1999b, Leishman 1999, Díaz et al. 2001) and just as great is the variety in methods of plant functional trait analyses. In this paper, I concentrate on single functional traits instead of functional groups to compare management treatments in temperate grasslands in the Southwest Germany (see Chapter 4). Adequate analyses can broadly be distinguished in univariate and multivariate methods. In univariate analyses, there is only one response variable so that each trait or attribute is analysed separately. In multivariate analyses, there are several response variables so that all considered traits are analysed together. Various ecologists recommend multivariate methods for functional trait analyses since traits may be related or interact with each other (e.g. Díaz & Marcelo 1997, Landsberg et al. 1999, Lavorel et al. 1999b, Pillar 1999). These interactions remain covered in univariate analyses and a trait response assessed by univariate analysis may be caused by the relation with another trait that primarily responds to the considered process. The objective of this paper is to compare univariate analysis (contingency table, χ^2-statistics) with multivariate analysis (ordination). The importance of correlated traits is being discussed.

Methods

Data set

Analyses were done using vegetation data of the “Fallow Experiments in Baden-Württemberg” which were initiated by K.F. Schreiber in 1975. The objective of the experiment is to evaluate different management treatments with respect to their suitability for maintaining the characteristic floristic composition of semi-natural grasslands (e.g. Schreiber 1977, Schiefer 1981, Schreiber 1997b). This study focused on the treatments grazing, mulching twice a year (mulching-2), mulching once a year (mulching-1) and burning once a year in winter. All treatments have been applied continuously since 1975. Further descriptions of the study design see Chapter 4. Table 4.1 lists the studied management treatments for each site and gives site descriptions. The sites were replications per treatment with one vegetation plot of 25 m^2 each. The percentage covers have been estimated on a fine scale following Schmidt et al. (1974). Here, the vegetation plots in 2000 were taken, after 25 years of management.

Plant Functional Traits

Eleven plant functional traits were selected that were supposed to be associated with the studied management treatments (see McIntyre et al. 1999, Weiher et al. 1999, Poschlod et al. 2000b). The traits were 'life form', 'plant height', 'canopy structure', 'specific leaf area' (SLA), 'storage organs', 'vegetative spread', 'plant persistence', 'seed bank longevity', 'start of flowering', 'duration of flowering' and 'seed mass'. All traits were classified with two to five attributes each. For descriptions of the classification criteria see Chapter 4. Each plant species was graded for each trait according to the attributes listed in Table 4.2. In total, 212 species were considered.

Data analysis

First, I looked for correlations among the traits. The 212 species were assigned to the attributes of two traits in contingency tables, respectively. Relations between each pair of traits were calculated using a coefficient of contingency V_{Cramer} (Brosius 1998)

$$V_{Cramer} = \sqrt{\frac{\chi^2}{N(k-1)}}$$

with Pearson χ^2, N being the total number of species and k being the minimal number of species per attribute of the two traits. V_{Cramer} is between 0 and 1 with 1 meaning absolute correlation. Comparisons of these coefficients among studies and data sets may be critical, however, remaining in this data set, the coefficients indicated the relative trait associations. Coefficients of contingency were calculated in SPSS 10.0.

Second, trait responses to management were analysed using univariate statistics, testing for independence of attribute distribution per trait from management treatments. Each trait was considered separately by determining the relative abundances of the attributes per trait for each of the four treatments. Attribute proportions per trait were calculated from the sum of the percentage covers of all plots per treatment. Attribute proportions per trait and treatment were listed in contingency tables. Standardised residuals of the cells indicated height and direction of the deviation from the expected values. The test of independence of treatments and attributes was done using Pearson χ^2. χ^2-statistics were calculated in SPSS 10.0.

Third, all attributes were analysed together using the multivariate technique NMS. The plots were arranged in an ordination diagram in attribute space considering all attributes together in order to find correlations with the management treatments. The distribution of attributes with respect to the treatments was not known so that it was inappropriate to use ordination techniques like PCA or DCA/CCA. NMS was chosen because this technique does not base on an underlying model but looks for the main structure in the data set (McCune & Grace 2002).

An attribute/plot-matrix was used considering the relative abundance of the attributes per trait. The dimensionality of the data set was assessed by starting with a 6-D solution and stepping down to a 1-D solution. A 2-D solution was taken finally. There were 50 replicates per dimensionality. The stability criterion was 0.0005 within 100 to 500 iterations. The Euclidean distance measure was used for the original data set. After the analysis, the treatments as well as the attributes were correlated with the two axes (Pearson coefficients). For this analysis, the treatments were transformed in dummy variables in a second matrix. Multivariate analyses were done in PCOrd 4.21.

Last, the results of the univariate analysis were compared with those of the multivariate analysis. For each treatment, attribute responses were considered with respect to the standardised residuals of the contingency tables (univariate) and the correlation coefficients with the treatment vectors in NMS ordination space (multivariate). Pearson correlation coefficients between attribute responses of both approaches were calculated in SPSS 10.0 for each treatment separately.

Results

The association matrix in Table 5.1 lists the coefficients of contingency for each pair of traits. 'Life form' demonstrated high coefficients of contingency with 'canopy structure', 'storage organ' and 'plant persistence'. Further high relations showed 'vegetative spread' and 'plant persistence' as well as 'seed bank longevity' and 'seed mass'. The trait 'life form' is an integrative trait comprising plant species strategies to survive cold winters (Raunkiaer 1934). It is thus a superior trait not comparable with the others and since 'life form' is well represented by three of the considered traits, it was let out of all further analyses.

Table 5.1 Matrix of associations between traits. Coefficients of contingency V_{Cramer} are between 0 and 1 (N = 212).

	life form	plant height	canopy structure	SLA	storage organ	veg. spread	plant per.	seed bank	start of flower.	duration flower.
plant height	0.28									
canopy structure	0.48	0.03								
SLA	0.19	0.12	0.12							
storage organ	0.44	0.09	0.06	0.06						
vegetative spread	0.39	0.05	0.01	0.08	0.14					
plant persistence	0.74	0.10	0.22	0.15	0.21	0.44				
seed bank	0.34	0.16	0.04	0.24	0.02	0.01	0.30			
start of flowering	0.18	0.29	0.20	0.13	0.15	0.11	0.09	0.02		
duration of flowering	0.36	0.15	0.09	0.09	0.16	0.03	0.16	0.18	0.05	
seed mass	0.33	0.21	0.18	0.21	0.11	0.12	0.20	0.46	0.08	0.21

Attribute proportions per trait for each treatment summarising all plots are pictured in Figure 5.1. Pearson χ^2 are presented in the same figure. Significant non-random distributions between treatments and attributes showed the traits 'canopy structure', 'storage organ', 'plant persistence', 'seed bank longevity' and 'seed mass'. The standardised residuals of each cell are presented in Table 5.2, left side.

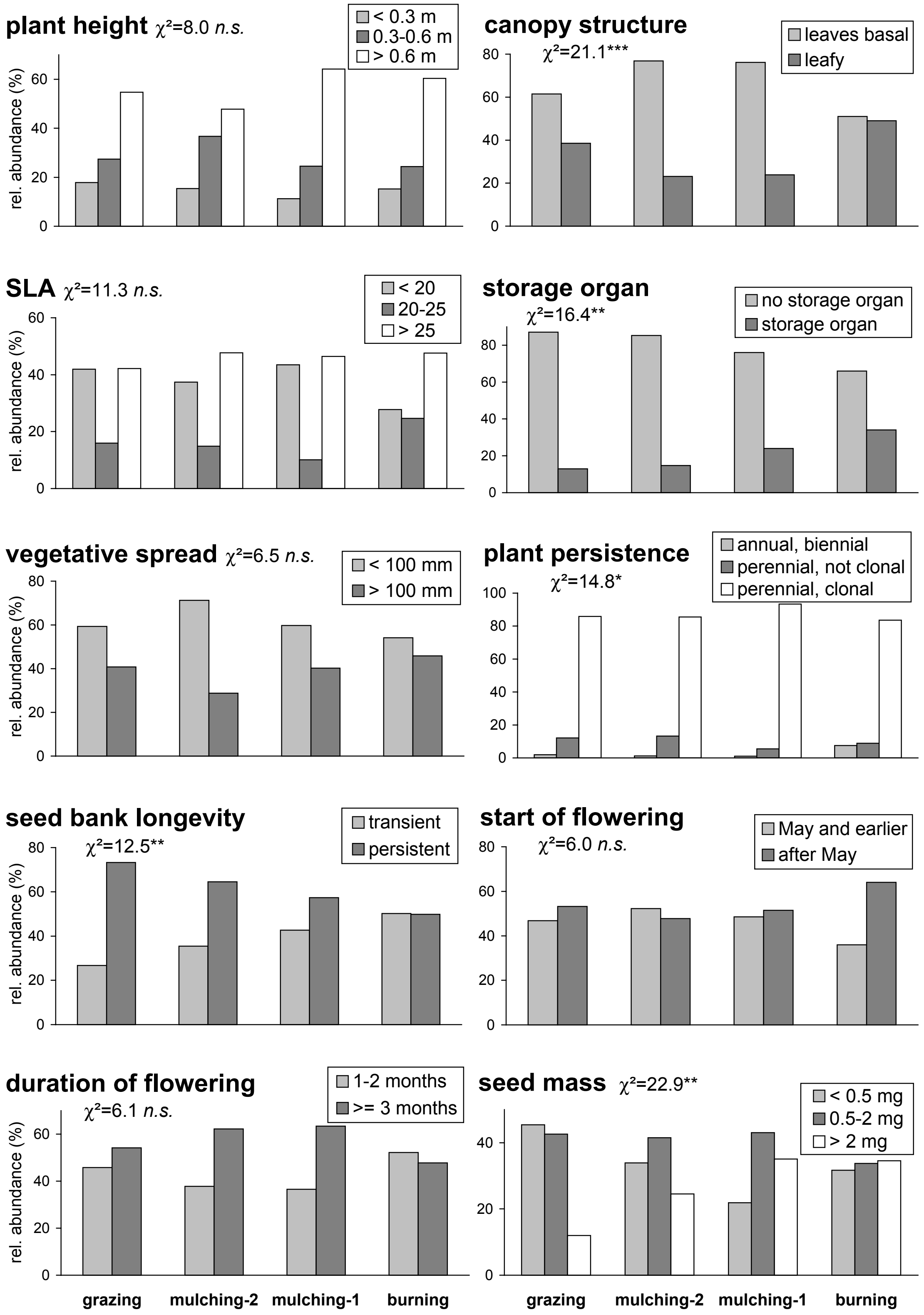


Figure 5.1 Relative species abundance of the attributes per trait considering the sum of all plots per treatment. χ^2 statistics test for non-random attribute distribution among the treatments for each trait. *** p<0.001, ** p<0.01, * p<0.05, *n.s.* not significant

Table 5.2 Relations between traits and treatments. The left site lists the standardised residuals of the cells of the contingency tables per trait (Figure 5.1), analysing the interactions between attribute distribution and treatments. The right site lists the Pearson correlation coefficients between the attributes and the treatment vectors of the NMS ordination diagram (Figure 5.2). N(grazing, mulching-1, mulching-2) = 9 and N(burning) = 6.

		stand. residuals of the contingency tables per trait				**correlation coefficients with NMS-treamtent vectors**			
		G	**M-2**	**M-1**	**B**	**G**	**M-2**	**M-1**	**B**
plant height	< 0.3 m	0.8	0.1	-1.0	0.1	0.6	0.3	-0.6	-0.4
	0.3-0.6 m	-0.2	1.6	-0.6	-0.8	-0.1	0.4	0.1	-0.4
	> 0.6 m	-0.3	-1.2	0.9	0.5	-0.4	-0.6	0.4	0.7
canopy structure	leaves basal	-0.6	1.3	1.2	-1.9	-0.1	0.5	0.1	-0.4
	leafy	0.9	-1.9	-1.7	2.6	0.1	-0.5	-0.1	0.4
SLA	< 20	0.7	-0.1	1.0	-1.6	-0.5	0.5	0.4	-0.4
	20-25	-0.1	-0.4	-1.6	2.0	0.0	-0.1	0.0	0.1
	> 25	-0.6	0.3	0.1	0.2	0.4	-0.4	-0.4	0.4
storage organ	no storage organ	1.0	0.7	-0.3	-1.4	0.4	0.3	-0.4	-0.4
	storage organ	-1.8	-1.4	0.5	2.7	-0.4	-0.3	0.4	0.4
vegetative spread	< 100 mm	-0.3	1.3	-0.1	-0.9	-0.3	0.7	0.2	-0.6
	> 100 mm	0.3	-1.6	0.2	1.1	0.3	-0.7	-0.2	0.6
plant persistence	annual, biennial	-0.6	-1.2	-1.2	2.9	0.0	-0.4	0.0	0.4
	perennial, not clonal	0.6	1.0	-1.3	-0.3	0.0	0.2	0.0	-0.2
	perennial, clonal	-0.1	-0.1	0.6	-0.4	0.0	0.1	0.0	-0.1
seed bank persistence	transient	-1.9	-0.6	0.7	1.8	-0.7	-0.2	0.7	0.3
	persistent	1.5	0.5	-0.5	-1.4	0.7	0.2	-0.7	-0.3
start of flowering	May and earlier	0.3	0.8	0.4	-1.5	0.0	0.8	-0.1	-0.8
	after May	-0.2	-0.8	-0.4	1.4	0.0	-0.8	0.1	0.8
duration of flowering	1-2 months	0.4	-0.8	-1.0	1.3	0.5	-0.4	-0.5	0.3
	≥ 3 months	-0.4	0.7	0.8	-1.2	-0.5	0.4	0.5	-0.3
seed mass	< 0.5 mg	2.1	0.1	-1.9	-0.2	0.9	-0.2	-0.8	0.1
	0.5-2 mg	0.4	0.2	0.4	-1.1	0.0	0.3	0.0	-0.3
	> 2 mg	-2.8	-0.4	1.6	1.6	-0.8	0.0	0.8	0.1

The ordination diagram of the NMS is documented in Figure 5.2, being split in (a) plots and (b) attributes for better presentation. Axis 1 represented R^2=51% and axis 2 represented R^2=32% of the variance in the data set which was evaluated by correlations between distances of the plots in the ordination space and distances of the plots in the original space. In summary, 83% of the variance in the attribute space was represented by both axes. The vectors in Figure 5.2a indicate the direction and extent of increasing importance of the treatments with grazing being focused at the bottom, mulching-2 at the left, mulching-1 at the top and burning at the right. At the first view, there was no distinct differentiation of the plots among the treatments but the orthogonal treatment vectors clearly showed that the structure in the data set separated among the treatments. Attribute vectors are plotted in Figure 5.2b. The traits ‘vegetative spread’, ‘start of flowering’ and ‘seed mass’ demonstrated strong correlations with the ordination axes. Table 5.2 (right side) lists the correlation coefficients between the attributes and the respective treatment vectors.

The correlation coefficients between attribute responses of univariate analysis (standardised residuals) and multivariate analysis (correlation with treatment vectors) were for grazing r = 0.76***, for mulching-2 r = 0.81***, for mulching-1 r = 0.65**, and for burning r = 0.79*** (N=24).

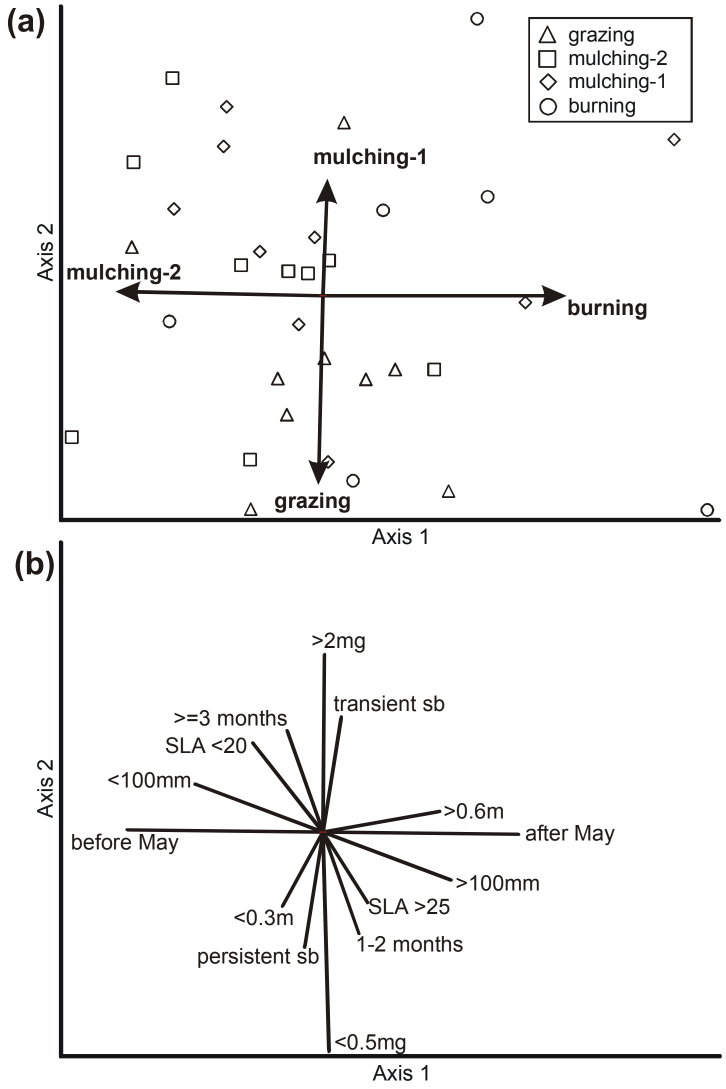


Figure 5.2 NMS ordination diagram of the plots in attribute space (biplot). (a) Plots and treatment vectors: vectors represent the correlations of the management treatments grazing, mulching-2 in June and August, mulching-1 in August, and burning in winter with the axes. (b) Attributes vectors: vectors represent the correlations of the attributes with the axes. Attributes that correlated less than r=0.2 with both axes are not presented. Proportion of variance represented by axis 1 = 0.51 and axis 2 = 0.32.

Discussion

Comparing univariate and multivariate analysis, there were high correlations of trait responses for each treatment despite completely different calculations. The main difference between univariate and multivariate analysis is that in the latter approach relations among the traits influence the result which is expressed by the arrangement of the plots in ordination space. Thus, we do not get information on functional response of each individual trait, but in relation to the other considered traits. The structure in the data set found by NMS clearly demonstrated differences of the treatments. All four treatments pointed in contrasting directions with grazing and mulching-1 as well as mulching-2 and burning being counterparts, respectively. Therefore, the correlation coefficients of grazing were opposed to mulching-1 and those of mulching-2 were generally opposed to burning (Table 5.2). However, those traits that were significantly associated with at least one of the treatments in the ordination analysis did not always show significant interactions between trait and treatments in the contingency tables which is discussed in the following.

A discrepancy between both analyses was found for the traits ‘seed bank longevity’ and ‘seed mass’ with a higher positive correlation of mulching-1 with ‘transient seed bank’ and ‘seed mass >2mg’ in NMS than expected from univariate analysis in comparison to burning (Table 5.2). In Figure 5.1 both treatments exhibited similar attribute distributions or even a relative promotion of ‘transient seed bank’ after burning. Both attributes, ‘transient seed bank’ and ‘seed mass >2mg’, strongly influenced the location of the mulching-1 plots as demonstrated by their long vectors in direction of the mulching treatment in Figure 5.2b (Legendre & Legendre 2000). Following, the correlation coefficients at the burning treatments were lower than expected which could be attributed to the orthogonal relation between mulching-1 and burning in the NMS ordination. Similarly, the attribute ‘annual/biennial’ showed a higher negative coefficient to mulching-2 in comparison to mulching-1 in NMS than expected from the univariate analysis (Table 5.2). Here, this negative correlation was probably due to the complementary relationship between mulching-2 and burning with burning being characterised by comparatively more annuals (Figure 5.1). As last example, the high abundance of species with a short flowering period at the burning treatment (‘1-2 months’, Figure 5.1) was not reflected in the NMS ordination (Table 5.2). Here, the impact of the high abundance of long flowering species at the mulching treatments seemed to dominate in the ordination.

These examples indicate that multivariate analyses may generate results that are clearly not due to single attribute responses but to the associations among the attributes. Correlated traits may largely determine the ordination outcome so that the results may rather depend on the selection of the traits than on the trait-environment relationships. At the other site, these results are possibly closer to the situation in nature with interacting traits.

A further aspect is that correlations among traits can be investigated more profoundly in ordination analyses. Regarding the traits ‘seed bank longevity’ and ‘seed mass’, it is known that small seeds are associated with a persistent seed bank (Thompson et al. 1993, Hodkinson et al. 1998, Thompson et al. 1998). This correlation was also found in this study (Table 5.1) and grazing encouraged species with a persistent seed bank as well as with small seeds (Figure 5.1). This observation generates the question if both traits responded independently to grazing or if one trait dominated the response of the other trait. Concentrating on univariate analysis, I might not go further into this question but the ordination gave hints to the dominant mechanisms. In ordination space, ‘seed mass <0.5mg’ was more correlated with grazing than ‘persistent seed bank’ (Table 5.2). This indicated that the attribute ‘small seeds’ dominated the attribute ‘seed bank persistence’. A further indication are the height of the correlation coefficients with the treatment vectors in comparison to the standardised residuals (Table 5.2) for ‘seed bank longevity’. As described above, the negative correlation of species with persistent seed bank with mulching-1 was stronger than with burning in the ordination, although Figure 5.1 clearly showed a higher relative abundance of species with a persistent seed bank at the mulching-1 treatment. The different pattern in ordination may again be explained by the dominance of the trait ‘seed mass’. Small seeded species were less abundant after mulching-1 in relation to burning (Figure 5.1 and Table 5.2). Thus, the strong negative response of small seeded species to mulching-1 seemed to have determined the strong negative response of species with a persistent seed bank in ordination space, which was not observed in univariate analysis. In this case, the correlation among traits appeared to dominate trait response to the treatments.

Conclusion

This study revealed that both approaches provided the same main trait responses apart from some differences. At this point, there is no general advantage of one of the approaches so that the selection of the analysis must be reasoned by the objective of the study. Univariate analyses give information about each single traits whereas multivariate analyses consider the attribute-associations. Using multivariate analyses we gain more information about correlated traits which may permit to differentiate the response of correlated traits to a process. Still, both approaches presented here are indirect methods and we obtain certainty about the mechanisms of a process only by direct, experimental testing. A crucial disadvantage of the multivariate methods is that the results are highly sensitive to the selection of traits. The result changes if different traits are included in the ordination analysis. Thus, results are never ‘definite’ and difficult to compare with other studies.

Finally, I argue that univariate analyses are reasonable if each trait is selected with ecological comprehension. This means that each trait should have its own ecological meaning and should be associated with an hypothesised process. If the knowledge of processes increases in the course of a study, further traits may easily be incorporated in the analysis. Additional multivariate analysis like ordination is useful if a more profound understanding of correlated traits is required. When restricting to multivariate methods, however, the traits must be selected carefully because correlated traits significantly influences the ordination outcome. In this case, it is advisable to look for correlations among the traits prior to analysis.

Chapter 6

Does germination success differ with respect to seed mass and germination season? Experimental testing of plant functional trait responses to management

Abstract

Plant functional trait responses on processes like grassland management have been analysed frequently, however, the scaling up from individual traits to the outcomes of vegetation dynamics have seldom been tested. In this study, germination success was analysed with respect to the interactions between management and two traits which are relevant for seedling recruitment: seed mass and germination season. Analysing vegetation data of the „Fallow experiments in Baden-Württemberg", which are located in Southwest Germany, these two traits were found to respond to management. Here, we present a germination experiment to test the relationships found in the "Fallow Experiments" between the two functional traits and management. The germination experiment took place in a semi-natural dry grassland in Northeast Germany. Considering a region with different climatic conditions allows for generalisation. Seeds of eight herbaceous species that differ with respect to seed mass and germination season were sown at mown, grazed and abandoned plots. Germination success was documented during the following year.

Contrary to the observations of the "Fallow Experiments", germination of small seeds was not promoted by mowing or grazing. Instead, small seeds germinated relatively more often than expected in the abandoned plots. A relationship between abandonment and gaps of bare soil that favour germination of small seeds was likely but could not be proved statistically. Germination of large seeds decreased more than germination of small seeds after abandonment which was similar to the observations of the "Fallow Experiments". Possibly, they suffered most from bad light conditions. Regarding germination season, mowing favoured autumn germination, explainable by the biomass removal in late summer. Contrary to our expectation, grazing showed relatively more spring germination than mowing, yet vegetation height was smallest in spring. Generally, germination season was found to be related to the temporal occurrence of favourable light conditions.

Introduction

Plant functional traits are biological characteristics of plants that respond to the dominant processes in an ecosystem (Keddy 1992b, Kelly 1996, Gitay & Noble 1997, Lavorel et al. 1997). There is growing interest in plant functional trait analyses since we gain information of the regulating mechanisms and we may scale down from the species level to the trait level. The trait level enables to compare sites with different species sets and permits to predict responses to specific processes. Most studies on plant functional trait responses to a specific process are indirect analyses that analyse the vegetation with respect to trait distribution (e.g. Díaz et al. 1998, Lavorel et al. 1999b, McIntyre et al. 1999, Köhler 2001). However, the effect of functional traits on the outcome of vegetation dynamics has seldom been proved by experiments.

This paper concerns the link between individual plant traits relevant for germination and seedling recruitment. Recruitment by seeds happens seldom in dense grassland vegetation, however, it is essential for population dynamics and the biodiversity in grasslands (Rusch & van der Maarel 1992, Tilman 1993, Kitajima & Tilman 1996, Eriksson & Eriksson 1997, Zobel et al. 2000). Here, the focus is on the two traits seed mass and germination season. Seed mass is an important characteristic of a plant species concerning seedling recruitment. In a variety of environmental conditions it was shown that the germination and establishment success increases with increasing seed mass (summarised in Leishman et al. 1995). A relative benefit of small seeded species or an increased germination of small seeds was observed repeatedly after soil disturbances (McConnaughay & Bazzaz 1987, Reader 1993, McIntyre et al. 1995, Thompson et al. 1996, Eriksson & Eriksson 1997). In contrast, Lavorel et al. (1999b) found seed mass not being related to disturbance. They stated that many correlated traits are important for regeneration e.g. seed production, dispersal, seed bank longevity, life cycle (see also Thompson & Baster 1992, Thompson et al. 1993, Leishman et al. 1995, Westoby 1998) and these correlated traits may therefore condition the response of seed mass. Concluding from a germination study of calcareous grassland species, Leishman (1999) stated that seed mass is not generally a good predictor for establishment ability but highly context dependent. Despite these controversial statements, it is widely accepted that large seeds show better germination success with decreasing light than small seeds, and that late successional species have mostly large seeds (Salisbury 1942, Fenner 1987, Osunkoya et al. 1994, Leishman et al. 1995, Hodkinson et al. 1998).

Species specific seasonal germination is supposed to be a response to temporal occurrence of regeneration niches (summarised in Schütz 2000, Grime 2001). Eriksson & Eriksson (1997) found germination in autumn being promoted through soil disturbances whereas Lavorel et al. (1994, 1998, 1999b) observed a promotion of germination in spring after soil disturbances. This difference may by due to different climates of the study sites with northern Europe in the first and southern Europe in the latter case. Generally, the seasonal timing of germination determines the degree of competition for light of the seedlings and is thus supposed to being related to the time of disturbance (McIntyre et al. 1999). Consequently, the removal of biomass by grazing or mowing in late summer should promote germination in autumn (see Olff et al. 1994).

The present paper aims at testing functional trait responses to management and abandonment identified by indirect analyses of vegetation data of the “Fallow Experiments in Baden Württemberg” (Schreiber 1977)(Chapter 2 to 4). For this reason, we employed a field experiment considering the managements mowing and grazing as well as abandonment. Since field experiments are highly time consuming, we restricted to studying the impact of the two traits seed mass and germination season on germination success. In the germination experiment, seeds of eight species were sown that differed in seed mass and germination season. The germination success was analysed with respect to traits and management.

The “Fallow Experiments” were conducted in Southwest Germany whereas the germination experiment was carried out in Northeast Germany. Considering two regions with different climatic conditions and different species sets additionally allows to generalise trait responses to management.

