

Impact of land-use practices on phytodiversity of mesic grasslands in a sub-mountainous region (Western Germany)

Dissertation zur Erlangung des Doktorgrades

(Dr. rer. nat.)

der Naturwissenschaftlichen Fachbereiche

der Justus-Liebig Universität Gießen

durchgeführt am

Institut für Landschaftsökologie und Ressourcenmanagement

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Gießen 2006

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The doctoral thesis „**Impact of land-use practices on phytodiversity of mesic grasslands in a sub-mountainous region (Western Germany)**” is based on the following three papers:

I. Wellstein, C., Otte, A. & Waldhardt, R.: Impact of site and management on the diversity of Central European mesic grassland. *Agriculture, Ecosystems & Environment* – *accepted*.

II. Wellstein, C., Otte, A. & Waldhardt, R.: Seed bank diversity in mesic grasslands and their relation to vegetation, management and site conditions. *Journal of Vegetation Science* – *accepted*.

III. Wellstein, C., Otte, A. & Waldhardt, R.: The population structure of three perennial grassland species (*Pimpinella saxifraga* L., *Leontodon autumnalis* L., *Sanguisorba officinalis* L.) in relation to management and habitat conditions. *Applied Vegetation Science* – *submitted*.

In paper **I**, I had the main responsibility for design, field work, data analysis and writing. The co-authors contributed valuable ideas and suggestions for this study.

In paper **II** and **III**, I had the main responsibility for design, field work, data analysis and performed the writing, while the co-authors contributed valuable comments.

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1 General Introduction

1.1 Background

For centuries, semi-natural grasslands have been created and maintained by human land use in Central Europe (Slicher van Bath, 1963). Due to their plant species richness they are highly relevant for the maintenance of biodiversity at multiple spatial scales. Generally, low productivity and recurrent disturbance by mowing or grazing are a prerequisite of high species diversity, while simultaneously hampering competitive exclusion and allowing for coexistence of many plant species (Huston 1994; Grime 2001). At the habitat scale, it has been proved that increased productivity by fertiliser application as well as abandonment or enhancement of disturbance frequency by mowing or grazing lead to changes in floristic composition and finally to a loss in species-richness (e.g. Burel et al. 1998; Korneck et al. 1998; Mac Donald et al. 2000). In Central Europe grasslands declined strongly in number and size over the five last decades due to abandonment of marginal agricultural areas, melioration and subsequent arable use. The remaining grassland areas often underwent intensification of land-use such as fertilisation by mineral fertiliser or manure, drainage or frequent mowing (e.g. Burel et al. 1998; Korneck et al. 1998; Mac Donald et al. 2000). Consequently, many types of unimproved semi-natural grasslands that were common several decades ago have become extinct or fragmented. Besides the particularly endangered wet meadows and dry calcareous grasslands, the formerly widespread mesic grasslands of the order *Arrhenatheretalia* (Tüxen 1931) are also currently in decline (Burel et al. 1998; Poschlod & Schumacher 1998; Mac Donald et al. 2000). This development has led to the inclusion of this habitat type in the European Fauna-Flora-Habitat Directive of the European Union (92/43/EEC, European Union 1992; Ssymank et al. 1998).

Particularly low-land grasslands were threatened by land use intensifications. In contrast, marginal regions, mainly within mountainous areas, are less agriculturally favourable. Such regions are traditionally associated with low-intensity management, and grassland habitats still predominate the agricultural landscape (e.g. Cousins & Eriksson 2002; Vandvik & Birks 2002; SRU 2004). Furthermore, according to OECD (2004), the common agricultural policy (CAP) reform is expected to ensure the maintenance of grassland areas. Due to these preconditions, such regions offer unparalleled opportunities to study different management regimes amongst other determinants influencing phytodiversity in mesic grasslands. The Lahn-Dill Highlands of central Hesse, Germany, are a typical example of marginal rural

landscapes: these are characterised by relatively unfavourable abiotic conditions for cultivation, such as cool climate and shallow soils (Frede & Bach 1999). Furthermore, unfavourable structural conditions for agriculture comprise small-scale part time farming along with alternative incomes in the vicinity. Since the 1950s, the Lahn-Dill Highlands have been subject to major agricultural land-cover changes, resulting in a decline in arable land and an increase in grassland and fallow land (Waldhardt & Otte 2003; Hietel et al. 2005, in press; Reger et al. accepted). In many places, non-intense grassland use has successively replaced the traditional, extremely small-parcelled crop production and crop/grassland rotation. There are different current grassland management regimes in the study area which provide strong differences in disturbance impact. The management regimes range from hay meadows with only one or two cuts per year to pastures grazed from May to September and silage meadows mown three times a year.

Management has a considerable influence on almost all aspects of grassland dynamics (Lennartson & Oostermeijer 2001). Hence, diverse management schemes can differently affect the dynamics and composition of plant communities and the dynamics of individual plant species. Species response to management may not only be manifested as presence/absence, but also in population demography, the alternations of which may anticipate possible floristic changes. Different cutting dates and frequencies may have a diversifying impact on vegetation (e.g. Kirkham & Tallowin 1995; Zechmeister et al. 2003) through differences in species' regenerative abilities. Grazing animals affect vegetation in several different ways: through direct biomass consumption, selective grazing, trampling, urination, defecation, and by acting as dispersal agents (Olf & Ritchie 1998). Consequently, there is a need to assess the suitability of the alternative management options in maintaining grassland communities (Bühler & Schmid 2001; Hegland et al. 2001; Colling et al. 2002). This is particularly true for mesic grasslands, for which knowledge about the quantitative importance of recent and historical management practices in relation to other determinants of plant species richness is scarce. In this context, the analysis of specific effects of management practices and site conditions on phytodiversity at the habitat scale is a challenge for scientific research.

Ecologically, mesic grasslands are characterised by a modest productivity and moderate variability in soil water potential. This leads to a relatively high diversity in species composition: The moderate range in productivity allows nutrient-demanding species as well as species depending on nutrient poor habitats. Besides species requiring moderate soil moisture, species that are adapted to alternations in soil moisture as well as those adapted to

relatively dry conditions can be found in these grasslands. Hence, mesic grasslands meet the habitat requirements both of competitive species and of stress strategists.

Phytodiversity is defined here as the share of biodiversity that is constituted by plants (cf. Noss 1990). In the thesis at hand the impact of management and site conditions on three different components of phytodiversity is studied at the habitat scale: the aboveground vegetation, the soil seed bank and the population biology of selected plant species' populations.

In the following paragraphs, these three components and their reliance on the respective determinants are introduced.

The impact of management and site conditions on aboveground vegetation

In traditional European phytosociology, management has been regarded as one of the most important factors differentiating vegetation types in mesic grasslands. Grazed (Cynosurion) and mown (Arrhenatherion) grasslands are usually separated at the high syntaxonomic level of the "alliance" (e.g. Dierschke 1994; Rodwell 1998). In addition to this expectation, the assemblage of plant species in seminatural grasslands is related to abiotic factors such as soil and topography (e.g. Cousins & Eriksson 2002; Sebastia 2004). In general, site fertility is regarded as a crucial factor for phytodiversity (e.g. Grime 1979). Furthermore, the age, site history, and traditional management practices that may have ceased long ago are also influencing factors (e.g. Partel & Zobel 1999; Cousins & Eriksson 2002; Waldhardt & Otte 2003; Sebastia 2004; Maurer et al. 2006). Several studies identified either environmental conditions (e.g. Vandvik & Birks 2002) or current management practices (e.g. Austrheim et al. 1999) to be more relevant for the explanation of floristic variance in grasslands. Moreover, species richness and composition of grassland vegetation depends on the pool of available species (Partel et al. 1996; Zobel et al. 1998; Partel & Zobel 1999).

However, knowledge is scarce about the quantitative importance of recent and historical management practices in mesic grasslands in relation to other determinants of plant species richness and floristic composition, the two major measures of phytodiversity. Such information is of particular relevance for the development of recommendations for future land use with respect to grassland diversity.

Significance of grassland soil seed banks

Soil seed banks are a source for re-establishment of species which are lost from the aboveground vegetation. Hence, maintenance and restoration of species-rich grasslands will

also depend on the soil seed bank (Grubb 1977; Fenner & Thompson 2005). However, Thompson et al. (1997) found that the investigation of seed banks has concentrated on productive agricultural habitats such as fertile grasslands. Relatively little is known about the seed bank communities and the respective ecology of species occurring in less productive semi-natural grasslands (Thompson et al. 1997: 21). For some grassland species such as *Trifolium repens* and *Agrostis capillaris*, which are common in mesic grasslands, there are clear indications for the presence of a persistent seed bank, but many grassland species lack a persistent seed bank (Rice 1989; Thompson et al. 1997; Bekker et al. 1998b, Bekker et al. 2000). However, it remains unclear to what degree the soil seed bank may contribute to the maintenance and restoration of species-rich mesic grasslands.

Since changes in land-use and management practices alter disturbance regimes (e.g. Gibson et al. 2005) they can have very distinct impacts on the seed bank and the established vegetation (Bekker et al. 1997; Smith et al. 2002). Theory predicts a close relationship between the degree of disturbance in a habitat and the percentage of species with long-term persistent seed banks (Thompson et al. 1998 (p.168); Grime 2001; Hölzel & Otte 2004). Despite this, few empirical studies of soil seed banks investigate the impact of different types of current management regimes.

Response of plant populations to management and site conditions

From a conservation perspective, it is necessary to develop criteria in order to make priorities for choosing appropriate management regimes that allow for high species diversity. The performance of viable (i.e. growing or stable) populations is one important criterion for selecting management regimes, since the dispersal capacity of many grassland species is limited in space and time. Thus, the possibility of species enrichment is restricted in floristically impoverished sites (e.g. Bakker et al. 1996; Donath et al. 2003). In semi-natural grasslands, perennial species are representative for a major part of the plant species in the community, since some 90% of the species are relatively long-lived perennials (Lindborg et al., 2005). Due to the differences in species traits such as disturbance tolerance and nutrient requirements, there may be a species-specific impact of the determinants management regime and site conditions. The evaluation of population stage structure has proved to be a useful method to describe the demographic viability of populations in cultural landscapes in relation to management (Bühler & Schmid 2001; Lennartsson & Oostermeijer 2001), management and site conditions (Oostermeijer et al. 1994; Colling et al. 2002; Bissels et al. 2004) or land

use change (Lindborg et al. 2005). Furthermore, populations have been evaluated in their natural habitats in landscapes dominated by natural disturbance regimes (García et al. 2002).

Thus, the objectives of this thesis are:

- I. To evaluate the relative impact of current and past management and site conditions - such as edaphic parameters and topography - on species richness and species composition of mesic grasslands.
- II. To assess the relative impact of management on the soil seed bank diversity, and to assess the capability of the seed bank to contribute to the maintenance and restoration of species-rich grasslands.
- III. To evaluate the population structure of three perennial grassland species (*Pimpinella saxifraga* L., *Leontodon autumnalis* L., *Sanguisorba officinalis* L.) in relation to management and site conditions such as edaphic parameters and light supply.

1.2 Objectives

The main objective of this study is to assess the impact of different management regimes on phytodiversity of mesic grasslands in the context of other important determinants. Three components of phytodiversity are investigated: the aboveground plant species richness and floristic composition, the seed bank plant species richness and floristic composition, and the population structure of three model species.

At first, the study is based on an evaluation of the vegetation composition and species richness of the established grassland vegetation and on the identification and assessment of their determinants (chapter 4). Due to the heterogeneity of the overall study region, there is a high variability of site conditions related to edaphic parameters, topography and the history of land use. To understand patterns of phytodiversity in the grassland stands, the relative importance of current and past management and site conditions such as edaphic parameters and topography was analysed in a comparative study.

If species are lost from the aboveground vegetation, the soil seed bank may offer a source for re-establishment. Knowledge on seed longevity is essential to assess the role of persistent soil seed banks in maintenance and restoration of sites (Bekker et al. 1997; Thompson et al. 1997; Hölzel & Otte 2004). Therefore we studied the species richness and composition of grassland soil seed banks, assessed the longevity of all present plant species and evaluated the impact of the different management regimes (chapter 5).

Knowledge about the effects of different types of grassland management on population viability and persistence of grassland species is of high importance. However, most of the recent studies investigated only single species (e.g. Bakker et al. 1980; Bissels et al. 2004; Gibson et al. 2005). In this study (chapter 6), the population stage structure of the model species *Pimpinella saxifraga* L., *Leontodon autumnalis* L. and *Sanguisorba officinalis* L. was analysed in relation to environmental conditions and under the different main management regimes which exist in the region.

In the following, the objectives of the thesis, as listed in the preceding chapter, are presented in detail. In chapter 7, the results of the individual studies (chapters 4-6) are summarised and discussed in a general discussion.

Relative impact of site conditions and management on grassland vegetation (Chapter 4)

This study deals with objective I, as it evaluates the relative impact of current and past management and site conditions such as edaphic parameters and topography on species richness and species composition of mesic grasslands of the order *Arrhenatheretalia* (Tüxen 1931) using two approaches. First, we compared vegetation types with respect to floristic composition, species richness, site conditions, grassland age as well as management. Secondly, we quantified the impact of these determinants on floristic composition of grasslands.

Seed bank diversity (Chapter 5)

The second study treats objective II, as it assesses the relative impact of management on the soil seed bank diversity, and the capability of the seed bank to contribute to the maintenance and restoration of species-rich grasslands. The main objectives were to analyse the floristic composition and size of the seed bank and to relate these to aboveground vegetation, site conditions and management. An additional goal was to test the effects of management regimes on functional aspects of the seed bank, such as seed mass, C-S-R strategy and seed longevity.

Population structure of *Pimpinella saxifraga*, *Leontodon autumnalis*, *Sanguisorba officinalis* (Chapter 6)

The study addressing objective III evaluates the population structure of three perennial grassland species (*Pimpinella saxifraga* L., *Leontodon autumnalis* L., *Sanguisorba officinalis*

L.) in relation to management, site conditions (nutrient availability, soil moisture, pH and light supply), vegetation structure and species composition.

The evaluation of management regimes is of high relevance for a successful maintenance of species-rich grassland communities. In this context the viability of model species populations may serve as a particularly useful indicator. We studied the stage structure in 16 populations of each of the perennial species *Pimpinella saxifraga*, *Leontodon autumnalis*, and *Sanguisorba officinalis* with respect to vegetation, site conditions and management. The main objective was to evaluate management options for the sustainable conservation of populations of these species in particular and species-rich grasslands in general. The results also provide useful information about how different management regimes affect populations of species differing in C-S-R strategy, clonal growth and requirements on edaphic conditions.

In chapter 7 the most important results of chapters 4, 5 and 6 are summarised and their significance for land-use practices is discussed.

2 Study area

The sub-mountainous Lahn-Dill Highlands (LDH) is located in Central Western Germany in the state of Hesse. The area covers about 900 km² and forms the eastern descent of the Rhenish Uplands. The strong geomorphologic heterogeneity of the region is accounted for by structuring the LDH in eleven geographic subunits (Meynen & Schmithüsen 1957; Klausning 1988). Nearly all of these were considered in the field studies by randomly selecting grassland sites spread over the whole study area (Fig.1). The ridges in the west-southeast region of the study area reach an altitude of 600 m a.s.l. (Schelde Forest, Hörre). Basins with low mounds at 200 up to 400 m a.s.l. are predominant in the northern and eastern part of the area (e.g. Niederweidbach Basin, Damshausen Mounds, Salzboede Valley). Almost in the centre of the area the planar Bottenhorn Uplands rise up to 500 m a.s.l. The subunits are mainly structured by geomorphology, but studies have shown that they also differ with regard to recent land cover and land-use history (Reger et al. accepted). Predominant soil types are moderately acidic Cambisols and Luvisols with possible gleysation in the valley floors; Regosols are limited to hilltop positions (Harrach 1998; Szibalski 2000).

The subatlantic climate of the LDH is characterised by a relatively cool and wet climate typical of sub-mountainous regions. Mean annual temperature and mean annual precipitation show a gradient from 6°C and 1100 mm in the raised western part to 7.5-8°C and 700mm in the eastern basin (Knoch 1950; HELELL 1981). However, the climate is largely modified by the local topography. In conjunction with the edaphic conditions, the wet climate results in a high variability of the soil-water potential.

Since the 1950s, the Lahn-Dill Highlands have been subject to major agricultural land-cover changes, resulting mainly in a decline in arable land and an increase in grassland and fallow land (Kohl 1978; Hietel et al. 2004, 2005, in press; Reger et al. accepted). In many places, larger-scaled low-intensity grassland management schemes have replaced the traditional, extremely small-parcelled crop production and crop/grassland rotation. The agricultural land of the LDH, which currently covers about 31% of the entire area, is dominated by grasslands; these cover more than half of the agricultural land area (Reger et al. accepted). Generally, the study region is characterised by a predominance of low-intensity farming, which has its origins in disadvantageous natural site conditions and the political and social history of the region (Nowak 1988, 1992). Iron mining had been the main industry from the Middle Ages to the early 20th Century, whereas agriculture in this region was traditionally based on small-scale farming and predominantly provided only sideline incomes (Hietel et al. 2005). Hence,

the study area is a typical example of marginal landscapes. Since 1976 the entire area has been included in the support scheme for less-favoured areas (EC Regulation No75/268). Typically, a large part of the landscape is managed by part-time farmers, who adhere to traditional agricultural practices (Hietel et al. 2005). The grasslands are partly managed according to EU-based agro-environmental schemes offered by the state of Hesse, focussing on grassland extensification (HMULF 2002). The adoption of agro-environmental schemes ensures a late first mowing not before mid-June, a low input of fertiliser ($< 30 \text{ kg N ha}^{-1} \text{ year}^{-1}$) or even a ban on fertilising, and extensive grazing with not more than 1.5 life weight units ha^{-1} (LWU). The grasslands of the study area are mainly grazed with cattle, but also with horses and on a few sites by sheep. As in many other low mountainous regions of central Europe (cf. Gigon 1999) these grasslands are embedded in a small-patch mosaic of arable fields, grassland fields, and old fields with shrub succession (Simmering et al. 2006). The latter are mainly occupied by *Cytisus scoparius* (Simmering et al. 2001). Fields vary in size from less than 0.5 to 5 ha (Reger et al. accepted).

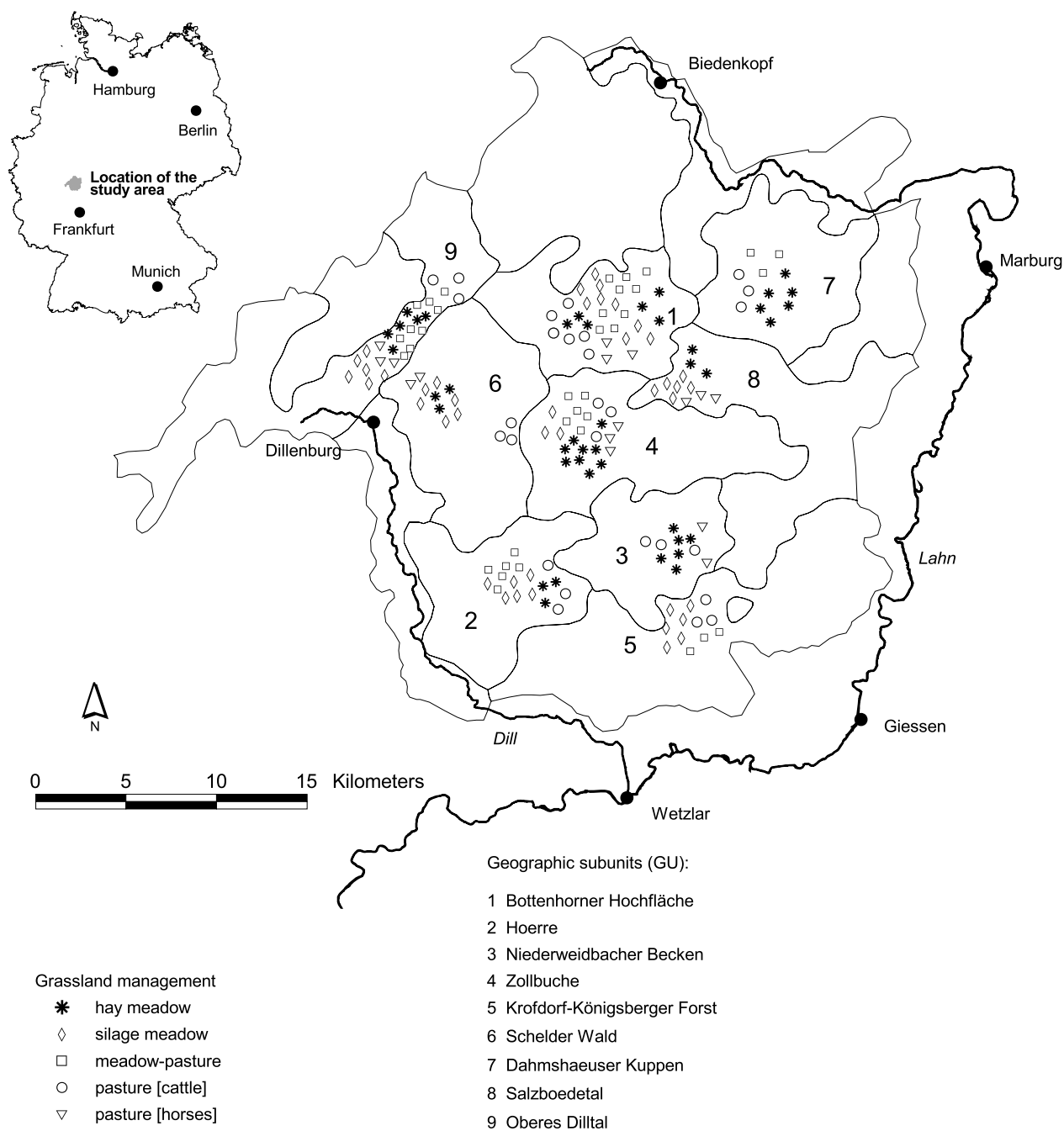


Fig. 1. Geographic situation of the study region Lahn-Dill Highlands and schematic distribution of the sampling sites, including information on management types, within geographic subunits.