Following the results of the “Fallow Experiments” we hypothesise for seed mass that

- mowing and grazing favour germination of small seeds
- abandonment favours germination of small seeds (<0.5 mg), whereas germination of larger seeds (0.5-2 mg) is inhibited

and for germination season that

- mowing and grazing favour germination of seeds germinating in autumn
- abandonment favours germination of seeds germinating in spring.

Methods

Study site

The study was conducted on a pasture of 300 ha in the Müritz National Park, Germany, with a high plant species richness (Jeschke 1982, Martin 1997). The pasture is managed by the Müritzhof in charge of the National Park with free ranging cattle, sheep and ponies in low intensities during the whole year without fertilizer application. Due to free ranging in a large area, there are intensively grazed as well as barely grazed or abandoned sites. The pasture contains divers vegetation types from nutrient poor to rich and dry to wet grasslands, wetlands and forests. The germination experiment was carried out on a dry grassland with clusters of the tree *Juniperus communis* (‘Wacholderheide’). Frequently, the clusters accreted to *Juniperus*-woods where no grazing took place any more.

In 2000, we selected 60 localities which are arranged regularly generating a grid of 30×30 m cells (Figure 6.1). 30 localities were in open parts of the grassland (Figure 6.1, black triangles) and here we installed exclosures of 1.5×1.5 m and 1 meter height each. The meadow treatment was applied within the exclosures with mowing once per year in August. We set up a permanent plot of 1×1 m in the centre of the exclosures to avoid edge effects. Adjacent to each exclosure, a respective permanent plot was installed on the pasture that reflects grazing. The 30 remaining localities were close to *Juniperus* shrubs with no or low grazing so that they were categorised as being abandoned despite being part of the pasture in principle (Figure 6.1, white triangles). Again, a permanent plot of 1×1 m was set up each which resulted in 90 permanent plots in total.

In any experiment there is a trade-off between the number of species and the number of replicates that are used, given the usual constraints of available labour and time. The high variability in germination success led to the decision to increase the number of replicates at the expense of the number of species in this experiment. Consequently, the results of trait responses bases only on eight species. In return, data on germination success are reliable for this study site.

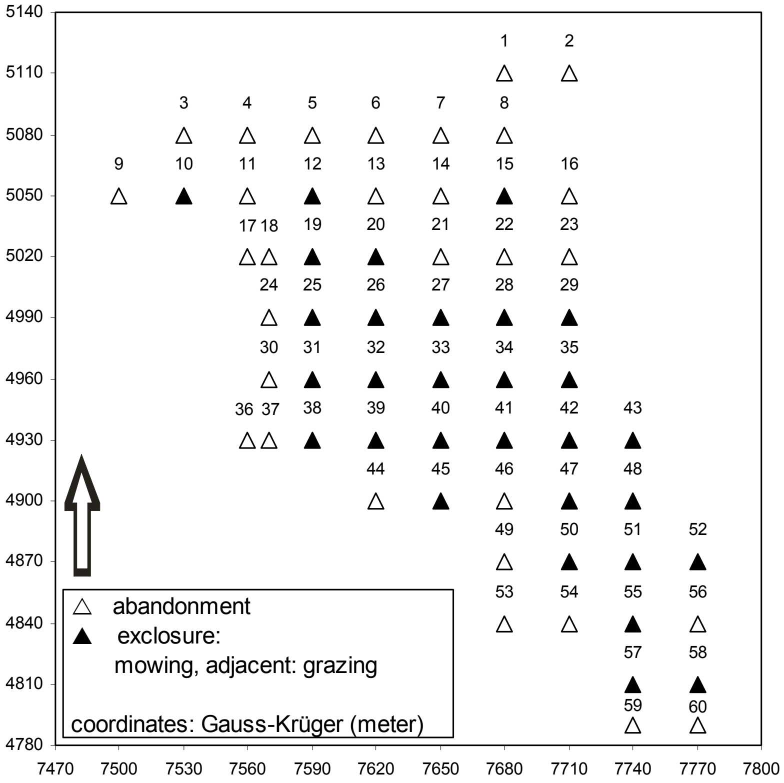


Figure 6.1 Experimental design. 60 localities arranged regularly generating a grid of 30×30 m cells. White triangles symbolise plots of abandonment, black triangles symbolise the exclosures including the plots of the meadow treatment neighboured by the plots of grazing.

Germination experiment

The species of the germination experiment were selected following three criteria: 1) the considered trait categories of seed mass and germination season should be represented evenly 2) seedlings should be unambiguous to identify and 3) the species should occur at the study site (Table 6.1). Seed mass was considered with two categories, small (<0.5 mg) and large (0.5-2 mg). The selected categories of germination season contained species that germinate mainly in autumn (autumn germination) and those that germinate mainly in spring (spring germination). The seeds were collected in late August 2001 at the pasture and sown after one week in the beginning of September. The number of seeds per species and plot is given in Table 6.1.

The permanent plots were subdivided into 20×20 cm subplots and each species was sown in an individual subplot to prevent strong interspecific competition of the seedlings. Germination success was determined by counting seedlings in October'01 for germination in autumn, in April'02 for germination in spring and in June'01 for establishment in the first year. Control of the seedlings of naturally sown seeds took place in one control-subplot per permanent plot.

Table 6.1 Species included in the experiment. Seed mass categories: small (<0.5 mg) and large (0.5-2 mg). Mean seed mass of 16×50 seeds per species is given. Number of sown seeds per plot and species. The nomenclature follows Wisskirchen et al. (1998).

	Thymus pulegioides	*Achillea millefolium*	*Leontodon hispidus*	*Armeria maritima*	*Linum catharticum*	*Euphrasia officinalis*	*Rhinanthus serotinus*	*Centaurea jacea*
germination season	autumn	autumn	autumn	autumn	spring	spring	spring	spring
seed mass (cat.)	small	small	large	large	small	small	large	large
seed mass (mg)	0.12	0.17	0.9	1.42	0.11	0.13	1.6	1.94
# seeds per plot	100	100	50	100	100	100	50	100

Plot characteristics

On all 90 plots we measured the following site factors: (1) height of the vegetation in Sep'01 and (2) Apr'02, (3) photosynthetic active radiation (PAR), (4) temperature at the soil surface, (5) percentage of bare soil, (6) percentage cover of moss layer, (7) height of the moss layer, (8) percentage cover of litter layer, (9) height of the litter layer and (10) pH-value. The factors height of the vegetation in Sep'01, photosynthetic active radiation (PAR), percentage of bare soil, percentage cover of moss layer, height of the moss layer, percentage cover of litter layer and height of the litter layer were measured in September'01. They were determined per subplot (eight subplots per plot) whereas the remaining factors pertained to the plots.

The PAR was acquired using a SunScan (UP GmbH, Cottbus) at the soil surface in combination with a Beam Fraction Sensor above the vegetation. With both values the percentage of PAR that reaches the soil surface in relation to the total PAR could be calculated. The pH-values were determined of a mixed soil-sample of three times 4 cm diameter and 2 cm depth located next to the plots. Sampling took place in Sep'01. PH-measurements were done with 10 g soil in 25 ml distilled water using a pH-meter CG 837 (Schott, Mainz). The temperature was measured using one Thermochrom iButton (Dallas, Semiconductor, Dallas-Texas) per plot. The iButtons were fixed at the soil surface, they measured every four hours from 20.04.02 to 02.06.02. The mean temperature of this period was taken.

Data analysis

During the experiment, locality 9 (abandonment) was destroyed by shrub clearing management. To keep the balanced design, the adjacent locality 10 (open vegetation: mowing and grazing) was excluded from the analyses, too. The germination success was reflected by the number of seedlings in relation to the number of seeds (percentage of seedlings in short). The germination success was corrected by the number of seedlings found in the control subplots, yet, germination was low in these controls.

First, the germination success of the three observation dates was analysed of each species separately. The maximal percentage of seedlings of the three observation dates of each plot and species was chosen for all further calculations. Next, the managements mowing, grazing and the abandonment were compared. Due to large variation of the percentage of seedlings, a non-parametric Kruskal-Wallis H-Test checked for differences among the observation dates and the managements followed by Mann-Whitney U-Tests for pair-wise comparisons.

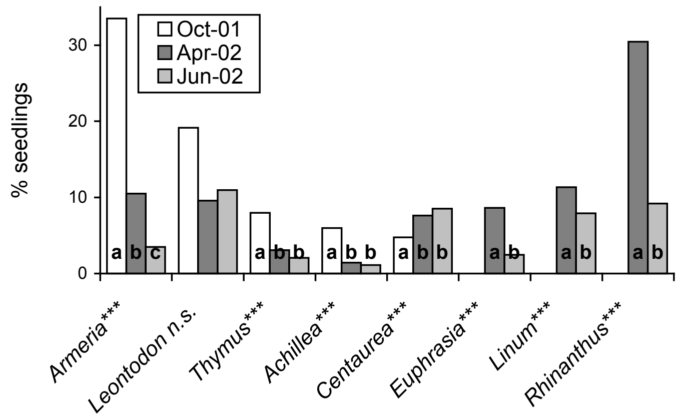
The percentage of seedlings was determined for each trait category, seed mass (small, large) and germination season (autumn, spring) per plot. Germination success was analysed for interactions between management and traits using two-factor ANOVA for both traits separately.

One-factor ANOVA tested for differences of the site factors among the managements. Correlations among the site factors were calculated using Spearman correlation coefficients. Finally, the variation of all grazed plots from open to abandoned localities was considered using the site factors with exclusion of the mown plots. The germination success was analysed for interactions among the site factors and trait categories using linear regressions with groups (GLM) for both traits separately. The site factors were the continuous variables and trait categories were the grouping variables. Percentage of bare soil was transformed by arcsin prior to analysis to optimise to normal distribution (Sokal & Rohlf 2000). All analyses except GLM were run in SPSS 10.0. GLM was done in Genstat 5.

Results

The germination success of each species is presented in Figure 6.2 for (a) the three sampling dates and (b) the management. The germination success is the number of seedlings in relation to the number of sown seeds. In the latter case, the maximal number of seedlings per plot was considered. All four species that germinate preferably in autumn demonstrated a higher percentage of seedlings in October than in April whereas the opposite was true for species that germinate preferably in spring. *Centaurea*, which was classified for germination in spring, clearly germinated already in autumn. Still, the percentage of seedlings increased significantly in April so that *Centaurea* remained in its initial category of spring germination despite its germination activity during the whole observation period. Regarding the maximal percentage of seedlings per plot, all species except *Centaurea* differed among the managements. Generally, germination success was highest when mowing and lowest in the abandoned plots.

(a) sampling date



(b) management

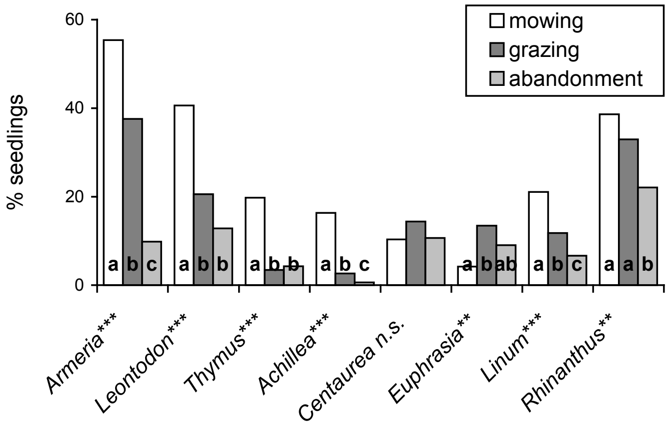
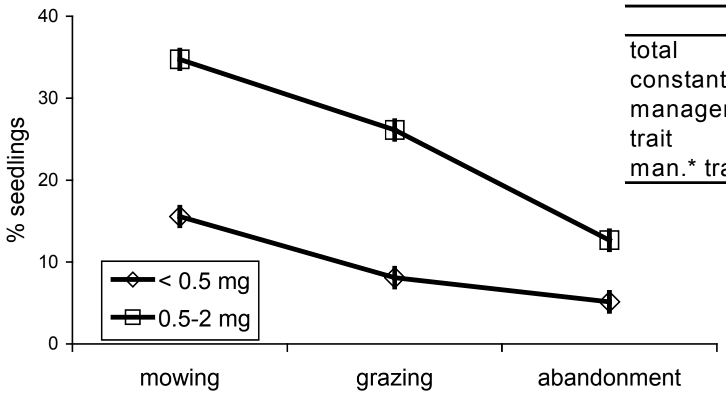


Figure 6.2 Percentage of seedlings per species with respect to (a) the three sampling dates and (b) management. The latter graph considers the maximal percentage of seedlings per plot and species. Percentages refer to all plots per date and managements, respectively. Testing for differences among the sampling dates and managements was done with data of each plot to consider plot variances, H-Test. Different letters indicate significant differences among sampling dates and managements, respectively, resulting from pair-wise comparisons (U-Test, $p<0.05$). *** $p<0.001$, ** $p<0.01$, *n.s.* not significant

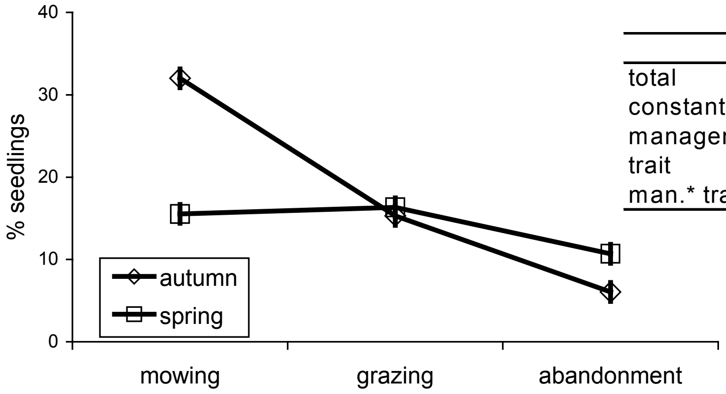
Figure 6.3 presents the maximal percentage of seedlings with respect to management and both traits. The ANOVA-analyses revealed significant interactions between management and traits, respectively. Regarding seed mass (Figure 6.3a), the germination success was generally higher for large than for small seeds. On the abandoned localities the germination success of small seeds was higher than expected. Regarding germination season (Figure 6.3b), seeds that germinate preferably in autumn demonstrated an ample benefit at the mown plots whereas spring germination was higher at the grazed and abandoned plots.

(a) seed mass



	df	F	
total	174		
constant	1	1335.56	***
management	2	101.96	***
trait	1	265.71	***
man.* trait	2	17.28	***

(b) germination season

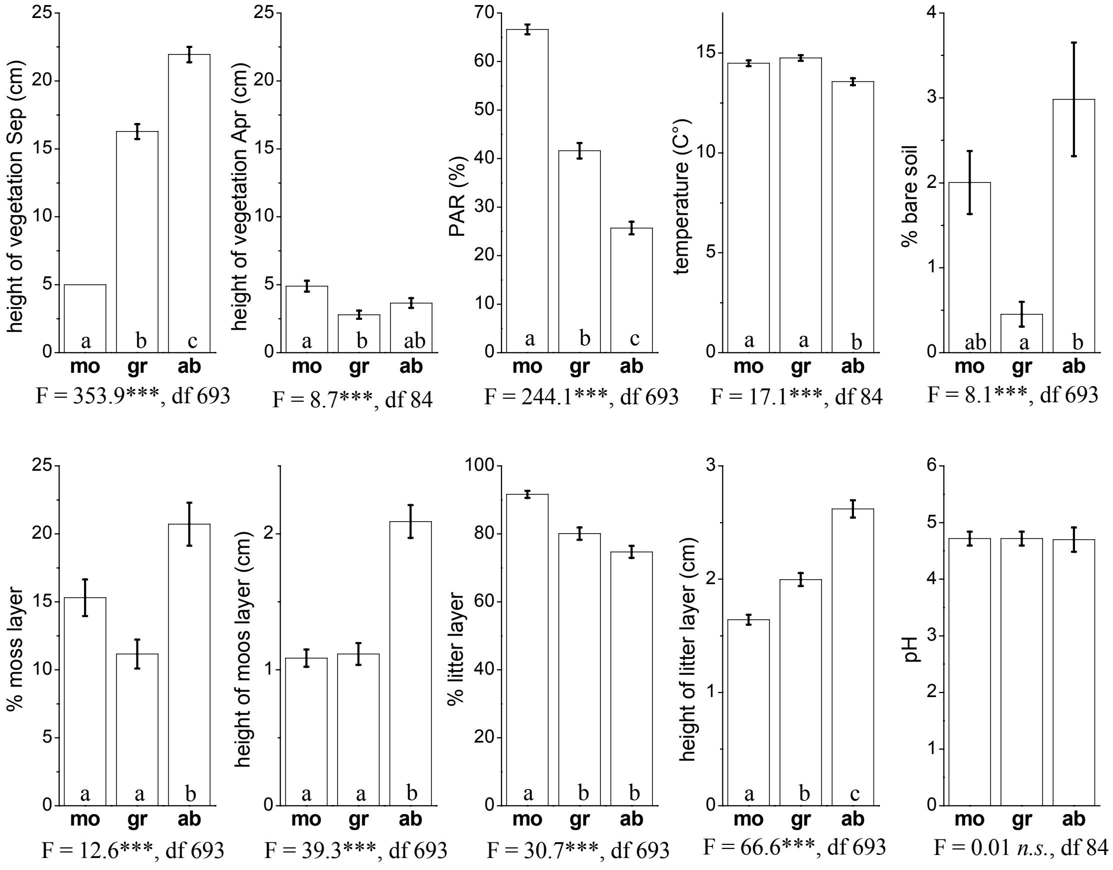


	df	F	
total	174		
constant	1	934.66	***
management	2	72.95	***
trait	1	12.27	**
man.* trait	2	37.57	***

Figure 6.3 Interactions between management and the trait categories of (a) seed mass and (b) germination season, tested by two-factor ANOVA. Mean and standard errors are presented. N = 29.

*** $p<0.001$, ** $p<0.01$

The permanent plots were characterised by several site factors as plotted in Figure 6.4 for each management. The pH-value was the only factor that did not differ significantly among the managements. Vegetation height at the grazed plots was high in autumn but short in spring. The PAR was measured in September and was thus highly correlated with the respective vegetation height (r = -0.76***, N = 696). The height of the litter layer was also significantly correlated with vegetation height in September (r = 0.56***, N = 696). Furthermore, percentage cover and height of the moss layer showed a strong correlation (r = 0.83***, N = 696).



F = 353.9***, df 693
F = 8.7***, df 84
F = 244.1***, df 693
F = 17.1***, df 84
F = 8.1***, df 693
F = 12.6***, df 693
F = 39.3***, df 693
F = 30.7***, df 693
F = 66.6***, df 693
F = 0.01 *n.s.*, df 84

Figure 6.4 Site factors of the mown (mo), grazed (gr) and abandoned (ab) plots. Mean and standard errors. One-factor ANOVA tested for differences among the managements. Different letters indicate significant differences of the managements resulting from pair-wise comparisons (Sheffé-Test, p<0.05).

*** p<0.001, *n.s.* not significant

Aiming to describe the variation of the grazed plots from open to abandoned localities all site factors except pH-value were considered. Table 6.2 lists the regression analyses testing for the influence of the site factors in interaction with the trait categories on germination success. These relationships are visualised in Figure 6.5. Four site factors, the height of the vegetation in September, PAR, temperature and height of the litter layer, showed a significant interaction with seed mass (Table 6.2). PAR also interacted with germination season, however, none of the other factors did. There was a stronger decrease in germination success of large than of small seeds with increasing height of the vegetation (Sep) and height of the litter layer as well as a stronger increase with increasing PAR and temperature (Figure 6.5). Regarding germination season, increasing PAR promoted the germination success of seeds germinating in autumn more than of those germinating in spring (Figure 6.5).

Table 6.2 Interactions between site factors of the grazed plots and the traits seed mass and germination season, tested by linear regression with groups (GLM). Site factors were the continuous and trait categories the grouping variables, df = 112. % of bare soil was arcsin transformed prior to analysis.
*** p<0.001, ** p<0.01, * p<0.05, *n.s.* not significant

	height of veg. (Sep)	height of veg. (Apr)	PAR%	temp.	% bare soil	% moss layer	height of moss layer	% litter layer	height of litter layer
seed mass									
R^2	60.3	51.2	66.5	58.8	42.5	47.0	49.9	41.9	55.2
F	59.1 ***	41.3 ***	77.2 ***	54.8 ***	29.3 ***	35.1 ***	39.3 ***	28.6 ***	48.3 ***
constant	11.3 ***	10.2 ***	3.3 *	-15.1 *n.s.*	2.9 ***	8.4 ***	8.7 ***	8.8 *	11.9 ***
factor	-0.3 *	-1.2 *	9.9 *	1.5 *n.s.*	7.7 *n.s.*	-0.1 *n.s.*	-1.4 *n.s.*	0.0 *n.s.*	-2.3 *
trait	23.0 ***	15.7 ***	5.4 **	-42.8 *	13.9 ***	13.8 ***	15.1 ***	10.9 *	21.5 ***
factor*trait	-0.5 **	-0.9 *n.s.*	23.3 ***	4.0 **	-14.9 *n.s.*	-0.1 *n.s.*	-1.3 *n.s.*	0.0 *n.s.*	-3.7 *
germination season									
R^2	26.1	16.6	33.5	20.7	0.8	11.5	13.4	2.6	21.1
F	14.5 ***	8.7 ***	20.3 ***	10.8 ***	1.3 *n.s.*	6.0 ***	7.0 ***	2.0 *n.s.*	10.7 ***
constant	22.6 ***	14.5 ***	2.4 *n.s.*	-31.3 *	10.5 ***	12.0 ***	13.4 ***	15.2 ***	22.0 ***
factor	-0.6 ***	-1.2 *	25.8 ***	3.0 ***	3.2 *n.s.*	-0.1 *n.s.*	-1.7 *	-0.1 *n.s.*	-4.9 ***
trait	-2.9 *n.s.*	4.9 *n.s.*	6.5 **	-4.3 *n.s.*	2.9 *	4.6 *	3.5 *n.s.*	-3.5 *n.s.*	-1.8 *n.s.*
factor*trait	0.3 *n.s.*	-0.7 *n.s.*	-12.0 *	0.5 *n.s.*	-3.8 *n.s.*	-0.1 *n.s.*	-0.5 *n.s.*	0.1 *n.s.*	1.9 *n.s.*

Discussion

The focus of this study was on the interactions between traits and management with respect to germination. Regarding the trait seed mass, there was a clear trend to more germination of large than of small seeds for all managements (Figure 6.3). Contrary to the hypothesis, germination of small seeds was not favoured by mowing or grazing in relation to abandonment. Instead, they were relatively promoted by abandonment (Figure 6.3) as well as by related site factors (increasing vegetation height, decreasing PAR and temperature, Table 6.2 and Figure 6.5). Grazing and sometimes mowing is characterised by the creation of gaps of bare soil through trampling or the mowing machinery. The positive effects of gaps in enhancing seedling recruitment is widely approved (summarised in Schütz 2000, Turnbull et al. 2000, Zobel et al. 2000). However, the outstanding importance of gaps for germination and establishment of small seeds is discussed controversially (see Introduction). In this study, the percentage of bare soil was low, particularly at the grazed plots (Figure 6.4) which may be due to low grazing intensities and indeed, grazing did not promote germination of small seeds. The percentage of bare soil was slightly higher at the abandoned plots and there is a relative promotion of germination of small seeds (Figure 6.3). The interaction between percentage of bare soil and seed mass, however, could not be verified statistically which may be due to the low variation in the percentage of bare soil among the plots (Table 6.2, Figure 6.4).

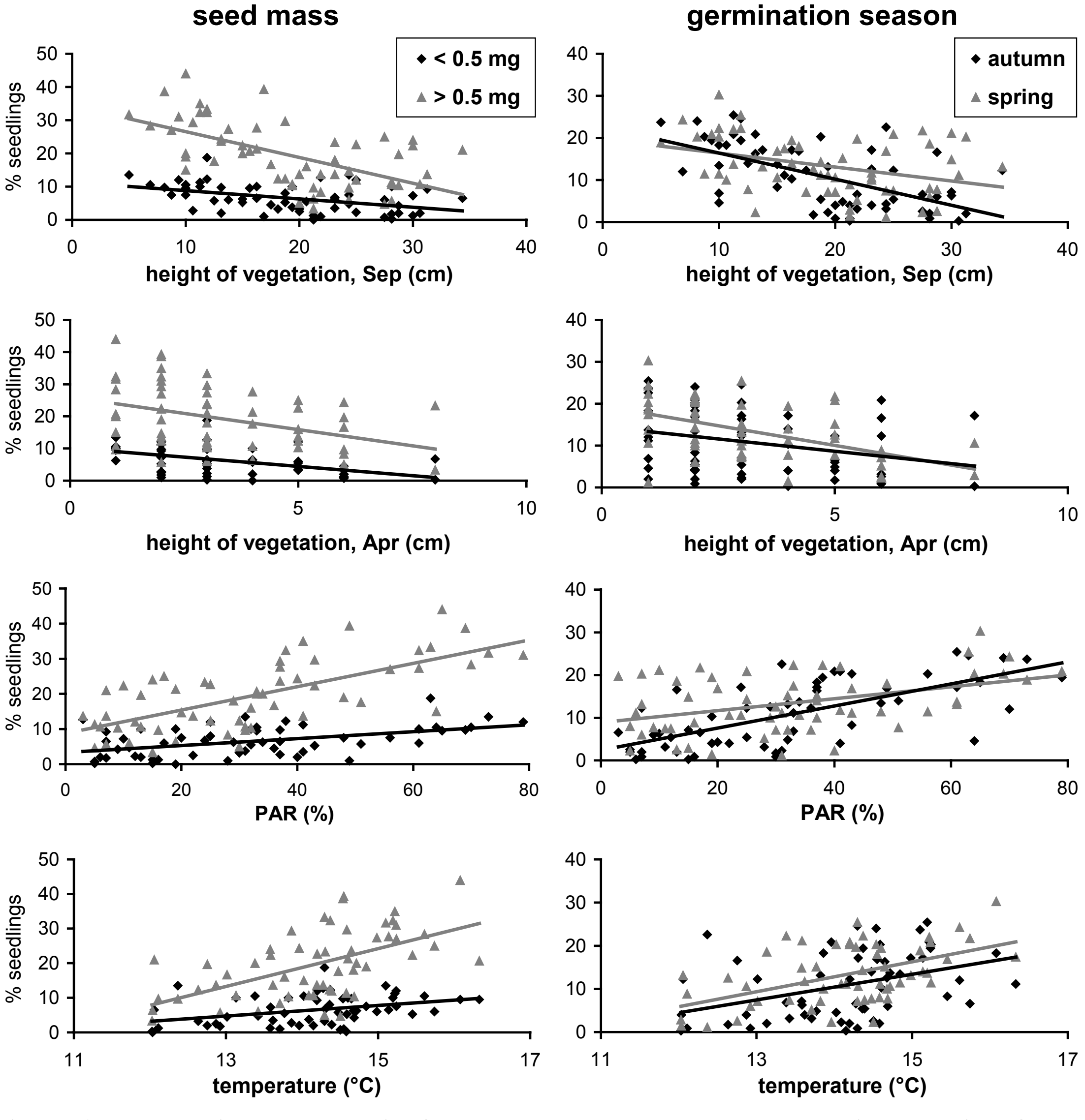


Figure 6.5 Interactions between site factors at the grazed plots and the trait categories of seed mass and germination season, visualised by regression lines of each trait category. Regression analyses see Table 6.2. The site factor height of moss layer is not presented because of high correlation with % cover moss layer. N = 59.

In a study of seedling recruitment in calcareous grassland, Ryser (1990) stressed the negative impact of physical hazards like drought or frost. He claimed that the positive effect of gaps on seedling recruitment is suspended by the shelter of neighbouring plants. In this germination experiment, all seeds showed decreasing germination with increasing height of the vegetation (Sep) or, conversely, increasing germination with increasing PAR and temperature (Figure 6.5). There is thus a general disadvantage by abandonment, and also larger seeds suffer from shading. Germination success of large seeds, however, decreased more than germination success of small seeds. Following Ryser (1990), the higher vegetation after abandonment can be a shelter for physical hazards as it effectively keeps the moisture and lowers fluctuations in temperature. This may be especially important for the germination of small seeds since small seeds do not have own reserves to outlast bad conditions (Leishman et al. 1995).

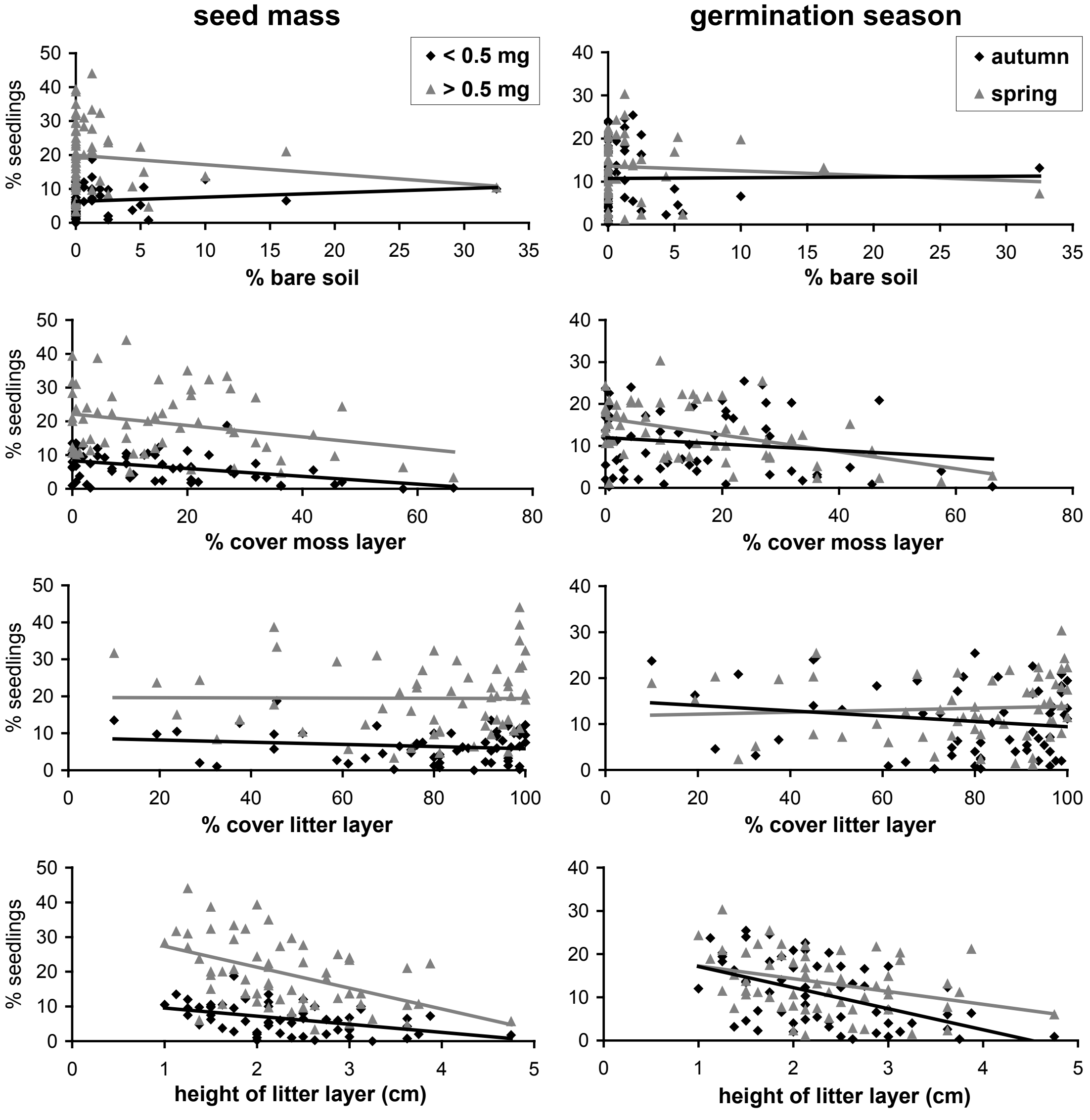


Figure 6.5 continued.

Furthermore, seedling recruitment is largely impaired by seed predation. Reader (1993) and Bonser & Reader (1998) demonstrated with cage-experiments that seed mass determines the attractiveness for predators (vertebrates and invertebrates) with small seeds being less attractive. Reasoning for the present study, small seeds might suffer less from predators than larger seeds, yet it was not studied if predation was higher in the abandoned plots.

Considering the effect of litter on seedling recruitment, Bosy et al. (1995) demonstrated, using four species, that germination of large seeds was less effected by litter than germination of small seeds (see also summary in Schütz 2000). In contrast, this study revealed the opposite trend with small seeds being less effected by litter than larger ones (Table 6.2). This does not mean that litter promoted germination of small seeds but probably, the litter layer effected germination success less than other factors.

Regarding the trait germination season, both hypotheses could partly be approved in this experiment. Mowing significantly favoured seeds that germinated mainly in autumn whereas spring germination was relatively enhanced by grazing and abandonment (Figure 6.3). It seems reasonable that the short vegetation in autumn after the mowing treatment enhanced instant germination. The same reason may explain the increased spring germination by grazing since the vegetation of the grazed plots was shortest in spring (Figure 6.4). The importance of short vegetation height for germination is further stressed by the negative relation between vegetation height in April and spring germination (Figure 6.5). Furthermore, decreasing PAR in September influenced germination in autumn negatively whereas germination in spring was less affected. When seeds germinate in spring, seedlings do not risk winter mortality. Thus, if the height of the vegetation is too high to promote germination in autumn, spring germination may be the better strategy for successful seedling recruitment (Schütz 2000). There was no relation between germination season and bare soil as discussed in the introduction which may again be due to low variance in the percentage of bare soil among the plots.

In conclusion, we could demonstrate in the germination experiment that the functional traits seed mass and germination season significantly determine germination success with respect to grassland management. The relationships identified using the vegetation data of the “Fallow Experiments” already indicated an impact of both traits on the outcome of vegetation. In indirect analyses, however, we cannot separate single processes so that these relationships could be artefacts conditioned by further processes e.g. of the established plants. Focusing on the process of germination by employing an experiment now allows to verify the observations of the “Fallow Experiments”. The relationships between both functional traits and management were similar in the different regions (Southwest and Northeast Germany) which claims for generality.

Chapter 7

Evaluation of plant trait responses to different grazing intensities using a mechanistic, spatially explicit simulation model

Abstract

Knowing about plant trait responses to the processes in an ecosystem helps to better understand the underlying mechanisms which is again a prerequisite for predictive purposes. Plant trait responses are often analysed using vegetation data, yet, experiments are necessary to prove the link between traits and vegetation dynamics. Mechanistic simulation models are useful experiments to study relations between plant traits and processes systematically. This paper deals with effects of different grazing intensities on trait composition using a mechanistic, spatially explicit simulation model. The model considers the competitive ability of the established plant, vegetative reproduction and seedling recruitment being the determinant processes of a plants life cycle in grassland. They are represented by the traits canopy height, vegetative spread and seed mass which are combined in 18 trait syndromes (strategies). The grazing gradient varies between no grazing (abandonment) and high grazing pressure.

Population dynamics of the 18 strategies were analysed with respect to trait composition. Canopy height influenced strategy abundances on both extremes of the grazing gradient with tall strategies being promoted after abandonment and short, rosette strategies becoming dominant at high grazing pressures. This relation is due to the plant fitness being related to its individual size. Concerning vegetative spread, the model results showed that long spreading was a superior strategy. Exceptions were in heterogeneous environments at a high spatial scale with lots of patches of unfavourable conditions through trees. Here, the risk of a spacer to arrive at a unfavourable site was high. The overall dominance of strategies with small seeds was attributed to their numerical advantage. They were again encouraged after increasing the number of favourable sites for germination through trampling.

This paper clearly demonstrates the profit of simulation models to investigate specific processes systematically in virtual experiments with well-defined conditions. However, a comparison with field data of the “Fallow Experiments in Baden-Württemberg” also exposes the limits of simulation studies since only a smallest fraction of the processes in nature can be considered.

Introduction

Grasslands made by grazing livestock are a common ecosystem worldwide. Grasslands are characterised by herbaceous vegetation with different amounts of woody species. The herbaceous vegetation may differ greatly among geographic regions e.g. with perennials dominating in temperate and annuals dominating in arid regions (Walter 1990, Ellenberg 1996). The processes induced by livestock, however, are similar like differential defoliation on a vertical gradient through grazing and soil disturbances caused by trampling. There is a great interest to generalise plant response to grazing. An important approach is to analyse changes on the trait level rather than on the species level. The focus is on plant traits which respond to the dominant ecosystem processes (Keddy 1992b, Kelly 1996, Gitay & Noble 1997, Lavorel et al. 1997). In the case of grazing it is being investigated which traits are sensitive to grazing and if these traits respond similar in different localities or regions (e.g. Noy-Meir et al. 1989, Díaz et al. 1992, Briemle & Schreiber 1994, McIntyre et al. 1995, Hadar et al. 1999, Landsberg et al. 1999, Lavorel et al. 1999a, Lavorel et al. 1999b, Sternberg et al. 2000, Bullock et al. 2001, Díaz et al. 2001, Dupré & Diekmann 2001, Köhler 2001). There are some general findings in trait responses to grazing suggesting that differential defoliation favours small or rosette species and that soil disturbances encourage short lived species. In a comparative analysis of grasslands in Argentina and Israel, Díaz et al. (2001) concluded that small canopy height and small leaf size helps to avoid grazing and high specific leaf area (SLA) enhances grazing tolerance.

Apart from field observation, mechanistic simulation models may be used to test the effects of grazing on plant trait responses systematically in a controlled system. By changing parameter values in sensitivity analyses, we get further insights into the system. Furthermore, the modelling approach allows to study the effects of different grazing intensities on the coexistence of plant species. As a matter of course, model systems cannot address all environmental factors and all species interactions influencing trait composition since they are highly simplified. However, in cases where experimental limitations impede the study of specific processes, simulation models have become an important tool in plant ecology. There are good examples of spatial simulation models studying the relation between resident and invader species, mostly in heterogeneous habitats with varying disturbance patterns (e.g. Weiner & Conte 1981, Crawley & May 1987, Czárán 1989, Czárán & Bartha 1989, Colasanti & Grime 1993, Dytham 1995, Lavorel & Chesson 1995, Winkler & Klotz 1997, Law & Dieckmann 2000, Loehle 2000). Coexistence of resident and invader species was often found to be due to a trade-off between competitive ability and dispersibility, with the invader species being more effective in seed dispersal (e.g. Czárán & Bartha 1989, Tilman 1994, Lavorel & Chesson 1995, Schippers et al. 2001).

The present paper aims to investigate effects of different grazing intensities on plant trait composition of the herbaceous vegetation of temperate grasslands. This study relies on a mechanistic simulation model to evaluate trait responses theoretically. The model considers survival of the established plant and regeneration to be the main processes in a plant's life cycle. At the grazing gradient, competition for light is supposed to mainly rule species interactions with tall species being better competitors for light (Grime 2001). Following, the competitive ability of the established plant is related to canopy height in this model (Weiher et al. 1999, Bullock et al. 2001). Regeneration strategies are the essential characteristics to explain population processes, species diversity and ecosystem response to changes of the environment (Schütz 2000). Regeneration may happen by vegetative growth or by seeds. Temperate grasslands are typically a dense sward where vegetative reproduction predominates whereas recruitment by seeds is rare (Thórhallsdóttir 1990, Arnthórsdóttir 1994, Eriksson & Jakobsson 1998, Otsus & Zobel 2002). Regarding vegetative reproduction, this model differentiates between no spread, short spreading and long spreading. The length of vegetative spread might be an important parameter with respect to habitat heterogeneity, depending on the distribution of favourable sites (de Kroon & van Groenendael 1990, Sutherland & Stillmann 1990). Regeneration by seeds is low in temperate grasslands but enhanced by soil disturbances through trampling (summarised in: Schütz 2000, Turnbull et al. 2000, Zobel et al. 2000). Since germination probability is positively related to seed mass (summarised in Leishman et al. 1995) this model considers small and large seeds.

Using a mechanistic, spatially explicit simulation model, I analyse the interactions of the three plant traits (1) canopy height, (2) vegetative spread and (3) seed mass in response to different grazing intensities (see Westoby 1998, Grime 2001). The combination of these traits leads to 18 trait syndromes in total which are called plant strategies. The paper asks in particular which traits or strategies are favoured along a grazing gradient and what are the responsible mechanisms. Finally, the model results are compared with field data of the "Fallow Experiments in Baden Württemberg" that investigated grazing management and abandonment after 25 years.

Model description

Plant traits and strategies

To simulate the population dynamics of herbaceous species with respect to a grazing gradient, I developed a simple, spatially explicit simulation model called PASTUREPOP with individual plants as modelling units. The model is written in Delphi 5 (Object Pascal).

The plant strategies of PASTUREPOP are combinations of three important plant traits of herbaceous grassland vegetation (trait syndromes), viz. canopy height, vegetative spread and the seed traits seed mass, seed number and seed bank. Table 7.1 lists the 18 strategy types evolved from the trait categories.

The model concentrates on perennials which are dominant in temperate grasslands. The perennials may be non-clonal or clonal. The clonal plants are distinguished with respect to the length of the vegetative spread. Canopy height is differentiated in three categories. The first category are short, rosette plants (10 cm height and 5 cm diameter), the second and third categories are erect, leafy plants of 3 cm diameter and 30 cm and 60 cm height, respectively.

The seed traits account for the trade-off between seed mass and seed number (Rees 1993, Leishman et al. 1995) as well as for the trade-off between seed mass and seed bank longevity (Thompson et al. 1993). Seed mass determines the germination probability, seed number determines the probability of a species to disperse seeds and seed bank longevity is a feature becoming advantageous if there is soil disturbance.

Seed mass is classified in small seeds (<0.5 mg) and large seeds (0.5-2 mg). The number of seeds produced per individual depends on the seed mass. It was assessed according to biomass calculations following Schippers et al. (2001). The mean annual biomass of semi-natural grassland is 500 g $\times$ m^{-2} (Rabotnov 1995). In Pasturepop, there can be one individual per 1 cm^2 which leads to an average individual biomass of 50 mg. When 8% of the plant biomass are invested in seed production (Harper 1977) this leads to 4 mg seeds per adult individual. Non-clonal perennials are presumed to invest up to three times as much energy in seeds as do clonal species (Abrahamson 1980) so that non-clonal species produce app. 12 mg seeds per adult. The resulting maximal number of seeds per strategy is given in Table 7.1. Finally, only small seeds (< 0.5 mg) have a persistent seed bank.

Table 7.1 Characterisation of the 18 plant strategies (S) and population parameters.

S	veg. spread (cm)	canopy height (cm)	plant diameter (cm)	CI tolerance	seed mass (mg)	seed number	seed bank	germ. prob.	species example	no of species
NRS	no spread	10	5	< 10	< 0.5	24	yes	0.1	*Orchis mascula*	4
NRL					0.5-2	6	no	0.3	*Leontodon autumnalis*	9
NMS		30	3	< 30	< 0.5	24	yes	0.1	*Cerastium holosteoides*	2
NML					0.5-2	6	no	0.3	*Lotus corniculatus*	3
NTS		60	3	< 60	< 0.5	24	yes	0.1		-
NTL					0.5-2	6	no	0.3	*Angelica sylvestris*	2
SRS	1 cm	10	5	< 10	< 0.5	8	yes	0.1		-
SRL					0.5-2	2	no	0.3		-
SMS		30	3	< 30	< 0.5	8	yes	0.1	*Festuca ovina*	6
SML					0.5-2	2	no	0.3	*Nardus stricta*	5
STS		60	3	< 60	< 0.5	8	yes	0.1	*Deschampsia cespitosa*	8
STL					0.5-2	2	no	0.3	*Dactylis glomerata*	8
LRS	10 cm	10	5	< 10	< 0.5	8	yes	0.1	*Hieracium pilosella*	20
LRL					0.5-2	2	no	0.3	*Scabiosa columbaria*	20
LMS		30	3	< 30	< 0.5	8	yes	0.1	*Achillea millefolium*	23
LML					0.5-2	2	no	0.3	*Carex flacca*	20
LTS		60	3	< 60	< 0.5	8	yes	0.1	*Leucanthemum vulgare*	15
LTL					0.5-2	2	no	0.3	*Galium verum*	10
JC	no	300	100	< 300	> 2 mg	1	no	1		

Abbreviations of the strategies following the traits. Vegetative spread: N – no spread, S – short , L – long; canopy height: R – rosette, M – medium, T – tall; seed mass: S – small, L – large. Canopy height determines plant diameter and CI tolerance for lateral growth. Seed mass and seed number are negative proportional, only small seeds have a persistent seed bank. Seed number of non-clonal plants is three times higher than of clonal plants. Seed mass determines the maximal germination probability according to Figure 7.3. Species example and number of species per strategy of the "Fallow experiments in Baden-Württemberg". The nomenclature follows Wisskirchen et al. (1998). Model population parameters of the woody species *Juniperus communis* (JC) are added.

Grazing gradient

The grazing intensity varies from no grazing at all (abandonment) to heavy grazing which is translated to a grazing gradient from intensity 0 to 10 in whole numbers. This model refers to sheep grazing several times a year at different stocking rates. An intermediate grazing intensity (G5) means that approximately 50% of the individuals are not grazed in one year whereas at high grazing intensity (G10) each individual is being grazed each time so that the vegetation is a short sward during the whole year. Trampling effects of sheep are relatively little in temperate grasslands. In the model, maximal 2.5% of the area is being disturbed by trampling at intensive grazing (see Demographic structure). Disturbance means here that the vegetation is destroyed so that there is bare soil.

Spatial structure

The spatial structure is a grid of 300×300 cells of 1 cm² (9m² in total). To avoid edge effects the grid space is modelled as a torus. Each cell may contain one plant individual. Here, each plant stem is referred to be an individual independent if a stems is a ramet of another individual (e.g. tussocks). The individuals are characterised by canopy height and plant diameter. Dependent on the plant diameter an individual may cover several cells in the Moore-neighbourhood. Consequently, a cell may contain one basis of an individual but the leaves of several surrounding individuals.

The model considers competition for light to be the main process ruling species interactions (see Introduction). Following, the survival and regeneration of species is determined by an internal variable describing competition intensity. According to Grime (2001), above ground and below ground competition are positively correlated so that canopy height is used as a simple parameter regulating competition intensity (CI) in PASTUREPOP. CI is calculated for each cell. Each individual contributes to the CI by its height and diameter in the way that in each cell covered by an individual the height of the individual is summed to the cell's CI. Through a cyclic calculation, the central cells of an individual obtain more CI than the marginal cells (pictured in Figure 7.1). The contribution of an individual *i* to the CI in cell *c* is determined by the distance of the cell from the basis of the individual ($dist_{c,i}$) and the height of the individual following formula (1)

$$CI_{i,c} = \left(\left(radius_i + 1\right) - dist_{c,i}\right) \times height_i . \tag{1}$$

The CI for each cell is calculated by summing up the CI_i of all individuals covering the cell *c*

$$CI_c = \sum_{i=1}^{n} CI_i \tag{2}$$

with *n* being the number of individuals covering cell *c*. The CI of a cell is between null and infinite. In herbaceous vegetation, the maximal CI of a cell is 76.

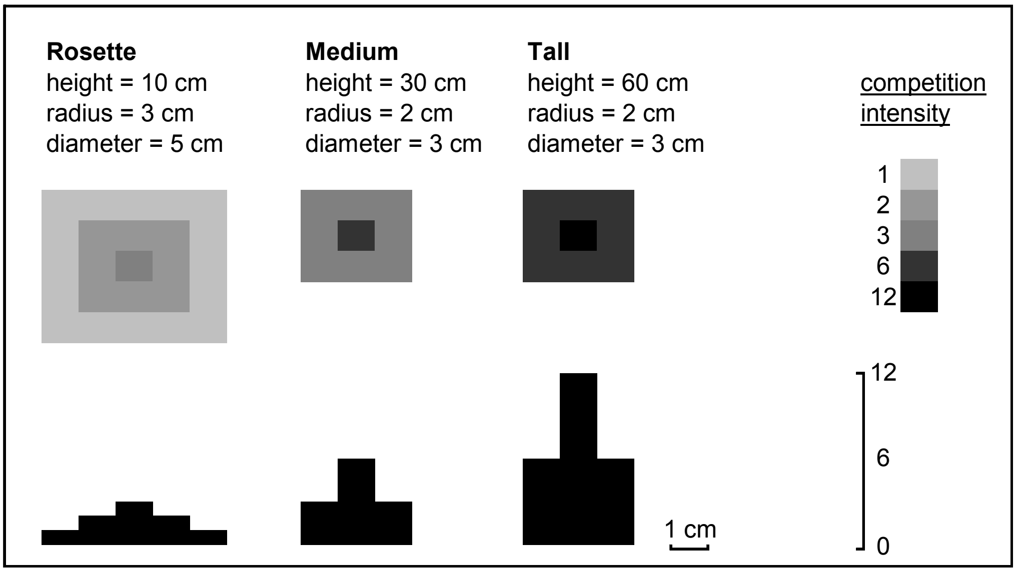


Figure 7.1 Plant canopy height categories and the respective contribution to the CI of each cell. A plant is defined by height and radius where a plant with radius = 1 cm covers one cell in the grid (corresponding to 1 cm diameter). For longer radii the diameter is proportional with radius = 2 cm equals diameter = 3 cm, radius = 3 cm equals diameter = 5 cm diameter etc. Horizontal as well as vertical aspects of the CI are given for all three canopy height categories.

Demographic structure

The model runs through the main processes of a perennials life cycle namely seed production, seed dispersal, germination, vegetative spread, vertical and lateral growth, and death (Figure 7.2). One time step of the model corresponds to one year. Grazing happens once per time step in the model but represents grazing several times a year at different stocking rates in the field (see Grazing gradient).

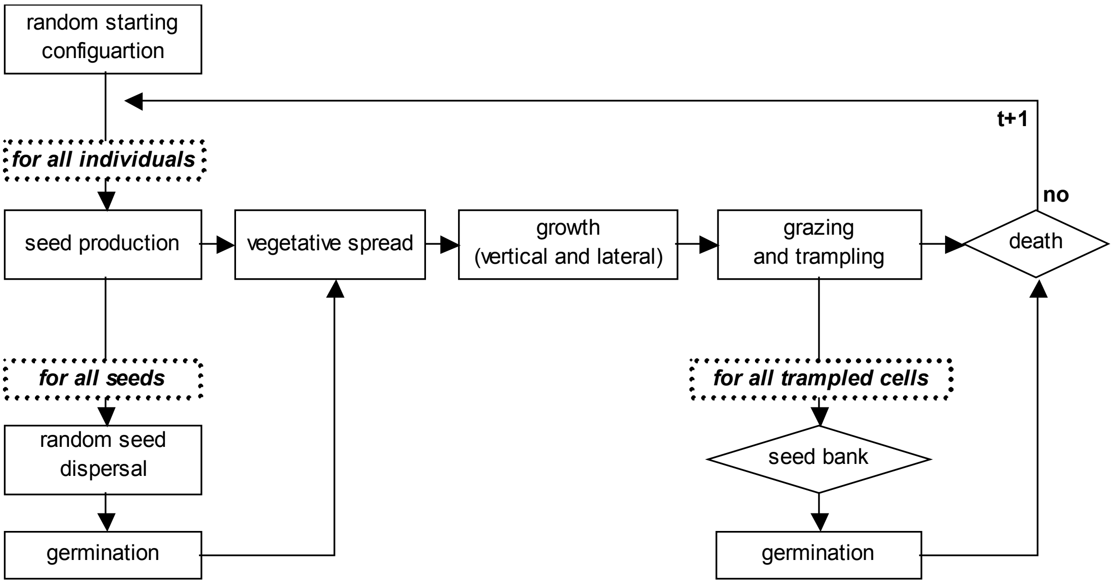
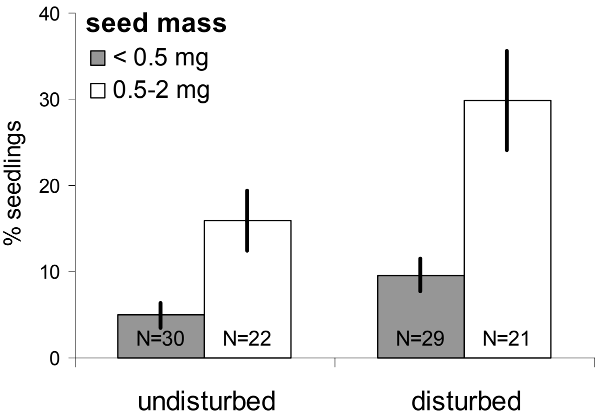


Figure 7.2 Course of the processes of the model. Description in the text.

At the start of the simulation, all strategies are distributed randomly at similar frequencies in the grid. The height and diameter of the individuals are random numbers between 1 and the maximal values in Table 7.1. All individuals that reach their maximal canopy height produce seeds. Total seed production is the product of the number of individuals with maximal canopy height and the specific seed number (Table 7.1) multiplied again by a random number between 0 and 1. Additionally, there is a constant seed input in the grid from outside for each strategy in number of its specific seed number. Seeds are dispersed randomly in the grid. Spatial aspects of seed dispersal are disregarded in PASTUREPOP since short distance seed dispersal of species occurring in the actual vegetation is not supposed to be a limiting factor within grassland communities (Turnbull et al. 2000). Seed input from external sites is clearly more dependent on the dispersibility of seeds, still the resulting dispersal rates are highly determined by seed abundance (Tackenberg 2001). A seed may germinate with a specific germination probability. The germination probability depends on the seed mass and the CI of the cell. Thus, seedlings do not compete with other seedlings as in many spatial vegetation models (e.g. Lavorel & Chesson 1995, Schippers et al. 2001) but with adult neighbours as claimed by Leishman (1999).

Evaluating eight sowing experiments from literature, I found significant differences in germination success between both seed mass categories (Figure 7.3). Additionally, the germination success of both categories was proportionally higher in disturbed than in undisturbed grassland. On the basis of this evaluation, the maximal germination probability in the model is set to 0.1 and 0.3 for the seed mass categories <0.5mg and 0.5-2 mg, respectively (Table 7.1). Maximal germination takes place if there is no CI in the cell and the germination probability decreases linearly to no germination at CI ≥ 100. With this criterion, germination is always possible in herbaceous vegetation but prohibited if a site is covered by a tree. A seedling is defined by a height of 10 cm and a radius of 1 cm. A seedling can establish only if the cell is not occupied by another individual.

Figure 7.3 Evaluation of eight sowing experiments from literature under consideration of two seed mass categories. Germination probability is equivalent to the proportion of germinated seeds. Only studies in semi-natural grasslands are considered. Some studies discriminated between disturbed and undisturbed grassland. N = no of species. (Miles 1972, Verkaar & Schenkeveld 1984, Klinkhamer & deJong 1988, Reader 1993, Hutchings & Booth 1996a, Jackel & Poschlod 1996, Kiviniemi & Eriksson 1999, Jakobsson & Eriksson 2000)



In the next step of the model run, all individuals able to spread vegetatively send a spacer of its specific length from their basis in a random direction. The spacer may establish only if the target cell is empty and if the cells CI is smaller than 150. The latter condition allows the reproduction in herbaceous vegetation but inhibits the reproduction in cells covered by a tree. A new ramet has always a height of 10 cm and a radius of 1 cm.

In the growth process, each individual grows vertically up to its maximal height in competition for light. Lateral growth means lateral expansion of the individuals. Lateral growth is only possible if there is enough space and light available. In the model, competitive ability is related to canopy height so that large plants can deal with more external CI than small plants. CI tolerance for lateral growth is proportional to the height of a strategy with tolerance=$\text{height}_{\text{max}}$ in cm (Table 7.1). For this process, the mean external CI covering the individual is calculated per cell following formula (3)

$$external - CI_i = \frac{\sum_{c=1}^{n} CI_c - CI_i}{n} \tag{3}$$

with n being the number of cells c covered by the individual i. If lateral growth is possible, an individual expands to its maximal diameter.