Since our main objective was to evaluate the impact of current management regimes on phytodiversity, we selected only grasslands that are managed within the local farming system. We excluded grasslands that are not included in local farming systems, i.e. grasslands of nature reserves receiving nature protection measures for maintenance. Due to the heavy influence on phytodiversity we did not aim to compare grasslands over a large gradient in soil moisture. Therefore wet grasslands were excluded and only mesic grasslands with species compositions referring to the order *Arrhenatheretalia* (Tüxen 1931) were investigated with

respect to management regimes and site conditions. To account for the topographic and edaphic heterogeneity of the region, 56 grassland fields (size 0.3 – 3 ha) were randomly selected within nine geographic units of the entire Lahn-Dill Highlands (Fig.1). Across all geographic units, the fields were categorised into management types (i-v; see below). Management types were almost evenly spread within the entire Lahn-Dill Highlands (Fig. 1). The five main types are: (i) silage meadows with early and frequent mowing (three cuts per year) and little fertiliser input (up to 30 kg N ha⁻¹ year⁻¹), (ii) hay meadows with late mowing in mid-June and one or two cuts per year, (iii) meadow-pastures with late mowing and subsequent cattle grazing, (iv) pastures grazed by cattle from May to September and (v) pastures grazed by horses between June and September. For the study on aboveground vegetation (chapter 4), all 56 sampling sites covering the five management types were sampled (Fig.1). For the study on the soil seed bank (chapter 5) and the study on the population structure of selected species (chapter 6) a subset of these sites spread over the whole study region and covering the four main important management types (hay meadows, silage meadows, meadow pastures and pastures grazed by cattle) was studied.

More detailed information with focus on the different research topics can be found in the material and methods as well as the study area sections of the chapters 4, 5 and 6.

3 Methods

This chapter summarises the sampling and data analysis methods used in the thesis.

3.1 Sampling of aboveground vegetation and other habitat variables

Different methods for sampling of vegetation and other habitat variables were applied. To describe species composition in the evaluation of aboveground floristic composition (chapters 4 and 5), the abundance of all vascular plant species was estimated on 5 x 5 m plots using a modified Braun-Blanquet scale (van der Maarel 1979). For the investigation of the population structure of three selected grassland species (chapter 6), several indicators of vegetation structure were estimated on 1 x 1 m plots: Total vegetation cover, the coverage of mosses, plant litter, the percentage of bare soil surface and the mean vegetation height. Moreover, light measurements were undertaken in each plot in this study (chapter 6). Using a Line Quantum Sensor of one meter length (LI-COR: LI-191SA) light intensity penetrating to the ground was recorded. Photosynthetically active radiation (PAR, 400-700 nm) was measured simultaneously at ground level and in full light above the canopy. Light penetration was expressed as a percentage of the latter value.

3.2 Soil nutrient analyses and ascertaining of other environmental parameters

For the evaluation of soil chemical parameters in chapters 4, 5 and 6 soil samples were collected and soil nutrient analyses were conducted. Plant-available phosphorus and potassium were determined using the Calcium-Acetate-Lactate extraction method (CAL). Total nitrogen and total carbon were assessed using a CN analyser (FlashEA 1112, Thermoquest). The pH values of the fine soil were determined in CaCl₂. As there were no limestone formations in the sampling areas, the total carbon of the soil represents the organic carbon and was used to calculate the organic matter in the soil samples. All analyses were done according to Steubing and Fangmeier (1992). The topographic position of the plots within the landscape was categorised in four classes from the valley floor to the upper slope. Furthermore, slope inclination (°), elevation (m a.s.l) and aspect were recorded. Aspect, i.e. the compass-direction of a slope, was characterized by Northness (cosine of aspect) and Eastness (sine of aspect). Additionally, the site conditions were characterised by calculating

cover-weighted averages of the vascular plant indicator values for moisture and nutrients for each plot (Ellenberg et al. 1992).

3.3 Seed bank analyses

For the investigation of the soil seed banks of grasslands (see chapter 5), soil seed samples were collected at each site by random collection of 20 cores of 10 cm depth. We analysed seed banks using the seedling emergence method over 4½ months (Roberts 1981; Thompson et al. 1997). After removing vegetative plant material the soil samples were transferred to Styrofoam trays and exposed under warm greenhouse conditions (day 25°C / night 15°C). The trays were watered regularly. Germinating seedlings were identified and removed once every week. Unidentifiable seedlings were transplanted into pots and grown until identification was possible.

3.4 Assessment of population biological parameters

In chapter 6 the population stage structure of the perennial species *Pimpinella saxifraga*, *Leontodon autumnalis* and *Sanguisorba officinalis* was investigated. For this purpose 16 grassland sites were chosen for each species where the respective model species was present. In each of the 16 populations two 1 m² plots were randomly selected and the total number of individuals in each plot was counted. To classify the life stage classes for each species the following growth parameters were measured for each individual: existence of cotyledons (all species); leaf morphology of the leaf blades on the ground rosette: length and width (*L. autumnalis*); number of pinnules (*P. saxifraga* and *S. officinalis*) (see chapter 6, Table 2); existence of flowering stalks (all species).

3.5 Data analysis

Several methods of both exploratory data analysis (e.g. ordination) and inferential statistics were applied in the thesis. The inferential statistics cover methods that allow statistical hypotheses testing, such as regression analysis and analysis of variance (Jongman et al. 1995). Analysis of complex data sets like plant community data often combines these two approaches (Jongman et al. 1995).

The following methods of multivariate analysis of ecological data were conducted:

- Detrended Correspondence Analysis (DCA) was used to explore gradients in the floristic composition of vegetation samples (chapters 4, 5, 6).
- Partial Canonical Correspondence Analysis (CCA) performed a decomposition of variance and was used to isolate the effect of management and other important determinants on floristic composition (chapters 4, 5).
- Two-Way Indicator Species Analysis (TWINSpan) (Hill 1979) allowed a classification of vegetation types of the sampled grasslands by examining the main groupings in the data set and the assignment of sampling sites to the respective groups in chapter 4.
- Indicator Species Analysis (Dufrêne & Legendre 1997) was applied to identify significant indicators of vegetation types (chapter 4) and of seed banks of differently managed grasslands (chapter 5).

Furthermore the following statistical methods were used:

- Multiple regression analysis (GRM module in Statistica) was performed to assess the importance of management and environmental variables in grasslands for the population structure of selected species (chapter 6).
- Multivariate analysis of variance (MANOVA) and covariance (MANCOVA) were applied to test for overall effects of possible determinants on the dependent variable of interest (chapters 4, 6).
- Univariate analysis of variance (ANOVA) and covariance (ANCOVA) were applied to test for differences between two groups of interest in normally distributed variables and variables that could be adequately transformed (e.g. the numbers of seeds in chapter 5). To analyse significant differences between several groups in detail, *post hoc* tests were used (e.g. Tukey's Honest-Significance test (HSD)) (chapters 4, 5, 6).
- In all cases of correlative analysis the non-parametric Spearman Rank Correlation was used (chapters 4, 6).

More detailed information with focus on the different research topics can be found in the material and methods sections of the chapters 4, 5, and 6.

4 Impact of site and management on the diversity of Central European mesic grassland

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Agriculture, Ecosystems and Environment: accepted

4.1 Abstract

The main objective was to quantify the relative impact of current management types on plant species-richness and composition of mesic grasslands with regard to other important determinants such as topography, soil chemical parameters and grassland age. The grasslands were (i) differentiated into management types and vegetation types, (ii) these types were tested for differences in site conditions and species-richness, and (iii) the relative impact of management, site conditions, grassland age and regional scale geomorphology on floristic composition was quantified. TWINSpan classification of the vegetation separated nutrient-poor from nutrient-rich sites. Results of ANCOVA revealed that vegetation types indicating high nutrient levels showed significantly higher contents of plant available phosphorous and younger grassland age. In partial CCA analyses, the geomorphology accounted for almost one third of explained variance. The current management had a relatively low explanatory value. Soil chemical variables and topography, in contrast, explained together almost twice as much variation in floristic composition.

Keywords:

Land use, Marginal landscape, Soil fertility, TWINSpan, Indicator Species Analysis, ANCOVA, Partial CCA

4.2 Introduction

Plant species-richness and floristic composition in grasslands are shaped not only by current site conditions, species pool and management but also by age, site history, and traditional ancient management practices that may have ceased long ago (e.g., Pärtel et al., 1996; Cousins and Eriksson, 2002; Waldhardt and Otte, 2003; Sebastiá, 2004). Phytodiversity over a broad range of environments has been shown to be determined mainly by the overall productivity and the land-use history of the study systems (e.g., Milchunas and Lauenroth, 1993). Studies on the relative importance of management and environmental factors on floristic composition in grasslands have shown either environmental conditions (e.g., Vandvik and Birks, 2002) or current management practices (e.g., Austrheim et al., 1999) to explain relatively more of the floristic variance. The assemblage of plant species in seminatural grasslands is often related to abiotic factors such as soil and topography (e.g., Cousins and Eriksson, 2002; Sebastiá, 2004). Soil fertility has been shown to be an important factor for phytodiversity (Janssens et al., 1998) and increasing amounts of fertilisers in agricultural practice are generally accepted as the main cause of the decline in grassland phytodiversity (e.g. Gough and Marrs, 1990; Smith, 1993; Korneck et al., 1998; Zechmeister et al., 2003). Grazing animals affect vegetation in several different ways, through direct biomass consumption, selective grazing, trampling, urination, defecation, and by acting as dispersal agents (Olf and Ritchie, 1998). Moreover, species-richness and species composition of grassland vegetation depend on the available species pool (Pärtel et al., 1996; Zobel et al., 1998).

Many grassland studies focus on the phytodiversity of highly endangered communities. In central Europe, these are unimproved semi-natural grasslands like the particularly endangered wet meadows and dry calcareous grasslands. But due to agricultural intensification and abandonment, the overall area of the formerly widespread mesophilous grassland of low mountainous regions is currently also in decline (Burel et al., 1998; Mac Donald et al., 2000). This has led to the inclusion of this habitat type in the European Fauna-Flora-Habitat Directive of the European Union (92/43/EEC, European Union, 1992; Ssymank et al., 1998). Given this background, the aim of this study was to assess and quantify the impact of former and current land use practices, site conditions, and regional scale geomorphology on the grassland phytodiversity of a marginal region, which is characterised by extremely small-scaled fields and highly diverse management schemes. Grassland management practices in the area provide strong differences in disturbance impact ranging from low-intensity pasturing without fertiliser application to mowing three times a year for fodder production (silage). The

specific questions addressed in this paper are:

1. How are grassland vegetation types differentiated in terms of floristic composition, species-richness and site conditions?
2. How important is current management in relation to other factors such as abiotic site conditions, grassland age and regional scale geomorphology for the floristic composition of grassland stands?

4.3 Material and Methods

Study region and sampling

The entire study region (Lahn-Dill-Highlands, Germany) has been included in the support scheme for less-favoured areas since 1976 (EC Regulation No75/268). Typically, a large part of the landscape is managed by part-time farmers, who adhere to traditional agricultural practices (Hietel et al., 2005). Since the 1950s, the Lahn-Dill Highlands have been subject to major agricultural land-cover changes, resulting mainly in a decline in arable land and an increase in grassland and fallow land (Hietel et al., 2005). In many places, extensive grassland use has replaced the traditional, extremely small-parcelled crop production and crop/grassland rotation. In the study region, a large part of the grasslands is managed according to EU-based agri-environmental schemes, focussing on grassland extensification. The adoption of the agri-environmental schemes ensures a late first mowing not before mid of June, a low input of fertiliser ($< 30 \text{ kg N ha}^{-1} \text{ year}^{-1}$) or even the ban of fertilising, and low-intensity pasturing with < 1.5 life weight units ha^{-1} (LWU). Pasturing on grasslands of the study area is done mainly with cattle, also with horses and few sites are grazed by sheep.

Predominant soil types are moderately acidic Cambisols and Luvisols with possible gleysation in the valley floors; Regosols are limited to hilltop positions. The climatic conditions in the region are relatively unfavourable, indicated by a mean annual temperature of 6 to 8°C and average annual precipitation ranging from 650 to 1100 mm. In conjunction with the edaphic conditions, the wet climate results in a high variability of the soil-water potential.

The Lahn-Dill Highlands are divided in different geomorphological subunits (GU) (Klausing, 1988) (see Table 1). The subunits are mainly structured by geomorphology, but they differ also with regard to recent land cover and land-use history (Hietel et al., 2005). The heterogeneity across these subunits may have had an effect on the development of different species pools in grassland vegetation, which may be due to a combined effect of contrasting large scale differences in soil properties, climate and land-use history.

To account for the topographical and edaphical heterogeneity of the region, 56 grassland fields (size 0.3 – 3 ha) were randomly selected within nine GU of the entire Lahn-Dill Highlands. Across all GUs, the fields were then categorised into management types (i-v; see below). Management types were almost evenly spread within the entire Lahn-Dill-Highlands (Table 1). To account for the sometimes high internal variability of vegetation within stands, three plots (5 m x 5 m) were randomly placed within each of the 56 fields and these were used as basic sampling unit. Geographical coordinates of plots were recorded using a Garmin GPS. To avoid edge effects, a minimum distance of 10m to the border of the fields was kept. The composition of vascular plant species was recorded within plots between May and September in 2003 and 2004. Species abundance was estimated on a modified Braun-Blanquet-scale (with cover degree 2 subdivided into 2a => 5 - 15% and 2b => 15 - 25%). The nomenclature of the vascular plant species followed Wisskirchen and Haeupler (1998).

Table 1. Distribution of plots with different management types within geomorphological subunits (GU) of the Lahn-Dill Highlands (Klausning, 1988) Management types: H, hay grassland; S, silage grassland; M, meadow; P[c], cattle grazed pasture; P[h], horse grazed pasture.

Geomorphological subunit (GU)	GU ID	Management types of plots (n=166)					Elevation a.s.l. [m]
		H	S	M	P[c]	P[h]	
Bottenhorn Uplands	1	6	9	9	6	3	470-530
Hoerre	2	3	6	6	3	0	330-410
Niederweidbach Basin	3	6	0	0	3	2	280-315
Zollbuche	4	9	3	6	3	3	340-490
Krofdorf-Königsberg Forest	5	0	6	3	3	0	320-390
Schelde Forest	6	3	6	0	3	2	350-420
Damhausen Mounds	7	6	0	3	3	0	280-340
Salzboede Valley	8	3	6	0	3	3	245-290
Upper Dill Valley	9	6	6	9	3	3	270-360

The current grassland management was classified based on information obtained from personal interviews with farmers conducted prior to the study in 2003. Additional background information was gained from the specific provisions of the agri-environmental schemes mentioned above. This combined data provided information on mowing intensity (frequency and time), grazing intensity (duration, number and kind of grazing individuals per area), the amount and type of fertiliser used. Five management practices were differentiated: (i) silage grassland with early and frequent mowing (three cuts per year) and little fertiliser input (up to 30 kg N ha⁻¹ year⁻¹), (ii) hay grassland with late mowing in mid-June and one or two cuts per year, (iii) meadows with late mowing and subsequent cattle grazing, (iv) cattle grazed pasture

(grazed from May to September) and (v) horse grazed pasture (grazed between June and September). The four last practices were characterised by the lack of fertiliser input. There was no aftermath grazing in case of management practices (i) and (ii).

Information on the consistency of management type was also derived from the personal interviews with farmers. All selected fields were managed accordingly for the last 25 years, i.e. since 1979. However, as major land-cover changes occurred during the first decades after World War II, and memories of farmers were incomplete for this period, the duration of grassland use was checked for each field by visual interpretation of black-and-white aerial photographs available from the years 1953, 1962, 1967, 1973, and 1979. The age (A) of grassland fields was quantified according to the determined land-cover at each of these dates. The probability that fields used as grassland in 1953 had also been traditionally used as grassland in prior times appeared to be very high. Thus, fields with an age of 50 years (grassland use in all photographs) were presumably ancient grasslands.

In autumn 2003, composite soil samples from each of the 168 plots were obtained by pooling 20 randomly sampled cores (3 cm diameter, 10 cm depth). Total nitrogen (N_t) and total carbon (C_t) levels were determined using a CN-analyser (FlashEA 1112, Thermoquest). Levels of plant available phosphorus (P_{CAL}) and potassium (K_{CAL}) were estimated by calcium-acetate-lactate (CAL) extraction method. PH-values of the fine soil were determined in $CaCl_2$. As there were no limestone formations in the sampling areas, the total carbon of the soil represented the organic carbon and was used to calculate the organic matter in the soil samples.

The relative topographic position of the plots within the landscape was categorised in four classes from the valley floor to the upper slope. Slope inclination ($^\circ$), elevation (m a.s.l) and aspect were recorded as well. Aspect, i.e. the compass-direction of a slope, was characterised by Northness (cosine of aspect) and Eastness (sine of aspect). Additionally, the site conditions were characterised by calculating cover-weighted averages of the vascular plants indicator values for moisture and nutrients (Ellenberg et al., 1992) for each plot.

Data analysis/Statistics

Prior to all analyses of this study, two data modifications were performed. First, according to an Outlier Analysis (included in the software package PC-ORD 4) two plots were omitted as multivariate outliers (McCune and Grace, 2002), resulting in a total of 166 plots for further analyses. Second, seasonal (first or second crop) and interannual (year 2003 or 2004) variation of the vegetation samples was tested by the method of Indicator Species Analysis

with ‘season’ and ‘year’ as grouping factors (Dufrêne and Legendre, 1997; McCune and Grace, 2002). To calculate the indicator value of a species, its mean abundance in one group compared with its mean abundance in all groups was multiplied by its relative frequency in the samples of that group. The obtained values were tested for significance by Monte Carlo statistics with 1000 random permutations (McCune and Mefford, 1999). ‘Year’ showed no significant differences of species occurrences. ‘Season’ resulted in significant differences of abundance and frequency of six species with an early phenology which were omitted from the data set. Correlation between species richness with and without these omitted species across all plots was 0.97 (Spearman’s r). The omitted species were not specific for particular management regimes, thus, exclusion of these species caused no bias in the comparison between management types. Adjusting the data for season-specific species resulted in reduction of species number by two species per plot on average.

Classification of vegetation types was achieved by a Two-Way Indicator Species Analysis (TWINSpan) (Hill, 1979). The TWINSpan run resulted in an ordered table that allowed examining the main groupings in the data set and the assignment of sampling sites to the respective clusters. Subsequently, Indicator Species Analysis (see above) was used to detect species characterising the groups (clusters) generated by TWINSpan. Numerical analyses were performed using the software package PC-ORD 4 (McCune and Mefford, 1999).

Multivariate Analysis of Covariance (MANCOVA) was carried out (using Wilks Lambda as test statistic) to test whether species-richness and site conditions differed among (i) the four TWINSpan clusters and (ii) the five management types. Significant differences between groups for particular dependent variables were assessed using subsequent one-way ANCOVAs with either (i) management type or (ii) cluster membership as fixed effect. In case of significant univariate effects, means were compared using Tukey Honest-Significance test (HSD) for unequal sample sizes.

To account for the effects of spatial autocorrelation in our data, the geographical coordinates of the plots were used to construct nine spatial variables, i.e. the terms of a cubic trend-surface polynomial (Borcard et al., 1992):

$$f(x, y) = b_1x + b_2y + b_3x^2 + b_4xy + b_5y^2 + b_6x^3 + b_7x^2y + b_8xy^2 + b_9y^3 \quad (1)$$

These were included as covariables in MANCOVA to partial out the spatial component of variation in analyses of variance. Multivariate and univariate ANCOVA and associated tests were carried out using STATISTICA 6.0 (Anon., 1998).