The growth process is followed by the grazing process which is split in two sub-processes: browsing which means removal of an individual's biomass to a height of 10 cm and trampling where all plants are eliminated. The probability of an individual to be grazed is proportional to the grazing intensity with $\text{prob}_{(\text{grazed})}$ = grazing-intensity × 0.1. If an individual is grazed it cannot produce seeds. Trampling happens as often as the grazing intensity is per square meter. The size of a step is 5×5 cm. Steps are set randomly. At each cell that was trampled the seed bank is activated. One strategy is selected randomly per trampled cell. If this strategy has a persistent seed bank, a seed may germinate according to the described germination process.

The last process of one time step is the death process. The survival probability of perennials is app. 0.8 which implies that perennials have an average longevity of about 5 years, but that 10% of the plants survive for more than 10 years and that 1% live for longer than 20 years (see also Schippers et al. 2001). To take into account that the probability of death decreases when an individual increases in size (Cook 1979) I added a fitness factor to the survival probability of 0.8. After calibration, the fitness factor was set between 0 and 0.03. It is determined by the size of an individual as listed in Table 7.2.

Table 7.2 Fitness factor added to the perennial survival probability of 0.8 depending on the individual size. Matrix of possible combinations of canopy height and plant diameter with the respective fitness factors [0 – 0.03].

	canopy height (species)	10 cm	30 cm		60 cm	
	height (ind)	10 cm	10 cm	30 cm	10 cm	60 cm
diameter (ind)	1 cm	0.0	0.0	0.015	0.0	0.2
	3 cm	0.015	0.015	0.03	0.1	0.3
	5 cm	0.03				

Woody species

The model system contains a woody species that characterises the process of abandonment. *Juniperus communis* was chosen as a typical woody species of semi-natural pastures grazed by sheep in Europe (García et al. 1999, García et al. 2000). Growth of *Juniperus* is prevented only under extreme grazing pressure. Its population parameters are appended to Table 7.1. The parameters refer to natural conditions, however, *Juniperus* is only used to determine the environmental conditions caused by a typical tree species so that the population structure of *Juniperus* is not of interest in PASTUREPOP. The maximal size of Juniperus is 3 m height and 1 m diameter which leads to a maximal CI of 1500 in the cell of the basis. The annual growth rate is set to 10 cm in height and 3 cm in radius. *Juniperus* is grazed or trampled only if it is smaller than 60 cm. In the model, *Juniperus* is sensitive to grazing and dies if more then 20 cm of its canopy height was removed by grazing. The survival probability is 0.8 if an individual is younger than 6 years, if it is older it does not die any more. *Juniperus* invades the model system through external seed input. The maximal germination probability is 1 and decreases linearly to no germination at CI ≥ 200 so that germination is possible in the outside margin of 6 cm of an adult tree.

Simulations

Effects of grazing

Figure 7.4 demonstrates the number of individuals of each strategy in the course of 100 time steps. During abandonment, when grazing was missing, there was an increasing number of *Juniperus* and these individuals covered large areas. Figure 7.5 pictures the CI at different grazing intensities, the large white areas visible at G0 indicate the cover of *Juniperus* individuals. In contrast, all herbaceous strategies declined in number but at different speed. At medium grazing pressure (G5), the development of the strategies was more divergent with three strategies becoming dominant (LMS, LTS, LRS). Strategies without clonal growth decreased quickly. *Juniperus* was less in number than without grazing but more importantly, most individuals remained small because of the grazing (Figure 7.5, G5). This feature was even more distinct at high grazing pressure (G10) and also the herbaceous strategies diverged more extremely. Non-clonal strategies decreased immediately whereas strategies with long vegetative spread were the dominant plants, ordered within this group after decreasing canopy height.

The relative abundances of the strategies along the grazing gradient are presented in Figure 7.6. Strategies without clonal growth were rare at all grazing intensities so that their proportion is not visible in Figure 7.6. There was an overall trend from strategies with short vegetative spread (S is first letter) at low grazing intensities to strategies with long vegetative spread (L is first letter) at high grazing pressure.

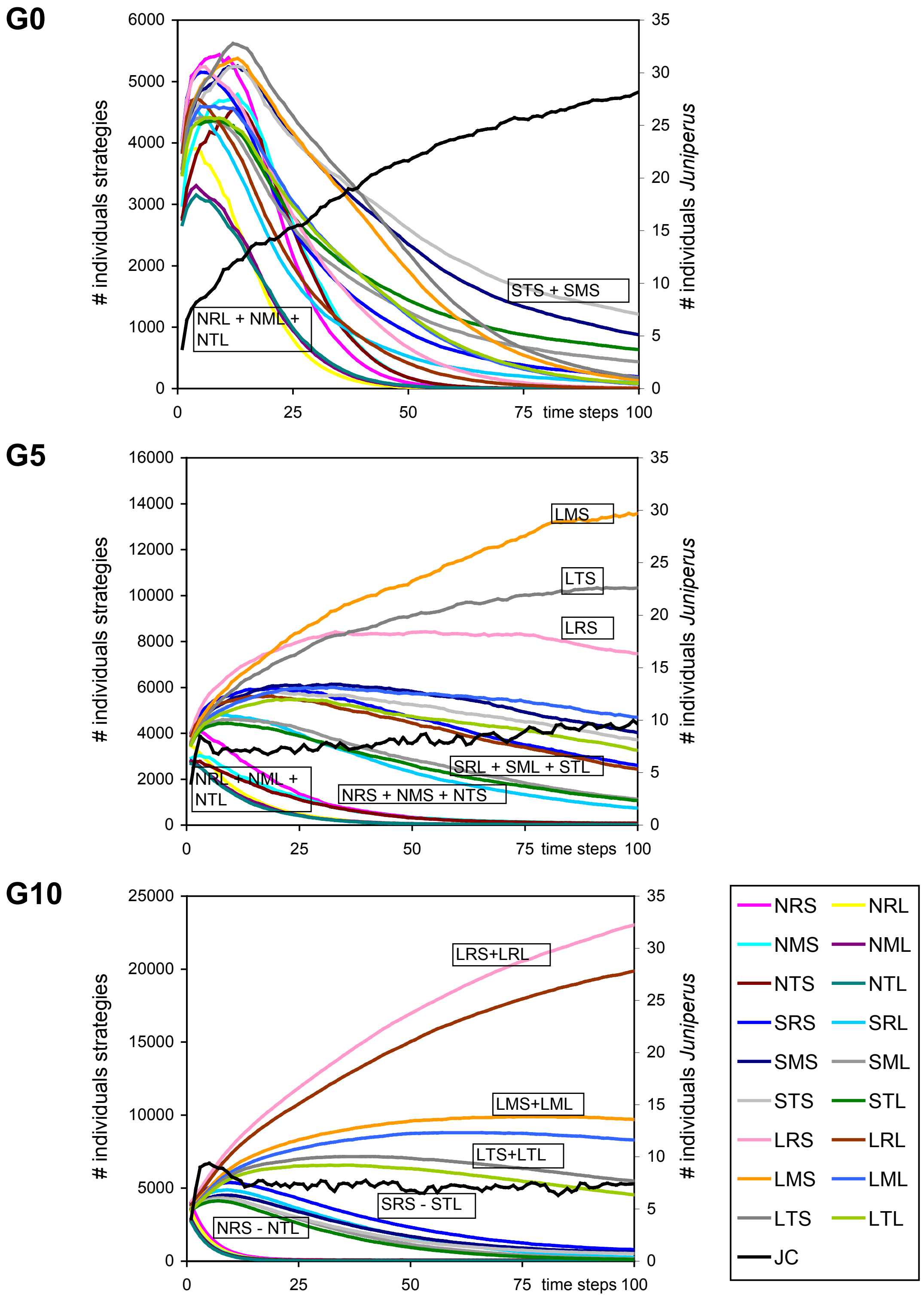


Figure 7.4 Number of individuals of the 18 plant strategies in the course of 100 time steps at different grazing intensities (left y-axis). Right y-axis and the black line represent the number of *Juniperus*-individuals (JC). Means of 50 simulation runs each. See Table 7.1 for strategy definitions.

Abbreviations of the strategies following the traits. Vegetative spread: N – no spread, S – short , L – long; canopy height: R – rosette, M – medium, T – tall; seed mass: S – small, L – large.

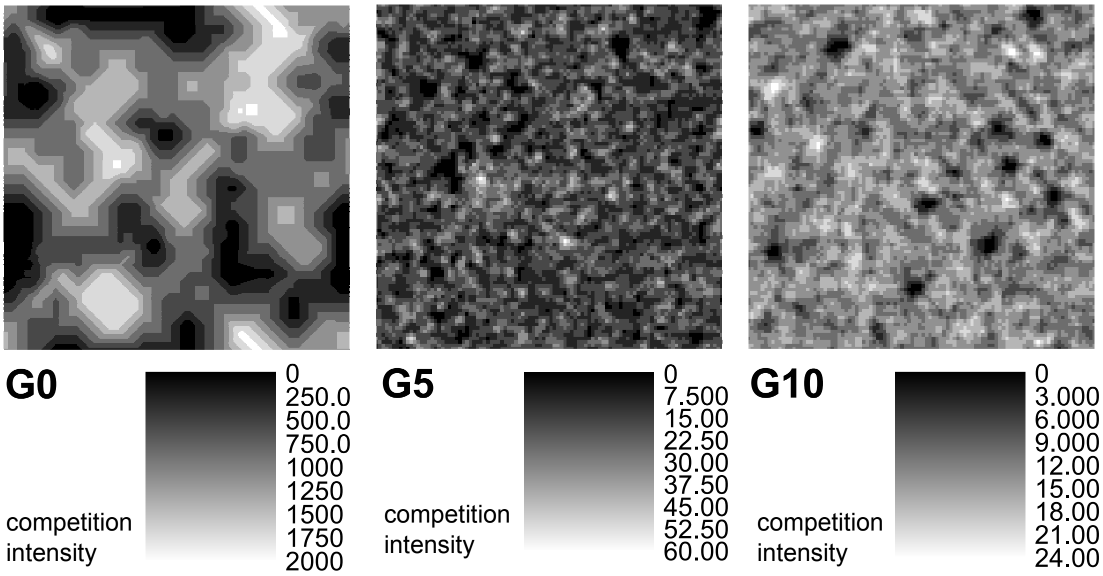


Figure 7.5 Examples of the distribution of the CI factor in the grid (3×3 m) at different grazing intensities G0, G5 and G10 after 100 time steps.

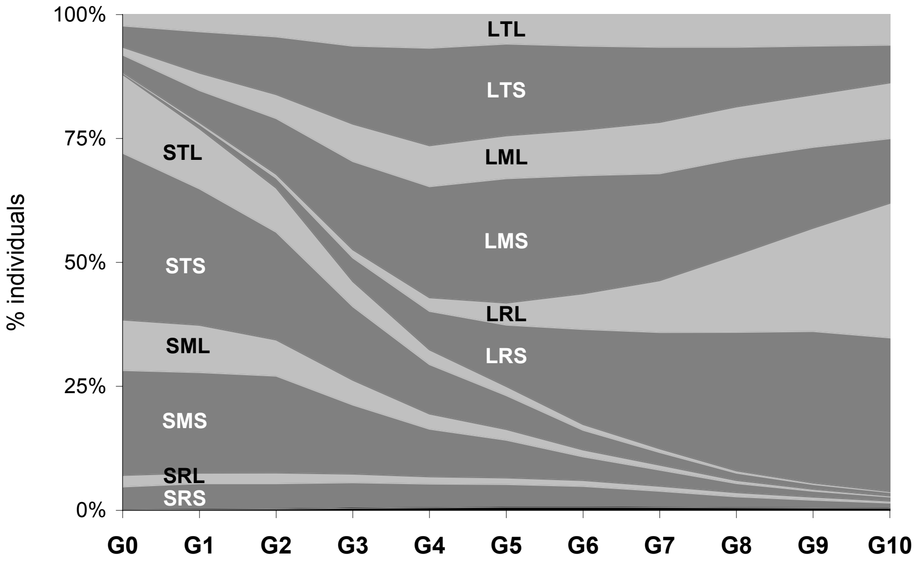


Figure 7.6 Percent individuals of the 18 plant strategies after 100 time steps at different grazing intensities. G0: no grazing to G10: high grazing pressure with all individuals being grazed. Non-clonal strategies are too rare to be visible in this presentation. Means of 50 simulation runs after 100 time steps for each grazing intensity.

Abbreviations of the strategies following the traits. Vegetative spread: N – no spread, S – short , L – long; canopy height: R – rosette, M – medium, T – tall; seed mass: S – small, L – large.

For all grazing intensities, trait features significantly influenced the abundance of individuals (Figure 7.7). There was a clear shift from strategies with a high canopy to rosette strategies with increasing grazing intensities whereby this change was strongly associated with a shift of strategies with short to those with long vegetative spread. Strategies without clonal growth were rare at all grazing intensities with app. 0.1% of the total vegetation. Seed mass strongly determined strategy success at lower grazing intensities with small seeds being favoured whereas seed mass were less important at high grazing pressure (G10).

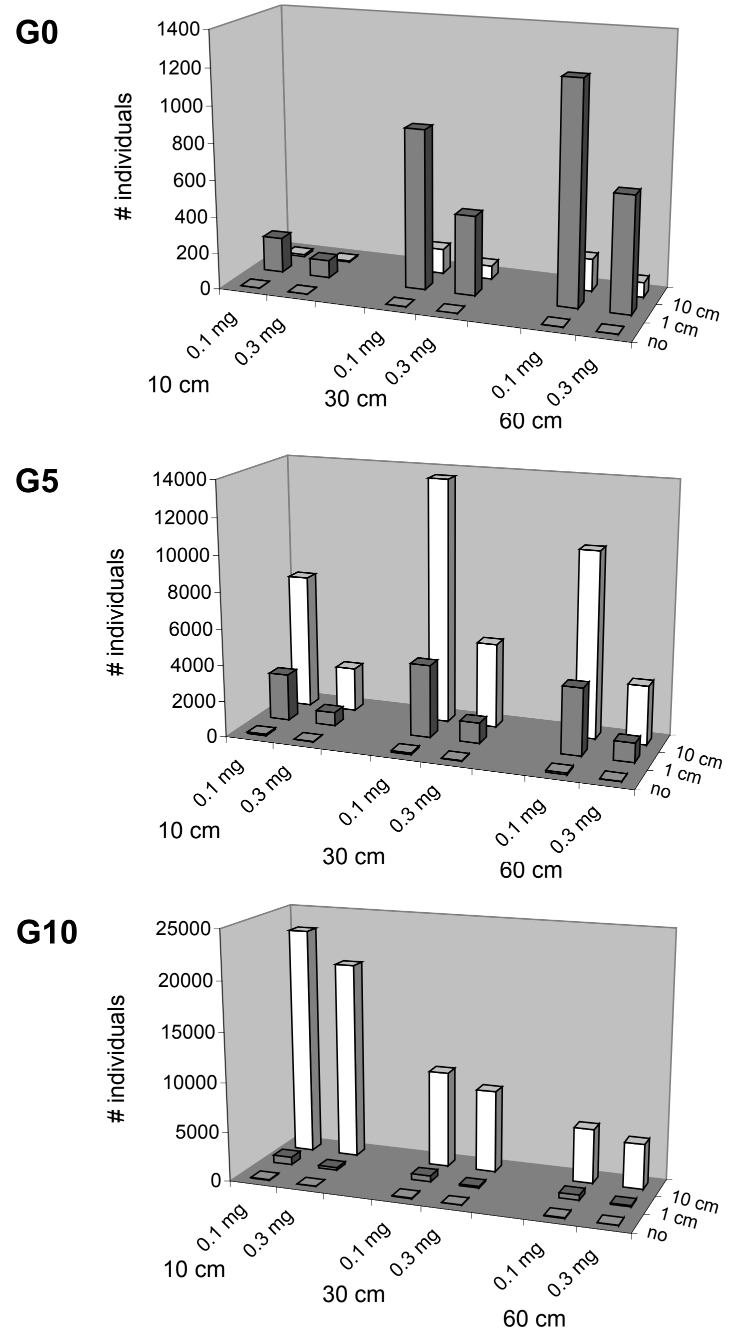


Figure 7.7 Interactions between the traits canopy height, seed mass (both on the x-axis) and vegetative spread (z-axis) at three grazing intensities (G0, G5, G10). Mean number of individuals of 50 simulation runs after 100 time steps.

The ANOVA-table (Table 7.3) indicates the importance of the three traits on abundance for each grazing intensity by the F-values. All statistics were done in SPSS 11.5. Vegetative spread most strongly determined abundance at all grazing intensities. At low and high grazing intensities (0+1 and 9+10) canopy height influenced abundance at the second degree. Contrary, all grazing intensities in between were more influenced by seed mass than by canopy height. At the highest grazing intensity, effects of seed mass were low.

Table 7.3 Trait effects along a grazing gradient from no grazing (G0) to high grazing pressure (G10). ANOVA with individuals as dependent and traits as independent variables, testing only for main effects. Explained variance of the model (R^2) and the F-values for each grazing intensity is given. Results of 50 simulation runs after 100 time steps.
*** $p<0.001$, ** $p<0.01$

	df	**G0**	**G1**	**G2**	**G3**	**G4**	**G5**	**G6**	**G7**	**G8**	**G9**	**G10**
R^2		0.56	0.60	0.50	0.50	0.61	0.68	0.77	0.83	0.83	0.80	0.76
total	900											
canopy height	2	113 ***	146 ***	105 ***	92 ***	83 ***	52 ***	20 ***	43 ***	128 ***	188 ***	222 ***
vegetative spread	2	423 ***	462 ***	272 ***	257 ***	454 ***	689 ***	1231 ***	1906 ***	1940 ***	1538 ***	1198 ***
seed mass	1	78 ***	139 ***	160 ***	209 ***	328 ***	415 ***	476 ***	440 ***	234 ***	86 ***	11.2 **

Coexistence

At high grazing pressure (G10) the strategy-pairs with different seed mass were similar abundant (Figure 7.4, Figure 7.7) which means that they could coexist. To test for stable coexistence of the strategy-pairs with different seed mass, I examined if both strategies can invade a monoculture population of the respective counterpart strategy, called the resident strategy here (Lavorel & Chesson 1995, Schippers et al. 2001). At the start of the model runs, half of the grid was occupied by the resident strategy. After 10 time steps, 1000 seeds of the invader strategy were randomly distributed in the grid. The development of the invader strategies was documented for 100 time steps. Figure 7.8 demonstrates the size of the populations of the invader strategies. Non-clonal strategies could not invade the established populations of the counterpart, they were averaged for better presentation in the diagram. Population sizes of the clonal strategies were averaged with respect to seed mass in the diagram due to high similarities. All clonal strategies could invade populations of the respective counterpart. Strategies with large seeds had higher abundances at the beginning due to the higher germination probability. With time, the strategies with small seeds increased more rapidly due to the higher seed number.

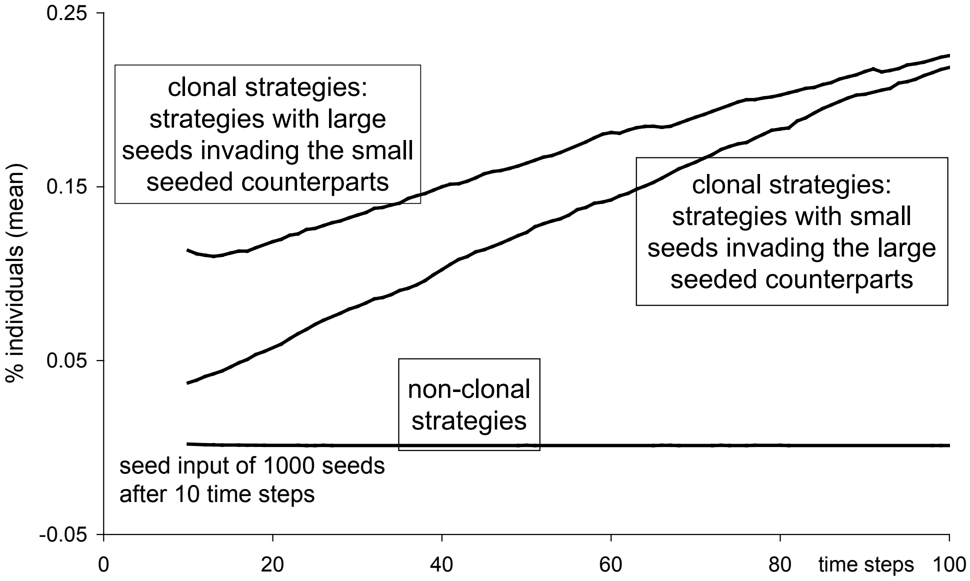


Figure 7.8 Tests for coexistence of two similar strategies each, differing only with respect to seed mass. A strategy invaded in a one-strategy population of the counterpart after 10 time steps by spreading 1000 seeds randomly. Mean percentage individuals of the invading strategies of 20 simulation runs each is given, averaged for similar population sizes (non-clonal strategies as well as clonal strategies separated with respect to seed mass). None of the strategies without clonal growth were invasive (line at the bottom).

Parameter sensitivity

Sensitivity analyses of specific parameters allow to test for the effects of these parameters on the model outcomes. In sensitivity analyses, a parameter is changed slightly and if the results change significantly, the model is sensitive to this parameter which must be considered in the interpretation. Here, I did not only test specific parameters for sensitivity but I addressed the following questions.

How large is the impact of the trampling procedure?

How large is the impact of the seed bank in the model?

What happens if an individual has several attempts for vegetative spreading?

How much must reproduction by seeds of non-clonal strategies be stressed so that they increase in abundance?

Sensitivity analyses were done for the grazing intensities G0, G5 and G10. Tests for sensitivity were calculated using ANOVA (SPSS 11.5) with individuals being the dependent variable. The independent variable was always the sensitivity parameter and optionally selected traits. The remaining traits were handled as co-variables. The sensitivity parameters as well as the results of the ANOVA analyses are documented in Table 7.4.

Table 7.4 Parameter values of the sensitivity analyses as well as results of ANOVA analyses for each sensitivity analysis and the grazing intensities G0, G5 and G10, respectively.
*** $p<0.001$, *n.s.* not significant

		trampling	**seed bank**	**attempts for vegetative spread**	**factor for seed production of the non-clonal strategies**
sensitivity parameter		trampling - no trampling	seed bank probability	1× – 2× – 3× – 4×	1× – 2× – 3× – 4× – 5×
ANOVA test variables		sens. parameter × strategies	sens. parameter, only strategies with small seeds	sens. parameter × vegetative spread	sens. parameter × vegetative spread
co-variables			canopy height, vegetative spread	canopy height, seed mass	canopy height, seed mass
df		17	2	6	8
G0	F			185.1 ***	4.6 ***
G5	F	17.3 ***	0.53 *n.s.*	105.6 ***	46.8 ***
G10	F	32.0 ***	1.7 *n.s.*	14.1 ***	0.005 *n.s.*

No trampling

Skipping the trampling process led to significant changes in strategy abundances for G5 and G10 (Table 7.4). Figure 7.9 presents the differences of the individuals per strategy with trampling process minus those without trampling process. These differences were related to the number of individuals with trampling process to obtain relative changes. There was a clear increase in strategies with short vegetative spread at both considered grazing intensities. Furthermore, large seeded strategies could notably increase with increasing grazing pressure at the expense of small seeded strategies.

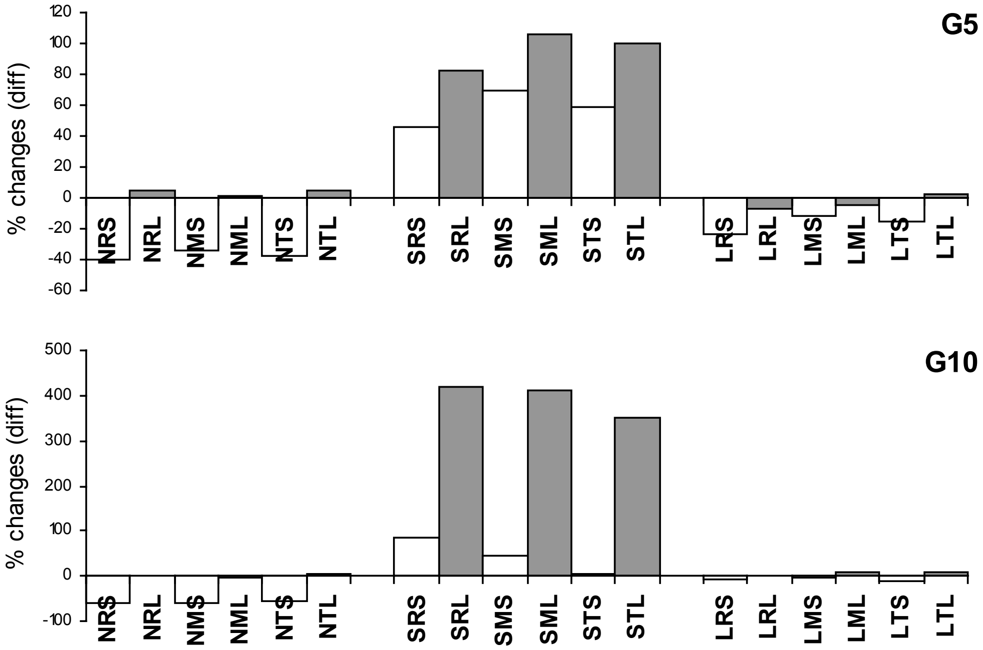


Figure 7.9 Effects of no trampling process within the grazing process on strategy abundances. Differences resulting from the number of individuals per strategy with trampling process minus those without trampling process are shown. Differences were related each to the respective number of individuals with trampling process to obtain percentage changes. Grazing intensities G5, G10. Mean numbers of 50 simulation runs after 100 time steps. ANOVA results of interactions between the sensitivity parameter and the plant strategies are documented in Table 7.4.

Abbreviations of the strategies following the traits. Vegetative spread: N – no spread, S – short , L – long; canopy height: R – rosette, M – medium, T – tall; seed mass: S – small, L – large.

Seed bank

In the model, the seed bank is activated after the trampling process in the way that one strategy or the tree species was chosen randomly (probability of 0.05 per strategy). Only strategies with a persistent seed bank could reach the germination process. In the sensitivity analysis the probability of seed bank germination was changed twice. Firstly, I considered no seed bank (prob. of null). Secondly, only strategies with a persistent seed bank were chosen after trampling and the amount of seed production was taken into account. This means that the probability of strategies without clonal growth to germinate from the seed bank was three times higher (prob. of 0.2) than the probability of clonal strategies (prob. of 0.067). Only strategies with a persistent seed bank were included in the ANOVA analysis (Table 7.4). The strategy abundances did not change after changing the probability of seed bank germination.

Attempts for vegetative spread

Increasing the number of attempts for vegetative spread does not mean that one individual may build several spacers per time step but have several attempts to find an empty cell for vegetative reproduction. The main effect of increasing the number of attempts was obvious if there was no grazing (G0 in Figure 7.10 and Table 7.4). Strategies with short vegetative spread dominated if individuals were restricted to one attempt for vegetative spread but long vegetative spreading became dominant if the number of attempts increased.

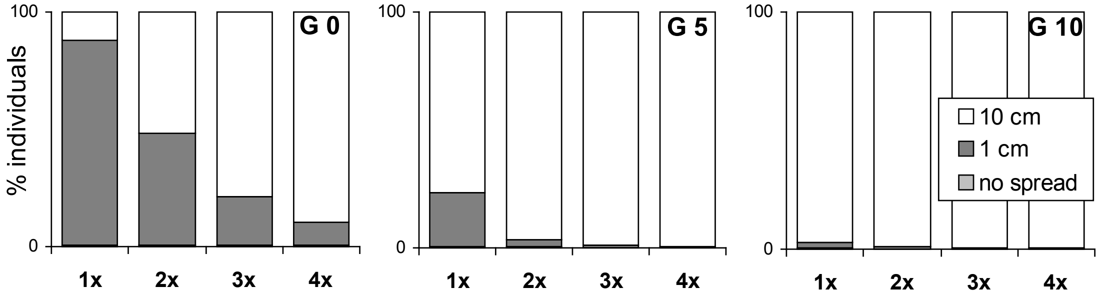


Figure 7.10 Effects of increasing numbers of attempts for vegetative spread (sensitivity parameter) on the abundance of individuals, grouped with respect to vegetative spread. Non-clonal strategies are too rare to be visible in this presentation. Grazing intensities G0, G5, G10. Mean numbers of 50 simulation runs after 100 time steps. ANOVA results of interactions between the sensitivity parameter and the trait vegetative spread are documented in Table 7.4.