Prior to ordination analyses, species with less than three occurrences across all plots were excluded to reduce their influence on ordination results. Subjecting the species data set (166 relevés, 114 species) to a Detrended Correspondence Analysis (DCA) (McCune and Grace, 2002) revealed a gradient length on the first axis of 2.34 SD, which showed a modest unimodal response and thus the appropriateness of CCA (Ter Braak and Šmilauer, 1998).

Environmental variables (see paragraph ‘environmental variables’) for CCA were selected by the CANOCO procedure of forward selection (Palmer, 1993). Except for Eastness, all examined variables yielded significant contributions to data structure and were retained for CCA. To receive ecologically interpretable variance components, the explanatory variables were grouped into the following five sets: Management type (M; including five different management types) (see Table 1); geomorphological subunit (GU; including nine different subunits) (see Table 1); soil chemical parameters (S; including organic carbon, total nitrogen, pH value, and plant available P and K contents); topography (T; including elevation a.s.l., slope inclination, topographic position, and Northness); grassland age (A). Spatial autocorrelation of plots (SP) was controlled for in CCA by including again a covariable matrix containing the terms of the cubic trend surface polynomial (equation 1) following Borcard et al. (1992). To distinguish between the gross and net effects of these sets on floristic composition, gross effects were first quantified by performing a series of CCAs (controlled for SP) for each set of explanatory variables. To obtain the net effect of a given set of variables, additionally a series of partial CCAs were performed controlling for all other sets (Økland and Eilertsen, 1994). For all CCAs, significance was tested by permutation tests (1000 permutations). The ratio of a given canonical eigenvalue to the sum of all eigenvalues (total inertia) was used to estimate the proportion of explained variation. CCAs were performed using the program package CANOCO (Ter Braak and Šmilauer, 1998).

4.4 Results

The TWINSpan classification of vegetation types resulted in four ecologically meaningful clusters: Judging from floristic differences between the clusters (Table 2) the first division in TWINSpan apparently separated nutrient-rich (clusters I, II) from nutrient-poor (clusters III, IV) sites.

Table 2. Indicator species (after Dufrêne and Legendre, 1997) of TWINSPAN clusters I-IV. Significance obtained by Monte-Carlo-Permutation test is given at three levels: * $P \leq 0.05$, ** $P \leq 0.01$, *** $P \leq 0.001$, Ind. value, indicator value. Species with non significant or low indicator values (< 25) are not shown; (N) notifies species indicating nutrient-rich habitats (Ellenberg nutrient value > 7 ; Ellenberg et al., 1992).

Cluster I (n = 32)	Ind. value	Cluster II (n = 65)	Ind. value
<i>Lolium perenne</i> (N)	47.6 ***	<i>Trisetum flavescens</i>	51.3 ***
<i>Phleum pratense s. str.</i> (N)	46.8 ***	<i>Arrhenatherum elatius</i> (N)	46.6 ***
<i>Taraxacum officinale</i> agg. (N)	46.2 ***	<i>Dactylis glomerata</i> agg.	36.6 ***
<i>Leontodon autumnalis</i>	40.8 ***	<i>Trifolium pratense</i>	33.5 ***
<i>Trifolium repens</i>	30.8 **	<i>Galium album</i>	33.5 ***
<i>Plantago major s. l.</i>	29.3 ***	<i>Achillea millefolium</i>	30.1 **
		<i>Heracleum sphondylium</i> (N)	28.6 **
		<i>Leucanthemum vulgare</i>	26.2 **

Cluster III (n = 39)	Ind. value	Cluster IV (n = 30)	Ind. value
<i>Festuca rubra</i>	43.1 ***	<i>Sanguisorba officinalis</i>	59 ***
<i>Deschampsia cespitosa</i> agg.	36.8 ***	<i>Lathyrus pratensis</i>	35.1 ***
<i>Ranunculus acris</i>	31.8 ***	<i>Leontodon hispidus</i>	34.4 ***
<i>Potentilla erecta</i>	31.8 ***	<i>Agrostis capillaris</i>	31.4 **
		<i>Holcus lanatus</i>	29.2 *
		<i>Centaurea jacea s.l.</i>	28 ***

Table 3. Mean values and standard error of site and vegetation parameters for TWINSPAN-derived clusters of grassland samples. Asterisks denote the significance levels revealed by univariate ANCOVA (* $P \leq 0.05$; ** $P \leq 0.01$; *** $P \leq 0.001$) after significant one-way MANCOVA ($F_{30,435} = 5.667$, $P < 0.001$). Different letters indicate significant differences among clusters, according to a Tukey test (for unequal n).

	Cluster I (n = 32)	Cluster II (n = 65)	Cluster III (n = 39)	Cluster IV (n = 30)
Age of grasslands (years)***	38±1.4 ^a	41±1.0 ^a	49±1.3 ^b	50±1.5 ^b
Number of species*	19±1.0 ^a	23±0.7 ^b	25±0.9 ^b	27±1.0 ^b
Elevation a.s.l.*	351±6.7 ^b	376±4.7 ^c	432±6.1 ^d	324±6.9 ^a
Total nitrogen (%)***	0.40±0.019 ^a	0.40±0.014 ^a	0.52±0.018 ^b	0.46±0.020 ^{a,b}
Organic matter (%)*	6.8±0.35 ^a	7.1±0.25 ^a	9.3±0.32 ^b	7.8±0.36 ^a
pH value [CaCl ₂]**	5.12±0.075 ^b	5.14±0.052 ^b	4.54±0.068 ^a	4.90±0.077 ^b
Phosphorus [mg/100g]***	7.4±0.63 ^b	7.8±0.44 ^b	3.9±0.57 ^a	3.1±0.65 ^a
Potassium[mg/100g]*	24±1.9 ^c	16±1.4 ^b	10±1.8 ^{a,b}	7±2.0 ^a
Moisture value (MV)*	5.25±0.066 ^b	5.00±0.047 ^a	5.51±0.060 ^c	5.56±0.069 ^c
Nutrient value (NV)***	6.4±0.11 ^c	5.8±0.07 ^b	5.0±0.10 ^a	5.2±0.11 ^a

This was confirmed by the MANCOVA analyses. The comparison of the derived clusters by MANCOVA revealed significant differences in average site conditions and species-richness ($F_{30,453} = 5.667$, $P < 0.001$). Tukey tests (Table 3) showed that clusters I and II contained the more fertile sites indicated by the higher content of available phosphorus, potassium, and higher Ellenberg nutrient values. Younger grasslands belonged exclusively to these clusters. In contrast, clusters III and IV contained less productive sites indicated by significantly lower contents of available phosphorus and potassium, and lower Ellenberg nutrient values. However, sites of these clusters were characterised by a significantly higher Ellenberg moisture value. Coherences between these explanatory variables became obvious also by significant, moderate correlation (Spearman's r) between the age of the fields and the available phosphorus ($r = -0.536$), total nitrogen ($r = -0.593$) and organic matter ($r = -0.528$) across all plots. There was also significant but low correlation of species richness and the explanatory variables age ($r = 0.371$), phosphorus ($r = -0.284$) and nutrient value ($r = -0.394$). At the level of the second TWINSpan division, the current grassland management became apparent. Cluster I predominantly contained sites with rather intense use for silage and pasture (Fig. 1).

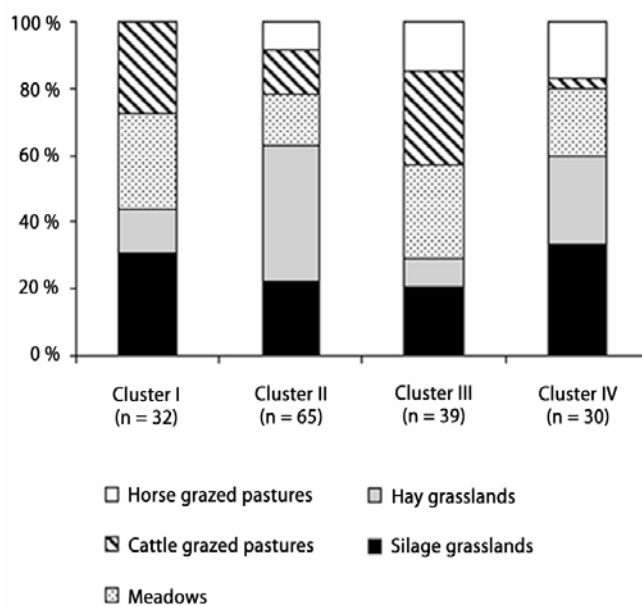


Figure 1. Percentage distribution of current management types of grassland samples within TWINSpan clusters, i.e. vegetation types.

Floristically, this was indicated by species preferring high nutrient levels and tolerating high levels of disturbance such as *Lolium perenne*, *Phleum pratense s. str.* and *Plantago major s. l.*, and ruderals such as *Taraxacum officinale* agg. (Table 2). Sites in this cluster contained significantly fewer species and were the youngest stands of all grasslands. Cluster II was dominated by hay grassland (Fig. 1) with species indicating nutrient-rich conditions such as *Arrhenatherum elatius* and *Heracleum sphondylium* (Table 2). Cluster III contained many pastures and meadows (Fig. 1). The impacts of grazing and relatively nutrient-poor and acidic site conditions were indicated by the dominance of species such as *Festuca rubra* and *Deschampsia caespitosa* agg.. This corresponded with low pH values and higher elevations of the stands (Table 3). Total nitrogen

and organic matter contents were also higher in the soils of these permanent grasslands. In contrast to cluster III, cluster IV predominantly contained stands with different mowing regimes and very few pastures (Fig. 1). Species characteristics of this cluster comprised indicators of base-rich and relatively nutrient-poor sites with an alternating moisture regime (Table 2).

In contrast to the differentiating results obtained by the comparison of vegetation types, grassland plots revealed only slight differences in site conditions and species-richness when compared with respect to their management type alone (MANCOVA $F_{40,559} = 2.7$, $P < 0.001$). Hay grasslands differed significantly from cattle grazed pastures in age and potassium content, and from meadows in their nitrogen and organic matter contents (Table 4). Species-richness differed significantly only between silage grasslands and meadows.

Table 4. Mean values and standard error of site and vegetation parameters for grassland samples of five different management types: H, hay grassland; S, silage grassland; M, meadow; P[c], cattle grazed pasture; P[h], horse grazed pasture. Asterisks denote the significance levels revealed by univariate ANCOVA (* $P \leq 0.05$; ** $P \leq 0.01$; *** $P \leq 0.001$) after significant one-way MANCOVA ($F_{40,559} = 2.700$, $P < 0.001$). Different letters indicate significant differences among management types, according to a Tukey test (for unequal n).

	H (n = 42)	S (n = 42)	M (n = 36)	P[c] (n = 30)	P[h] (n = 16)
Age of grasslands (years)*	41 ± 1.3 ^a	41 ± 1.3 ^a	46 ± 1.5 ^{a,b}	48 ± 1.5 ^b	46 ± 2.3 ^{a,b}
Number of species**	25 ± 0.9 ^{a,b}	22 ± 0.9 ^a	26 ± 1.0 ^b	23 ± 1.1 ^{a,b}	22 ± 1.4 ^{a,b}
Elevation a.s.l. **	355 ± 5.7 ^a	371 ± 5.7 ^{a,b}	398 ± 6.1 ^c	383 ± 6.7 ^{b,c}	367 ± 9.2 ^{a,b,c}
Total nitrogen (%)*	0.40 ± 0.017 ^a	0.45 ± 0.017 ^{a,b}	0.48 ± 0.018 ^b	0.44 ± 0.020 ^{a,b}	0.40 ± 0.027 ^{a,b}
Organic matter (%)**	7.0 ± 0.30 ^a	7.8 ± 0.30 ^{a,b}	8.6 ± 0.33 ^b	7.8 ± 0.36 ^{a,b}	7.1 ± 0.49 ^{a,b}
pH value [CaCl ₂] n.s.	4.97 ± 0.068	5.02 ± 0.068	4.87 ± 0.072	5.04 ± 0.080	4.79 ± 0.110
Phosphorus [mg/100g] n.s.	5.6 ± 0.58	6.5 ± 0.58	6.1 ± 0.63	6.8 ± 0.68	3.7 ± 0.94
Potassium [mg/100g]**	10 ± 1.7 ^a	15 ± 1.7 ^{a,b}	16 ± 1.9 ^{a,b}	20 ± 2.1 ^b	12 ± 2.8 ^{a,b}
Moisture value (MV)*	5.1 ± 0.06 ^a	5.3 ± 0.06 ^{a,b}	5.3 ± 0.07 ^{a,b}	5.3 ± 0.07 ^{a,b}	5.5 ± 0.10 ^b
Nutrient value (NV) n.s.	5.6 ± 0.11	5.9 ± 0.11	5.5 ± 0.12	5.6 ± 0.13	5.3 ± 0.17

Classification results for vegetation and management types confirmed the importance of site conditions for floristic composition and revealed a moderate impact of management. Taking all sets of variables into account as constraining variables in CCA and controlling for spatial autocorrelation, they explained 27.9% of total variation in floristic composition (Table 5). After controlling for the other sets, each set studied here still yielded a significant net effect on floristic composition in partial CCA. Comparing the net effects, the geomorphological

subunit (GU) explained almost one third (8.5%) of explained variance. The current management practice (M) had an explanatory value of 4.2%, which indicates its moderate role for the floristic variance. The net effects of site conditions, i.e. soil (S) and topography (T), in contrast, explained together almost twice as much variation in floristic composition (10.2%). Grassland age (A) explained only 1.8% of the variance.

Table 5. Results of selected CCA analyses adjusted for the spatial component (SP), isolating the effect of the age of sampled grasslands (A), geomorphological subunit (GU), management type (M), soil chemical parameters (S), and topography (T) as explanatory variables on the vegetation (n = 166). Expl. Var. = Explanatory variables; Covar. = Covariables; Eigenv. = Sum of all canonical eigenvalues – measure for explanatory power of the explanatory variables (total inertia = 2.333); % = percentage of explained variance; *F* = F-ratio for the test of significance of all canonical axes (test on the trace), *P* = corresponding probability value obtained by the Monte-Carlo-permutation test (1000 permutations).

Expl. Var.	Covar.	Eigenv.	%	<i>F</i>	<i>P</i>
M,S,T,A,GU	SP	0.651	27.9	2.576	0.001
SP	-	0.088	3.8	3.205	0.001
<i>Net effects</i>					
GU	S,T,A,M,SP	0.198	8.5	2.352	0.001
T	S,A,M,GU,SP	0.140	6.0	2.182	0.001
S	T,A,M,GU,SP	0.099	4.2	1.856	0.001
M	S,T,A,GU,SP	0.097	4.2	2.257	0.001
A	S,T,M,GU,SP	0.043	1.8	4.017	0.001
<i>Gross effects</i>					
GU	SP	0.235	10.1	2.416	0.001
T	SP	0.193	8.3	2.622	0.001
S	SP	0.144	6.2	2.297	0.001
M	SP	0.121	5.2	2.396	0.001
A	SP	0.056	2.4	4.408	0.001

4.5 Discussion

With respect to the impact of site conditions, differences between vegetation types of relatively nutrient-rich (clusters I and II) and nutrient-poor sites (clusters III and IV) were floristically well characterised by indicator species (Table 2). The results of Indicator Species Analysis were supported by ANCOVA results, which confirmed that plant-available phosphorus and potassium as well as the mean Ellenberg nutrient values were significantly higher in younger grassland sites (clusters I and II), in contrast to the species-rich long-term grasslands (clusters III and IV, Table 3). Correlation between organic matter and total nitrogen with grassland age were in line with other studies indicating self-mulching in long-term grasslands (e.g., Gough and Marrs; 1990).

Since most grassland species lack a long-term persistent seed bank (Thompson et al., 1997), their soil seed banks are rapidly depleted. Additionally, ploughing of grassland allotments will also deplete the soil seed bank of species with long-term persistent seeds (e.g., Bakker et al., 1991). Therefore, species of grassland communities may only re-establish in abandoned arable land by dispersal from elsewhere. Dispersal limitation is a constraint in intensively managed regions where grassland habitats are often fragmented and source populations may be far away from a site (Bischoff, 2002). Even under favourable conditions, with viable remnant populations of species in the vicinity of such sites as in the study area, dispersal is an uncertain and time-demanding process (e.g., Bischoff, 2002). It remains an open question as to what extent the lower species-richness of the nutrient-richer and younger sites can be attributed to enhanced competitive exclusion (resulting from the higher soil fertility levels), compared to factors that limit dispersal.

Relative impact of management types and site conditions

The degree of floristic variance that was explained by the current grassland management type in CCA was relatively low in the present study (4.2%; Table 5). In contrast, the geomorphological subunit (GU) of the sampled grasslands explained the highest amount of floristic variance. Even after adjustment for all other determinants (soil chemical parameters, topography, grassland age, management type, spatial component), GU retained remarkable explanatory power (8.5%), which can be interpreted as a strong influence of local species pools (Pärtel et al., 1996) on floristic composition of grassland relevés. On the other hand, when accounting for the effect of GU, spatial component and all other explanatory sets (management type, soil chemical parameters, topography, grassland age), each set dropped some percent in the amount of explained variance, but remained significant. The fact that only 27.9% of the total variance in floristic composition could be explained by these sets is not surprising (Lepš and Šmilauer, 2003), given the complexity of the natural communities studied. Another study in the treeline-ecotone of the Swiss Alps reported differences in species-richness between traditionally mown stands compared to sites grazed for up to 50 years by cattle (Fischer and Wipf, 2002). Aftermath and winter grazing has been shown to be important to maintaining the characteristic species composition of upland meadows in northern England (Smith & Rushton, 1994).

But why did the current management type prove to be only moderately important in our study? One possible explanation may be the low overall level of land-use intensity compared to other studies and the lack of any steep gradient in the intensity of current grassland

management. In contrast, Zechmeister et al. (2003) demonstrated the impact of land-use practices on species-richness along a strong gradient in land-use intensity with a range of fertilisation levels between 0 and 168 kg N ha⁻¹ year⁻¹. The total species-richness of these grasslands differed significantly in response to the level of fertiliser application (below or above 90 kg N ha⁻¹ year⁻¹) and in response to mowing frequency (range from two to four cuttings per year). Studies of modern grassland management often investigate the influence of the cutting regime together with the level of fertilisation because these are commonly connected in practice.

Conclusions for management practices

In accordance with other studies our analyses show that there is a wide variety of low-intensity management options to contribute to the maintenance of mesic grassland diversity in Europe (e.g., Cousins and Eriksson, 2002; Vandvik and Birks, 2002; Zechmeister et al., 2003; Pykälä, 2005). Even though they have been applied for the least 25 years, currently applied management types did not appear to cause severe constraints on current floristic composition and species-richness of the studied grassland sites. In particular, meadows with an intermediate disturbance impact on the plant biomass, the sward, and the topsoil may support higher species-richness. Differences in phytodiversity were only partly related to the variation of low-intensity management types in this study. Edaphic parameters, topography and regional scale geomorphology had a relatively higher impact on species composition. Our results also suggested that historical land use with fertiliser application on ex-arable fields caused a differentiation in the productivity of the stands that has lasted to the present.

Acknowledgements

We are grateful to Norbert Hölzel for critical comments and suggestions in statistical analysis and data interpretation. Josef Scholz-vom Hofe provided assistance in field work and the soil chemical analyses, Oliver Ginzler helped in collecting the relevés. We thank Dietmar Simmering for critical revision of this paper and Lutz Eckstein and two anonymous referees for helpful comments and linguistic improvement. We are very grateful to the landowners who allowed us to use their fields.

This study was carried out as a part of the Deutsche Forschungsgemeinschaft (DFG) project ‘Land-use Options for Peripheral Regions (SFB 299)’. We would like to thank the DFG for financial assistance.

5 Seed bank diversity in mesic grasslands and their relation to vegetation, management and site conditions

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Journal of Vegetation Science: accepted

5.1 Abstract

Question: (i) Is there an impact of different management types (i.e., hay meadow, silage meadow, meadow-pasture, pasture) on the size and composition of the seed bank of mesic grassland (*Arrhenatheretalia*)? (ii) How strong is the effect of management on the seed bank in relation to aboveground vegetation, edaphic factors and land-use history? (iii) Are there differences in C-S-R plant strategy types and seed longevity between managements?

Location: Lahn-Dill Highlands in central-western Germany.

Methods: Aboveground vegetation and the soil seed bank of 63 plots (at 21 sites) in mesic grasslands were studied. Differences between management types in quantitative seed bank traits and functional characteristics were tested by ANOVA. The impact of management, aboveground vegetation, site conditions and land-use history on seed bank composition were analyzed by partial CCAs.

Results: Management had no significant impact on species richness and density of the seed bank but significantly influenced their floristic composition and functional characteristics. CCA revealed that even after adjustment for soil chemical parameters and aboveground vegetation management still had significant impact on seed bank composition. ANOVA revealed that silage meadows contained higher proportions of R-strategy compared to hay meadows. In contrast, in hay meadows and meadow-pastures proportions of S-strategy were higher than in silage meadows.

Conclusions: The type of grassland management has relatively little impact on quantitative seed bank traits. Management types with a high degree of disturbance lead to an increase of species following a ruderal strategy in the seed bank. Irrespective of management type only a limited proportion of characteristic grassland species is likely to re-establish from the seed bank after disappearance from aboveground vegetation.

Keywords: grazing; mowing; semi-natural grassland; land-use; marginal region; C-S-R strategy; seed accumulation index (SAI).

Nomenclature: Wisskirchen & Haeupler (1998)

Abbreviations: ANOVA = Analysis of variance; C-S-R = Competition-Stress-Ruderality; CCA = Canonical Correspondence Analysis; SAI = Seed Accumulation Index.

5.2 Introduction

Despite a sharp decline in mesic grasslands all over Europe due to intensification and abandonment (e.g., Mac Donald et al. 2000), these habitats are still a typical feature of marginal regions, mainly within mountainous areas associated with traditional low intensity management. They have been a topic of several studies on the aboveground flora focussing on the maintenance and restoration of species rich plant communities, for the ecological evaluation of land-use and for modelling purposes. Soil seed banks are a source for re-establishment of species which are lost from the aboveground vegetation. Hence, maintenance and restoration of species rich grasslands will also depend on the soil seed bank (Grubb 1977; Fenner & Thompson 2005). In contrast, the investigation of seed banks is concentrated on productive agricultural habitats such as fertile grasslands. Therefore relatively little is known about the seed bank communities and the respective ecology of species occurring in less productive semi-natural grasslands (Thompson et al. 1997: 21).

Basically, the composition of a seed bank depends on the contribution of present and former aboveground plant communities (Rice 1989), seed rain from adjacent areas (Hutchings & Booth 1996) and on seed longevity (Rice 1989). Especially the historical composition of the aboveground vegetation has often been identified as one key factor that determines the subsequent composition of the seed bank (Bekker et al. 1997).

However, few studies on soil seed banks investigated the impact of different types of current management. Changes in land-use and management practices can have very distinct impacts on the seed bank and the established vegetation (Bekker et al. 1997; Smith et al. 2002) since they alter disturbance regimes (e.g., Gibson et al. 2005), whereas the impact of site conditions on soil seed bank is considered to be mainly indirect. For example, the soil nutrient level is an important factor influencing composition of aboveground vegetation rather than having a direct species specific influence on seeds.

Disturbance of grassland swards through grazing creates gaps for seed germination (Burke & Grime 1996), while at the same time limiting the rate of recolonization (e.g., Bakker et al. 1996, Osem et al. 2006). Also different cutting dates and frequencies can have large impact on aboveground vegetation composition (e.g., Zechmeister et al. 2003) through differences in species regenerative abilities. Germination of small seeds is supposed to be favoured through open vegetation and topsoil disturbances (Grime 2001; Fenner & Thompson 2005) which are typical of grazed sites.

Reactions to disturbance differ since species are adapted in distinct ways to these impacts. Species groups can be differentiated through C-S-R strategies. The triangular model of

ecological primary strategies (Grime 1988) discriminates strategies of competitiveness, stress tolerance and ruderality using resource availability and disturbance as two orthogonal dimensions for plant classification. Moreover, differences of seed attributes such as seed mass are important in determining seed bank behaviour. Seed mass and seed longevity were found to be negatively correlated since smaller seeds are more likely to become buried (Bekker et al. 1998a; Hölzel & Otte 2004). Due to its disturbance tolerance and the capacity of fast colonization, the ruderal (pioneer) strategy, along with a higher proportion of seeds with lower seed mass, would be expected mainly in management types with higher disturbance impact, e.g. pastures and silage meadows. Theory predicts a close relation between the degree of disturbance in a habitat and the percentage of species with long-term persistent seed banks (Thompson et al. 1998 (p.168); Grime 2001; Hölzel & Otte 2004).

To evaluate the regeneration and maintenance potential of species rich plant communities of mesic grasslands from the seed bank, the persistence of seeds can be assessed by calculating the seed accumulation index (SAI) which has high correlation with the seed longevity index (Hölzel & Otte 2004). The SAI expresses the tendency of a species to accumulate seeds in the soil relative to its cover in the established vegetation using the frequency and abundance of seeds in the soil seed bank relative to the frequency and abundance of a species in the aboveground vegetation. Much research, however, suggests that seed longevity of grassland plant species is low (Rice 1989; Thompson et al. 1997; Bekker et al. 1998b, Bekker et al. 2000).

Given this background, the aim of this study was to assess and quantify the seed bank diversity of mesic grasslands and its relation to aboveground vegetation, seed longevity of species, current management and site conditions. Grasslands of the Lahn-Dill Highlands (Hesse, Germany) have been subject to traditional low intensity management ranging from grazing and mowing without fertilization to silage meadows with low fertilization and early mowing until today. These management practices provide strong differences in disturbance impact ranging from hay meadows with only one or two cuts per year to pastures grazed from May to September and silage meadows mown three times a year.

The main objective of this study was to analyse the effects of management on seed bank diversity. Specifically we hypothesised that (1.) current management regime has a significant impact on seed bank composition even after adjustment for other important factors such as overlying vegetation type and edaphic conditions, and (2.) management regimes with greater

levels of disturbance (silage meadows, pastures) select for more ruderal plant functional types, which is reflected in the composition of the seed bank.

5.3 Material and Methods

Study region

The Lahn-Dill-Highlands cover about 900 km² of Hesse, Germany. These highlands are a typical example of marginal rural landscapes, which are characterised by relatively unfavourable abiotic conditions for cultivation (Frede & Bach 1999) such as cool climate and shallow soils. Since the 1950s, the Lahn-Dill Highlands have been subject to major agricultural land-cover changes, consisting mainly of a decline in arable land and an increase in grassland and fallow land (Waldhardt & Otte 2003; Hietel et al. 2005). In many places, non-intense grassland use has successively replaced the traditional, extremely small-parcelled crop production and crop/grassland rotation. In the study region a large part of the grassland is managed according to EU-based agri-environmental schemes offered by the state of Hesse, focussing on low intensity grassland use.

Current grassland management and land use history

The current grassland management was classified based on information obtained from personal interviews with farmers conducted prior to the study in 2003. Four management practices were differentiated: (i) hay meadows with late mowing in mid-June and one or two cuts per year, (ii) silage meadows with early and frequent mowing (three cuts per year) and little fertiliser input, (iii) meadow-pastures with late mowing and subsequent cattle grazing, and (iv) pastures grazed by cattle from May to September. Except type (ii) that obtains up to 30 kg N ha⁻¹ year⁻¹ all other managements are characterized by a present lack of fertiliser input. All selected sites were managed accordingly for the last 25 years, i.e. since 1979. We checked the former duration of grassland use for each site by visual interpretation of available black-and-white aerial photographs from the years 1953, 1962, 1967, 1973, and 1979. We quantified the age (A) of grassland sites according to the determined land-cover (land use) at each of these dates. The studied grasslands are either long-term-grasslands or were under arable cultivation before 1979. Thus, the factor age is a measure of land use history.

Sampling design

A total of 21 sites (five to six sites per management type) spread over the whole study region were chosen for seed bank and vegetation sampling. On each site, three randomly situated

permanent plots of 25 m² were analysed. To avoid edge effects, for each permanent plot a minimum distance of 10 m to the border of the site was kept.

Sampling of vegetation and seed bank

Species composition of vascular plants in aboveground vegetation was sampled in 2003 and 2004 on the 25 m² permanent plots. Species cover-abundance was visually estimated on a modified Braun-Blanquet-scale (with cover degree 2 subdivided into 2a and 2b).

Sampling of seed banks was carried out in February 2004 when cold stratification had taken place naturally during the winter period. Within each 25 m² permanent plot, 20 cores of 10 cm depth were taken at random locations using a soil corer of 3 cm in diameter. After removing the litter layer soil cores were divided into 0-5 cm and 5-10 cm sections. Thus, the data represent the soil seed bank in the strict sense without the superficial diaspore litter deposited during the preceding vegetation period. The soil samples represent 141 cm² of the soil surface and 1410 cm³ of the soil volume in each plot and were thus well above the minimum requirements for studies of seeds in grasslands (Oomes & Ham 1983). Using this sampling setup the minimal detectable density with a 95% confidence level was ca. 214 seeds m⁻² based on a Poisson distribution of seeds (Thompson et al. 1997).

Following the seedling emergence method (Roberts 1981; Thompson et al. 1997) the soil samples were concentrated by eliminating the coarse stones and vegetative plant material and transferred in a 2 cm thin layer to 18 cm x 28 cm styrofoam trays. The trays were exposed under warm greenhouse conditions and watered regularly. Seedlings were identified and removed once every week and later once every few weeks. Unidentifiable seedlings were transplanted into pots and grown until identification was possible. In case of identification to the genus level only, seedlings were pooled (*Betula ssp.* and *Carex ssp.*). After 4 ½ months <1% germination and no additional species were recorded and the experiment was terminated.

Site characteristics/Soil nutrients

In autumn 2003, soil samples were collected by randomly taking 20 cores of 10 cm depth and 3 cm diameter within each of the permanent plots. We determined total nitrogen (Nt) and total carbon (Ct) levels using a CN-analyser (FlashEA 1112, Thermoquest), amounts of plant available phosphorus (P_{CAL}) and potassium (K_{CAL}) using the calcium-acetate-lactate (CAL) extraction method and pH (in CaCl₂) of the fine soil. As there were no limestone formations in the sampling areas the total carbon of the soil represents the organic carbon and was used to calculate the organic matter in the soil samples.

Data analysis

Cover-weighted averages of the Ellenberg indicator values for soil nutrients (NV) and soil moisture (MV) given by Ellenberg et al. (1992) were calculated for aboveground vegetation of each plot. Similarity between established vegetation and seed bank of each plot was determined using the Euclidian distance after standardizing the data (Z-transformation) (McCune & Grace 2002).

To evaluate the regeneration and maintenance potential of target communities of mesic grasslands, the persistence of seeds was assessed by calculating the seed accumulation index (SAI, Hölzel & Otte 2004). The SAI is a continuous estimator of seed persistence which combines two indices to express the relationship between the presence of a certain species in aboveground vegetation and in the soil seed bank. The first index relates the plot frequency of a certain species in the soil seed bank (SB_f) to its frequency in aboveground vegetation (AV_f) and seed bank:

$$AV/SB_{freq} \text{ index} = (SB_f / (SB_f + AV_f)) * 100 \quad (1)$$

The second index relates the total number of seeds recorded in the seed bank over all plots (SB_q) to the cumulative cover of a certain species over all plots (AV_q) plus the total number of seeds:

$$AV/SB_{quant} \text{ index} = (SB_q / (SB_q + AV_q)) * 100 \quad (2)$$

Both indices range between 0 (only present in aboveground vegetation) and 100 (only present in the soil seed bank). To integrate quantitative aspects of species occurrence in aboveground vegetation and seed bank, Hölzel & Otte (2004) merged the two indices into a single one, the SAI, by the addition of both indices and division by two.

SAI was calculated across all sampled plots ($n = 63$) for all 207 species recorded in the study (Appendix 1). For seed bank species, mean abundance-weighted (i.e. weighted for seed density) SAI value was calculated for each plot. Abundance-weighted (i.e. weighted for seed density) calibrated C-S-R strategy types by Grime et al. (1988) were calculated for each plot based on the species found in the soil seed bank. The calibration of unbalanced C-S-R radii for species was performed according to Ejrnæs & Bruun (2000). We allocated a total of 60 points to each species divided on the three strategies C, S and R. A species recorded as R/CSR was consequently assigned to ten points for competitive ability, ten points for stress tolerance and 40 points for ruderal adaptation. Only species categorized by Grime et al. (1988) were included in the analysis when considering C-S-R as dependent variable; they

comprised about 80% of the entire species pool and all of the frequent and abundant species. Uncategorized species always had low abundances, i.e. less than five seeds per plot. Data on seed mass of common species were derived from Korsmo (1930), Grime et al. (1988), Hölzel & Otte (2004) and Otte et al. (2006). Mean abundance-weighted seed weight of seed bank species was calculated for each plot.

To test for differences between the four management types in (i) site characteristics, (ii) similarity between established vegetation and seed bank and (iii) differences in functional traits of seed bank species, we calculated one-factorial analyses of variance (Table 1, Fig. 2, Fig. 3). Prior to analyses, for each variable tested mean values for each site were obtained by averaging the values of the respective three plots and the numbers of seeds were log-transformed to fulfill the assumption of normally distributed data required for ANOVA. In case of significance, ANOVA was followed by the Tukey HSD test for unequal sample sizes. To keep the type I error at 5% despite multiple testing, the significance level α was adjusted by the sequential Bonferroni procedure (Holm 1979). ANOVA and associated tests were carried out using STATISTICA 6.0 (Anon. 1998).

Two-way analysis of variance was performed to test the effects of the four management types and the two soil depths on (a) species richness (α -diversity) of seed bank species (calculated as mean species number per 25 m²) and (b) seed density (calculated as mean number of seeds m⁻²). In a second step, ruderal species, i.e. typical species of disturbed habitats according to Ellenberg et al. (1992) and Oberdorfer (1994) which occurred only irregularly were excluded from the analysis. For this reduced data set of the seed bank *with grassland species only*, which made up 70% of the species in the seed bank, tests (a) and (b) were repeated. The second analysis was considered to be more meaningful for assessing the potential of the seed bank for contributing to the maintenance of mesic grassland vegetation. Untransformed mean values of species richness and seed density for each management type and soil depth are given in Table 2.

The relative importance of current management, aboveground vegetation and other important factors on floristic composition of the seed bank was quantified by a series of Canonical Correspondence Analyses (CCA). In order to assess the appropriateness of CCA, we first subjected the seed bank species data set to a Detrended Correspondence Analysis (DCA) (McCune and Grace 2002). DCA revealed a gradient length of 3.23 SD on the first axis, which indicates the appropriateness of a unimodal response model (Ter Braak & Smilauer

1998). We also performed a DCA of the aboveground vegetation species matrix resulting in three ordination axes representing 23.52% of the total variance in species data. The sample scores of the three DCA-axes were subsequently used as constraining ('environmental') variables in canonical correspondence analyses (CCA) of the seed bank matrix. Prior to CCAs, all examined variables were submitted to a forward selection procedure (Lepš & Šmilauer 2003). They all yielded significant contributions ($p < 0.05$) to data structure and were therefore retained for CCA. To receive ecologically interpretable variance components, the explanatory variables were grouped into the following four sets: Management type (M; including four different management types); soil chemical parameters (S; including organic matter, total nitrogen, pH value, and plant available P and K contents); Aboveground Vegetation (AV; DCA axes scores of vegetation relevés); grassland age (A). In order to isolate the effect of these sets of explanatory variables on seed bank composition we performed a decomposition of variance by running a series of partial CCAs as proposed by Ter Braak & Šmilauer (1998, p.258). All ordinations were done with CANOCO 4 software (Ter Braak & Šmilauer 1998).

Significant indicators of management types were detected by the method of Indicator Species Analysis (Dufrêne & Legendre 1997, McCune & Grace 2002). To calculate the indicator value of a species, its mean abundance in one group compared with its mean abundance in all groups is multiplied by its relative frequency in the samples of that group. The obtained values were tested for significance with a Monte Carlo permutation test (1000 random permutations). Indicator Species Analysis was done with PC-ORD (McCune & Mefford 1999).

5.4 Results

The aboveground vegetation contained 151 taxa, 56% (84 species) of these were represented also in the soil seed bank. A total of 9209 seedlings emerged from the soil samples which could be assigned to 140 different taxa, 128 in 0-5 cm and 107 in 5-10 cm depth. The observed seed densities ranged from 5 225 to 24 421 with a mean of 10 367 seeds m^{-2} over all sites. The soil seed bank was dominated by a few species which occurred with high densities (see Appendix 1): *Trifolium repens* (1274 seeds m^{-2}), *Agrostis capillaris* (1029 seeds m^{-2}), *Plantago lanceolata* (952 seeds m^{-2}), *Juncus bufonius* (883 seeds m^{-2}), *Leontodon autumnalis* (778 seeds m^{-2}), *Poa trivialis* (545 seeds m^{-2}), and *Cerastium holosteoides* (482 seeds m^{-2}).

These seven species contributed 50% of all seeds found, whereas the majority of species had lower seed densities (see Appendix 1).

The application of the SAI to our data set resulted in a continuous and differentiated ranking of species (Appendix 1). Species with high accumulation of seeds in the soil, i.e. high SAI, which are likely to form a long time persistent seed bank were mostly scarce or absent in aboveground vegetation. Exceptional species which were frequent in the seed bank but also in the aboveground vegetation were *Anthoxanthum odoratum*, *Cerastium holosteoides*, *Holcus lanatus*, *Leontodon autumnalis*, *Luzula campestris*, *Plantago lanceolata*, *Poa trivialis* and

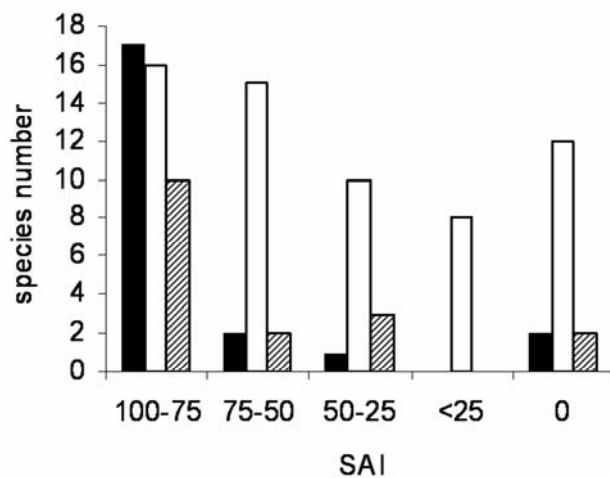


Fig. 1. Absolute frequencies of species of disturbed habitats, grassland habitats and other habitats in different seed accumulation index (SAI) classes ($n = 100$ species; only species with a frequency of at least three plots of 21 were included).

- D = species of disturbed habitats ($n = 22$)
- G = species of grassland habitats ($n = 61$)
- ▨ others ($n = 17$)

Veronica chamaedrys. A comparison of absolute frequencies of frequent species ($n = 100$, frequency at least three from 21 sites; Appendix 1, Fig. 1) of different habitat types over five classes of SAI revealed that most species of disturbed habitats (86%, $n = 22$) and a remarkable proportion of species from grassland habitats (51%, $n = 61$), such as

Anthoxanthum odoratum and *Poa trivialis*, showed high SAI values ($SAI \geq 50$). The species with preferences for ‘other habitats’ with high SAI values (71%, $n = 17$) consisted mostly of plants related to disturbed situations e.g. *Solidago virgaurea*, *Epilobium angustifolium*, and *Aethusa cynapium* or anemochorous pioneers like *Betula ssp.*

and *Salix caprea* as well as undetermined groupings of *Carex ssp.* Species with low SAI values ($SAI < 50$) were mostly grassland species.

Differences between management types

Tests of several environmental factors for differences between management types (Table 1) revealed that all variables had non-significant effects and showed no ecologically meaningful differences among managements. As revealed in one-way ANOVA (Table 1), similarity between species composition of established vegetation with those of the respective seed bank

(Euclidian distance) was not affected by management type, and also mean SAI of seed bank species did not show significant differences between management types.

Two-way ANOVA revealed no significant differences in the quantitative traits species richness (α -Diversity) and seed density between management types, but soil depth was a significant factor for these quantitative traits ($p \leq 0.0005$, adjusted $\alpha = 0.0125$). There was no interaction between management and soil depth. The result was identical when only grassland species were considered. Comparing the two depth fractions, the upper soil layer contained higher species richness (seed bank; seed bank of grassland species only) (29 vs. 21; 25 vs. 16) and seed density (7700 vs. 2667; 7088 vs. 1915) (Table 2).

Table 1. Abiotic site conditions, similarity between aboveground vegetation and seed bank and the seed accumulation index (SAI) of four management types. Mean values \pm standard deviation for sites of each management type are given. For the variable ‘age of grasslands’ the range is given in brackets. Differences between management types were not significant (one-way ANOVA).