Number of seeds of the non-clonal perennials

In the model, non-clonal strategies spend three times as much energy in seed production than clonal strategies. In this sensitivity analysis, I varied the multiplication factor from 1 to 5. At all grazing intensities, the number of non-clonal strategies increased with increasing multiplication factor, yet the total strategy abundances varied drastically (Figure 7.11). At G0 and G5, there was a strong push between factor 4 and 5 but only for small seeded strategies (NRS, NMS, NTS) whereas at G10, strategy abundances increased continuously for both seed mass categories. The ANOVA analysis revealed significant interactions between the multiplication factor and the trait vegetative spread for G0 and G5 but not for G10 (Table 7.4). Summarising, a significant increase in non-clonal strategies started at a multiplication factor of 5 and was not observed at a high grazing pressure.

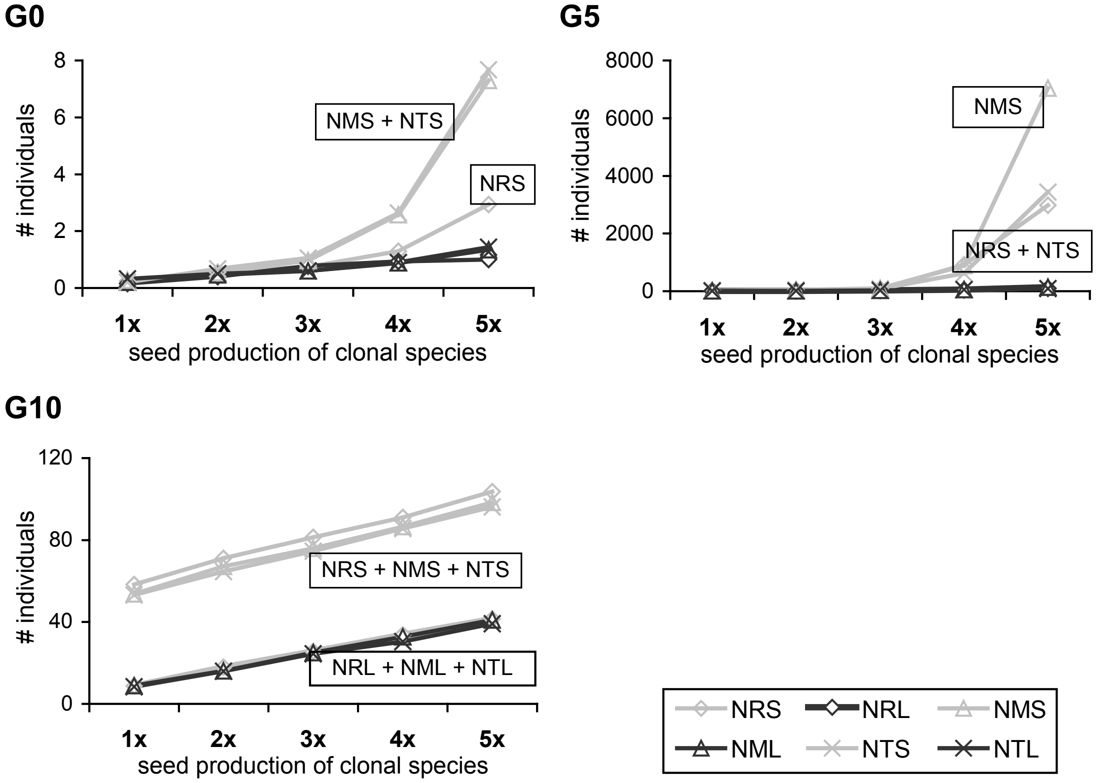


Figure 7.11 Effects of the seed number of non-clonal strategies in relation to the clonal strategies. The categories are the factors being multiplied with the respective seed number of the clonal strategies. Mean number of individuals of the six non-clonal strategies are presented for the grazing intensities G0, G5, G10 of 50 simulation runs after 100 time steps. ANOVA results of interactions between the sensitivity parameter and the trait vegetative spread are documented in Table 7.4.

Abbreviations of the strategies following the traits. Vegetative spread: N – no spread, S – short , L – long; canopy height: R – rosette, M – medium, T – tall; seed mass: S – small, L – large.

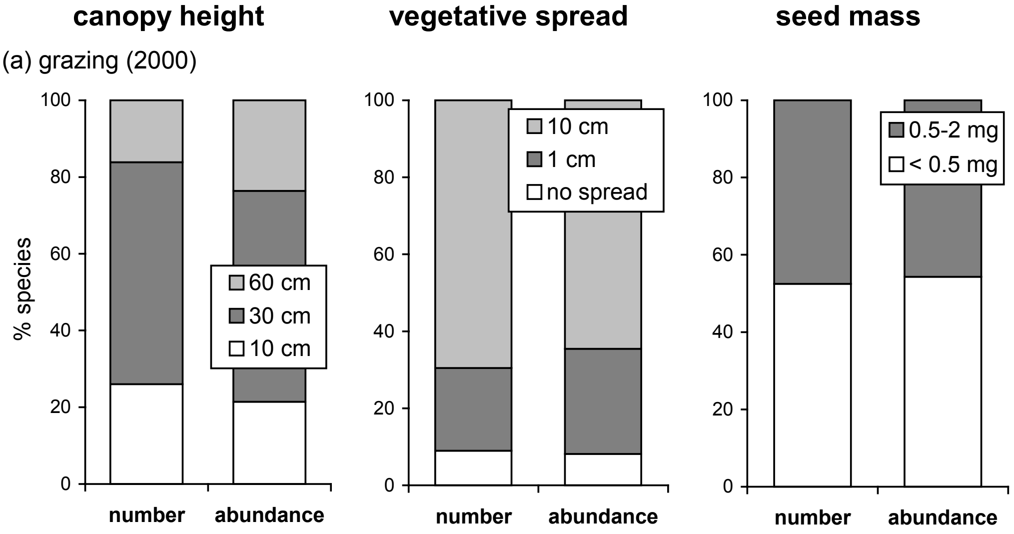
Field data of the "Fallow Experiments"

To compare the model results with field data, I used vegetation data of the "Fallow Experiments in Baden-Württemberg" which were carried out by K.F. Schreiber since 1975 (Schreiber 1977). In this experiment, different management treatments have been evaluated on semi-natural grasslands during 25 years (for the description of the experiment see Chapter 3 and 4). In the present analysis, only the grazed and the abandoned fields were considered. Grazing took place at low intensities which is about G3-G5 in the model. I took vegetation relevés of one permanent plot per site and field, including 9 sites of grazing and 14 sites of abandonment (site description see Chapter 2 and 4).

The species of the "Fallow Experiment" were allocated to the 18 strategies and tested for responses to grazing and abandonment. The analyses of Chapter 2 to 4 also consider trait responses to management and abandonment, yet by analysing all traits separately. The model deals with plant individuals so that trait syndromes (named strategies) instead of single traits are regarded. Since it is not possible to scale from trait responses to species behaviour by simply combining traits it is not reasonable to compare the results of the single trait studies with the model results of trait syndromes.

In total, 138 species could be assigned to the 18 strategies. Canopy height was taken from Rothmaler (1994). All rosette and semi-rosette species were assigned to the strategies with a short canopy height (10 cm), independent of their actual canopy height in the field. The erect species were allocated to the remaining height categories according to the minimum plant height in Rothmaler (1994). Data on vegetative spread referred to the types in the database CLOPLA1 of Klimeš et al. (1997): non-clonal (types 1, 2, 4, 12, 16-20), short vegetative spread (types 6, 7 (grass species) and 9) and long vegetative spread (types 3, 5, 7 (except grasses), 8, 10, 11, 13-15). Seed masses were means of own measurements and data of various literature. Table 7.1 gives a species example for each strategy. The strategies NTS, SRS and SRL were not represented in the dataset of the "Fallow Experiments". Still, I considered all strategies in the model to gain information of all theoretical trait combinations.

Trait composition after grazing and abandonment was analysed in Figure 7.12 including all strategies. For grazing, trait composition of species number was compared with species abundance in 2000. For abandonment, trait composition of species abundances was compared between 1976 and 2000. Regarding the trait vegetative spread, there was no significant trend neither after grazing nor after abandonment. Comparing grazing and abandonment, there was a slight trend from small growing species after grazing to tall growing species after abandonment as observed in the simulation study (Figure 7.12). Seed mass also showed different tendencies between grazing and abandonment. After abandonment, the strategies with small seeds increased significantly whereas at the grazing treatment, strategies with large seeds were relatively frequent.



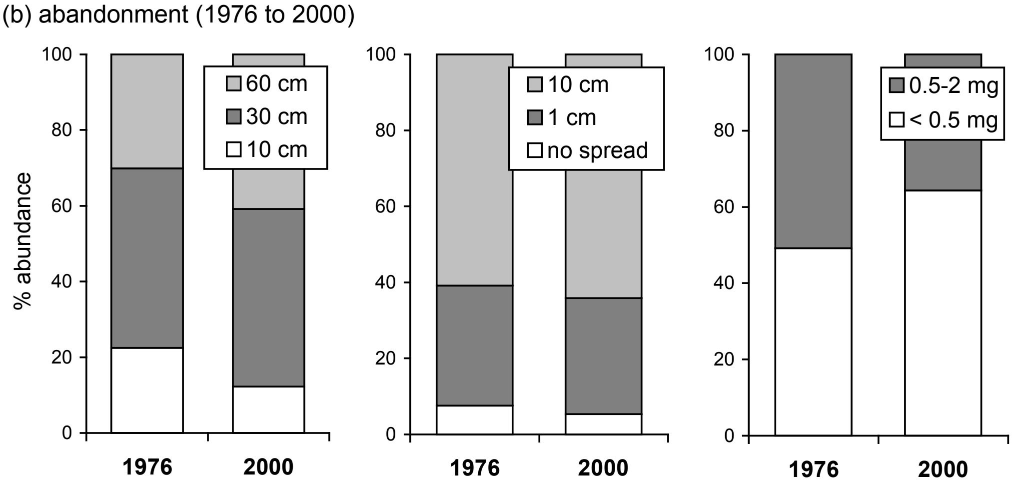


Figure 7.12 Proportions of the strategies combined with respect of the three traits canopy height, vegetative spread and seed mass. Grazing: comparison between species number and species abundances in 2000 (N=9). Abandonment: comparison between 1976 and 2000 (N=14) using species abundances.

Discussion

Canopy height

Canopy height is known to be a major trait with respect to grazing intensity through biomass removal (McIntyre et al. 1999, Poschlod et al. 2000b). Small species are promoted because of differential defoliation on a vertical gradient whereas tall species are better competitors for light if removal of the biomass is missing (Weiher et al. 1999, Grime 2001).

In the model, canopy height determined strategy abundance strongly on both extremes of the grazing gradient but it was of minor importance at intermediate grazing pressures (Table 7.3). This relation is attributed to the fitness factor which is determined by the size of an individual in the model. The fitness factor again determines the survival probability with fitness being positively related to survival. After abandonment, tall plants clearly out-competed rosette plants whereas plants of intermediate height might keep abundance. Without biomass removal, the CI increases (Figure 7.5) so that light becomes a limited resource for small plants. They may hardly grow to their full diameter so that the survival probability is reduced in comparison to tall plants. The opposite is true at high grazing intensities where rosette plant significantly out-compete erect plants. Light conditions are good with a generally low CI through grazing (Figure 7.5) but tall plants loose more biomass if grazed than small, rosette plants which reduces their survival probability. At intermediate grazing levels, the effects of biomass removal interact with the effects of competition for light which results in a balance among the height classes with a slight promotion of plants with intermediate height (Figure 7.7).

This trend could also be found in the field data (Figure 7.12) although it was less explicit. Grazing intensity at the “Fallow Experiments” was rather low and at the abandoned fields the growth of tree species was often rare. Following, the grazed sites sometimes very much resembled the abandoned sites with a high sward so that differences are blurred. Still, tall species were relatively favoured after abandonment which again means for the model that the regulation by the fitness factor and thus by the individual size is reasonable.

Vegetative spread

Regeneration properties are essential for population dynamics (de Kroon & van Groenendael 1990, Stöcklin 1992, Arnthórsdóttir 1994, Bullock et al. 1995, Eriksson & Jakobsson 1998, Otsus & Zobel 2002) which is accounted for in PASTUREPOP. In the model, reproduction by vegetative means is significantly most important for strategy abundance which can be seen in the low proportion of strategies without clonal growth for all grazing intensities (Figure 7.6, Figure 7.7). Apart from the contrast between non-clonal and clonal strategies, there is an interesting shift along the grazing gradient with respect to the length of vegetative spread. The model considers two extremes with 1 cm and 10 cm spreading. The length of vegetative spread is an important parameter with respect to habitat heterogeneity which means that a habitat varies between favourable and unfavourable sites (Sutherland & Stillmann 1990, Stöcklin 1992, Hutchings & Wijesinghe 1997, Klimeš et al. 1997). Considering the model system, there are two different spatial scales of habitat heterogeneity. The higher scale of heterogeneity regards the difference between tree species and herbaceous vegetation. Here, unfavourable sites are those covered by a tree because of the high CI that prohibits the establishment of ramets whereas all sites covered by herbaceous plants are relatively favourable. The lower scale of heterogeneity regards the herbaceous vegetation without trees. Here, unfavourable sites are cells being occupied by other individuals whereas all empty cells are favourable sites.

Short vegetative spread is expected to be advantageous if it is more likely to find good growing conditions near the mother plant despite intraspecific competition. This could be a good strategy in the case of high tree abundance which means high heterogeneity at the higher spatial scale. Long vegetative spread should be advantageous if the probability is high to find slightly better conditions in some distance to the mother plant. This strategy could be advantageous at the lower scale of heterogeneity if there are patches of empty cells. In totally homogenous habitats with empty cells distributed regularly at the site, both strategies should be equally successful on the assumption that the costs for short and long spreading are the same. Since in nature, plants must invest more energy to produce long spacers than short spacers (de Kroon & van Groenendael 1990), species with short vegetative spread are supposed to be promoted.

In PASTUREPOP, I did not include costs for spreading. Here, close spreading (1 cm) was a successful strategy at abandonment whereas long spreading strategies (10 cm) out-competed all other strategies at high grazing pressure (Figure 7.7). After abandonment (G0), the heterogeneity at high spatial scale increased with increasing growth of *Juniperus*. *Juniperus*-trees prevented the establishment of ramets so that the probability of long spacers to arrive at unfavourable conditions was high. There was thus a promotion of short spreading strategies. At intermediate grazing intensities the advantage of short spreading changed to the benefit of long spreading until long spreading strategies were absolutely dominant (Figure 7.4). The extreme competitive advantage of long spreading strategies at high grazing intensities was facilitated by the effects of trampling. Through trampling, there were gaps of empty cells randomly distributed at the site leading to heterogeneity at the low spatial scale (Figure 7.5). Thus, the probability to find an empty cell was higher for a long spacer than for a short spacer. The positive effect of trampling on long vegetative spread demonstrates Figure 7.9 since strategies with short spacers might increase when the trampling process was led out. The importance of the feature for vegetative spread was highest at G7/G8 (F-values in Table 7.3). Possibly, small scale habitat heterogeneity was highest at these grazing intensities with 20-30% of the individuals not being grazed but with a considerable amount of gaps of empty cells.

Comparing the competitive ability of short with long distance dispersal of seeds in simulation studies (e.g. Czárán & Bartha 1989, Lavorel & Chesson 1995, Schippers et al. 2001), strategies with long distance dispersal have always been the superior strategy. The same is true considering vegetative spread in the present analysis despite the different spatial scales between seed dispersal and vegetative spreading. Without grazing (G0), strategies with short vegetative spread dominated only if individuals were restricted to one attempt for vegetative spreading (Figure 7.10). If the risk to not reproduce vegetatively due to unfavourable conditions was reduced through more possible attempts, long spreading became again the most successful strategy.

Looking at the field data of the "Fallow Experiments", there was no clear interaction between management and vegetative spread (Figure 7.12). The first argument to explain this inconsistency with the simulation data is that in the field, the vegetation after abandonment sometimes very much resembled the vegetation after grazing due to low grazing intensities. Second, field sites are generally highly variable and heterogeneous with respect to abiotic as well as to biotic conditions in contrast to the model system. In the field, there are numerous factors affecting vegetative spreading (Abrahamson 1980, Hutchings & Wijesinghe 1997) whereas the simulation study disregarded abiotic conditions except the effects of grazing and trampling and reduced the biotic interactions to competition for light. It is thus not surprising not to observe the same clear trends as in the model situation. Third, plant traits may be inter-correlated. Consequently, other traits related to vegetative spread might primarily respond to the ecosystem processes in the field so that they actually determined species abundances. In contrary, this simulation study permitted to investigate the original effect of spreading distances in a defined environment.

Seed mass

Reproduction by seeds is the second regeneration strategy considered in PASTUREPOP. Seed mass is a core trait for seedling recruitment since seed mass determines germination success under different light conditions (Fenner 1987, Leishman et al. 1995, Eriksson 1997, Schütz 2000). Abandonment of grassland is correlated with increasing seed mass (Fenner 1987, Leishman 1999) whereas germination of small seeds is supposed to be favoured through open vegetation and soil disturbances (Reader 1993, McIntyre et al. 1995, Eriksson & Eriksson 1997). The latter conditions are typical for grazed sites. However, the eight published sowing experiments evaluated in Figure 7.3 did not observe that germination probability of small seeds increased in relation to larger seeds after soil disturbances. Basing on this evaluation, the model assumes that the germination probability of small seeds is generally three times lower than that of large seeds. For example, at a CI factor of 25, which is typical for sites of intermediate grazing intensity (Figure 7.5), the germination probability of small seeds is 0.075 whereas that of large seeds is 0.225. The advantage of the small seeded strategies is that they might produce more seeds due to the trade-off between seed mass and seed number. Jakobsson & Eriksson (2000) confirmed "that the trade-off between seed size and seed number is reflected in a trade-off between the number of recruitment attempts and the probability that the recruitment attempt will succeed, by showing that larger seeds produce larger seedlings and have higher recruitment success". In PASTUREPOP, the number of small seeds is four times higher than of the large seeds. Following, both seed mass and seed number determine seedling recruitment in the model.

The results of the ANOVA showed that the seed traits importantly affected strategy abundance at intermediate grazing intensities whereas they were less important at high grazing pressure (Table 7.3). Generally, small seeded strategies were more frequent than large seeded strategies indicating that a high seed number always dominated a higher germination probability. The trade-off in PASTUREPOP is asymmetric since there are four times more seeds but only three times less germination probability which explains the competitive advantage of small seeded strategies. However, Schippers et al. (2001) found in a spatial vegetation model focusing on strategies reproducing only by seeds that plant strategies with large seeds were always inferior to small seeded strategies if the trade-off was balanced (10× more seeds against 10× higher germination probability). Thus, the numerical disadvantage of large seeds seems generally to dominate the higher germination success. In the present model, this relation was less significant after abandonment which may be attributed to the decreasing numbers of “safe sites” (sensu Harper 1977). Germination happens only if light conditions are sufficient. This means that the CI of a cell must be less than 100 which is seldom on late successional sites (see Figure 7.5, G0).

The impact of seed mass was again less obvious in highly grazed sites (Figure 7.7, G10). Here, each individual was grazed so that there was only external seed input but no seed production at the site itself. External seed input is subjected to the same conditions with four times more small seeds than large seeds, however, the numerical advantage of small seeds seems to be reduced. The minor role of seed mass at high grazing pressure could be checked in the tests for coexistence (Figure 7.8). For each strategy pair with respect to seed mass, the invader strategy could invade a monoculture population of the respective counterpart. Information on the mechanisms gives the sensitivity analysis when the trampling process was skipped (Figure 7.9). Large seeded strategies increased when there was no trampling which means that large seeds only profit from biomass removal. In the other way round, this observation shows that soil disturbances through trampling enhance germination of small seeds. There were more empty cells due to trampling and the probability of a small seed to be dispersed to an empty cell was higher than for larger seeds due to higher seed numbers. Comparably, McIntyre et al. (1995) found soil disturbances being positively related to the dispersibility of seeds. As mentioned above, some germination surveys observed an increased seedling recruitment of small seeds in relation to larger seeds after soil disturbances. The simulation results now indicate that this could be due to the higher seed number of small than of larger seeds.

The field data of the “Fallow Experiment” confirms the discussed relationships (Figure 7.12). Grazing intensities at the field sites were low so that trampling events were expected to be rare whereas abandoned grassland vegetation is characterised by gaps of bare soil at the ground. This implies that small seeded strategies were favoured by abandonment but not by grazing.

In PASTUREPOP, trampling also implies the activation of the seed bank which should favour small seeded strategies because of their persistent seed bank. Anyway, comparing the abundances of small seeded strategies with and without seed bank consideration (Table 7.4) no significant differences could be revealed. Thus, the overall advantage of small seeded strategies cannot be attributed to seed bank longevity in PASTUREPOP.

Strategies without clonal growth may only reproduce by seedling recruitment. However, the configurations taken in the model cannot ensure the survival of these strategies in a mixed vegetation. Furthermore, in the analyses of coexistence between two strategies differing only with respect to seed mass (Figure 7.8), none of the non-clonal strategies could invade the counterpart. This demonstrates that populations of non-clonal strategies are not sustainable in the model, also without interspecific competition. They do not go extinct because of the external seed input. Obviously, PASTUREPOP underestimates seed production with maximal 24 seeds per individual and time step (Jakobsson & Eriksson 2000). In nature, seed production is often higher than 1000 seeds per individual and year (e.g. *Achillea millefolium*) so that the population dynamics of strategies that rely on seedling recruitment for reproduction are not well represented in the model. Raising the seed number of the strategies, however, slows down the model runs strongly and seedling recruitment becomes the dominant way of regeneration which is not the case in temperate grasslands. In the model configuration as presented, seedling recruitment was already considerable high with a maximum of about 50 seeds per m² of strategy LMS at G6. In average, 3% to 10% of the seeds germinated and established at high grazing pressure (G10). Increasing the amount of seed number only of the non-clonal strategies led to higher abundances in the vegetation which was most obvious at medium grazing intensities (Figure 7.11). Here, half of the individuals were not being grazed so that they produced seeds. Additionally, soil disturbances through trampling guaranteed a specific amount of 'safe sites' and the CI was generally low. As discussed above, however, small seeded strategies were largely favoured and they out-competed the large seeded strategies due to the four times higher seed number. At high grazing pressure (G10) the seed availability increased only linearly since no individual could produce seeds.

Summary

The aim of this thesis is to investigate plant functional trait responses to grassland management and succession in order to gain a better understanding of the patterns and the underlying mechanisms. Significant trait responses are identified and can be further used for predictive purposes. The thesis employs three different approaches to the analysis of functional traits in relation to environmental factors associated with grassland management.

The first approach (chapters 2 to 5) used vegetation data of the ”Fallow Experiments in Baden-Württemberg” (Prof. K.F. Schreiber) to analyse the processes of management treatments and abandonment in grassland vegetation. The management treatments grazing, mulching and burning in winter were compared after 25 years and succession series were analysed from the abandoned fields. Using permanent plot surveys, the data set was based on 14 study sites. I structured the results regarding the survival of the established plant, regeneration by vegetative growth and regeneration by seedling recruitment.

For established plants, the main difference between abandonment and grassland management is that the latter effects a regular removal of biomass. In this study, abandonment generally led to an increase in plant height in the competition for light. Due to differential defoliation on a vertical gradient, grazing and mulching favoured plants that accumulated most of their leaves close to the ground. In contrast to that, burning deleted all leaves right down to the ground so that plants with basal leaves were not promoted. The absence of biomass removal resulted in better nutrient conditions at the succession plots. The effect of this was slightly reflected in an increase in plants with a high specific leaf area (SLA) and a decrease in plants with storage organs. The existence of storage organs was especially advantageous after burning in winter for resprouting in the next year.

Regeneration by vegetative growth was the dominant regeneration strategy. Burning and abandonment enhanced species with long spacers indicating that the higher investment in vegetative spread was ‘worthwhile’. Spreading mainly happened below ground by rhizomes so that the spacers were not destroyed during the burning event. Additionally, rhizomes ensured nutrient supply for the new ramets and facilitated establishment after burning as well as in the dense vegetation of abandoned grasslands. In contrast, grazing favoured vegetative spread above ground by stolons which were able to effectively colonise bare ground micro-sites.

Although regeneration by seedling recruitment is generally rare in grassland vegetation, annuals were found to increase in the course of abandonment. This must be attributed to the shaded sites leading to patches of bare soil. Patches of bare soil created by burning also promoted the establishment of annuals on the burned fields. The time of biomass removal correlated well with the germination season, with autumn germination being favoured after grazing during the vegetation period and spring germination being promoted after the burning event in winter. Large seed mass was advantageous to successfully recruit in the dense and shaded vegetation of the succession sites whereas grazing promoted both small-seeded species and species with a persistent seed bank to some extent. Surprisingly, small-seeded species also increased after abandonment. The phenology of seed production was found to

correlate with grassland management in that succession promoted species with a short flowering period as well as species not restricted to early flowering.

The second approach (chapter 6) experimentally investigated the impact of functional traits on the outcome of vegetation dynamics. In a germination experiment comparing mown, grazed and abandoned plots, I tested whether the traits seed mass and germination season influenced the germination success. In the experiment, both traits significantly interacted with the management in terms of germination success. Contradictory to the results of the first approach, germination of small seeds was not promoted by mowing or grazing. This is thought to be due to the absence of soil disturbances in the experiment. In contrast, small seeds suffered less from adverse light conditions after abandonment than larger seeds, which is in line with the observations of the ”Fallow Experiments”. It is suggested that small seeds profit from the abandoned vegetation to some extent, as it provides a shelter from physical hazards. Large seeds were not considered in the experiment. Results of the ”Fallow Experiments” suggested germination season to be related to the time of biomass removal to catch optimal light conditions. This was confirmed in the germination experiment.

Using a mechanistic simulation model, the third approach (chapter 7) systematically investigated the performance of specific plant functional traits along a grazing gradient. The model PASTUREPOP analysed the competitive ability of the established plant, vegetative reproduction and seedling recruitment. These processes were represented by the traits canopy height, vegetative spread and seed mass which were combined in trait syndromes (strategies). Confirming the results of the ”Fallow Experiments”, canopy height was found to be strongly related to the grazing gradient with ‘tall strategies’ being promoted after abandonment and ‘short, rosette strategies’ becoming dominant at high grazing pressures. Long vegetative spread by spacers was a superior strategy in all environments except those characterised by adult tree species as these considerably increased the risk of a spacer to arrive at unfavourable conditions. This could explain why in the ”Fallow Experiments” a promotion of long spacers was restricted to the abandoned sites without tree cover. Although germination probability was related to seed mass, ‘small-seeded strategies’ continued to dominate over strategies with larger seeds. This could be attributed to their numerical advantage since the model accounted for the trade-off between seed mass and seed number. Grazing again enhanced ‘small-seeded strategies’. Due to their higher seed numbers these plants were better able to utilise soil disturbances through trampling.

In conclusion, using vegetation data to investigate trait responses to environmental factors such as grassland management (indirect approach) permits to screen the performance of various functional traits. In these analyses, several underlying mechanisms of management and succession could be identified. However, conclusive evidence of the influence of functional traits on the outcome of vegetation dynamics can only be obtained by experiments (direct approach). I carried out a field experiment as well as a simulation experiment to test the link between traits and vegetation dynamics and to gain a deeper insight into the underlying mechanisms. The following paragraph gives an example.

In contrast to the medium seed mass category, small seeds were positively related to abandonment in the vegetation data of the “Fallow Experiments”. Exclusively focusing on the ”Fallow Experiments”, this relationship could also be attributed to further correlated traits instead of germination features. However, the germination experiment confirmed the link between small seeds and germination success after abandonment. One possible explanation is that gaps enhance germination of small seeds. However, neither the vegetation data nor the germination experiment found any evidence of such a relationship. The modelling approach explicitly accounted for the trade-off between seed mass and seed number and here, gaps promoted the germination of small seeds because of the higher probability of a small seed to be dispersed into a gap. This relationship could be responsible for the pattern in the vegetation data but not in the germination experiment with a defined number of sown seeds. Another possible explanation is that small seeds profited not so much from the actual gaps as from the abandoned vegetation which acted as a protection against physical hazards. Furthermore, seed predation, which is more severe for large than for small seeds, might increase after abandonment. Both latter possibilities might serve to explain the relationship observed in the field study but fail to do so as far as the modelling approach is concerned. It is thus to conclude that there is no one-dimensional explanation for the positive relationship between small seeds and abandonment.

Zusammenfassung

Diese Arbeit untersucht die Reaktion von biologischen Pflanzenmerkmalen auf Grünlandmanagement und Sukzession mit dem Ziel, ein besseres Verständnis der Muster und der wirkenden Mechanismen zu erlangen. Merkmale mit deutlichen Reaktionen können später zu Vorhersagezwecken herangezogen werden. Zur Analyse der Zusammenhänge zwischen Merkmalen und Umweltfaktoren verfolgte ich drei verschiede Ansätze.

Im ersten Ansatz (Kapitel 2 bis 5) wurden Vegetationsdaten der von Prof. K.F. Schreiber durchgeführten „Bracheversuche Baden-Württembergs“ analysiert. Auf 14 unterschiedlichen Standorten erfolgt seit 1975 Grünlandmanagement und Brache (Sukzession). In dieser Arbeit untersuchte ich die Maßnahmen Beweidung, Mulchen und Brennen im Winter nach 25 Jahren sowie die Sukzessionsverläufe. Management und Brache wurden anhand von Vegetationsaufnahmen von Dauerbeobachtungsflächen hinsichtlich der Sensitivität von biologischen Merkmalen ausgewertet. Die Beschreibung der Ergebnisse ist nach drei Aspekten im Lebenszyklus von Pflanzen strukturiert: Überleben der etablierten Pflanzen, vegetative Reproduktion und generative Reproduktion.

Für das Überleben der etablierten Pflanzen ist die regelmäßige Biomasseentnahme durch das Management der entscheidende Unterschied zur Brache. Auf den Bracheparzellen erhöhte sich der Anteil an großen Arten, wohingegen Beweidung und Mulchen Arten mit bodennahen Blättern förderte (z.B. Rosettenpflanzen). Dieses ist darauf zurückzuführen, dass beide Managementmaßnahmen die Biomasse nur bis kurz über der Bodenoberfläche entnehmen. Im Gegensatz dazu wird durch Brennen die ganze oberirdische Biomasse entfernt, so dass Pflanzen mit bodennahen Blättern nicht selektiv gefördert wurden. Durch fehlende Biomasseentnahme auf den Bracheparzellen verbesserten sich die Nährstoffbedingungen geringfügig, was sich in mehr Arten mit hoher spezifischer Blattfläche (SLA) und weniger Arten mit Speicherorganen widerspiegelte. Das Ausbilden von Speicherorganen war besonders vorteilhaft nach Brennen im Winter für den Wiederaustrieb im nächsten Jahr.

Die meisten Arten reproduzierten sich vegetativ. Brennen und Brache förderten Arten mit langen Ausläufern, wobei die Ausbreitung hauptsächlich unterirdisch, d.h. über Rhizome erfolgte. Der Vorteil von unterirdischen Ausläufern ist zum Einen, dass diese nicht durch das Brennen zerstört werden. Zum Anderen dienen Rhizome der Nährstoffspeicherung, was das Austreiben von Sprossen nach dem Brennen wie auch in der dichten Vegetation der Bracheparzellen unterstützt. Im Gegensatz dazu förderte Beweidung Arten mit oberirdischen Ausläufern, die effektiv offene Bodenstellen besiedeln können.

Generative Reproduktion, also die Vermehrung über Samen, erfolgt in Grünlandvegetation selten. Auf den Bracheparzellen mit starkem Aufkommen von Gehölzen war eine Zunahme an einjährigen Arten zu verzeichnen, was möglicherweise in einer Zunahme an offenen Bodenstellen durch Beschattung im Laufe der Sukzession begründet liegt. Ebenso wurden einjährige Arten durch offene Bodenstellen infolge von Brennen gefördert. Der Zeitpunkt der Biomasseentnahme durch das Management war deutlich mit der Keimsaison der Arten korreliert.

Herbstkeimer wurden durch Beweidung während der Vegetationsperiode und Frühjahrskeimer durch Brennen im Winter gefördert. Arten mit schweren Samen nahmen im Laufe der Sukzession zu, da schwere Samen auch in dichter Vegetation oder unter Beschattung keimen und sich etablieren können. Beweidung förderte Arten mit kleinen Samen und einer persistenten Samenbank. Erstaunlicher Weise nahmen Arten mit kleinen Samen auch auf den Bracheparzellen zu. Die Phänologie der Samenproduktion korrelierte in dem Sinne mit dem Grünlandmanagement, dass während der Sukzession Arten zunahmen, die eine kurze Blühperiode aufweisen oder die nicht auf frühes Blühen spezialisiert sind.

Im zweiten Ansatz (Kapitel 6) wurde der Einfluss von biologischen Merkmalen auf die Vegetationsdynamik experimentell geprüft. In einem Keimversuch untersuchte ich, ob die Merkmale Samengewicht und Keimsaison den Keimerfolg hinsichtlich Mahd, Beweidung und Brache bestimmen. Beide Merkmale zeigten signifikante Interaktionen mit dem Management. Mahd und Beweidung förderten jedoch nicht die Keimung von kleinen Samen, wie von den Ergebnisse der Bracheversuche erwartet. Eine mögliche Erklärung ist das Fehlen von Bodenstörungen auf den Mahd- und Beweidungsflächen im Keimversuch. Hingegen litten kleine Samen weniger als größere Samen unter den Brachebedingungen, was in Übereinstimmung mit den Bracheversuchen ist. Möglicherweise konnten kleine Samen mehr von der Brache-Vegetation profitieren mit ihrer Funktion als Schutz vor Trockenheit und Dürre. Ausgehend von den Ergebnissen der Bracheversuche wurde erwartet, dass die Keimsaison mit dem Zeitpunkt der besten Lichtbedingungen korreliert ist, was im Keimversuch bestätigt wurde.

Im dritten Ansatz (Kapitel 7) analysierte ich den Zusammenhang zwischen biologischen Merkmalen und Beweidungsintensität systematisch mit Hilfe eines mechanistischen Simulationsmodells. Das Modell PASTUREPOP betrachtete drei Aspekte aus dem Lebenszyklus der Pflanzen: Konkurrenzfähigkeit der etablierten Pflanze, vegetative Reproduktion und Reproduktion über Samen. Diese Prozesse wurden von den Merkmalen Pflanzenhöhe, Ausläuferlänge und Samengewicht repräsentiert, welche zu Merkmals-Syndromen (Strategien) kombiniert wurden. Die Pflanzenhöhe korrelierte deutlich mit der Beweidungsintensität, wie es auch bei den Bracheversuchen beobachtet wurde. Große Pflanzen wurden bei fehlender Beweidung gefördert, wohingegen kleine Rosettenpflanzen bei hohen Beweidungsintensitäten dominierten. Die Ausbildung von langen Ausläufern war grundsätzlich die erfolgreichste Strategie. Eine Ausnahme bildeten baumbewachsene Standorte, wo das Risiko eines langen Ausläufers groß war, auf eine nicht besiedelbare Stelle zu treffen. Dieser Sachverhalt könnte erklären, warum in den Bracheversuchen nur in Bracheparzellen ohne deutlichen Baumzuwachs Arten mit langen Ausläufern gefördert wurden. Das Samengewicht bestimmte die Keimwahrscheinlichkeit, aber dennoch dominierten die Strategien mit kleinen Samen. Da das Modell den ‚trade-off' zwischen Samengewicht und Samenproduktion berücksichtigt, liegt der Erfolg der kleinen Samen in ihrem numerischen Vorteil begründet. Dieser numerische Vorteil wurde weiterhin durch Beweidung aufgrund der Bodenstörungen unterstützt.

Zusammenfassend lässt sich sagen, dass die Analyse von Vegetationsdaten zur Untersuchung der Reaktion von funktionellen, biologischen Merkmalen auf Grünlandmanagement geeignet ist, um viele biologische Merkmale zu betrachten. Mit dieser Arbeit konnte ein besseres Verständnis der Mechanismen vieler Prozesse des Grünlandmanagements und der Sukzession erreicht werden. Gewissheit über den Einfluss eines Merkmales auf die Vegetationsdynamik kann jedoch nur über Experimente erlangt werden. In dieser Arbeit ergänzte ich die indirekten Analysen der Vegetationsdaten im ersten Ansatz mit den zwei experimentellen Ansätzen (Keimversuch und Simulationsmodell), um den Bezug einzelner Merkmale zur Vegetationsdynamik zu prüfen und einen tieferen Einblick in die Mechanismen zu erhalten. Dies sei im Folgenden beispielhaft dargestellt.

In den Vegetationsdaten der Bracheversuche waren kleine Samen im Vergleich zu größeren Samen positiv mit Brache assoziiert. Bei Beschränkung auf die Vegetationsdaten kann nicht differenziert werden, ob diese Beziehung ggf. durch weitere, korrelierte Merkmale bedingt wurde und nicht auf die Keimereignisse zurückgeht. Diese Beobachtung unterstützend wurde aber auch im Keimversuch der Zusammenhang zwischen kleinen Samen und Keimerfolg unter Brachebedingungen gefunden. Eine mögliche Erklärung ist, dass offene Bodenstellen die Keimung von kleinen Samen fördern, was aber weder durch die Vegetationsdaten der Bracheversuche noch durch den Keimversuch unterstützt wurde. Im Simulationsexperiment dagegen wurde eine Förderung von kleinen Samen durch offene Bodenstellen beobachtet. Dafür verantwortlich ist der im Modell berücksichtigte ‚trade-off' zwischen Samengewicht und Samenproduktion, so dass die Wahrscheinlichkeit größer war, dass ein kleiner als ein großer Same in die offenen Stellen ausgebreitet wurde. Dieser ‚trade-off' könnte das Muster in den Vegetationsdaten der Bracheversuche erklären, jedoch nicht die Ergebnisse des Keimversuches, da hier eine definierte Anzahl an Samen ausgesät wurde. Eine weitere Erklärungsmöglichkeit ist, dass kleine Samen weniger von den offenen Bodenstellen als von der Brache-Vegetation profitieren, welche einen Schutz vor physikalischen Gefahren darstellt. Weiterhin steigt möglicherweise der Predationsdruck in der Brache und kleine Samen leiden weniger unter Predation als größere Samen. Diese beiden Möglichkeiten können die Beobachtung in den Feldversuchen, nicht aber in dem Simulationsmodell erklären. Aus dem Beispiel ist zu schlussfolgern, dass es keine monokausale Erklärung für die positive Beziehung zwischen kleinen Samen und Brache gibt.

References

Abrahamson, W.G. (1980) Demography and vegetative reproduction. In *Demography and evolution in plant populations.* (ed O.T. Solbrig), pp. 89-106. Blackwell Scientific Publications, Oxford.

Arnthórsdóttir, S. (1994) Colonization of experimental patches in a mown grassland. *Oikos* **70**, 73-79.

Austin, M.P. (1981) Permanent quadrats: An interface for theory and practice. *Vegetatio* **46**, 1-10.

Bakker, J.P. (1989) Nature management by grazing and cutting. Kluwer Academic Publishers, Dortrecht.

Bakker, J.P., Elzinga, J.A., & de Vries, Y. (2002a) Effects of long-term cutting in a grassland system: perspectives for restoration of plant communities on nutrient-poor soil. *Applied Vegetation Science* **5**, 107-120.

Bakker, J.P., Marrs, R.H., & Pakeman, R.J. (2002b) Long-term vegetation dynamics: successional patterns and processes. *Applied Vegetation Science* **5**, 2-6.

Bakker, J.P., Olff, H., Willems, J.H., & Zobel, M. (1996a) Why do we need permanent plots in the study of long-term vegetation dynamics? *Journal of Vegetation Science* **7**, 147-156.

Bakker, J.P., Poschlod, P., Strykstra, R.J., Bekker, R.M., & Thompson, K. (1996b) Seed bank and seed dispersal: important topics in restoration ecology. *Acta Bontanica Neerlandica* **45**, 461-490.

Bekker, R.M., Verweij, G.L., Bakker, J.P., & Fresco, L.F.M. (2000) Soil seed bank dynamics in hayfield succession. *Journal of Ecology* **88**, 594-607.

Berlin, G.I., Linusson, A.C., & Olsson, E.G.A. (2000) Vegetation changes in semi-natural meadows with unchanged management in southern Sweden, 1965-1990. *Acta Oecologica* **21**, 125-138.

Bobbink, R. & Willems, J.H. (1987) Increasing dominance of Brachypodium pinnatum (L.) Beauv. in chalk grasslands: a threat to a species-rich ecosystem. *Biological Conservation* **40**, 301-314.

Bobbink, R. & Willems, J.H. (1993) Restoration management of abandoned chalk grassland in the Netherlands. *Biodiversity and Conservation* **2**, 616-626.

Bonn, S. & Poschlod, P. (1998) Ausbreitungsbiologie der Pflanzen Mitteleuropas. Grundlagen und kulturhistorische Aspekte. Quelle & Meyer, Wiesbaden.

Bonser, S.P. & Reader, R.J. (1998) Species and biomass dependence of an indirect effect of vegetation on seedling recruitment. *Ecoscience* **5**, 207-212.

Bornkamm, R. (1981) Rates of change in vegetation during secondary succession. *Vegetatio* **47**, 213-220.

Bosy, J. & Reader, R. (1995) Mechanisms underlying the suppression of forb seedling emergence by grass (*Poa pratensis*) litter. *Functional Ecology* **9**, 635-639.

Boutin, C. & Keddy, P.A. (1993) A functional classification of wetland plants. *Journal of Vegetation Science* **4**, 591-600.

Briemle, G. & Schreiber, K.F. (1994) Zur Frage der Beeinflussung pflanzlicher Lebens- und Wuchsformen durch unterschiedliche Landschaftspflegemaßnahmen. *Tuexenia* **14**, 229-244.

Brosius, F. (1998) SPSS 8.0: Professionelle Statistik unter Windows. MITP-Verlag GmbH, Bonn.

Brown, V.K. (1992) Plant succession and life history strategy. *Trends in Ecology and Evolution* **75**, 143-144.

Bühl, A. & Zöfel, P. (2000) SPSS Version 9. Einführung in die moderne Datenanalyse unter Windows. Addison-Wesley, München.

Bullock, J.M., Franklin, J., Stevenson, M.J., Silvertown, J., Coulson, S.J., Gregory, S.J., & Tofts, R. (2001) A plant trait analysis of responses to grazing in a long-term experiment.

Journal of Applied Ecology **38**, 253-267.

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

Campbell, B.D. & Grime, J.P. (1992) An experimental test of plant strategy theory. *Ecology* **73**, 15-29.

Campbell, B.D., Stafford Smith, D.M., & Ash, A.J. (1999) A rule-based model for the functional analysis of vegetation change in Australasian grasslands. *Journal of Vegetation Science* **10**, 723-730.

Chytrý, M., Sedláková, I., & Tichý, L. (2001) Species richness and species turnover in a successional heathland. *Applied Vegetation Science* **4**, 89-96.

Clements, F.E. (1916) Plant succession: an analysis of the development of vegetation. Carnegie Inst. Washington Publishers 242, Washington.

Colasanti, R.L. & Grime, J.P. (1993) Resource dynamics and vegetation processes: a deterministic model using two-dimension cellular automata. *Functional Ecology* **7**, 169-176.

Connell, J.H. & Slatyer, R.O. (1977) Mechanisms of succession in natural communities and their role in community stability and organization. *The American Naturalist* **111**, 1119-1144.

Cook, R.E. (1979) Patterns of juvenile mortality and recruitment in plants. In *Topics in plant population biology.* (eds O.T. Solbrig, S. Jain, G.B. Johnson & R.H. Raven), pp. 207-231. Columbia University Press, New York and Guildford.

Crawley, M.J. & May, R.M. (1987) Population dynamics and plant community structure: competition between annuals and perennials. *Journal of Theoretical Biology* **125**, 475-489.

Czárán, T. (1989) Coexistence of competing populations along an environmental gradient: a simulation study. *Coenoses* **2**, 113-120.

Czárán, T. & Bartha, S. (1989) The effect of spatial pattern on community dynamics; a comparison of simulated and field data. *Vegetatio* **83**, 229-239.

Davies, A. & Waite, S. (1998) The persistence of calcareous grassland species in the soil seed bank under developing and established shrub. *Plant Ecology* **136**, 27-39.

de Kroon, H. & van Groenendael, J. (1990) Regulation and function of clonal growth in plants: an evaluation. In *Clonal growth in plants.* (eds J. van Groenendael & H. de Kroon), pp. 177-186. SPB Academic Publishing, The Hague, The Netherlands.

Deng, H.J. (2001) Succession from farmland to heathland: a case for conservation of nature and historic farming methods. *Biological Conservation* **97**, 319-330.

Díaz, S., Acosta, A., & Cabido, M. (1992) Morphological analysis of herbaceous communities under different grazing regimes. *Journal of Vegetation Science* **3**, 689-696.

Díaz, S., Cabido, M., Zak, M., Martinez Carretero, E., & Aranibar, J. (1999) Plant functional traits, ecosystem structure and land-use history along a climatic gradient in central-western Argentina. *Journal of Vegetation Science* **10**, 651-660.

Díaz, S. & Marcelo, C. (1997) Plant functional types and ecosystem function in relation to global change. *Journal of Vegetation Science* **8**, 463-474.

Díaz, S., Marcelo, C., & Casanoves, F. (1998) Plant functional traits and environmental filters at regional scale. *Journal of Vegetation Science* **9**, 113-122.

Díaz, S., Noy-Meir, I., & Cabido, M. (2001) Can grazing response of herbaceous plants be predicted from simple vegetative traits? *Journal of Applied Ecology* **38**, 497-508.

Dupré, C. & Diekmann, M. (2001) Differences in species richness and life-history traits between grazed and abandoned grasslands in southern Sweden. *Ecography* **24**, 275-286.

Dyer, A.R., Goldberg, D.E., Turkington, R., & Sayre, C. (2001) Effects of growing conditions and source habitat on plant traits and functional group definition. *Functional Ecology* **15**, 85-95.

Dytham, C. (1995) The effect of habitat destruction pattern on species persistence: a cellular model. *Oikos* **74**, 340-344.

Ellenberg, H. (1996) Vegetation Mitteleuropas mit den Alpen., 5. ed. Ulmer, Stuttgart.

Ellenberg, H. & Müller-Dombois, D. (1967) A key of Raunkiaer plant life forms with revised subdivision. *Berichte des Geobotanischen Institutes der Eidg Technischen Hochschule, Stiftung Rübel* **37**, 56-73.

Ellenberg, H., Weber, H.E., Dull, R., Wirth, V., Werner, W., & Paulissen, D. (1992) Zeigerwerte von Pflanzen in Mitteleuropa. *Scripta Geobotanica* **18**.

Eriksson, A. & Eriksson, O. (1997) Seedling recruitment in semi-natural pastures: the effects of disturbance, seed size, phenology and seed bank. *Nordic Journal of Botany* **17**, 469-482.

Eriksson, O. (1997) Clonal life histories and the evolution of seed recruitment. In *The ecology and evolution of clonal plants.* (eds H. de Kroon & J. van Groenendael), pp. 211-226. Backhuys Publishers, Leiden, The Netherlands.

Eriksson, O. & Jakobsson, A. (1998) Abundance, distribution and life histories of grassland plants: a comparative study of 81 species. *Journal of Ecology* **86**, 922-933.

Fenner, M. (1987) Seed characteristics in relation to succession. In *Colonization, succession and stability.* (eds A.J. Gray, M.J. Crawley & P.J. Edwards), pp. 103-114. Blackwell Scientific Publications, Oxford.

Fischer, M. & Wipf, S. (2002) Effect of low-intensity grazing on the species-rich vegetation of traditionally mown subalpine meadows. *Biological Conservation* **104**, 1-11.

Foster, B.L. & Tilman, D. (2000) Dynamic and static view of succession: Testing the descriptive power of the chronosequence approach. *Plant Ecology* **146**, 1-10.

García, D., Zamora, R., Gómez, J.M., Fordano, P., & Hódar, J.A. (2000) Geographical variation in seed production, predation and abortion in Juniperus communis throughout its range in Europe. *Journal of Ecology* **88**, 436-446.

García, D., Zamora, R., Hodar, J.A., & Gomez, J.M. (1999) Age structure of Juniperus communis L. in the Iberian peninsula: Conservation of remnant populations in Mediterranean mountains. *Biological Conservation* **87**, 215-220.

Gaudet, C.L. & Keddy, P.A. (1988) A comparative approach to predicting competitive ability from plant traits. *Nature* **334**, 242-243.

Gillison, A.N. & Carpenter, G. (1997) A generic plant functional attribute set and grammar for dynamic vegetation description and analysis. *Functional Ecology* **11**, 775-783.

Gitay, H. & Noble, I.R. (1997) What are functional types and how should we seek them? In *Plant functional types - their relevance to ecosystem properties and global change.* (eds T.M. Smith, H.H. Shugart & F.I. Woodward), pp. 3-19. Cambridge University Press, Cambridge.

Glenn-Lewin, D.C. & van der Maarel, E. (1992) Patterns and processes of vegetation dynamics. In *Plant succession: theory and prediction.* (eds D.C. Glenn-Lewin, R.K. Peet & T.T. Veblen), pp. 11-59. Chapman & Hall, London.

Grime, J.P. (1974) Vegetation classification by reference to strategies. *Nature* **250**, 26-31.

Grime, J.P. (2001) Plant strategies, vegetation processes, and ecosystem properties., 2. ed. John Wiley & Sons, Ltd, Chichester.

Grime, J.P., Hodgson, J.G., & Hunt, R. (1988) Comparative Plant Ecology. Chapman & Hall, London.

Hadar, L., Noy-Meir, I., & Perevolotsky, A. (1999) The effect of shrub clearing and grazing on the composition of a Mediterranean plant community: functional groups versus species. *Journal of Vegetation Science* **10**, 673-683.

Harper, J.L. (1977) Population Biology of Plants. Academic Press, London.

Herben, T. (1996) Permanent plots as tools for plant community ecology. *Journal of Vegetation Science* **7**, 195-202.

Hobbs, R.J. (1997) Can we use plant functional types to describe and predict responses to environmental change? In *Plant Functional Types. Their relevance to ecosystem properties and global change.* (eds T.A. Smith, H.H. Shugard & F.I. Woodward), pp. 66-90. Cambridge University Press, Cambridge.

Hodgson, J.G. (1990) The role of autecological accounts. In *Calcareous grasslands - ecology* *and management. Proceedings of a BES/NCC symposium at University of Sheffield* (eds S.H. Hillier, D.W.H. Walton & D.A. Wells), pp. 161-168. Bluntisham Books, Bluntisham.

Hodkinson, D., Askew, A., Thompson, K., Hodgson, J., Bakker, J., & Bekker, R. (1998) Ecological correlates of seed size in the British flora. *Functional Ecology* **12**, 762-766.

Huhta, A.P. & Rautio, P. (1998) Evaluating the impacts of mowing: a case study comparing managed and abandoned meadow patches. *Annales Botanici Fennici* **35**, 85-99.

Huhta, A.P., Rautio, P., Tuomi, J., & Laine, K. (2001) Restorative mowing on an abandoned semi-natural meadow: short-term and predicted long-term effects. *Journal of Vegetation Science* **12**, 677-686.

Hunt, R. & Cornelissen, J. (1997) Component of relative growth rate and their interrelations in 59 temperate plant species. *New Phytologist* **135**, 395-417.

Hutchings, M.J. & Booth, K.D. (1996a) Studies of the feasibility of re-creating chalk grassland vegetation on ex-arable land. II. Germination and early survivorship of seedlings under different management regimes. *Journal of Applied Ecology* **33**, 1182-1190.

Hutchings, M.J. & Booth, K.D. (1996b) Studies on the feasibility of re-creating chalk grassland vegetation on ex-arable land. I. The potential role of the seed bank and the seed rain. *Journal of Applied Ecology* **33**, 1171-1181.

Hutchings, M.J. & Wijesinghe, D.K. (1997) Patchy habitats, division of labour and growth dividends in clonal plants. *Trends in Ecology and Evolution* **12**, 390-394.

Hyatt, L.A. & Casper, B.A. (2000) Seed bank formation during early secondary succession in a temperate deciduous forest. *Journal of Ecology* **88**, 516-527.

Jackel, A.K. & Poschlod, P. (1996) Why are some plant species of fragmented continental dry grassland frequent and some rare? - The role of germination and establishment. In *Species survival in fragmented landscapes.* (eds J. Settele, C. Margules, P. Poschlod & K. Henle), pp. 194-203. Kluwer Academic Publishers, Dortrecht.

Jakobsson, A. & Eriksson, O. (2000) A comparative study of seed number, seed size, seedling size and seedling recruitment in grassland plants. *Oikos* **88**, 494-502.

Jensen, K. & Schrautzer, J. (1999) Consequences of abandonment for a regional fen flora and mechanisms of successional change. *Applied Vegetation Science* **2**, 79-88.

Jeschke, L. (1982) Die Bedeutung des Naturschutzgebietes "Ostufer der Müritz" für die Erhaltung bedrohter Pflanzenarten. *Natur und Naturschutz in Mecklenburg* **18**, 63-71.

Kahmen, S. & Poschlod, P. (in press) Plant functional trait repsonse to grassland succession over 25 years. *Journal of Vegetation Science*.

Kahmen, S., Poschlod, P., & Schreiber, K.F. (2002) Conservation management of calcareous grasslands. Changes in plant species composition and response of functional traits during 25 years. *Biological Conservation* **104**, 319-328.

Kalamees, R. & Zobel, M. (1997) The seed bank in an Estonian calcareous grassland: comparison of different successional stages. *Folia Geobotanica Phytotaxonomica* **32**, 1-14.

Kapfer, A. (1988) Versuche zur Renaturierung gedüngten Feuchtgrünlandes - Aushagerung und Vegetationsentwicklung. *Dissertationes Botanicae* **120**.

Keddy, P.A. (1992a) Assembly and response rules: two goals for predicitve community ecology. *Journal of Vegetation Science* **3**, 157-164.

Keddy, P.A. (1992b) A pragmatic approach to functional ecology. *Functional Ecology* **6**, 621-626.

Kelly, C.K. (1996) Identifying plant functional types using floristic data bases: Ecological correlates of plant size. *Journal of Vegetation Science* **7**, 417-424.

Kiefer, S. (1998) Wiederherstellung brachgefallener oder aufgeforsteter Kalkmagerrasen. *Berichte des Institutes für Landschafts- und Pflanzenökologie der Universität Hohenheim, Beiheft 7*.

Kitajima, K. & Tilman, D. (1996) Seed banks and seedling establishment on an experimental productivity gradient. *Oikos* **76**, 381-391.

Kiviniemi, K. & Eriksson, O. (1999) Dispersal, recruitment and site occupancy of grassland plants in fragmented habitats. *Oikos* **86**, 241-253.

Kleyer, M. (1995) Biological traits of vascular plants. A database. *Arbeitsberichte des Instituts für Landschaftsplanung und Ökologie* **2**.

Kleyer, M. (1999) The distribution of plant functional types on gradients of disturbance intensity and resource supply in an agricultural landscape. *Journal of Vegetation Science* **10**, 697-708.

Klimeš, L., Klimešová, J., Hendriks, R., & van Groenendael, J. (1997) Clonal plant architectures: a comparative analysis of form and function. In *The ecology and evolution of clonal plants* (eds H. de Kroon & J. van Groenendael), pp. 1-29. Backhuys Publishers, Leiden, the Netherlands.

Klinkhamer, P.G.L. & deJong, T.J. (1988) The importance of small-scale disturbance for seedling establishment in Cirsium vulgare and Cynoglossum officinale. *Journal of Ecology* **76**, 383-392.

Köhler, B. (2001) Mechanisms and extent of vegetation changes in differently managed limestone grasslands. *Dissertationes ETH, Zürich* **14227**.

Krüsi, B. (1981) Phenological methods in permanent plot research. *Veröffentlichungen des Geobotanischen Institutes der ETH, Stiftung Rübel* **75**.