Management type	Hay meadow (n = 6)	Silage meadow (n = 5)	Meadow-pasture (n = 5)	Pasture (cattle) (n = 5)
<i>Environmental factors</i>				
Age of grasslands (years)	41 \pm 3 [30-50]	40 \pm 4 [25-50]	48 \pm 4 [40-50]	50 \pm 4 [40-50]
Elevation a.s.l. (m)	362 \pm 35	370 \pm 39	421 \pm 39	351 \pm 39
Total nitrogen (%)	0.40 \pm 0.05	0.45 \pm 0.05	0.51 \pm 0.05	0.40 \pm 0.05
Organic matter (%)	7.0 \pm 0.8	7.8 \pm 0.9	9.0 \pm 0.9	6.7 \pm 0.9
pH value (CaCl ₂)	4.9 \pm 0.2	4.8 \pm 0.2	4.6 \pm 0.2	5.26 \pm 0.2
Phosphorus (mg 100g ⁻¹)	4.8 \pm 2	5.9 \pm 2	6.2 \pm 2	7.0 \pm 2
Potassium (mg 100g ⁻¹)	9 \pm 6	20 \pm 7	15 \pm 7	24 \pm 7
Moisture value (MV)	4.9 \pm 0.1	5.2 \pm 0.1	5.4 \pm 0.1	5.3 \pm 0.1
Nutrient value (NV)	5.5 \pm 0.3	6.0 \pm 0.3	4.9 \pm 0.3	5.9 \pm 0.3
<i>Similarity between established vegetation and seed bank</i>				
Euclidian distance	19 \pm 2	19 \pm 3	21 \pm 3	19 \pm 2
<i>Seed accumulation index</i>				
SAI	66 \pm 3	70 \pm 4	68 \pm 4	70 \pm 4

Table 2. Species richness (α -diversity, calculated as mean species richness per 25m² plot) and seed density (calculated as mean number of seeds per m²) in the vegetation and seed bank of four management types (n = 21). Untransformed mean values \pm standard deviation for sites of each management type are given. Two-way ANOVA with management and soil depth showed significant main effects for soil depth while differences between management types and the interaction were not significant.

Management type	Depth (cm)	Hay meadow (n = 6)	Silage meadow (n = 5)	Meadow-pasture (n = 5)	Pasture (cattle) (n = 5)
<i>Established Vegetation</i>					
Species richness/plot (25m ²)		36 \pm 3	32 \pm 3	41 \pm 3	34 \pm 3
<i>Seed bank</i>					
Species richness/plot (25m ²)	0-5	28 \pm 3	26 \pm 3	31 \pm 3	29 \pm 3
Species richness/plot (25m ²)	5-10	20 \pm 3	19 \pm 3	20 \pm 3	24 \pm 3
Species richness/plot (25m ²)	0-10	35 \pm 3	32 \pm 3.5	36 \pm 3.5	37 \pm 3.5
Number of seeds m ⁻²	0-5	7687 \pm 1584	7891 \pm 1735	7778 \pm 1735	7447 \pm 1735
Number of seeds m ⁻²	5-10	1773 \pm 1045	2624 \pm 1044	3735 \pm 1044	2714 \pm 1044
Number of seeds m ⁻²	0-10	9460 \pm 2111	10515 \pm 2312	11513 \pm 2312	10161 \pm 2312
<i>Seed bank of grassland species only</i>					
Species density/plot (25m ²)	0-5	26 \pm 3	21 \pm 3	29 \pm 3	22 \pm 3
Species density/plot (25m ²)	5-10	17 \pm 3	14 \pm 3	17 \pm 3	17 \pm 3
Species density/plot (25m ²)	0-10	29 \pm 3	24 \pm 3	32 \pm 3	28 \pm 3
Number of seeds m ⁻²	0-5	7510 \pm 1529	7366 \pm 1675	6567 \pm 1675	6823 \pm 1675
Number of seeds m ⁻²	5-10	1521 \pm 714	1674 \pm 783	2558 \pm 783	1986 \pm 783
Number of seeds m ⁻²	0-10	9031 \pm 1809	9040 \pm 1982	9125 \pm 1982	8809 \pm 1982

Indicator Species Analysis revealed significant indicators for management types (Table 3). In contrast to the management types with mowing regime, in the seed bank under pastures mainly ruderal species (according to Ellenberg et al. 1992) such as *Plantago major* and *Urtica dioica* occurred as indicators. Among indicator species for silage meadows were arable weeds (e.g. *Capsella bursa-pastoris*). Meadows and meadow-pastures contained a number of indicator species characteristic of relatively nutrient poor site conditions such as *Luzula campestris* and *Potentilla erecta* which are considered as stress tolerators (Grime et al. 1988). Analyses of variance showed differences in composition of C-S-R strategy of seed bank species between management types (Fig. 2).

Table 3. Indicator species of the grassland seed bank samples (Dufrière & Legendre 1997). Significance obtained by Monte-Carlo-Permutation test is given at three levels: * $p \leq 0.05$, ** $p \leq 0.01$, *** $p \leq 0.001$; IV = indicator value. Species with non significant or low indicator value (< 25) are not shown; (A) notifies arable weeds; (D) notifies ruderal species typical of disturbed habitats according to Ellenberg et al. (1992).

Hay meadows (n = 18)	IV	Silage meadows (n = 15)	IV
<i>Anthoxanthum odoratum</i> ***	52	<i>Leontodon autumnalis</i> *	34.6
<i>Plantago lanceolata</i> **	39.6	<i>Capsella bursa-pastoris</i> * (A)	25.4
<i>Trifolium pratense</i> **	39.5		
<i>Holcus lanatus</i> *	36.4		
<i>Poa angustifolia</i> *	31.1		
<i>Luzula campestris</i> *	26.8		
<i>Trifolium campestre</i> *	25.5		

Meadow-pastures (n = 15)	IV	Pastures (n = 15)	IV
<i>Deschampsia cespitosa</i> ***	47.4	<i>Rumex obtusifolius</i> *** (D)	50.2
<i>Juncus bufonius</i> ** (D)	45	<i>Poa trivialis</i> **	40.2
<i>Juncus conglomeratus</i> **	36.1	<i>Urtica dioica</i> ** (D)	38.6
<i>Festuca rubra</i> **	28.3	<i>Plantago major</i> * (D)	29.5
<i>Alchemilla xanthochlora</i> **	25		
<i>Potentilla erecta</i> **	25		

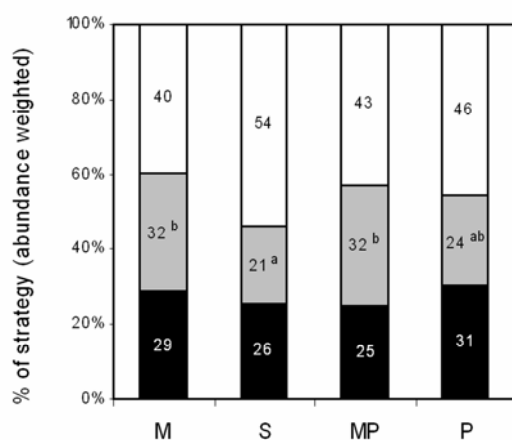


Fig. 2. Differences in the proportion of C-R-S strategies of soil seed bank species between management types. Different letters denote significant differences between management types according to Tukey HSD Test after one-way ANOVA. (□) R = ruderality (F = 3.21; p = 0.049; adjusted α is 0.025), (■) S = stress (F = 5.24; p = 0.0096; adjusted α is 0.017), (■) C = competitiveness (n.s.), according to Grime (1988). M = hay meadows (n = 6), S = silage meadows (n = 5), MP = meadow-pastures (n = 5), P = pastures (n = 5).

While competitors such as *Dactylis glomerata* were evenly distributed across types, stress strategy, represented for example by *Luzula campestris*, *Pimpinella saxifraga*, *Carex ovalis* and *Veronica chamaedrys*, was significantly higher in meadows (32%) and meadow-pastures (32%) than in silage-meadows (21%). Among all management types the ruderal strategy embodied nearly half of the C-S-R scheme. It is represented by species such as *Cerastium*

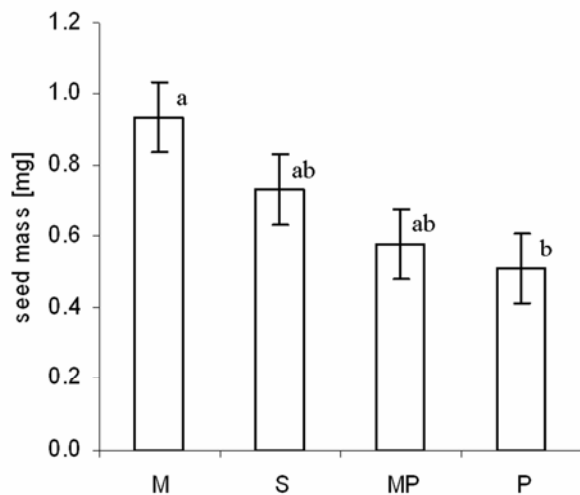


Fig. 3. Comparison of mean abundance weighted seed mass of soil seed bank species between management types (M = hay meadows; S = silage meadows; MP = meadow pastures; P = pastures). Different letters denote significant differences ($p < 0.05$) according to Tukey Test after one-way ANOVA.

glomeratum, *Gnaphalium uliginosum*, *Juncus bufonius*, *Leontodon autumnalis*, *Plantago major*, *Veronica serpyllifolia* and *Viola arvensis*. While the proportion of ruderal strategy was high in silage meadows (54%), it was lower (closely to significance after Bonferroni correction) in hay meadows (40%), meadow-pastures (43%) and (46%) pastures were intermediate. Seed mass showed significant differences between hay-meadows (0.9 g) and pastures (0.5 g) (Fig. 3).

Relative importance of management in relation to other factors

In contrast to the similarity of the quantitative traits of seed banks among management types, CCA displayed a significant ($p < 0.001$) impact of current management on species composition of the soil seed bank (12.8% explained variance, Table 4). This was true even after adjustment for the aboveground vegetation and soil chemical parameters which also significantly influenced the floristic composition of the soil seed bank and contributed 16.1 and 17.0% of explained variance, respectively. Soil chemical parameters explained the highest amount of variance in seed bank composition even after adjustment for aboveground vegetation and management. The age of sites had a low but still significant explanatory value.

Table 4. Results of CCA analyses isolating the effect of different sets of variables on the soil seed bank ($n = 63$ plots). Variable sets: A = age of sampled grasslands; AV = aboveground vegetation (sample scores of DCA axes); M = management type; S = soil chemical parameters. EV = Explanatory variables; CV = Covariables; V = Sum of all canonical eigenvalues – measure for explanatory power of the explanatory variables (total inertia = 2.763); % = percentage of explained variance; F = F-ratio statistics for the test on the trace, p = corresponding probability value obtained by the Monte-Carlo-permutation test (1000 permutations).

EV	CV	V	%	F	p
S	-	0.470	17.0	2.336	0.001
AV	-	0.445	16.1	3.780	0.001
M	-	0.353	12.8	2.882	0.001
A	-	0.098	3.5	2.243	0.001
S	M	0.393	14.2	2.101	0.001
S	M, AV	0.289	10.5	2.181	0.001
AV	M	0.318	11.5	2.840	0.001
AV	M, S	0.215	7.8	2.024	0.001
M	AV	0.226	8.2	2.016	0.001
M	AV, S	0.213	7.7	2.005	0.001

5.5 Discussion

In our study, neither similarity of species composition between seed bank and aboveground vegetation nor quantitative seed bank traits, i.e. α -diversity and seed density, were significantly affected by current management. Other studies mostly found that intensified management resulted in an increase of seed density due to a higher number of nutrient demanding ruderal species and in a higher similarity between established vegetation and seed banks (e.g., Bekker et al. 1997; Matus et al. 2005). In contrast, characteristic grassland species, in particular those growing on more nutrient-poor conditions, were largely eliminated from the seed bank. In our study, such significant quantitative differences in the number of seeds between management types could not be observed, most likely due to the overall very low intensity of grassland use in the study region.

While there were no quantitative differences, grassland management had significant impact on species composition and the distribution of plant functional strategy types in the seed bank. Partial CCA indicated that management was a significant factor for seed bank composition even after adjustment for other important factors, i.e. overlying vegetation type and soil chemical parameters (Table 4). Gradients in actual aboveground vegetation had high explanatory value and significantly influenced seed bank species composition, which was also shown in other habitats (e.g., Looney & Gibson 1995). The effect of soil chemical parameters on seed bank composition is rather mediated by its effect on composition of established

vegetation of recent and former periods than by a direct influence on seed bank composition (Bekker et al. 1997).

Differences in species identity and abundance between management types potentially imply differences in functional features. In our study an effect of current management on species composition was most obvious by an accumulation of ruderal species in the soil seed bank under pastures and silage meadows (Fig. 2, Table 3). The significant occurrence of certain nutrient demanding ruderals on grazed sites reflects the higher degree of soil disturbance in this management type. Ruderal strategy is connected with rapid growth and generative reproduction and thus the tolerance of disturbance and capacity of fast colonization (pioneers). Similarly, in silage meadows the increased amount of ruderals reflects the high degree of disturbance by frequent mowing in this management type. In silage meadows a considerable proportion of sites (40%) underwent past changes in land-use from arable to grassland which is reflected by some relict arable weeds in the lower soil layer able to build up a long-term persistent seed bank. Similar phenomena have been reported by other authors from European grasslands (e.g., Bekker et al. 1997; López-Mariño et al. 2000; Hölzel et al. 2001).

In contrast to silage meadows and permanent pastures, hay meadows and meadow pastures are characterized by a higher proportion of the stress strategy, which probably reflects a lower degree of disturbance and a lower nutrient availability. This is best exemplified by the occurrence of certain stress tolerant grassland species such as *Luzula campestris*, *Pimpinella saxifraga*, *Festuca rubra* and *Potentilla erecta* (Grime et al 1988).

Average seed mass decreased from hay meadows via silage meadows to meadow pastures and pastures. The significant differences in average seed mass between hay meadows and pastures found in our study are consistent with the results from other studies. Germination of small seeds is supposed to be favoured through open vegetation and topsoil disturbances (Grime 2001, Fenner & Thompson 2005) which are typical of grazed sites. In contrast, the higher competition by established vegetation in closed swards of hay and silage meadows favours large-seeded species (e.g., Hölzel 2005).

A comparison of SAI values between species with different habitat preferences (Fig. 1) revealed that species of disturbed habitats were characterised by high SAI values. This is in line with the results and general conclusion from Thompson et al. (1998, p.168), Grime (2001) and Hölzel & Otte (2004), which predict that increasing habitat disturbance selects for increased seed persistence. However, the disturbance gradient comprised by the different

management types of the present study was not reflected by differences in the SAI of seed bank species (Table 1). While our finding of a high proportion of grassland species present in the seed bank with low SAI values is in line with research of Bekker et al. (2000) suggesting that seed longevity of grassland plant species is low, we also found a remarkable amount of frequent grassland species with high seed accumulation. The latter have a lower risk of extinction, especially if these species are also present in the aboveground vegetation. However, ploughing of grassland allotments will also deplete the soil seed bank of species with long-term persistent seeds (Bakker et al. 1991).

Conclusions

We conclude that in mesic grasslands of our study region (1.) current management is a main important factor influencing seed bank composition even after adjustment for overlying vegetation type and edaphic factors. (2.) Management regimes with a high degree of disturbance, i.e. silage meadows and pastures, lead to an increase of species following a ruderal strategy in the seed bank. Irrespective of management type only a limited proportion of characteristic grassland species is likely to re-establish from the seed bank after disappearance from aboveground vegetation.

Acknowledgements

For his help with methodology of seed bank sampling, seed bank analysis and valuable comments on the manuscript we would like to thank in particular Norbert Hölzel. Josef Scholz-vom Hofe helped with sampling the seed banks, Lutz Eckstein and Tobias Donath gave useful comments on the paper and polished the English. We are thankful to Alessandro Chiarucci, David Ackerly, Simon Pierce and an anonymous referee, who gave many suggestions for improvement of a former version of this paper. We thank the DFG for financial assistance.

Appendix 1. Habitat, Seed Accumulation Index (SAI), absolute frequency and abundance per site ($n = 21$) in aboveground vegetation (AV) and soil seed bank (SB) (separate listing of soil seed bank at two depths in parentheses) for all 207 species recorded in the study. Abundance in AV is given as cumulative cover, in SB as mean, minimum and maximum seed density (number of seeds/m²) across all sites. For species in the SB which are also present in AV mean seed density is given in bold. Habitat classifications (D = disturbed habitats; G = grassland habitats; M = moist habitats; W = woody habitats; u = unclassified) according to Ellenberg et al. (1992) and Oberdorfer (1994).

Species	Habitat	SAI	Frequency		AV	Abundance		
			AV	SB		AV	SB 0-10 (0-5, 5-10) Seeds per m ²	
				0-10 (0-5, 5-10)			Mean	Minimum
<i>Achillea millefolium</i>	G	15	19	5 (4, 2)	27	76 (65, 59)	24 (24, 24)	260 (165, 95)
<i>Aethusa cynapium</i>	u	100		3 (1, 3)		95 (24, 87)	47 (24, 24)	142 (24, 142)
<i>Agrostis capillaris</i>	G	49	20	17 (17, 15)	692	1029 (859, 192)	24 (24, 24)	6430 (5910, 520)
<i>Agrostis stolonifera</i>	u	73	4	12 (5, 9)	22	89 (147, 37)	24 (24, 24)	496 (426, 95)
<i>Ajuga reptans</i>	G	72	7	8 (5, 6)	6	216 (236, 91)	24 (24, 24)	1182 (898, 284)
<i>Alchemilla monticola</i>	G	28	6	3 (3, 0)	7	24 (24, 0)	24 (24, 0)	24 (24, 0)
<i>Alchemilla xanthochlora</i>	G	61	4	1 (1, 1)	5	591 (47, 544)	591 (47, 544)	591 (47, 544)
<i>Anagallis arvensis</i>	D	100		2 (0, 2)		24 (0, 24)	24 (0, 24)	24 (0, 24)
<i>Anthoxanthum odoratum</i> agg.	G	68	12	15 (14, 6)	18	345 (355, 35)	24 (24, 24)	1253 (1253, 95)
<i>Aphanes arvensis</i>	D	58	1	1 (0, 1)	<1	24 (0, 24)	24 (0, 24)	24 (0, 24)
<i>Arabidopsis thaliana</i>	D	100		12 (11, 8)		329 (172, 257)	24 (24, 24)	1277 (520, 780)
<i>Arenaria serpyllifolia</i> agg.	u	33	2	1 (1, 0)	2	24 (24, 0)	24 (24, 0)	24 (24, 0)
<i>Arrhenatherum elatius</i>	G	6	18	5 (3, 3)	570	43 (39, 32)	24 (24, 24)	118 (71, 47)
<i>Atropa bella-donna</i>	W	100		1 (0, 1)		24 (0, 24)	24 (0, 24)	24 (0, 24)
<i>Bellis perennis</i>	G	59	9	5 (5, 4)	9	246 (142, 130)	47 (24, 24)	544 (236, 449)
<i>Betula</i> ssp.	u	100		5 (1, 4)		33 (47, 30)	24 (47, 24)	47 (47, 47)
<i>Calamagrostis epigejos</i>	u	100		2 (2, 0)		35 (35, 0)	24 (24, 0)	47 (47, 0)
<i>Campanula rotundifolia</i> agg.	G	53	3	2 (1, 2)	3	106 (118, 47)	24 (118, 24)	189 (118, 71)
<i>Capsella bursa-pastoris</i>	D	100		6 (6, 6)		280 (150, 130)	71 (47, 24)	1017 (615, 402)
<i>Cardamine pratensis</i> agg.	G	75	7	10 (9, 9)	7	118 (92, 39)	47 (24, 24)	260 (213, 71)
<i>Carex nigra</i>	M	77	1	3 (3, 1)	2	426 (142, 851)	24 (24, 851)	1229 (378, 851)
<i>Carex ovalis</i>	G	93	1	3 (3, 2)	<1	1545 (591, 1430)	24 (24, 24)	4468 (1631, 2837)
<i>Carex pilulifera</i>	G	100		1 (1, 0)		118 (118, 0)	118 (118, 0)	118 (118, 0)
<i>Carex</i> ssp. agg.	u	100		3 (2, 2)		394 (532, 59)	47 (118, 47)	1017 (946, 71)
<i>Carpinus betulus</i>	W	65	1	1 (1, 0)	<1	47 (47, 0)	47 (47, 0)	47 (47, 0)
<i>Centaurea jacea</i> s.l.	G	14	10	4 (3, 1)	59	41 (47, 24)	24 (24, 24)	95 (95, 24)
<i>Cerastium glomeratum</i>	D	100		7 (4, 7)		108 (71, 68)	24 (24, 24)	260 (165, 236)
<i>Cerastium holosteoides</i>	G	78	17	20 (20, 19)	22	482 (332, 158)	95 (95, 24)	993 (946, 473)
<i>Chenopodium album</i>	D	100		8 (4, 8)		86 (59, 56)	24 (24, 24)	213 (95, 142)
<i>Chenopodium ficifolium</i>	D	100		1 (1, 0)		24 (24, 0)	24 (24, 0)	24 (24, 0)
<i>Chenopodium polyspermum</i>	D	100		2 (0, 2)		47 (0, 47)	47 (0, 47)	47 (0, 47)
<i>Cirsium arvense</i>	D	61	2	2 (2, 1)	6	260 (130, 260)	24 (24, 260)	496 (236, 260)
<i>Cirsium vulgare</i>	D	52	4	6 (6, 1)	9	32 (28, 24)	24 (24, 24)	47 (47, 24)
<i>Clematis vitalba</i>	W	100		1 (1, 0)		24 (24, 0)	24 (24, 0)	24 (24, 0)
<i>Convolvulus arvensis</i>	D	58	1	1 (1, 0)	<1	24 (24, 0)	24 (24, 0)	24 (24, 0)
<i>Crataegus monogyna</i> s.l.	W	100		2 (2, 0)		485 (485, 0)	47 (47, 0)	922 (922, 0)
<i>Dactylis glomerata</i> agg.	u	32	20	13 (12, 2)	179	138 (146, 24)	24 (24, 24)	426 (426, 24)
<i>Deschampsia cespitosa</i> agg.	u	49	5	3 (3, 1)	30	299 (268, 95)	24 (24, 95)	615 (520, 95)
<i>Epilobium angustifolium</i>	W	100		3 (2, 1)		24 (24, 24)	24 (24, 24)	24 (24, 24)
<i>Epilobium montanum</i>	W	100		2 (0, 2)		24 (0, 24)	24 (0, 24)	24 (0, 24)
<i>Epilobium parviflorum</i>	M	100		1 (1, 0)		24 (24, 0)	24 (24, 0)	24 (24, 0)
<i>Epilobium tetragonum</i> s.l.	D	100		4 (2, 2)		24 (24, 24)	24 (24, 24)	24 (24, 24)
<i>Erophila verna</i> ssp. <i>verna</i>	G	84	1	4 (3, 1)	<1	24 (24, 24)	24 (24, 24)	24 (24, 24)

SEED BANK DIVERSITY IN MESIC GRASSLANDS AND THEIR RELATION TO VEGETATION, MANAGEMENT AND SITE CONDITIONS

App. 1, cont. Species	Habitat	SAI	Frequency		Abundance			
			AV	SB	AV	SB 0-10 (0-5, 5-10) Seeds per m ²		
				0-10 (0-5, 5-10)		Mean	Minimum	Maximum
<i>Euphorbia helioscopia</i>	D	100		1 (1, 1)		165 (95, 71)	165 (95, 71)	165 (95, 71)
<i>Festuca ovina</i> agg.	G	100		1 (1, 0)		24 (24, 0)	24 (24, 0)	24 (24, 0)
<i>Festuca pratensis</i> s.l.	G	6	7	1 (1, 0)	52	47 (47, 0)	47 (47, 0)	47 (47, 0)
<i>Festuca rubra</i>	G	13	19	9 (9, 0)	803	55 (55, 0)	24 (24, 0)	118 (118, 0)
<i>Fragaria viridis</i>	W	100		1 (1, 0)		24 (24, 0)	24 (24, 0)	24 (24, 0)
<i>Fumaria officinalis</i> s.l.	D	100		1 (0, 1)		24 (0, 24)	24 (0, 24)	24 (0, 24)
<i>Galeopsis segetum</i>	u	100		1 (1, 0)		24 (24, 0)	24 (24, 0)	24 (24, 0)
<i>Galium album</i>	G	11	13	3 (3, 0)	35	32 (32, 0)	24 (24, 0)	47 (47, 0)
<i>Glechoma hederacea</i>	D	32	6	4 (3, 1)	7	24 (24, 24)	24 (24, 24)	24 (24, 24)
<i>Gnaphalium sylvaticum</i>	W	100		1 (1, 1)		165 (95, 71)	165 (95, 71)	165 (95, 71)
<i>Gnaphalium uliginosum</i>	D	100		7 (5, 7)		162 (52, 125)	47 (24, 47)	449 (71, 426)
<i>Helicotrichon pubescens</i>	G	17	4	1 (1, 0)	5	24 (24, 0)	24 (24, 0)	24 (24, 0)
<i>Heracleum sphondylium</i>	G	3	18	2 (2, 0)	85	24 (24, 0)	24 (24, 0)	24 (24, 0)
<i>Hieracium umbellatum</i>	W	60	6	5 (5, 1)	8	104 (95, 47)	24 (24, 47)	284 (236, 47)
<i>Holcus lanatus</i>	G	60	21	18 (18, 13)	139	503 (470, 45)	24 (24, 24)	2151 (2080, 95)
<i>Hypericum humifusum</i>	D	100		2 (2, 0)		35 (35, 0)	24 (24, 0)	47 (47, 0)
<i>Hypericum maculatum</i> s.l.	G	64	5	5 (4, 3)	16	270 (207, 173)	71 (24, 71)	757 (591, 284)
<i>Hypericum perforatum</i>	W	94	1	6 (3, 5)	<1	106 (110, 61)	24 (24, 24)	331 (213, 118)
<i>Hypericum tetrapterum</i>	G	68	5	4 (3, 2)	5	319 (102, 485)	24 (24, 71)	1135 (236, 898)
<i>Hypochaeris radicata</i>	G	39	8	3 (3, 2)	10	79 (63, 24)	24 (24, 24)	142 (118, 24)
<i>Isolepis setacea</i>	D	100		1 (0, 1)		47 (0, 47)	47 (0, 47)	47 (0, 47)
<i>Juncus articulatus</i>	G/M	100		7 (3, 6)		111 (110, 75)	24 (24, 24)	520 (189, 331)
<i>Juncus bufonius</i>	D	100		15 (11, 14)		883 (520, 537)	24 (24, 24)	8369 (3948, 4421)
<i>Juncus conglomeratus</i>	G/M	94	2	15 (11, 9)	2	241 (116, 260)	24 (24, 24)	2742 (804, 1939)
<i>Juncus effusus</i>	G/M	78	2	3 (1, 2)	1	221 (449, 106)	24 (449, 24)	449 (449, 189)
<i>Lamium purpureum</i> s.l.	D	86	1	3 (3, 2)	1	118 (24, 142)	24 (24, 142)	165 (24, 142)
<i>Lapsana communis</i>	D	100		1 (0, 1)		24 (0, 24)	24 (0, 24)	24 (0, 24)
<i>Lathyrus pratensis</i>	G	32	9	3 (3, 0)	12	63 (63, 0)	24 (24, 0)	142 (142, 0)
<i>Leontodon autumnalis</i>	G	60	14	13 (13, 4)	115	778 (758, 65)	24 (24, 24)	5106 (5035, 118)
<i>Leontodon hispidus</i>	G	40	5	4 (3, 2)	31	100 (118, 24)	24 (47, 24)	236 (213, 24)
<i>Leucanthemum vulgare</i> agg.	G	58	16	14 (11, 8)	87	426 (494, 65)	24 (24, 24)	1726 (1608, 142)
<i>Linum catharticum</i>	G	100		2 (2, 2)		47 (24, 24)	47 (24, 24)	47 (24, 24)
<i>Lolium perenne</i>	G	8	14	3 (3, 0)	194	63 (63, 0)	24 (24, 0)	95 (95, 0)
<i>Lotus corniculatus</i>	G	30	11	6 (6, 3)	29	63 (43, 39)	24 (24, 24)	118 (118, 71)
<i>Lotus pedunculatus</i>	G	87	1	2 (1, 2)	3	473 (284, 331)	118 (284, 118)	827 (284, 544)
<i>Luzula campestris</i>	G	66	12	12 (10, 9)	21	136 (123, 45)	24 (24, 24)	449 (378, 71)
<i>Matricaria recutita</i>	D	100		1 (1, 1)		189 (95, 95)	189 (95, 95)	189 (95, 95)
<i>Myosotis arvensis</i>	D	100		1 (1, 1)		71 (47, 24)	71 (47, 24)	71 (47, 24)
<i>Myosotis discolor</i>	G	80	1	3 (1, 2)	<1	24 (24, 24)	24 (24, 24)	24 (24, 24)
<i>Myosotis ramosissima</i>	G	70	2	3 (3, 0)	1	32 (32, 0)	24 (24, 0)	47 (47, 0)
<i>Ononis repens</i>	G	58	1	1 (1, 0)	<1	24 (24, 0)	24 (24, 0)	24 (24, 0)
<i>Oxalis stricta</i>	D	100		2 (1, 2)		47 (24, 35)	24 (24, 24)	71 (24, 47)
<i>Papaver rhoeas</i>	D	100		1 (1, 1)		47 (24, 24)	47 (24, 24)	47 (24, 24)
<i>Persicaria amphibia</i>	M	100		1 (0, 1)		24 (0, 24)	24 (0, 24)	24 (0, 24)
<i>Persicaria maculosa</i>	D	100		1 (0, 1)		24 (0, 24)	24 (0, 24)	24 (0, 24)
<i>Pimpinella saxifraga</i>	G	31	15	5 (5, 0)	31	99 (99, 0)	24 (24, 0)	307 (307, 0)
<i>Plantago lanceolata</i>	G	63	21	21 (21, 12)	231	952 (905, 83)	24 (24, 24)	3924 (3806, 284)
<i>Plantago major</i> s.l.	D	90	2	11 (9, 8)	2	146 (126, 59)	24 (24, 24)	969 (709, 260)
<i>Plantago media</i>	G	26	5	2 (1, 1)	7	24 (24, 24)	24 (24, 24)	24 (24, 024)
<i>Poa angustifolia</i>	G	96	2	15 (15, 6)	1	98 (74, 59)	24 (24, 24)	260 (142, 142)

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SITE CONDITIONS

App. 1, cont. Species	Habitat	SAI	Frequency		Abundance			
			AV	SB	AV	SB 0-10 (0-5, 5-10) Seeds per m ²		
			0-10 (0-5, 5-10)		Mean	Minimum	Maximum	
<i>Poa palustris</i>	G	100		1 (1, 0)		71 (71, 0)	71 (71, 0)	71 (71, 0)
<i>Poa pratensis</i> s. str.	G	31	16	8 (5, 7)	38	53 (28, 41)	24 (24, 24)	118 (47, 95)
<i>Poa trivialis</i> s. str.	G	72	11	18 (17, 15)	51	545 (430, 167)	24 (24, 24)	1962 (1300, 662)
<i>Polygonum aviculare</i> agg.	D	100		5 (2, 4)		47 (24, 47)	24 (24, 24)	118 (24, 118)
<i>Potentilla erecta</i>	G	69	2	1 (1, 1)	2	827 (544, 284)	827 (544, 284)	827 (544, 284)
<i>Prunella vulgaris</i>	G	79	4	6 (6, 1)	2	91 (79, 71)	24 (24, 71)	189 (165, 71)
<i>Ranunculus acris</i>	G	17	19	6 (6, 3)	96	79 (63, 32)	24 (24, 24)	142 (142, 47)
<i>Ranunculus auricomus</i> agg.	G	87	1	3 (3, 1)	<1	39 (32, 24)	24 (24, 24)	47 (47, 24)
<i>Ranunculus bulbosus</i>	G	73	3	9 (8, 1)	5	55 (59, 24)	24 (24, 24)	260 (260, 24)
<i>Ranunculus flammula</i>	M	100		1 (1, 1)		402 (284, 118)	402 (284, 118)	402 (284, 118)
<i>Ranunculus nemorosus</i>	G	100		3 (2, 1)		32 (35, 24)	24 (24, 24)	47 (47, 24)
<i>Ranunculus repens</i>	u	80	5	12 (10, 6)	27	333 (267, 221)	24 (24, 24)	1040 (520, 544)
<i>Rhinanthus minor</i>	G	46	3	2 (2, 0)	24	343 (343, 0)	142 (142, 0)	544 (544, 0)
<i>Rubus idaeus</i>	W	100		3 (1, 2)		32 (24, 35)	24 (24, 24)	47 (24, 47)
<i>Rumex acetosa</i>	G	47	18	15 (14, 6)	59	104 (100, 28)	24 (24, 24)	260 (260, 47)
<i>Rumex crispus</i>	D	72	2	2 (2, 0)	3	567 (567, 0)	71 (71, 0)	1064 (1064, 0)
<i>Rumex obtusifolius</i>	D	90	2	4 (4, 3)	1	272 (106, 221)	24 (24, 71)	520 (355, 426)
<i>Sagina procumbens</i>	D	100		3 (2, 2)		47 (35, 35)	24 (24, 24)	95 (47, 47)
<i>Salix caprea</i>	W	100		4 (3, 2)		35 (24, 35)	24 (24, 24)	47 (24, 47)
<i>Sanguisorba minor</i> s.l.	G	30	3	1 (1, 1)	27	189 (142, 47)	189 (142, 47)	189 (142, 47)
<i>Sanguisorba officinalis</i>	G	14	14	3 (3, 0)	323	197 (197, 0)	71 (71, 0)	378 (378, 0)
<i>Scirpus sylvaticus</i>	G	100		2 (1, 1)		35 (24, 47)	24 (24, 47)	47 (24, 47)
<i>Silene flos-cuculi</i>	G	76	4	7 (6, 5)	6	226 (185, 95)	24 (24, 47)	851 (780, 165)
<i>Solanum nigrum</i>	D	100		1 (1, 1)		71 (24, 47)	71 (24, 47)	71 (24, 47)
<i>Solidago virgaurea</i>	u	100		2 (1, 2)		83 (71, 47)	24 (71, 24)	142 (71, 71)
<i>Sonchus asper</i>	D	100		3 (1, 2)		24 (24, 24)	24 (24, 24)	24 (24, 24)
<i>Stellaria graminea</i>	G	68	6	8 (7, 3)	6	77 (68, 47)	24 (24, 24)	331 (236, 95)
<i>Stellaria media</i> agg.	D	83	2	6 (4, 3)	1	28 (24, 24)	24 (24, 24)	47 (24, 24)
<i>Taraxacum officinale</i> agg.	u	28	20	17 (15, 8)	535	185 (165, 83)	24 (24, 24)	969 (851, 331)
<i>Thlaspi arvense</i>	D	100		3 (2, 2)		638 (390, 567)	71 (236, 71)	1608 (544, 1064)
<i>Trifolium campestre</i>	G	100		11 (10, 8)		123 (97, 47)	24 (24, 24)	402 (331, 118)
<i>Trifolium pratense</i>	G	44	21	19 (18, 15)	408	391 (334, 95)	24 (24, 24)	1820 (1608, 520)
<i>Trifolium repens</i>	G	59	20	21 (21, 20)	605	1274 (1017, 271)	71 (71, 24)	5177 (4634, 780)
<i>Tripleurospermum perforatum</i>	D	100		1 (1, 0)		71 (71, 0)	71 (71, 0)	71 (71, 0)
<i>Trisetum flavescens</i>	G	2	18	1 (1, 0)	131	24 (24, 0)	24 (24, 0)	24 (24, 0)
<i>Urtica dioica</i> subsp. <i>dioica</i>	D	91	2	10 (7, 6)	3	104 (78, 83)	24 (24, 24)	378 (331, 213)
<i>Veronica arvensis</i>	G	10	7	1 (1, 0)	4	24 (24, 0)	24 (24, 0)	24 (24, 0)
<i>Veronica chamaedrys</i> s.l.	G	80	10	17 (15, 12)	22	467 (408, 152)	24 (24, 24)	1962 (1702, 473)
<i>Veronica persica</i>	D	100		1 (1, 1)		426 (95, 331)	426 (95, 331)	426 (95, 331)
<i>Veronica serpyllifolia</i>	G	94	3	17 (16, 13)	2	213 (160, 82)	24 (24, 24)	733 (567, 331)
<i>Vicia angustifolia</i>	G	20	4	1 (0, 1)	3	24 (0, 24)	24 (0, 24)	24 (0, 24)
<i>Vicia cracca</i> agg.	G	11	11	2 (2, 0)	18	35 (35, 0)	24 (24, 0)	47 (47, 0)
<i>Vicia hirsuta</i>	D	69	4	3 (2, 3)	2	79 (71, 32)	24 (24, 24)	165 (118, 47)
<i>Vicia</i> spp.	u	100		1 (1, 0)		24 (24, 0)	24 (24, 0)	24 (24, 0)
<i>Vicia tetrasperma</i>	D	100		1 (0, 1)		24 (0, 24)	24 (0, 24)	24 (0, 24)
<i>Viola arvensis</i>	D	100		5 (2, 3)		24 (24, 24)	24 (24, 24)	24 (24, 24)
<i>Viola riviniana</i>	W	81	1	2 (2, 1)	<1	118 (95, 47)	95 (47, 47)	142 (142, 47)

SEED BANK DIVERSITY IN MESIC GRASSLANDS AND THEIR RELATION TO VEGETATION, MANAGEMENT AND SITE CONDITIONS

App. 1, cont. Species	Habitat	SAI	Frequency		Abundance		
			AV	SB	AV	SB 0-10 (0-5, 5-10) Seeds per m ²	
				0-10 (0-5, 5-10)		Mean	Minimum
Species in aboveground vegetation only							
<i>Achillea ptarmica</i> agg.	G	0	2		2		
<i>Aegopodium podagraria</i>	D	0	1		3		
<i>Alchemilla</i> ssp.	u	0	2		2		
<i>Alopecurus pratensis</i>	G	0	12		30		
<i>Anthriscus sylvestris</i>	G	0	12		15		
<i>Arctium lappa</i>	D	0	1		2.5		
<i>Artemisia vulgaris</i>	D	0	1		<1		
<i>Bistorta officinalis</i>	G	0	5		15		
<i>Briza media</i>	G	0	1		1		
<i>Bromus hordeaceus</i>	u	0	5		11		
<i>Bromus racemosus</i>	G	0	1		<1		
<i>Campanula rapunculus</i>	W	0	2		1		
<i>Carex flacca</i>	u	0	1		<1		
<i>Carex pallescens</i>	G	0	1		2.5		
<i>Carex panicea</i>	M	0	1		<1		
<i>Carex spicata</i>	W	0	1		<1		
<i>Carex</i> spp.	u	0	1		1		
<i>Centaurea scabiosa</i> subsp. <i>scabiosa</i>	G	0	1		2.5		
<i>Cirsium acaule</i>	G	0	1		3		
<i>Cirsium palustre</i>	G	0	3		2		
<i>Colchicum autumnale</i>	G	0	2		21		
<i>Crepis biennis</i>	G	0	8		26		
<i>Crepis capillaris</i>	G	0	1		1		
<i>Cynosurus cristatus</i>	G	0	4		44		
<i>Danthonia decumbens</i>	G	0	1		<1		
<i>Daucus carota</i>	D	0	3		2		
<i>Dianthus deltooides</i>	G	0	1		<1		
<i>Elymus caninus</i>	D	0	1		1		
<i>Elymus repens</i>	D	0	3		24		
<i>Equisetum arvense</i>	u	0	2		1		
<i>Euphrasia officinalis</i> s.l.	G	0	1		2.5		
<i>Filipendula ulmaria</i>	G	0	2		3		
<i>Galium saxatile</i>	G	0	1		3.5		
<i>Galium verum</i> agg.	G	0	4		11		
<i>Geranium pusillum</i>	D	0	1		<1		
<i>Helicotrichon pratense</i>	G	0	2		1		
<i>Hieracium lachenalii</i>	W	0	1		<1		
<i>Hieracium laevigatum</i>	W	0	1		5		
<i>Hieracium pilosella</i>	G	0	3		3.5		
<i>Hieracium sabaudum</i>	W	0	2		7.5		
<i>Hieracium</i> spp.	u	0	2		1		
<i>Holcus mollis</i>	W	0	1		<1		
<i>Knautia arvensis</i> s.str.	G	0	8		25		
<i>Lysimachia nummularia</i>	u	0	3		3		
<i>Malva moschata</i>	G	0	1		2.5		
<i>Molinia caerulea</i> s. str.	u	0	1		<1		
<i>Myosotis scorpioides</i> agg.	G	0	2		1		

SEED BANK DIVERSITY IN MESIC GRASSLANDS AND THEIR RELATION TO VEGETATION, MANAGEMENT AND SITE CONDITIONS

App. 1, cont. Species	Habitat	SAI	Frequency		Abundance		
			AV	SB	AV	SB 0-10 (0-5, 5-10) Seeds per m ²	
				0-10 (0-5, 5-10)		Mean	Minimum
<i>Myosotis spp.</i>	u	0	1		<1		
<i>Nardus stricta</i>	G	0	1		3		
<i>Phelum pratense s.str.</i>	G	0	9		103		
<i>Phyteuma nigrum</i>	G	0	2		1		
<i>Poa annua</i>	D	0	1		<1		
<i>Polygala serpyllifolia</i>	G	0	1		<1		
<i>Prunus spinosa agg.</i>	W	0	1		<1		
<i>Ranunculus ficaria</i>	W	0	1		<1		
<i>Rhinanthus alectorolophus s.l.</i>	u	0	1		<1		
<i>Rumex acetosella subsp. acetosella</i>	u	0	1		<1		
<i>Saxifraga granulata</i>	G	0	3		2.5		
<i>Senecio jacobaea</i>	G	0	2		1		
<i>Silaum silaus</i>	G	0	2		1		
<i>Succisa pratensis</i>	G	0	2		4		
<i>Thymus pulegioides s.l.</i>	G	0	2		1		
<i>Trifolium dubium agg.</i>	G	0	9		8.2		
<i>Trifolium medium</i>	W	0	1		2.5		
<i>Valerianella locusta</i>	D	0	1		<1		
<i>Vicia sepium</i>	u	0	2		1		
<i>Vicia villosa s.l.</i>	D	0	1		<1		

6 The population structure of three perennial grassland species (*Pimpinella saxifraga* L., *Leontodon autumnalis* L., *Sanguisorba officinalis* L.) in relation to management and habitat conditions

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Applied Vegetation Science: submitted

6.1 Abstract

Question: (i) Is there an impact of extensive mowing and grazing regimes (management) and habitat conditions on population stage structure of three indicator species of mesic long-term grasslands (*Arrhenatheretalia*)? (ii) Are there interspecific differences linked to C-S-R plant strategy type and clonal growth between managements?