Landsberg, J., Lavorel, S., & Stol, J. (1999) Grazing response groups among understorey plants in arid rangelands. *Journal of Vegetation Science* **10**, 683-696.

Lavorel, S. & Chesson, P. (1995) How species with different regeneration niches coexist in patchy habitats with local disturbances. *Oikos* **74**, 103-114.

Lavorel, S. & Garnier, E. (2002) Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grain. *Functional Ecology* **16**, 545-556.

Lavorel, S., Lepart, J., Debussche, M., Lebreton, J.D., & Beffy, J.L. (1994) Small scale disturbance and the maintenance of species diversity in Mediterranean old fields. *Oikos* **70**, 455-473.

Lavorel, S., McIntyre, S., & Grigulis, K. (1999a) Plant response to disturbance in a Mediterranean grassland: How many functional groups? *Journal of Vegetation Science* **10**, 661-672.

Lavorel, S., McIntyre, S., Landsberg, J., & Forbes, T.D.A. (1997) Plant functional classifications: from general groups to specific groups based on response to disturbance. *Trends in Ecology and Evolution* **12**, 474-478.

Lavorel, S., Rochette, C., & Lebreton, J.D. (1999b) Functional groups for response to disturbance in Mediterranean old fields. *Oikos* **84**, 480-498.

Lavorel, S., Touzard, B., Lebreton, J.D., & Clément, B. (1998) Identifying functional groups for response to disturbance in an abandoned pasture. *Acta Oecologica* **19**, 227-240.

Law, R. & Dieckmann, U. (2000) A dynamical system for neighbourhoods in plant communities. *Ecology* **81**, 2137-2148.

Legendre, P. & Legendre, L. (2000) Numerical Ecology, 2. ed. Elsevier, Amsterdam.

Leishman, M.R. (1999) How well do plant traits correlate with establishment ability? Evidence from a study of 16 calcareous grassland species. *New Phytologist* **141**, 487-496.

Leishman, M.R. & Westoby, M. (1992) Classifying plants into groups on the basis of associations of individual traits - evidence from Australien semi-arid woodlands. *Journal of Ecology* **80**, 417-424.

Leishman, M.R., Westoby, M., & Jurado, E. (1995) Correlates of seed size variation: a comparison among five temperate floras. *Journal of Ecology* **83**, 517-530.

Loehle, C. (2000) Strategy space and the disturbance spectrum: A life-history model for tree species coexistence. *American Naturalist* **156**, 14-33.

MacGillivray, C.W., Grime, J.P., & Team, T.I.S.P.T. (1995) Testing predictions of resistence and resilience of vegetation subjected to extreme events. *Functional Ecology* **9**, 640-649.

Margalef, R. (1963) On certain unifying principles in ecology. *The American Naturalist* **97**, 357-374.

Martin, D. (1997) Erfahrungen mit der Extensiv-Haltung von Fjällrindern im Müritz-Nationalpark. *Schriftenreihe für Landschaftspflege und Naturschutz* **54**, 161-175.

McConnaughay, K. & Bazzaz, F. (1987) The relationship between gap size and performance of several colonizing annuals. *Ecology* **68**, 411-416.

McCune, B. & Grace, J.B. (2002) Analysis of ecological communities. MjM Software Design, Gleneden Beach, Oregon.

McIntyre, S., Lavorel, S., Landsberg, J., & Forbes, T.D.A. (1999) Disturbance response in vegetation - towards a global perspective on functional traits. *Journal of Vegetation Science* **100**, 621-630.

McIntyre, S., Lavorel, S., & Tremont, R.M. (1995) Plant life-history attributes: their relationship to disturbance response in herbaceous vegetation. *Journal of Ecology* **83**, 31-44.

Miles, J. (1972) Experimental establishment of seedlings on a southern english heath. *Journal of Ecology* **60**, 225-234.

Miles, J. (1987) Vegetation succession: past and present perceptions. In *Colonization, succession and stability* (eds A.J. Gray, M.J. Crawley & P.J. Edwards), pp. 1-29. Blackwell Scientific Publications, Oxford.

Moog, D., Kahmen, S., & Poschlod, P. (submitted) Application of CSR- and LHS-strategies for the distinction of differently managed grasslands. *Basic and Applied Ecology*.

Moog, D., Poschlod, P., Kahmen, S., & Schreiber, K.F. (2002) Comparison of species composition between different grassland management treatments after 25 years. *Applied Vegetation Science* **5**, 99-106.

Neitzke, A. (1991) Vegetationsdynamik in Grünlandbrachen. *Arbeitsberichte Lehrstuhl Landschaftsökologie Münster* **13**.

Noble, I. & Gitay, H. (1996) A functional classification for predicting the dynamics of landscapes. *Journal of Vegetation Science* **7**, 329-336.

Noy-Meir, I., Gutman, M., & Kaplan, Y. (1989) Responses of mediterranean grassland plants to grazing and protection. *Journal of Ecology* **77**, 290-310.

Odum, E.P. (1969) The strategy of ecosystem development. *Science* **164**, 262-270.

Olff, H., Pegtel, D.M., van Groenendael, J.M., & Bakker, J.P. (1994) Germination strategies during grassland succession. *Journal of Ecology* **82**, 69-77.

Osunkoya, O., Ash, J., Hopkins, M., & Graham, A. (1994) Influence of seed size and seedling ecological attributes on shade-tolerance of rain-forest tree species in northern Queensland. *Journal of Ecology* **82**, 149-163.

Otsus, M. & Zobel, M. (2002) Small-scale turnover in a calcareous grassland, its pattern and components. *Journal of Vegetation Science* **13**, 199-206.

Pausas, J.G. (1999) Response of plant functional types to changes in the fire regime in Mediterranean ecosystems: A simulation approach. *Journal of Vegetation Science* **10**, 717-722.

Pickett, S.T.A., Cadenasso, M.L., & Bartha, S. (2001) Implications from the Buell-Small Succession Study for vegetation restoration. *Applied Vegetation Science* **4**, 41-52.

Pickett, S.T.A., Collins, S.L., & Armesto, J.J. (1987) A hierarchical consideration of causes and mechanisms of succession. *Vegetatio* **69**, 109-114.

Pillar, V.D. (1999) On the identification of optimal plant functional types. *Journal of Vegetation Science* **10**, 631-640.

Poschlod, P., Dannemann, A., Kahmen, S., Melzheimer, V., Biedermann, H., Mengel, C., Neugebauer, K., & Pantle, I. (2000a) Genes in the landscape. Change in central European land use and its impact on genetic diversity of plants. *Schriftenreihe für Vegetationskunde* **32**, 111-127.

Poschlod, P., Deffner, A., Beier, B., & Grunicke, U. (1991) Untersuchungen zur Diasporenbank von Samenpflanzen auf beweideten, gemähten, brachgefallenen und aufgeforsteten Kalkmagerrasenstandorten. *Verhandlungen der Gesellschaft für Ökologie* **20**, 893-903.

Poschlod, P., Fischer, S., & Kiefer, S. (1996) A coenotical approach of plant population viability analysis on successional and afforested calcareous grassland sites - Towards an ecological flora data base. In *Species survival in fragmented landscapes* (eds J. Settele, C.

Margules, P. Poschlod & K. Henle), pp. 219-229. Kluwer Academic Publishers, Dordrecht.

Poschlod, P., Kiefer, S., Tränkle, U., Fischer, S., & Bonn, S. (1998) Plant species richness in calcareous grasslands as affected by dispersability in space and time. *Applied Vegetation Science* **1**, 75-90.

Poschlod, P., Kleyer, M., & Tackenberg, O. (2000b) Databases on life history traits as a tool for risk assessment in plant species. *Zeitschrift für Ökologie und Naturschutz* **9**, 3-18.

Poschlod, P. & Schumacher, W. (1998) Rückgang von Pflanzen und Pflanzengesellschaften des Grünlandes - Gefährdungsursachen und Handlungsbedarf. *Schriftenreihe für Vegetationskunde* **29**, 83-99.

Prach, K. & Pysek, P. (1994) Clonal plants - what is their role in succession? *Folia Geobotanica et Phytotaxonomica* **29**, 307-320.

Prach, K., Pysek, P., & Smilauer, P. (1997) Changes in species traits during succession: a search for pattern. *Oikos* **79**, 201-205.

Pywell, R.F., Bullock, J.M., Roy, D.B., Warman, L., Walker, K.J., & Rothery, P. (2003) Plant traits as predictors of performance in ecological restoration. *Journal of Applied Ecology* **40**, 65-77.

Raunkiaer, C. (1934) The life forms of plants and statistical plant geography. Being the collected papers of C. Raunkiaer, translated into English by H.G. Carter, A.G. Tansley and Miss Fansboll. Claredon Press, Oxford.

Reader, R.J. (1993) Control of seedling emergence by ground cover and seed predation in relation to seed size for some old-field species. *Journal of Ecology* **81**, 169-175.

Rees, M. (1993) Trade-offs among dispersal strategies in British plants. *Nature* **366**, 150-152.

Rennwald, E. (2000) Verzeichnis und Rote Liste der Pflanzengesellschaften Deutschlands. *Schriftenreihe für Vegetationskunde* **35**.

Roberts, D.W. (1996a) Landscape vegetation modelling with vital attributes and fuzzy system theory. *Ecological Modelling* **90**, 175-184.

Roberts, D.W. (1996b) Modelling forest dynamics with vital attributes and fuzzy system theory. *Ecological Modelling* **90**, 161-173.

Rothmaler, W. (1994) Exkursionsflora von Deutschland. Gefäßpflanzen: Atlasband., 8. ed. Gustav Fischer, Jena, Stuttgart.

Rothmaler, W. (1999) Exkursionsflora von Deutschland. Gefäßpflanzen: Grundband., 8. ed. Spektrum Akademischer Verlag, Heidelberg, Berlin.

Rusch, G. & van der Maarel, E. (1992) Species turnover and seedling recruitment in limestone grasslands. *Oikos* **63**, 139-146.

Ryser, P. (1990) Influence of gaps and neighbouring plants on seedling establishment in limestone grassland. Experimental field studies in northern Switzerland. *Veröffentlichungen des Geobotanischen Institutes der ETH, Stiftung Rübel* **104**.

Ryser, P., Langenauer, R., & Gigon, A. (1995) Species richness and vegetation structure in a limestone grassland after 15 year management with six biomass removal regimes. *Folia Geobotanica Phytotaxonomica* **30**, 157-167.

Salisbury, E.J. (1942) The reproductive capacity of plants. Bell, London.

Schiefer, J. (1981) Bracheversuche in Baden-Württemberg. *Beihefte zu den Veröffentlichungen für Naturschutz und Landschaftspflege in Baden-Württemberg* **22**.

Schippers, P., van Groenendael, J., Vleeshouwers, L.M., & Hunt, R. (2001) Herbaceous plant strategies in disturbed habitats. *Oikos* **95**, 198-210.

Schmidt, W. (1981) Ungestörte und gelenkte Sukzession auf Brachäckern. *Scripta Geobotanica* **15**.

Schmidt, W., Dierschke, H., & Ellenberg, H. (1974) Vorschläge zur vegetationskundlichen Untersuchung auf Dauerprobeflächen. Ms. Göttingen.

Schreiber, K.F. (1977) Zur Sukzession und Flächenfreihaltung auf Brachland in Baden-Württemberg. *Verhandlungen der Gesellschaft für Ökologie* **Göttingen 1976**, 251-263.

Schreiber, K.F. (1987) Sukzessionsuntersuchungen auf Grünlandbrachen und ihre Bewertung für die Landschaftspflege. Erfassung und Bewertung anthropogener

Vegetationsveränderungen, Teil 2. In *Tagungsbericht des Internationalen Symposiums der Vereinigung für Vegetationskunde, Halle/Saale 1986* (eds R. Schubert & W. Hilbig), pp. 275-284, Universität Halle-Wittenberg.

Schreiber, K.F. (1997a) 20 Jahre Erfahrung mit dem kontrollierten Brennen auf den Bracheversuchen Baden-Württemberg. *NNA-Berichte* **10**, 59-71.

Schreiber, K.F. (1997b) Sukzessionen - Eine Bilanz der Grünlandbracheversuche in Baden-Württemberg. *Veröffentlichungen PAÖ* **23**.

Schreiber, K.F. (2001) 25 Jahre Landschaftspflegemaßnahmen in den Bracheversuchsflächen in Baden-Württemberg. *NZH Akademie Berichte* **2**, 5-42.

Schütz, W. (2000) The importance of seed regeneration strategies for the persistence of species in the changing landscape of Central Europe. *Zeitschrift für Ökologie und Naturschutz* **9**, 73-83.

Semenova, G.V. & van der Maarel, E. (2000) Plant functional types - a strategic perspective. *Journal of Vegetation Science* **11**, 917-922.

Silvertown, J. & Dodd, M. (1997) Comparing plants and connecting traits. In *Plant life histories.* (eds J. Silvertown, M. Franco & J.L. Harper), pp. 3-16. Cambridge University Press, Cambridge.

Skarpe, C. (1996) Plant functional types and climate in a southern African savanna. *Journal of Vegetation Science* **7**, 397-404.

Sokal, R. & Rohlf, F.J. (2000) Biometry., 3. ed. W.H. Freeman and Company, New York.

Sternberg, M., Gutman, M., Perevolotsky, A., Ungar, E.D., & Kigel, J. (2000) Vegetation response to grazing management in a Mediterranean community: a functional group approach. *Jounal of Appplied Ecology* **37**, 224-237.

Stöcklin, J. (1992) Umwelt, Morphologie und Wachstumsmuster klonaler Pflanzen - eine Übersicht. *Botanica Helvetica* **102**, 3-21.

Sutherland, W.J. & Stillmann, R.A. (1990) Clonal growth: insights from models. In *Clonal growth in plants: regulation and function.* (eds J. van Groenendael & H. de Kroon), pp. 95-111. SPB Academic Publishing, The Hague, The Netherlands.

Tackenberg, O. (2001) Methoden zur Bewertung gradueller Unterschiede des Ausbreitungspotentials von Pflanzenarten. - Modellierung des Windausbreitungspotentials und regelbasierte Ableitung des Fernausbreitungspotentials. *Dissertationes Botanicae* **347**.

Thompson, K., Bakker, J.P., & Bekker, R.M. (1997) The soil seed banks of north west Europe: methodology, density and longevity. Cambridge University Press, Cambridge.

Thompson, K., Bakker, J.P., Bekker, R.M., & Hodgson, J.G. (1998) Ecological correlates of seed persistence in soil in the north-west European flora. *Journal of Ecology* **86**, 163-169.

Thompson, K., Band, S.R., & Hodgson, J.G. (1993) Seed size and shape predict persistence in soil. *Functional Ecology* **7**, 236-241.

Thompson, K. & Baster, K. (1992) Establishment from seed of selected Umbelliferae in unmanaged grassland. *Functional Ecology* **6**, 346-352.

Thompson, K., Hillier, S.H., Grime, J.P., Bossard, C.C., & Brand, S.R. (1996) A functional analysis of a limestone grassland community. *Journal of Vegetation Science* **7**, 371-380.

Thompson, K., Hodgson, J.G., Grime, J.P., & Burke, M.J.W. (2001) Plant traits and temporal scale: evidence from a 5-year invasion experiment using native species. *Journal of Ecology* **89**, 1054-1060.

Thórhallsdóttir, T.E. (1990) The dynamics of a grassland community: a simultaneous investigation of spatial and temporal heterogeneity at various scales. *Journal of Ecology* **78**, 884-908.

Tilman, D. (1993) Species richness of experimental productivity gradients: how important is colonization limitation? *Ecology* **74**, 2179-2191.

Tilman, D. (1994) Competition and biodiversity in spatially structured habitats. *Ecology* **75**, 2-16.

Turnbull, L.A., Crawley, M.J., & Rees, M. (2000) Are plant populations seed-limited? A review of seed sowing experiments. *Oikos* **88**, 225-238.

Van der Valk, A.G. (1992) Establishment, colonization and persistence. In *Plant succession:*

theory and prediction. (eds D.C. Glenn-Lewin, R.K. Peet & T.T. Veblen), pp. 60-102. Chapman & Hall, London.

Van Dijk, G. (1991) The status of semi-natural grasslands in Europe. In *The conservation of lowland dry grassland birds in Europe.* (eds P.D. Goriup, L.A. Batten & J.A. Norton), pp. 15-36. Joint Nature Conservation Committee, Peterborough.

Verkaar, H.J. & Schenkeveld, A.J. (1984) On the ecology of short-lived fabs in chalk grasslands: life-history characteristics. *New Phytologist* **98**, 659-672.

WallisDeVries, M.F., Poschlod, P., & Willems, J.H. (2002) Challenges for the conservation of calcareous grasslands in northwestern Europe: integrating the requirements of flora and fauna. *Biological Conservation* **104**, 265-273.

Walter, H. (1990) Vegetation und Klimazonen., 6. ed. Ulmer, Stuttgart.

Weiher, E., Clarke, G.D.P., & Keddy, P.A. (1998) Community assembly rules, morphological dispersion, and the coexistence of plant species. *Oikos* **81**, 309-322.

Weiher, E., van der Werf, A., Thompson, K., Garnier, M., & Eriksson, O. (1999) Challenging Theophrastus: a common core list of plant traits for functional ecology. *Journal of Vegetation Science* **10**, 609-620.

Weiner, J. & Conte, P.T. (1981) Dispersal and neighbourhood effects in an annual plant competition modell. *Ecological Modelling* **13**, 131-147.

Westoby, M. (1998) A leaf-height-seed (LHS) plant ecology strategy scheme. *Plant and Soil* **199**, 213-227.

Westoby, M., Leishman, M., & Lord, J. (1997) Comparative ecology of seed size and dispersal. In *Plant life histories.* (eds J. Silvertown, M. Franco & J.L. Harper), pp. 143-162. Cambridge University Press, Cambridge.

Willems, J.H. (1990) Calcareous grasslands in Continental Europe. In *Calcareous grasslands - ecology and management. Proceedings of a BES/NCC symposium at University of Sheffield* (eds S.H. Hillier, D.W.H. Walton & D.A. Wells), pp. 3-10. Bluntisham Books, Bluntisham.

Wilson, J.B. & Lee, W.G. (2000) C-S-R triangle theory: community-level predictions, tests, evaluation of criticisms, and relation to other theories. *Oikos* **91**, 77-96.

Wilson, P.J., Thompson, K., & Hodgson, J.G. (1999) Specific leaf area and leaf dry matter content as alternative predictors of plant strategies. *New Phytologist* **143**, 155-162.

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

Wisskirchen, R., Haeupler, H., & Albers, F. (1998) Standardliste der Farn- und Blütenpflanzen Deutschlands. Ulmer, Stuttgart.

Zobel, M., Otsus, M., Liira, J., Moora, M., & Möls, T. (2000) Is small-scale species richness limited by seed availability or microsite availability? *Ecology* **81**, 3274-3282.

List of the vegetation plots of the different treatments in 1975 and 1999 and species attributes of the plant functional traits. Vegetation plots with percentage covers. Trait code see **Table 3.3**, nd = no data.

	grazing		mowing		mulching		burning		leaving fallow		life form	life cycle	growth form	runners	lateral spread	fecundity	seed mass	germ. season
	1975	1999	1975	1999	1975	1999	1975	1999	1975	1999								
total percentage cover	95	95	95	90	95	85	95	85	98	95								
Acer pseudoplatanus				0.1							4	2	3	1	3	1	3	1
Achillea millefolium	1	0.5	3	2	1	0.5	1	1	0.5	0.5	1	2	3	3	3	1	1	1
Agrostis capillaris	3	5	3	4	1	1			1		3	2	3	1	2	nd	1	nd
Alchemilla monticola					0.5	0.1	0.5	1		0.5	3	2	4	1	1	nd	1	nd
Anthoxanthum odoratum	1	1	1	5	1	1	3		1		3	2	1	1	1	1	1	1
Arenaria serpyllifolia		0.5									5	1	1	1	1	1	1	1
Arrhenatherum elatius	0.5		1	1	0.5	1	0.5				3	2	1	1	1	1	3	nd
Asperula cynanchica	1	1	1	0.1	0.5		0.5		1		3	2	3	1	2	nd	nd	nd
Avenula pratensis		1		4				1			3	2	1	1	1	nd	3	nd
Avenula pubescens	0.5		1		0.5		0.5	0.5	0.5	1	3	2	1	1	1	1	2	1
Brachypodium pinnatum		3	1	8	1	7	3	50	1	50	2	2	1	3	3	1	3	2
Briza media	1		1	5	0.5	1	1	0.5	1		3	2	1	2	2	nd	1	1
Bromus erectus	30	20	30	40	40	40	30	8	40	15	3	2	1	1	1	1	3	nd
Campanula rotundifolia	0.5		1	3	0.5	0.5	0.5	0.5		0.5	3	2	4	3	2	1	1	3
Carex caryophyllea	3		3		5		0.5		3		2	2	1	3	2	nd	2	2
Carex flacca	3		3		3		8		8	0.5	2	2	1	3	3	1	1	2
Carex montana					0.5						3	2	1	1	1	nd	nd	nd
Carlina acaulis	0.5	1	1	3	0.5	1	0.5		0.5		3	2	4	1	1	nd	2	1
Carpinus betulus				5		0.5		1			4	2	3	1	1	1	3	1
Centaurea jacea			1	0.5	0.5		0.5	1	1		3	2	3	1	1	1	2	2
Cerastium holosteoides	0.5	0.5	1	1	0.5		0.5		0.5		1	2	1	1	1	1	1	nd
Cirsium acaule	0.5	0.1	8	2	3		5		8		3	2	2	1	1	nd	nd	nd
Colchicum autumnale										0.1	2	2	2	1	1	1	3	nd
Cruciata laevipes						0.1					3	2	3	2	2	nd	nd	nd
Cynosurus cristatus	3	3	1	3	3	0.5	3		1		3	2	1	1	1	1	2	3
Dactylis glomerata	0.5		1		0.5	3	3	0.5	1		3	2	1	1	1	1	2	1
Festuca ovina	1		1	10	1	0.5	1	1	0.5	5	3	2	1	1	1	1	1	nd
Festuca pratensis						1					3	2	1	1	1	1	2	1
Festuca rubra	5		3		5	7	3	3	3	5	3	2	1	3	3	1	2	1
Fragaria vesca										1	3	2	4	2	3	1	1	3
Fraxinus excelsior										0.5	4	2	1	1	3	1	3	2
Galium pumilum		0.5		3	1	2	0.5			0.5	3	2	3	2	1	nd	nd	nd
Galium verum	5	3	5	4	3	3	3	4	3	3	3	2	3	1	3	1	2	3
Genistella saggitalis					0.5						1	2	3	2	1	nd	nd	nd
Gentianella ciliata										0.5	3	2	3	1	1	nd	nd	nd
Helianthemum nummulariu	3	1	5	2	5	2	3	2	3	5	1	2	1	2	2	1	2	1
Hieracium pilosella	15	20	8	3	3		1		5		3	2	2	2	3	1	1	1
Hippocrepis comosa	5	0.5	8	2	1	0.5	3		5		1	2	1	1	1	nd	nd	nd
Holcus lanatus						2					3	2	1	1	2	1	1	1

	grazing		mowing		mulching		burning		leaving fallow		life form	life cycle	growth form	runners	lateral spread	fecundity	seed mass	germ. season
	1975	1999	1975	1999	1975	1999	1975	1999	1975	1999								
total percentage cover	95	95	95	90	95	85	95	85	98	95								
Hypericum perforatum				1		3		10		1	3	2	3	3	3	2	1	2
Knautia arvensis						0.5					3	2	4	1	1	1	3	1
Koeleria pyramidata	3	1	5	15	1	2	1	1	3	1	3	2	1	1	1	1	3	1
Leontodon hispidus		3			1		0.5				3	2	2	1	2	1	2	nd
Leucanthemum vulgare	1		1	4	1		3		1		3	2	4	1	1	1	2	3
Linum cartharticum	0.5	0.5	1	1	0.5	0.5	0.5		0.5		5	1	3	1	1	1	1	2
Lotus corniculatus	1	1	1	0.5	3		3	1	1		3	2	1	1	1	1	2	3
Luzula campestris	1		1	3	0.5	0.5	1				3	2	1	3	2	1	2	1
Medicago falcata								0.5			3	2	1	1	1	nd	2	nd
Medicago lupulina	1	0.5	1	2	1		5		1		5	2	1	1	1	1	3	nd
Orobanche vulgaris								0.5			2	1	3	1	1	nd	nd	nd
Picea abies										0.1	4	2	3	1	1	nd	nd	1
Pimpinella saxifraga	1	1	1	1	0.5		1	0.5	1	0.5	3	2	4	1	1	1	2	2
Pinus sylvestris										2	4	2	3	1	1	nd	nd	1
Plantago lanceolata	3	3	3	8	1	2	3	1	3		3	2	2	1	1	1	2	3
Plantago media	8	10	5	1	8		10	0.5	10		3	2	2	1	1	1	1	3
Poa pratense	0.5				0.5	2			0.5	10	3	2	1	3	2	1	1	3
Poa trivialis								3			3	2	1	3	2	1	1	1
Potentilla erecta					0.5	0.5		2			3	2	1	1	2	nd	nd	nd
Potentilla heptaphylla	0.5		1	1	0.5		0.5		0.5		3	2	1	1	1	nd	nd	nd
Potentilla neumanniana	1	1	1	1	0.5	0.1	0.5		0.5	0.5	3	2	1	1	1	nd	2	nd
Primula veris			1	4	1	15		1		0.5	3	2	2	1	1	1	2	2
Prunella grandiflora	1		3		3		5	4	3		3	2	1	1	1	nd	2	nd
Prunella vulgaris		7	1	3	0.5				0.5	0.5	3	2	3	3	2	1	2	3
Ranunculus bulbosus	0.5		1	1	1	0.5	1		1		2	2	4	1	1	1	3	1
Salvia pratensis								0.1			3	2	4	3	1	1	2	nd
Sanguisorba minor	3		1	8	3	5	3	2	3	2	3	2	4	1	1	1	3	3
Scabiosa columbaria	5	10	8	5	5		8	1	5		3	2	4	3	1	1	3	3
Senecio jacobea								0.5			3	2	3	1	1	1	1	nd
Taraxacum officinale		1									3	2	2	1	1	1	2	nd
Teucrium chamaedrys											1	2	3	3	3	nd	2	nd
Thymus pulegioides	20	40	20	5	10		15		10	0.5	1	2	1	2	3	1	1	nd
Trifolium medium				0.5							3	2	3	3	3	1	3	1
Trifolium ochroleucon				2							3	2	1	1	1	nd	nd	nd
Trifolium pratense	3	5	3	1	3		8		3		3	2	1	1	1	1	2	1
Trifolium repens	1	3	1	2	1	3	8	6	0.5		1	2	nd	2	3	1	2	1
Trisetum flavescens	0.5		1		0.5		1		0.5		3	2	1	1	1	1	1	1
Veronica chamaedrys				3	1			0.5		0.5	1	2	3	3	2	1	1	3
Veronica officinalis				1							1	2	3	2	2	nd	1	3

Species of the “Fallow Experiments of Baden-Württemberg” with allocated traits and model strategies (Chapter 7). Species of the succession analysis (Chapter 2) and of the management analyses (Chapter 4+5) are indicated by crosses. Description of the traits and strategies see respective chapters. Life from (1: therophytes, 2: geophytes, 3: hemicryptophytes, 4: chamaephytes, 5: phanerophytes); plant height (1: <0.3m, 2: 0.3-0.6m, 3: >0.6m); canopy height (1: leaves basal, 2: leafy); SLA (1: <20, 2: 20-25, 3: >25); storage organ (1: no storage organ, 2: storage organ); vegetative spread (1: <100mm, 2: ≥100mm); plant persistence (1: annual, biennial, 2: not clonal perennial, 3: clonal perennial); seed bank longevity (1: transient, 2: persistent); start of flowering (1: May and earlier, 2: after May); duration of flowering (1: 1-2 months, 2: ≥3 months); seed mass (1: <0.5mg, 2: 0.5-2mg, 3: >2mg).