Location: Lahn-Dill Highlands in central-western Germany.

Methods: The population structure of *Pimpinella saxifraga* L., *Leontodon autumnalis* L. and *Sanguisorba officinalis* L. was analysed on 48 grassland sites, which differed in management regime (i.e., silage meadows, hay meadows, meadow-pastures, pastures) and habitat conditions (e.g., nutrient availability and vegetation structure).

Results: Species responded differently to habitat conditions and significant effects were stage-specific. The main variables of influence were soil moisture, nutrient availability, and litter coverage. Management regimes had significant effects on population stage structure of the study species but accounted for less of the explained variance than differences between populations (i.e. sites). Especially meadow-pastures provided higher seedling recruitment and early establishment, whereas the response of adult stages varied between management regimes. The stress strategist *P. saxifraga* responded positively to the regime with low disturbance (hay meadows), while the ruderal strategist *L. autumnalis* had higher densities of generative individuals in regimes with high disturbance (silage-meadows, pastures). Significant inter-specific differences in densities of adult stages were linked to different strategies of clonal propagation.

Conclusion: Viable populations of all three species may occur under all regimes of current management. Thus, from a conservation perspective, a wide range of management options was confirmed for the study region.

Keywords: demography, long-living perennial, low-intensity land use, mesic grasslands, management regimes, marginal region, recruitment

Nomenclature: Wisskirchen & Haeupler (1998)

6.2 Introduction

Semi-natural grasslands of Europe have been created and maintained by human land-use over hundreds of years and in the last decades underwent a sharp decline due to intensification and abandonment (e.g., Burel et al. 1998; Mac Donald et al. 2000). However, in contemporary marginal regions, mainly within mountainous areas, these habitats still predominate the agricultural land (e.g., Cousins & Eriksson 2002; Vandvik & Birks 2002; SRU 2004). In such regions traditional low intensity grasslands represent a land use option until today. Agri-environmental schemes as introduced in the early 1990s in Europe (European Communities 1985) benefit the environment and biodiversity of grasslands by compensating farmers financially for loss of income associated with conservation measures (e.g., Critchley et al. 2004; Knop et al. 2006) such as prescriptions for management schemes, e.g. the ban of fertilizer application, the date of the first mowing or the amount of grazing animals (LWU, life weight units ha⁻¹). Furthermore, according to OECD (2004), the common agricultural policy (CAP) reform is expected to ensure the maintenance of grassland areas as well as to lead to a particular increase of pasture land along with extensification.

Management has a considerable influence on almost all aspects of grassland dynamics (Lennartson & Oostermeijer 2001) and diverse management schemes can differently affect the dynamics and composition of plant communities and individual plant species. Species response to management may not only be manifested as presence/absence, but also in population demography, the changes of which may anticipate possible floristic changes. The different disturbance regimes have a major impact on seed availability and on suitable safe sites (Grubb 1977; Harper 1977), which are key factors for reproduction and successful recruitment in plant populations (Eriksson & Ehrlén 1992). Grazing disturbs grassland sward creating gaps that facilitate seedling recruitment while at the same time limiting the rate of recolonization (Bullock et al. 1995; Bakker et al. 1996; Burke & Grime 1996). Also a higher mowing frequency as applied in silage meadows supports open vegetation and soil disturbances (McIntyre et al. 1995; Eriksson & Eriksson 1997). Different cutting dates and frequencies can have large impact on plants (e.g., Kirkham & Tallwin 1995; Zechmeister et al. 2003) through differences in species regenerative abilities, furthermore they differently influence light competition (Lepš 1999). Differences in population structure were shown to be also related to habitat conditions such as nutrient availability, soil moisture and vegetation structure (e.g. Colling et al. 2002; Bissels et al. 2004) that, given extensive management schemes, are

largely not related to current management. However, viable seedlings are necessary for population growth-rates to remain stable or positive.

From a conservation perspective, it is necessary to develop criteria to make priorities for choosing appropriate management regimes that allow for high species diversity. The performance of viable (i.e. growing or stable) populations is one important criterion for selecting management regimes, since the dispersal capacity of many grassland species is limited in space and time, thus restricting possibility of species enrichment in floristically impoverished sites (e.g., Bakker et al. 1996; Donath et al. 2003). Particularly, when there is no time or money for detailed demographic monitoring of individual plants over a period of years, information on population structure can reveal important information on the demographic status and future outlook of a population and their relation to management but also to environmental factors (Oostermeijer et al. 1994; Hegland et al. 2001; Eckstein et al. 2004). This method has proved useful to describe the demographic viability of populations in cultural landscapes in relation to management (Bühler & Schmid 2001; Lennartsson & Oostermeijer 2001), management and site conditions (Oostermeijer et al. 1994; Colling et al. 2002; Bissels et al. 2004) or land use change (Lindborg et al. 2005) as well as evaluating populations in their natural habitats in landscapes dominated by natural disturbance regimes (García et al. 2002).

In the present study we used this approach to assess the suitability of different mowing and grazing regimes (management regimes) for the preservation of species-rich mesic grasslands (order *Arrhenatheretalia*) in a mountainous marginal region in Germany. There are different current management regimes in the study area, which provide strong differences in disturbance impact, ranging from hay meadows with only one or two cuts per year to pastures grazed from May to September and silage meadows mown three times a year. Consequently, there is a need to assess the suitability of the alternative management options in maintaining grassland communities (Bühler & Schmid 2001; Hegland et al. 2001; Colling et al. 2002). For this purpose, we studied characteristic but also abundant species from the monitored community as suggested by Bühler & Schmid (2001). Additionally, in regions that underwent land-use change with conversion from arable land to grassland, long-term grasslands, i.e. at least 20 years up to 50 years of grassland use, were evaluated to have higher species richness (Waldhardt & Otte 2003; Wellstein et al. accepted,a) and contain indicator species for long-term grassland use (Donath et al. 2003). The perennial herbs *Pimpinella saxifraga*, *Leontodon autumnalis* and *Sanguisorba officinalis* that predominantly occur in managed grasslands

(Oberdorfer 1994) were present under all current management regimes of the study region. They are also indicator species of long-term grassland use (Donath et al. 2003; Wellstein unpubl.). Furthermore, in semi-natural grasslands, perennial species are representative for a major part of the plant species in the community, since some 90% of the species are relatively long-living perennials (Lindborg et al. 2005). For all these reasons *P. saxifraga*, *L. autumnalis* and *S. officinalis* were chosen for this study. While *P. saxifraga* due to its dependence upon infertile grassland habitats and low colonizing ability is a currently declining species, *L. autumnalis* is relatively mobile and appears to be increasing by exploiting some artificial habitats (Grime et al. 1988). Due to the differences in species traits such as tolerance to disturbance and nutrient requirements, we expected a species specific impact of the determinants management regime and habitat conditions. Specifically, we hypothesized that management regimes with higher disturbance (silage meadows and pastures) should be beneficial for populations of the ruderal species *L. autumnalis*, whereas populations of the stress strategist *P. saxifraga* should be negatively affected, and also the tall herb *S. officinalis* should not benefit from enhanced levels of disturbance. Finally, we intended to identify management regimes that positively affect the demographic viability of the three study species in order to provide advice on the best long-term conservation management.

The main objectives of the study were (i) to quantify the impact of management regimes and habitat characteristics, i.e. site conditions (nutrient availability, soil moisture, pH, and light supply), vegetation structure and species composition, on population stage structure and (ii) to evaluate management options for the sustainable conservation of populations of the three species and species-rich mesic grasslands in general.

6.3 Material and Methods

Study species

Three species were selected as study species: *Pimpinella saxifraga* L., *Leontodon autumnalis* L. and *Sanguisorba officinalis* L. (hereafter referred to as *P. saxifraga*, *L. autumnalis* and *S. officinalis*). The choice of species was based on three criteria: they should be fairly common (medium frequency ca. 60 %) in semi-natural grasslands, occur under all four currently applied management regimes and they should be indicators of long-term grasslands. Some life-cycle characteristics of the species are summarised in Table 1.

Table 1. Life-history traits for the study species *Sanguisorba officinalis*, *Pimpinella saxifraga*, *Leontodon autumnalis*. NV=Ellenberg nutrient value; MV=Ellenberg moisture value. Data on life-form, strategy, germination were based on Grime et al. (1988), data on height, flowering and seed set were based on Rothmaler (2002), data on seed bank were based on Wellstein et al. (accepted,b), data on clonal growth were based on Klimeš et al. (1997).

Traits	<i>S. officinalis</i>	<i>P. saxifraga</i>	<i>L. autumnalis</i>
Life-form	perennial	perennial	perennial
Strategy	CSR	S/SR	R/CSR
Ellenberg NV;MV	5;6	2;3	5;5
Height (cm)	30 – 100 – (150)	(10) 30 – 60	15 – 45
Growth form	Semi-rosette	Semi-rosette	Rosette
Flowering	VI–IX	VII–IX	VI–X
Seed set	VIII–IX	VIII–X	VI–X
Germination	spring (autumn)	spring, chilling	spring (autumn)
Seed bank	transient	transient	persistent
Clonal growth	Frequent (stem-origin, rhizom)	Limited (root- and stem-origin)	Frequent (stem-origin, rhizom)
Storage organ		Primary root and lower stem	

All three species are long-living herbaceous perennial plants. *P. saxifraga* (*Apiaceae*) predominantly occurs in nutrient poor meadows and pastures but also in *Pinus*-forests and in heathlands, indicates nutrient poor and relatively dry conditions and is pollinated by insects. The species is considered to be a character species of the class *Festuco-Brometea* (Oberdorfer 1994). *P. saxifraga* did not show vegetative reproduction in the field, although it may occasionally reproduce vegetatively (Lindborg et al. 2005). *L. autumnalis* (*Asteraceae*) predominantly occurs in nutrient rich pastures, lawns, steppe-communities and is pollinated by insects as well as by auto-pollination. The species is considered to be a character species of the alliance *Cynosurion* (Oberdorfer 1994). In contrast to the other two species, *L. autumnalis* has a persistent seed bank (Wellstein et al. accepted,b). *S. officinalis* (*Rosaceae*) predominantly occurs in wet meadows and fens but also in wet meadows on nutrient and base rich soils, indicates an alternating moisture regime and is pollinated by insects. The species is considered to be a character species of the order *Molinetalia* (Oberdorfer 1994). In contrast to *P. saxifraga*, *L. autumnalis* and *S. officinalis* showed vegetative propagation in the field.

Study area and sampling

The Lahn-Dill-Highland is a marginal, sub-mountainous region with predominance of grassland areas in central western Germany. Since the 1950s, the Lahn-Dill Highlands have been subject to major agricultural land-cover changes, resulting mainly in a decline in arable land and an increase in grassland and fallow land (Hietel et al. 2004). In many places, extensive grassland use has replaced the traditional, extremely small-parcelled crop production and crop/grassland rotation. Until today this study region is characterised by the predominance of low-intensity farming that originates from disadvantageous natural site conditions and the political and social history of the region (Nowak 1988). The mean annual temperature is 6 to 8°C and the average annual precipitation ranges from 650 to 1100mm. In conjunction with the edaphic conditions, the relatively wet climate results in a high variability of the soil-water potential.

To investigate whether demographic structure of populations of the three selected study species reflect differences in management regimes and habitat conditions of long term grasslands, 48 populations (16 populations per species) were selected. These differed in the management regime (four regimes with a replication of 4 sites per species-management combination) and showed variance in habitat conditions (i.e. structure and composition of the vegetation and soil chemical parameters). All studied populations were situated in grassland sites to which a particular management regime had been applied for at least 25 years. The investigated grasslands received the following management regimes: (i) silage meadows with early mowing, high mowing intensity (three cuts per year) and little fertiliser input (up to 30 kg N ha⁻¹ year⁻¹), (ii) hay meadows with late mowing in mid-June and one or two cuts per year, (iii) meadow-pastures with late mowing and subsequent cattle grazing and (iv) pastures with rotational grazing by cattle between May and September. The three latter practices were characterised by the lack of fertiliser input; the amount of grazing cattle did not exceed 1.5 life weight units ha⁻¹.

We conducted the sampling in August and early September 2004 (03.08.04 to 07.09.04), i.e. during the secondary growth. 2004 was a year with average climatic conditions; the preceding year (2003) was characterized by a hot and dry summer. In each population two randomly selected plots of 1 m² were analysed, yielding a total of 96 samples (32 per species). For each study species the total number of individuals was counted in each plot, using a predefined classification of phenological stages (Tab. 2, see also below). Although clonal propagation may occur in the selected species, each

rosette was considered as an individual. The habitat variables related to structure and composition of the vegetation was measured in each plot: the coverage of all plants, mosses, plant litter as well as the percentage of bare soil surface was estimated, all vascular plant species we determined and cover-abundance was visually estimated on a modified Braun-Blanquet-scale (with cover degree 2 subdivided into 2a = >5-15% and 2b = >15-25%). Compositional gradients in the vegetation of the study plots were represented by the scores of the first two axes of a Detrended Correspondence Analyses (DCA) on square root transformed cover data (species with less than three occurrences were excluded) for the data set of each species (n=32 plots). The vegetation data were also used to calculate cover weighted means of the Ellenberg indicator values for nutrients, moisture and light (Ellenberg et al. 1992). As soil related habitat variables we measured the pH value (in CaCl₂) of the fine soil as well as amounts of plant available phosphorus (P_{CAL}) and potassium (K_{CAL}) using the calcium-acetate-lactate (CAL) extraction method. The soil samples were taken from three randomly situated permanent plots of 25 m² per each site as established in a previous study. Within each 25 m² permanent plot, 20 cores of 10 cm depth were taken at random locations using a soil corer of 3 cm in diameter.

As a further habitat variable relative light intensity penetrating to the ground was measured using a Line Quantum Sensor of one meter length (LI-COR: LI-191SA). We recorded photosynthetic active radiation (PAR, 400-700 nm) at ground level relative to an above canopy reference sensor repeating the measurement four times at random locations within each plot.

Classification of life stages

To describe the stage structure of populations of each study species, four different phenological stage classes (i-iv) were used. These stage classes were based on the following growth parameters: existence of cotyledons (all species); leave morphology of the leaf blades of the ground rosette: length and width (*L. autumnalis*), number of pinnules (*P. saxifraga* and *S. officinalis*) (see Table 2); existence of flowering stalks (all species); clonal growth (all species). Stage classes: (i) Seedlings (s) of all three species had cotyledons and up to three of four primary leaves. (ii) Juveniles (j) of *L. autumnalis* had up to 6 leaves with a length up to 20 cm and were only slightly serrate (width up to 10 mm); juveniles of *P. saxifraga* had up to 6 leaves and up to 9 pinnules, *S. officinalis* juveniles had up to 7 pinnules. (iii) Vegetative adults (v) of *L. autumnalis* were

characterised by a rosette with up to 15 leaves. The leaves were up to 28 cm long and had more serrate structure (width up to 20 mm); vegetative adults of *P. saxifraga* had up to 9 leaves and up to 13 pinnules and *S. officinalis* had leaves with up to 13 pinnules. (iv) Generative adults (g) normally had one or more flowering stalks. Rosette characters are similar to those of vegetative plants, but leaves of *L. autumnalis* were strongly serrate (width up to 45 mm). Rosettes whose flowering stalks had been grazed were also considered as generative adults.

Generally, this classification of phenological stages was very robust in the field. In their early growth period, vegetative individuals of clonal origin of *L. autumnalis* and *S. officinalis* showed growth parameters similar to juvenile individuals. They were identified as vegetative individuals by the lack of a well developed primary root and by the detection of the organs of their clonal origin to which they were connected.

Table 2. Growth parameters in phenological stage classes of the study species *Sanguisorba officinalis*, *Pimpinella saxifraga*, *Leontodon autumnalis*. MV = Mean value.

<i>P. saxifraga</i> (n=1900)	seedlings	juveniles	vegetative adults	generative adults
Number of ground leaves	up to 4 (MV 2.6)	up to 6 (MV 2.8)	up to 9 (MV 3.9)	up to 9 (MV 1.6)
Number of pinnules	up to 3 (MV 1.0)	up to 9 (MV 5.3)	up to 13 (MV 9.1)	up to 15 (MV 5.5)
<i>L. autumnalis</i> (n=1500)	seedlings	juveniles	vegetative adults	generative adults
Number of ground leaves	up to 3 (MV 2.2)	up to 6 (MV 3.8)	up to 15 (MV 7.1)	up to 20 (MV 8.9)
Length of longest ground leaf (cm)	up to 10 (MV 7)	up to 20 (MV 16)	up to 28 (MV 20)	up to 30 (MV 22)
Width of longest ground leaf (mm)	up to 0.45 (MV 3.6)	up to 10 (MV 6.8)	up to 20 (MV 13.0)	up to 45 (MV 23.3)
<i>S. officinalis</i> (n=2000)	seedlings	juveniles	vegetative adults	generative adults
Number of ground leaves	up to 3 (MV 1.3)	up to 4 (MV 2)	up to 7 (MV 2.7)	up to 8 (MV 3)
Number of pinnules	up to 3 (MV 3)	up to 7 (MV 5.1)	up to 13 (MV 8.8)	up to 13 (MV 9.1)

Data analysis

For each population the density of individuals of the different life stage classes per m² was calculated. To test for the overall effect of species and management and their interaction on stage densities we applied a MANOVA, using the robust Pillai's trace for interpretation of results (Quinn & Keough 2002). Prior to analysis mean values for each allotment (population) were calculated (n=48). In case of significance, the analysis was followed by a Tukey's test.

The relationship between habitat variables, management and the density of each stage class was investigated by multiple regression analysis. Spearman rank correlation coefficients between predictor variables were examined to detect collinearity (Quinn &

Keough 2002). Site conditions were not intercorrelated with the management regimes. However, omission of other, intercorrelated variables resulted in the following variables remaining in the analysis: management and ten habitat variables, related to nutrient availability (contents of plant available P and K, mean Ellenberg nutrient value), to soil moisture (mean Ellenberg moisture value), to soil acidity (pH value), to vegetation structure (cover of total vegetation, litter and bryophytes) and to light availability (relative light intensity, mean Ellenberg light value). These were chosen as predictor variables in the multiple regression model. If necessary, data were transformed prior to analyses to meet assumptions of analysis of variance (Zar 1999). For the design of models in multiple regressions the forward selection procedure was applied. As a measure for the relative contribution of each factor to the total variability in the density of the respective live stage class, we used the ratio of the sum of squares of the factor of interest to the total sum of squares (i.e. for all factors and the error).

To analyse the counts of individuals per plot and to test for differences in the demographic status of the three species between management regimes we used two-way analysis of variance (ANOVA) with the densities of each life stage of each species as dependent variable and with management regime as well as population as factors; population was used as a nested random factor within management regimes and refers to the established population of a site. In case of significance the analysis was followed by a Tukey's test ($\alpha < 0.05$). As a measure for the relative contribution of each of the two factors to the total variability in the density of the respective live stage class, we used the ratio of the sum of squares of a single factor to the total sum of squares (i.e. for both factors and the error).

Regression analyses were carried out with the General Linear Model module of STATISTICA 6.0 (Anon. 2002). MANOVA, ANOVA and associated tests were performed using SAS 8.2 (Anon. 1999).