species	**life form**	**plant height**	**canopy str.**	**SLA**	**st. organ**	**veg. spread**	**p. persistence**	**seed bank l.**	**start of flow.**	**duration of flow.**	**seed mass**	**model strategy**	**management**	**succession**
Acer campestre	5	3	2	1	1	1	2	1	1	1	3			x
Acer platanoides	5	3	2	3	1	1	2		1	1	3		x	x
Acer pseudoplatanus	5	3	2	2	1	1	2	1	1	1	3		x	x
Achillea millefolium	3	3	2	1	2	2	3	1	2	2	1	LMS	x	x
Achillea ptarmica	3	3	2	1	2	2	3	1	2	2	1	LMS		x
Aegopodium podagraria	2	3	2	2	2	2	3	2	2	1	3			x
Agrimonia eupatoria	3	3	2	2	1	1	3	1	2	2	3		x	x
Agrostis canina	3	2	1	3	1	2	3	2	2	2	1	LMS	x	x
Agrostis capillaris	3	3	1	3	1	2	3	2	2	1	1	LMS	x	x
Agrostis stolonifera	3	3	1	2	1	2	3	2	2	1	1	LMS	x	x
Ajuga genevensis	3	1	1	3	1	2	3	2	1	2	2	LRL		x
Ajuga reptans	3	1	1	3	2	2	3	2	1	2	2	LRL	x	x
Alchemilla glabra	3	1	1	1	1	1	3		1	2	1	LRS		x
Alchemilla monticola	3	1	1	1	1	1	3		1	2	1	LRS	x	x
Alopecurus pratensis	3	3	1	1	1	1	3	2	1	1	2	STL	x	x
Anagallis arvensis	1	1	2		1	1	1	2	2	2	2			x
Anemone nemorosa	2	1	1	3	2	2	3	1	1	2	3		x	x
Angelica sylvestris	3	3	2		1	1	2	1	2	2	2	NTL	x	x
Anthoxanthum odoratum	3	2	1	3	1	1	3	2	1	1	1	SMS	x	x
Anthriscus sylvestris	3	3	2	3	1	1	2	1	1	2	3		x	x
Anthyllis vulneraria	3	1	1	1	1	1	2	1	1	2	3		x	
Arabis hirsuta	3	3	1		1	1	1	2	1	2	1		x	
Arenaria leptoclados	1	1	2	2	1	1	1	2	1	2	1		x	x
Arnica montana	3	2	1	2	2	2	3	1	2	1	2	LRL	x	x
Arrhenatherum elatius	3	3	1	3	1	1	3	1	2	1	3		x	x
Arum maculatum	2	2	1		2	1	2	1	1	2	3			x
Asperula cynanchica	3	1	2		1	2	3	2	2	2	2	LML	x	x
Astragalus cicer	3	2	2		2	1	2		2	2	3		x	
Astragalus glycyphyllos	3	3	2	3	2	1	2		2	1	3		x	
Betula pendula	5	3	2	1	1	1	2	2	1	1	3			x
Brachypodium pinnatum	2	3	1	3	2	2	3	1	2	1	3		x	x
Brachypodium sylvaticum	3	3	1		1	1	3	1	2	1	3		x	
Briza media	3	2	1	3	1	1	3	1	1	1	1	SMS	x	x
Bromus erectus	3	3	1	1	1	1	3	2	1	2	3		x	x
Bromus hordeaceus	1	3	1	3	1	1	1	2	1	2	3		x	
Bromus sterilis	1	2	1	3	1	1	1	1	1	1	3		x	
Calluna vulgaris	4	3	2	1	1	1	3	2	2	2	1	LTS	x	x
Caltha palustris	3	1	1	1	1	2	3	1	1	2	2	LRL	x	x
Campanula glomerata	3	2	1		1	1	3		2	2	1	LRS	x	x
Campanula patula	3	2	1	3	1	1	1	2	1	2	1		x	
Campanula rapunculoides	3	3	1		2	2	3		2	2	1	LRS		x
Campanula rotundifolia	3	1	1	3	2	2	3	2	2	2	1	LRS	x	x
Cardamine pratensis	3	2	1	3	1	1	3	2	1	2	2	LRL	x	x
Carex acutiformis	2	3	1		1	2	3	2	2	1	2	LTL		x
Carex brizoides	3	3	1	3	1	2	3		1	1	1	LTS	x	x
Carex caryophyllea	2	1	1	2	1	2	3	1	1	2	2	LML	x	x

species	life form	plant height	canopy str.	SLA	st. organ	veg. spread	p. persistence	seed bank l.	start of flow.	duration of flow.	seed mass	model strategy	management	succession
Carex echinata	3	2	1	1	1	1	3	1	1	1	2		x	
Carex flacca	2	2	1	1	2	2	3	2	1	2	2	LML	x	x
Carex ovalis	3	2	1	3	1	1	3	2	2	1	1	SMS	x	x
Carex pairae	3	2	1		1	1	3		1	2	3		x	x
Carex pallescens	3	2	1	2	1	1	3	2	1	2	2		x	
Carex panicea	2	2	1	2	1	2	3	2	1	1	3		x	x
Carex parviflora	3	1	1	1	1	2	3		1	1	2	LML	x	x
Carex pilulifera	3	2	1		1	1	3	2	1	1	2	SML	x	x
Carlina acaulis	3	2	1		1	1	3	1	2	2	3		x	x
Carpinus betulus	5	3	2	1	1	1	2	1	1	1	3		x	
Carum carvi	3	3	2		2	1	2	1	1	2	3			x
Centaurea jacea	3	3	2	1	1	1	3	1	2	2	2	LML	x	x
Centaurea nigra	3	3	2	3	2	1	3	2	2	1	3		x	
Centaurea scabiosa	3	3	2	1	1	1	3	1	2	1	3		x	x
Cerastium arvense	4	1	2	3	1	1	3	2	1	2	1	LMS	x	x
Cerastium glomeratum	1	2	2		1	1	1	2	1	2	1		x	
Cerastium holosteoides	4	2	2	3	1	1	2	2	1	2	1	NMS	x	x
Chamaespartium sagittale	4	1	2	3	1	2	3		1	1			x	x
Cirsium acaule	3	1	1	1	2	1	2	1	2	2	3		x	x
Cirsium arvense	2	3	1	1	2	2	3	2	2	2	2	LRL	x	x
Cirsium eriophorum	3	3	1		1	1	1	2	2	2			x	
Cirsium palustre	3	3	1	1	1	1	2	2	2	2	2	NRL	x	x
Cirsium vulgare	3	3	1	1	1	1	3	1	2	2	3		x	x
Colchicum autumnale	2	2	1		2	1	2	1	2	2	3			x
Convolvulus arvensis	2	3	2		2	2	3	2	2	2	3		x	x
Cornus sanguinea	5	3	2	3	1	1	2	2	1	1	3		x	
Coronilla varia	3	2	2		1	2	3	2	2	2	3		x	
Crataegus laevigata	5	3	2		1	1	2	1	1	1	3			x
Crataegus monogyna	5	3	2	1	1	1	2	1	1	1	3			x
Crepis biennis	3	3	1		2	1	1		1	2	2			x
Crepis mollis	3	2	2		1	1	2		2	2	2	NTL	x	x
Crepis paludosa	3	3	2		1	1	3	1	2	2			x	x
Cruciata laevipes	3	2	2	3	1	2	3	1	1	2			x	x
Cuscuta epithymum	1	2	2		1	1	1		2	2	1		x	
Cynosurus cristatus	3	2	1		1	1	3	1	2	1	2	STL	x	x
Dactylis glomerata	3	3	1	3	1	1	3	2	1	1	2	STL	x	x
Danthonia decumbens	3	2	1	1	1	1	3	1	2	1	2	SML	x	x
Daucus carota	3	3	1	1	2	1	2	2	2	2	2	NRL	x	x
Deschampsia cespitosa	3	3	1	1	1	1	3	2	2	1	1	STS		x
Deschampsia flexuosa	3	2	1	1	1	1	3	1	2	2	1	STS	x	x
Elymus repens ssp. arenosus	2	3	1	1	2	2	3	2	1	2	3		x	x
Epilobium montanum	3	3	2	3	1	1	3	2	2	2	1	LMS		x
Epilobium obscurum	3	3	2		1	1	3		2	2	1	LTS		x
Epilobium palustre	3	2	2		1	1	3	2	2	2	1		x	
Epilobium tetragonum	3	3	2	1	1	1	3	2	2	1	1	LTS		x
Eupatorium cannabinum	3	3	2	3	2	1	3	2	2	2	1		x	
Euphorbia cyparissias	3	1	2	3	2	2	3	2	1	1	3		x	x
Euphorbia verrucosa	3	2	2		2	1	2	2	1	1	3			x
Euphrasia officinalis	1	2	2	3	1	1	1	2	1	2	1		x	x
Fagus sylvatica	5	3	2	3	1	1	2	1	1	1	3		x	
Festuca ovina	3	2	1	1	1	1	3	1	1	2	1	SMS	x	x
Festuca pratensis	3	3	1	3	1	1	3	1	2	1	2	STL	x	x
Festuca rubra	3	3	1	1	1	1	3	2	2	1	2	STL	x	x
Filipendula ulmaria	3	3	2	1	2	2	3	1	2	2	2	LTL	x	x
Fragaria vesca	3	1	1	1	1	1	3	2	1	1	1	LRS	x	x
Fragaria viridis	3	1	1	1	1	2	3	1	1	1	1	LRS		x
Frangula alnus	5	3	2	3	1	1	2	1	1	1	3			x
Fraxinus excelsior	5	3	2	1	1	1	2	1	1	1	3		x	x
Galeopsis tetrahit	1	3	2	3	1	1	1	2	2	2	3		x	x

species	**life form**	**plant height**	**canopy str.**	**SLA**	**st. organ**	**veg. spread**	**p. persistence**	**seed bank l.**	**start of flow.**	**duration of flow.**	**seed mass**	**model strategy**	**management**	**succession**
Galium aparine	1	3	2	3	1	1	1	1	2	2	3			x
Galium mollugo	3	3	2	3	1	2	3	1	1	2	2	LML	x	x
Galium palustre ssp. elongatum	3	3	2	3	1	2	3	2	1	2				x
Galium palustre ssp. palustre	3	3	2	3	1	2	3	2	1	2				x
Galium pumilum	3	2	2	3	1	2	3	1	2	2			x	x
Galium saxatile	4	1	2	3	1	1	3	2	2	2	2	LML	x	x
Galium uliginosum	3	2	2	3	1	2	3	1	2	2	1	LMS		x
Galium verum	3	2	2	2	1	2	3	1	2	2	2	LTL	x	x
Genista anglica	4	3	2		1	1	2		1	1				x
Genista tinctoria	4	2	2	1	1	1	2	1	2	2	3		x	
Gentianella ciliata	3	1	2		1	2	3	1	2	2	1	LMS		x
Geranium columbinum	1	2	1		1	1	1		2	1			x	x
Geranium dissectum	1	2	1		1	1	1	2	1	2	3			x
Geranium pratense	3	2	1		2	2	3	2	2	2	3		x	
Geranium purpureum	1	2	1	3	1	1	1	2	1	2	3			x
Geranium pyrenaicum	3	3	1	3	2	1	3		1	2	3		x	
Geranium robertianum	1	2	1	3	1	1	1	2	1	2	3			x
Geranium sylvaticum	3	2	1		2	2	3	1	1	2	3		x	x
Geum urbanum	3	3	1	3	2	1	3	1	1	2	3		x	
Glechoma hederacea	2	2	2	3	1	2	3	2	1	2	2	LTL		x
Gnaphalium sylvaticum	3	2	1	2	1	1	2	2	2	2	1		x	
Helianthemum nummularium	4	1	2	1	1	1	3	2	2	2	2	LML	x	x
Helictotrichon pratense	3	3	1	1	1	1	3	1	1	1	3			x
Helictotrichon pubescens	3	3	1	1	1	1	3	1	1	1	2	STL	x	x
Heracleum sphondylium	3	3	2	1	1	1	3	2	2	2	3		x	x
Hesperis matronalis	3	3	2		1	1	1		1	2				x
Hieracium lachenalii	3	3	1		1	1	3	2	2	2	1	LRS		x
Hieracium lactucella	3	1	1		1	2	3	1	1	2	1	LRS		x
Hieracium pilosella	3	1	1	2	1	2	3	1	1	2	1	LRS	x	x
Hieracium sabaudum	3	3	2		2	1	3	2	2	2	2	LTL		x
Hippocrepis comosa	3	1	2	1	1	1	3	1	1	2	3		x	x
Holcus lanatus	3	3	1	3	1	1	3	2	2	2	1	STS	x	x
Holcus mollis	2	3	1	3	1	2	3	1	2	2			x	x
Hypericum hirsutum	3	3	2		1	2	3	2	2	1				x
Hypericum maculatum	3	2	2	2	1	2	3	2	2	1	1	LMS	x	x
Hypericum perforatum	3	2	2	3	2	2	3	2	2	1	1	LTS	x	x
Hypochaeris radicata	3	2	1		1	1	3	2	2	2	2	LRL		x
Impatiens glandulifera	1	3	2		1	1	1		2	1	3		x	
Inula conyzae	3	3	1		2	2	3		2	2	1	LRS		x
Iris pseudacorus	2	3	1	1	2	2	3	1	1	1	3		x	x
Juncus acutiflorus	2	3	1	1	2	1	3	2	2	2	1	STS	x	x
Juncus conglomeratus	3	3	1	1	2	1	3	2	1	2	1	SMS		x
Juncus effusus	3	3	1	1	2	1	3	2	2	2	1	STS	x	x
Knautia arvensis	3	3	1	2	2	1	3	1	2	1	3		x	x
Koeleria pyramidata	3	3	1	1	1	1	3	1	2	1	2	STL	x	x
Lamium purpureum	1	2	2		1	1	1	2	1	2	2			x
Lathyrus latifolius	3	3	2		2	1	3		2	1	3			x
Lathyrus linifolius	2	1	2	3	2	2	3	1	1	2	3			x
Lathyrus pratensis	3	3	2	3	1	2	3	1	2	2	3		x	x
Lathyrus tuberosus	2	3	2	3	2	2	3		2	2				x
Leontodon autumnalis	3	2	1	3	2	1	2	1	2	2	2	NRL	x	x
Leontodon hispidus	3	2	1	3	2	1	2	2	2	2	2	NRL	x	x
Leucanthemum vulgare	3	3	2	1	1	2	3	2	2	2	1	LTS	x	x
Linaria vulgaris	2	3	2		1	2	3	2	2	2	1	LMS	x	
Linum catharticum	1	1	2	3	1	1	1	2	2	1	1		x	x
Lolium perenne	3	2	1	3	1	1	3	2	1	2	2	SML	x	x
Lotus corniculatus	3	2	2	3	2	1	2	2	2	2	2	NML	x	x
Lotus uliginosus	3	2	2	3	2	1	2	2	2	1	1	NMS	x	x
Luzula campestris	3	1	1	3	1	2	3	2	1	1	2	LML	x	x

species	**life form**	**plant height**	**canopy str.**	**SLA**	**st. organ**	**veg. spread**	**p. persistence**	**seed bank l.**	**start of flow.**	**duration of flow.**	**seed mass**	**model strategy**	**management**	**succession**
Luzula luzuloides	3	3	1	2	1	2	3	2	2	1	1	LTS	x	
Lychnis flos-cuculi	3	3	1	2	1	1	3	2	1	2	1	LRS	x	x
Lysimachia nummularia	4	2	1	3	1	2	3	1	1	2	1	LMS		x
Lysimachia vulgaris	3	3	2	3	2	1	3	2	2	2	1	LTS		x
Lythrum salicaria	3	3	2		2	1	3	1	2	2	1	STS		x
Medicago lupulina	1	2	2	3	1	1	1	2	1	2	2		x	x
Melilotus officinalis	3	3	2		2	1	1		2	2	3		x	x
Meum athamanticum	3	2	1	1	1	1	3		1	1	3			x
Muscari botryoides	2	1	1		2	1	2		1	1				x
Myosotis arvensis	1	2	2		1	1	1	2	1	2	1		x	x
Myosotis nemorosa	3	1	1	3	1	1	2	2	1	1	1	NRS	x	x
Nardus stricta	3	1	1	1	1	1	3	1	1	1	2	SML	x	x
Ononis repens	4	2	2	2	1	1	3	1	2	1	3		x	x
Ophrys apifera	2	2	1		2	1	2		1	1	1		x	
Origanum vulgare	3	2	2	3	1	1	3	2	2	2	1	SMS	x	
Phalaris arundinacea	2	3	2	2	2	2	3	2	2	1	1	LTS	x	x
Phleum pratense	3	3	1	2	1	1	3	2	2	2	2	SML	x	x
Phyteuma nigrum	3	2	1		1	1	3	1	1	2	1	LRS		x
Phyteuma spicatum	3	3	1		2	2	3	1	1	2				x
Picea abies	5	3	2	1	1	1	2	1	1	2	3			x
Picris hieracioides	3	2	1	3	1	1	1	2	2	2	2			x
Pimpinella major	3	3	2	1	2	1	3	1	2	2	3		x	x
Pimpinella saxifraga	3	2	1	1	2	2	3	1	2	2	2	LRL	x	x
Pinus sylvestris	5	3	2	1	1	1	2	1	1	1	3			x
Plantago lanceolata	3	2	1	1	1	1	3	2	1	2	2	LRL	x	x
Plantago major	3	1	1	3	1	1	3	2	2	2	1		x	
Plantago media	3	2	1	1	1	1	3	2	1	2	1	LRS	x	x
Platanthera bifolia	2	2	1		2	1	2		1	2	1	NRS	x	
Poa chaixii	3	3	1	2	1	1	3	1	2	1				x
Poa nemoralis	3	3	1		1	1	3	1	2	1	2	STL		x
Poa pratensis	3	3	1	3	1	2	3	2	1	1	1	LMS	x	x
Poa trivialis	3	3	1	2	1	2	3	2	2	1	1	LTS	x	x
Polygala comosa	3	1	2	2	1	1	2	1	1	1			x	x
Polygala serpyllifolia	3	1	2		1	1	2		1	2	2	NML		x
Polygala vulgaris	3	1	2	2	1	1	2	1	1	2	2	NML	x	x
Polygonum bistorta	2	3	1	3	2	2	3	1	1	2	3		x	x
Potentilla erecta	3	1	2	3	2	1	3	2	1	2	1	LMS	x	x
Potentilla heptaphylla	3	1	1	1	1	1	3		1	2	2	LRL	x	x
Potentilla reptans	3	1	1	3	1	2	3	2	2	2	1	LRS	x	x
Potentilla sterilis	3	1	1		2	2	3	2	1	2			x	x
Potentilla tabernaemontani	3	1	2	1	1	1	3	2	1	2	2	LML	x	x
Primula elatior	3	1	1		2	1	3	1	1	2	2	LRL	x	x
Primula veris	3	1	1	1	2	1	3	1	1	2	2	LRL	x	x
Prunella grandiflora	3	1	2	2	1	1	3	2	2	2	2	LML	x	x
Prunella vulgaris	3	1	2	2	2	2	3	2	2	2	2	LML	x	x
Prunus avium	5	3	2	1	1	1	2	1	1	1	3			x
Prunus domestica	5	3	2		1	1	2	1	1	1	3			x
Prunus spinosa	5	3	2	1	1	1	2	1	1	1	3		x	x
Quercus petraea	5	3	2	3	1	1	2	1	1	1	3		x	x
Quercus robur	5	3	2	1	1	1	2	1	1	1	3		x	x
Quercus rubra	5	3	2	3	1	1	2		1	1	3		x	x
Ranunculus aconitifolius	3	2	1		1	1	2		1	2	2	NRL	x	x
Ranunculus acris	3	3	1	2	1	1	2	2	1	2	2	NRL	x	x
Ranunculus auricomus	3	2	1		1	1	2	1	1	1	2	NRL	x	x
Ranunculus bulbosus	2	2	1	2	2	1	2	2	1	2	3		x	x
Ranunculus ficaria	2	1	1		2	1	2	1	1	2				x
Ranunculus flammula	3	2	1	1	1	2	3	2	1	2			x	
Ranunculus repens	3	2	1	1	1	2	3	2	1	2	3		x	x
Rhinanthus alectorolophus	1	3	2	2	1	1	1	2	1	2	3		x	x

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Rhinanthus minor	1	2	2	1	1	1	1	2	1	2	2		x	x
Rosa canina	5	3	2	1	1	1	2	1	2	1	3		x	x
Rubus fruticosus	5	3	2	1	1	1	2		2	1	3		x	x
Rumex acetosa	3	3	1	2	2	1	3	2	1	2	2	LRL	x	x
Rumex acetosella	3	1	1	3	1	1	3	2	1	2	1	LRS	x	x
Salvia pratensis	3	2	1	2	2	1	3	1	1	2	2	LRL	x	x
Salvia verticillata	3	2	2		2	1	3		2	2			x	
Sanguisorba minor	3	2	1	1	1	1	3	2	1	2	2		x	x
Sanguisorba officinalis	3	3	1	1	1	2	3	1	2	2	2		x	x
Scabiosa columbaria	3	2	1	1	2	1	3	2	2	2	2	LRL	x	x
Senecio erucifolius	3	3	2	1	2	1	3	2	2	2	1	LTS	x	x
Senecio jacobaea	3	3	2		2	2	3	2	2	2	1	LTS	x	
Senecio ovatus	3	3	2	2	2	1	3	1	2	2	3			x
Silene dioica	3	3	1	3	1	1	3	2	1	2	2	LRL	x	x
Silene nutans	3	2	1	3	2	2	3	2	1	2	1	LRS		x
Silene vulgaris	3	2	2	3	2	2	3	2	1	2	2	LML		x
Solidago virgaurea	3	3	2	1	2	1	3	1	2	2	2	LML	x	x
Stachys palustris	2	3	2	2	2	1	3	1	2	2	2	LTL	x	x
Stellaria graminea	3	2	2	3	1	2	3	2	1	2	1	LMS	x	x
Stellaria holostea	4	1	2	3	1	2	3	1	1	1				x
Succisa pratensis	3	3	1	1	1	1	2	1	2	2	2	NRL	x	x
Taraxacum sect. Ruderalia	3	2	1	3	1	1	3		1	2	2	LRL	x	x
Teucrium chamaedrys	4	1	2	1	1	2	3	2	2	1	2	LML		x
Teucrium scorodonia	3	2	2	2	1	2	3	2	2	2	2	LTL	x	x
Thlaspi perfoliatum	1	1	1		1	1	1		1	2	1		x	x
Thymus chamaedrys	4	2	2		1	2	3		2	2	1	LMS	x	x
Thymus pulegioides	4	2	2	3	1	2	3	2	2	2	1	LMS	x	x
Torilis japonica	1	3	2		1	1	1	2	2	2	2		x	x
Tragopogon pratensis	3	2	1	3	2	1	2	2	1	2	3		x	x
Trifolium campestre	1	1	2		1	1	1	2	2	2	1		x	x
Trifolium dubium	1	1	2	3	1	1	1	2	1	2	1		x	x
Trifolium medium	3	2	2	1	1	2	3	1	2	2	3		x	x
Trifolium montanum	3	2	2	2	2	1	3		1	2	2		x	
Trifolium ochroleucon	3	2	2		2	1	2		2	1			x	
Trifolium pratense	3	2	2	2	2	1	3	2	2	2	2	LML	x	x
Trifolium repens	4	2	2	3	1	2	3	2	1	2	1	LMS	x	x
Trisetum flavescens	3	3	1	3	1	1	3	1	1	1	1	STS	x	x
Urtica dioica	3	3	2	3	1	2	3	2	2	2	1	LTS		x
Vaccinium myrtillus	4	2	2	3	2	2	3	1	1	2	1	LMS	x	x
Valeriana dioica	3	1	1		1	2	3	1	1	1	2	LRL		x
Valeriana officinalis	3	3	1	2	2	1	3	1	1	2	1	LRS	x	x
Valerianella carinata	1	2	1		1	1	1		1	1	1			x
Valerianella locusta	1	1	1		1	1	1		1	1	2		x	x
Verbascum nigrum	3	3	1		2	1	1	2	2	2	1			x
Veronica arvensis	1	1	2		1	1	1	2	1	2	1		x	x
Veronica austriaca	4	2	2	2	1	1	3	2	1	2	1	LMS	x	x
Veronica chamaedrys	4	2	2	3	1	1	3	2	1	2	1	LMS	x	x
Veronica officinalis	4	1	2	3	1	2	3	2	2	2	1	LMS	x	x
Vicia cracca	3	3	2	1	1	2	3	1	2	2	3		x	x
Vicia hirsuta	1	2	2		1	1	1	2	2	1	3		x	
Vicia sativa	1	2	2	3	1	1	1	2	1	2			x	x
Vicia sepium	3	2	2	3	1	2	3	1	1	1	3		x	x
Vicia tetrasperma	1	2	2	3	1	1	1	2	2	1	3		x	
Viola arvensis	1	1	2		1	1	1	2	1	2	2		x	
Viola canina	3	1	2	3	1	1	3	2	1	1	2	LML	x	x
Viola hirta	3	1	1		1	1	3	1	1	1	3		x	x
Viola palustris	3	1	1		1	1	3	1	1	1			x	
Viola reichenbachiana	3	1	2		1	1	3		1	2	3		x	
Viola riviniana	3	1	2		1	1	3	1	1	2			x	

Dank

Ich bedanke mich herzlich bei Prof. Dr. Peter Poschlod für die Betreuung der Arbeit. Bereits während des Studiums motivierte er mich mit seinen Ideen und seiner wissenschaftlichen Neugier. Besonders hervorheben möchte ich seinen internationalen wissenschaftlichen Austausch, in den er seine Mitarbeiterinnen und Mitarbeiter frühzeitig einführt.

Diese Arbeit wurde im Rahmen des MOSAIK Projektes durchgeführt, finanziert vom Bundesministerium für Bildung und Forschung (BMBF, FKZ 01 LN 0007). Die Mitarbeit in dem von Prof. Dr. Michael Kleyer geleiteten MOSAIK Projekt war durch zielorientierte Diskussionen und nette Stimmung geprägt.

Dank gebührt Michael Kleyer für die Begutachtung der Dissertation.

Das Nationalparkamt Müritz ermöglichte die Freilandarbeit im Nationalpark. Dem Müritzhof (Waren) danke ich für die Unterstützung beim Auf- und Abbau der Exclosures.

Ein großer Dank geht an Prof. Karl-Friedrich Schreiber, der 1975 die „Bracheversuche in Baden-Württemberg“ ins Leben rief und diese noch immer enthusiastisch begleitet. Seine Hilfsbereitschaft sowie die Bereitstellung aller Vegetationsaufnahmen weiß ich sehr zu schätzen. Diese Daten waren die Grundlage für die Auswertung der Zusammenhänge zwischen biologischen Merkmalen (traits) und Grünlandmanagement. Kirsten Mitlacher führte die Vegetationsaufnahmen im Jahr 2000 durch, auf denen ein Großteil dieser Auswertungen beruhen. Die Bracheversuche werden vom Ministerium für Ernährung und ländlichen Raum in Baden-Württemberg finanziert. Das Ministerium leistet die Unterhaltung der Flächen und die Durchführung des Grünlandmanagements.

Bei Prof. Achim Poetke und seiner Arbeitsgruppe möchte ich mich herzlich für wegweisende Diskussionen über das Simulations-Modell bedanken. Weiterhin war der Kurs „Modellierung und Simulation für Ökologie und Artenschutz“ in Pesina hervorragend. Besonderer Dank gilt Martin Hinsch, der mir große Hilfe bei der Programmierung von PASTUREPOP leistete und geduldig alle aufkommenden Fragen diskutierte.

Der Arbeitsgruppe in Marburg, insbesondere Christina Mengel, sowie der Arbeitsgruppe in Regensburg möchte ich herzlich danken für die schöne gemeinsame Zeit. Mein größter Dank gilt Oliver Tackenberg für die thematische, praktische und freundschaftliche Begleitung während der Promotion. Die Datenbanken, die ich zur Analyse heranzog, basieren zu großen Teilen auf seiner Vorarbeit. Danke für die regelmäßigen Diskussionen und für die hilfreichen Kommentare zu den Manuskripten der Arbeit. Beim Aufbau der Exclosures auf der Wachholderheide (Müritzhof) stand er tatkräftig zu Seite zusammen mit Matthias Jäger und Markus Kleinschmidt. Tanja Reinhold und Sarah Wanning waren eine große Hilfe bei der Durchführung des Keimversuches im Herbst 2001.