6.4 Results

Interspecific differences in population structure

MANOVA across all life stage classes resulted in an overall significant species effect (Pillai's Trace=0.93420993, $F_{8,68}=7.45$; $p < 0.0001$) on stage density whereas there was no overall effect of management or the interaction term (species*management) probably due to the high variability among populations. Tukey test after univariate ANOVA confirmed significant differences among species for the adult stages with significantly lower mean density of vegetative adults in *P. saxifraga* compared to *L. autumnnalis*

($p=0.0309$) and *S. officinalis* ($p=0.0015$) and significant differences in the generative adult stage with a significantly higher mean density of flowering individuals in *L. autumnalis* compared to *S. officinalis* ($p<0.001$) and *P. saxifraga* ($p<0.001$) (Table 3).

Table 3. Results of univariate ANOVA after significant MANOVA (Pillai's Trace=0.93420993, $F_{8,68}=7.45$; $p<0.0001$) on the effects of species and management across all life stage classes (untransformed data). D.f. = degrees of freedom; MS = Mean sum of squares.

	Source of variation	Df	MS	F	p
Seedlings	species	2	9140	1.94	0.1584
	management	3	8785	1.87	0.1530
	species*management	6	3110	0.66	0.6818
	error	36	4710		
Juveniles	species	2	1603	2.15	0.1310
	management	3	942	1.26	0.3013
	species*management	6	350	0.47	0.8257
	error	36	745		
Vegetative adults	species	2	7864	7.59	0.0018
	management	3	551	0.53	0.6633
	species*management	6	1530	1.48	0.2137
	error	36	1036		
Generative adults	species	2	7552	17.83	<0.0001
	management	3	331	0.78	0.5117
	species*management	6	377	0.89	0.5120
	error	36	423		

Relationships between habitat variables and population structure

The sets of study sites of each of the three study species are characterized as mesic grassland habitats and therefore all have the same range of the habitat conditions nutrient availability, soil moisture and pH. Nutrient availability of the study sites ranged from 2.5 to 12.6 mg*100g⁻¹ plant available P and from the Ellenberg nutrient value 4.2 to 6.7; soil moisture ranged from the Ellenberg moisture value 4.4 to 5.7; the pH value ranged from 4.2 to 6.6. In multiple regression analyses, habitat conditions explained different parts of the variation in the population structure of *P. saxifraga* (32% among seedlings, 29% among vegetative adults, 30% among generative adults), of *S. officinalis* (7% among seedlings) and of *L. autumnalis* (74% among generative adults). The main variables of influence were the nutrient availability and soil moisture. Multiple regression analyses confirmed a strong negative relationship between soil moisture and

the density of seedlings of *P. saxifraga*, whereas vegetative adults were significantly positive correlated with moisture (Fig. 1).

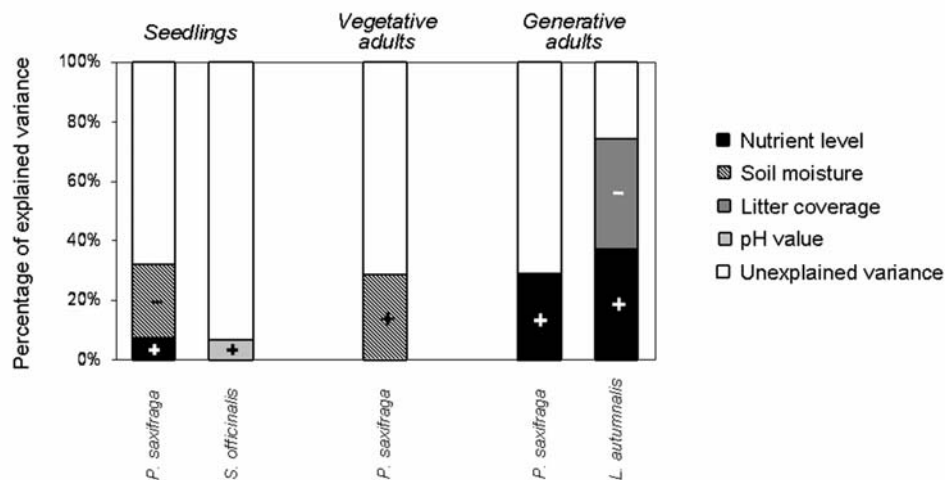


Fig. 1. Stepwise multiple regression of the relationship between the density of four life stage classes of the study species (*Pimpinella saxifraga*, *Leontodon autumnalis*, *Sanguisorba officinalis*) and habitat characteristics on the population level (n = 16). For the full model 11 predictor variables were chosen (see Methods for details). Forward selection of variables was used (p<0.05). Positive or negative correlation is indicated by “+” or “-“ inside bars. Soil moisture refers to the Ellenberg moisture value, nutrient availability refers to contents of plant available phosphorus or the Ellenberg nutrient value.

Nutrient availability was significantly positive correlated with seedlings and generative adults. The studied populations of *S. officinalis* showed a significantly positive correlation between seedling density and pH value. *L. autumnalis* populations showed a strong negative relationship between the coverage of litter (ranging from 5% to 35%) and the density of generative adults and a strong positive relationship between this stage and the nutrient availability. This indicates that species generally responded differently to site conditions and that significant effects were stage-specific.

Impact of management on population structure

Univariate two-way ANOVAs calculated for each species separately revealed significant differences between management regimes for most stage classes, however, explained amounts of population variation were mostly relatively low (Table 4). For *S. officinalis* these effects were caused mainly by relatively high densities of seedlings and juveniles in meadow-pastures as compared to the other three management regimes (Fig. 2.). This holds true also for seedlings of *L. autumnalis*, whereas in its juvenile stage class differences were significant only between meadow-pastures and hay-meadows. For seedlings and juveniles, *P. saxifraga* showed higher densities in meadows and

meadow-pastures than in silage meadows and pastures, but differences were not significant. The density of adults of *P. saxifraga* was highest in hay-meadows and differed for vegetative adults significantly from all other management regimes and for generative adults significantly from silage-meadows. The densities of generative adults of *L. autumnalis* showed significantly higher values in pastures compared to hay-meadows. The vegetative adult stage class of *S. officinalis* showed significantly higher densities in silage-meadows than in hay-meadows and the generative adult stage class showed significantly higher values in meadow-pastures as compared with all other management regimes. Densities of flowering plants were significantly lower in hay-meadows than in silage-meadows and pastures.

For all stages of the three study species the factor population (nested in management) was significant and explained a higher amount of variation than management (Table 4). From data of an additional seed addition experiment also conducted in 2004 we could estimate germination and establishment probabilities for each of the three species (Wellstein unpubl.). Combined with the respective seedling density of the present study (Fig. 2), the resulting estimated annual establishment success of the species varied among management regimes. Accordingly, populations of *P. saxifraga* may have between 6 and 22 new recruits per m² and year, and *L. autumnalis* between 3 and 36. *S. officinalis* showed the lowest establishment success and only in case of meadow-pastures between 3 and 7 new recruits may be expected annually, whereas the other management regimes will not enable recruitment each year.

Table 4. Results of a two-way ANOVA on the effects of management regimes and population on density of the respective life stage class. df = degrees of freedom; MS = Mean sum of squares; vc (%) = relative contribution of individual factors to total variation.

	Source of variation	df	MS	F	p	vc (%)
<i>Pimpinella saxifraga</i>						
Seedlings	management	3	4151.1	2.9	0.0668	7.1
	population(man.)	12	11654.5	8.2	0.0001	79.8
	error	16	1427.7			13.0
Juveniles	management	3	177.0	1.7	0.2096	7.3
	population(man.)	12	418.4	4.0	0.0057	69.4
	error	16	104.9			23.2
Vegetative adults	management	3	565.5	5.2	0.0106	24.3
	population(man.)	12	295.8	2.7	0.0316	50.9
	error	16	108.4			24.8
Generative adults	management	3	159.6	4.4	0.0201	8.5
	population (man.)	12	381.4	10.4	< 0.0001	81.1
	error	16	36.6			10.4
<i>Leontodon autumnalis</i>						
Seedlings	management	3	25064.3	17.2	< 0.0001	25.9
	population(man.)	12	16001.5	11.0	< 0.0001	66.0
	error	16	1475.3			8.1
Juveniles	management	3	2454.2	3.7	0.0333	11.5
	population(man.)	12	3823.7	5.8	0.0008	71.9
	error	16	659.3			16.5
Vegetative adults	management	3	891.4	1.9	0.1764	6.7
	population(man.)	12	2443.7	5.1	0.0016	74.0
	error	16	478.2			19.3
Generative adults	management	3	1854.4	4.8	0.0149	15.1
	population(man.)	12	2084.6	5.3	0.0012	67.9
	error	16	390.5			17.0
<i>Sanguisorba officinalis</i>						
Seedlings	management	3	793.7	26.9	< 0.0001	23.6
	population(man.)	12	604.3	20.4	< 0.0001	71.8
	error	16	29.6			4.7
Juveniles	management	3	653.4	7.1	0.003	31.8
	population(man.)	12	227.8	2.5	0.0464	44.3
	error	16	92.1			23.9
Vegetative adults	management	3	5765.7	4.7	0.015	22.0
	population(man.)	12	3475.3	2.9	0.0262	53.2
	error	16	1216.3			24.8
Generative adults	management	3	156.9	21.3	<0.0001	31.7
	population(man.)	12	74.6	10.1	<0.0001	60.3
	error	16	7.4			7.9

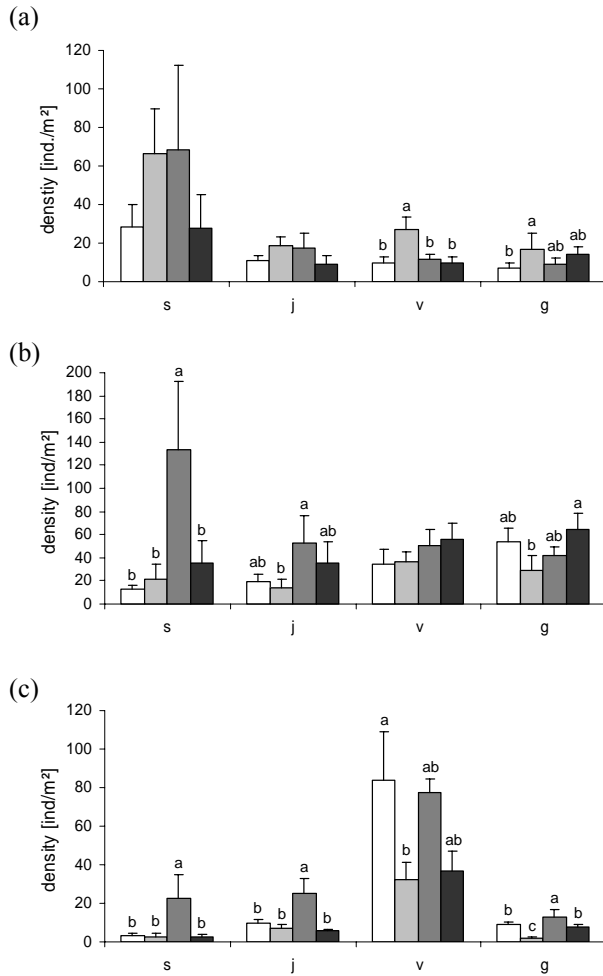


Fig. 2. Density of different life-stage classes (s=seedlings, j=juveniles, v=vegetative adults, g=generative adults) of the investigated grassland species (a) *Pimpinella saxifraga*, (b) *Leontodon autumnalis*, (c) *Sanguisorba officinalis*, and among-population variability (mean \pm SD) with respect to different management regimes. Letters indicate if means differ significantly among managements regimes within each life stage class at $\alpha < 0.05$ (Tukey's test). Management regimes: \square silage meadows, \square meadows, \blacksquare meadow-pastures, \blacksquare pastures.

6.5 Discussion

Impact of habitat conditions on population structure

This study confirmed a species as well as stage specific impact of habitat conditions at the population level. Large differences in the density of life stages were observed among populations of each of the three study species. These differences in population structure were strongly related to habitat conditions, whereas management regime exerted relatively weak effects. The main variables of influence were the nutrient availability, soil moisture and litter accumulation. Higher nutrient availability indicated by the Ellenberg nutrient value or the content of plant available phosphorus led to an increase in the number of *P. saxifraga* seedlings, and in the density of generative adults

of *P. saxifraga* and *L. autumnalis*. Nutrient availability is a major important factor controlling population structure of long-living perennial plants of wet grasslands such as *Serratula tinctoria* (Bissels et al. 2004) and *Scorzonera humilis* (Colling et al. 2002). In *Serratula*, seedlings were negatively affected while density of vegetative adults increased with higher nutrient availability. Similarly, in *Scorzonera* different age states responded differently to nutrient availability, viz. with reduced recruitment of new genets and increased growth of surviving genets. An increase of nutrient availability enhances productivity and competition at a site. Therefore, such negative effects on seedling establishment may be related to higher litter accumulation at more productive sites as proposed by Tilman (1993) or to competition for light with the surrounding vegetation (Lepš 1999). In our study, there was no effect of the litter layer or of the light supply at the soil surface on seedling density in the secondary growth. Other studies, in contrast, found light supply at the soil surface as a major factor controlling reproduction (e.g., Eckstein 2005) and recruitment (e.g., Jensen & Meyer 2001; Bissels et al. 2004). Another experimental study on the effect of fertilisation on regeneration by seeds (Rusch & Fernández-Palacios 1995) reported species specific effects of increased nutrient availability. In our study, the sites inhabited by *P. saxifraga* populations were rather nutrient poor, what may allow a benefit for growth and reproduction through a slightly increased nutrient availability even for a species indicative for nutrient poor conditions (Oberdorfer 1994). Thus, nutrient availability enhances fitness of stress strategists rather than enhancing growth of competitors whose dominance is unlikely under such harsh site conditions.

Significant relationships between soil moisture and the density of stage classes of *P. saxifraga* showed that, in contrast to seedlings, vegetative adults were more numerous in habitats with higher soil moisture. This species, which is indicative for relatively dry soil conditions (Ellenberg et al. 1992; Oberdorfer 1994) may profit only as established, adult individual from higher soil moisture. Findings for the wet grassland species *Scorzonera humilis* (Colling et al. 2002) demonstrate a positive effect of soil moisture (measured by Ellenberg moisture value) on seedling density.

In contrast to *P. saxifraga* and *L. autumnalis*, *S. officinalis* showed rarely significant correlations within the range of habitat conditions of the investigated mesic grasslands. This may be due to a wider amplitude in ecological requirements of the species or due to a higher plasticity. Our results merely indicate that a higher pH level provides somewhat more suitable conditions for germination of seedlings of *S. officinalis*, a

species known to be indicative of more base rich sites. There is also the possibility that other factors, which were not included in our analysis, influenced population variation, e.g., stochastic events such as years with extreme climatic conditions.

Although light availability was not a significant factor in the respective regression model, there was a significantly negative relationship between cover of litter and density of *L. autumnalis* generative adults. This may be interpreted as an inhibitive effect of the litter layer in late summer on development of flowering stalks. According to Grime et al. (1988), *L. autumnalis* appears to be intolerant of shading. Our results and the comparisons with the findings of other studies confirm that species, generally, react differently to site conditions and significant effects are stage-specific.

Effects of management

In our study we found only slightly significant impacts of the different extensive grazing and mowing regimes on population structure of the perennial study species. Meadow-pastures were characterized by significantly higher densities of seedlings and juveniles, mostly in contrast to all other management regimes. In *P. saxifraga*, also hay meadows provided a high seedling density. The higher seedling recruitment and early establishment in meadow-pastures is most likely a combined effect of, first, the lower damage to adult plants and their seeds by subsequent grazing with relatively low intensity in the secondary growth, and, second, the provision of gaps by sward disturbance, which may enhance recruitment of new individuals. For all three study species higher germination and establishment rates in gaps were detected in the additionally applied seed addition experiment (Wellstein unpubl.). This is in line with other studies (e.g. Bullock et al. 1995; Lennartsson & Oostermeijer 2001) suggesting more suitable conditions for species establishment due to trampled gaps. By the example of the biennial *Gentianella campestris* meadow-pastures were shown to be the best conservation sites due to high values for seed production and establishment of rosettes (Lennartsson & Oostermeijer 2001). In contrast to such low grazing intensity, effects of grazing intensity in heavily grazed fens were reported by Bühler & Schmid (2001) on populations of the perennial species *Succisa pratensis* with a destruction of flowering stalks by grazing cattle leading to reduced seed set and lower seedling recruitment.

Whereas with respect to recruitment all species profited from intermediate disturbance in meadow-pastures, the adult stages (vegetative and generative) responded differently

to management regimes in our study. The stress strategist *P. saxifraga* responded positively to the regime with low disturbance, i.e. hay-making, whereas *L. autumnalis* and *S. officinalis* had higher densities of generative individuals in regimes with high disturbance, i.e. silage-meadows and pastures. Irrespective of management regime, significant inter-specific differences in densities of adult stages were linked to different strategies of clonal propagation. Specifically, the ruderal strategist *L. autumnalis* showed high densities of generative adults compared to the other species. *S. officinalis* and *L. autumnalis* as species with effective vegetative reproduction showed higher densities of vegetative adults as compared to *P. saxifraga*.

That there is no overall significant effect of management across species and stages could also be confirmed by MANOVA. Generally, differences between population performances in the different management regimes did not reflect different population types, i.e. regressive populations vs. stable or growing ones. Viable populations of *P. saxifraga*, *L. autumnalis* and *S. officinalis*, as defined by relatively high numbers of seedlings and juveniles, occurred under all management regimes. The calculation of the establishment success based on seedling densities indicated that there will be a contribution of several newly recruited individuals each year for *P. saxifraga* and *L. autumnalis* in all management regimes. In *S. officinalis* this holds true only for meadow-pastures, the other regimes will not enable recruitment in each year. As indicated by the relatively high proportion of vegetative adults in *S. officinalis*, the reduced generative reproduction, compared to the other two study species, seems to be at least partly compensated by a raised importance of clonal propagation. Long life spans may buffer populations against rapid extinction as a consequence of, e.g. a series of years with low or no reproduction or germination, if extant individuals survive (Watson et al. 1997). In this context annual seedling recruitment becomes less important to ensure persistence of populations. *L. autumnalis* additionally persists in the seed bank (Wellstein et al. accepted,b).

Conclusions

Our results clearly showed that viable populations of *P. saxifraga*, *L. autumnalis* and *S. officinalis* may occur under all current management regimes in mesic grasslands of the marginal study region. For mesic grasslands of comparable regions, this confirms the wide options of extensive regimes of management. There is neither a limitation in the timing of the first cut nor in choosing between the options of mowing or grazing.

Especially intermediate levels of disturbance as provided by mowing with subsequent grazing (meadow-pastures) supported viable populations of the perennial study species. Modern nature conservation should also support sustainable use of sites that are not included in special programs (i.e. covered by the EU/OECD) by research and management advice. In accordance with other studies, our results suggest that the analysis of population structure of long-living perennials is particularly useful to evaluate the suitability of different management options for the preservation of semi-natural grassland species (e.g., Bühler & Schmid 2001; Hegland et al. 2001; Colling et al. 2002).

Acknowledgements

We are grateful to Tobias W. Donath for providing help in the statistical analyses with SAS, K. Ekschmitt and J. Ahlemeyer also provided statistical advice. We thank Stefanie Bissels for suggestions in field work and data analysis and Oliver Ginzler for assistance in field work. Lutz Eckstein, T.W. Donath and Norbert Hölzel gave valuable comments on the paper. We are grateful to the landowners who allowed us to conduct the study on their grassland fields.

This study was carried out as a part of the Deutsche Forschungsgemeinschaft (DFG) project 'Land-use Options for Peripheral Regions (SFB 299)'. We would like to thank the DFG for financial assistance.

7 General Discussion and Synthesis

In this chapter the main results of the different research topics (chapters 4, 5 and 6) are summarized and their significance for land-use practices is discussed.

Relative impact of site conditions and management on phytodiversity (Chapter 4)

In chapter 4 we evaluated different vegetation types and compared these, along with different grassland management types, with respect to species richness, site conditions and grassland age. Analyses of vegetation types confirmed that nutrient levels were significantly higher in the two vegetation types with younger grassland sites than in the two vegetation types of species-rich long-term grasslands. The younger grassland sites underwent an historical land use change. The fertiliser application on these ex-arable fields probably caused an increase of productivity that has lasted until the present. It remains an open question as to what extent the lower species-richness of the nutrient-richer and younger sites can be attributed to enhanced competitive exclusion (resulting from the higher soil fertility levels), compared to factors that limit dispersal. This question has also not yet been clarified in the context of other studies. However, dispersal limitation is a constraint in intensively managed regions where grassland habitats are often fragmented and source populations may be far away from a site (Poschlod et al. 1996). Even under favourable conditions with viable remnant populations of species in the vicinity of such sites, as in the study area, dispersal is an uncertain and time-demanding process (Donath et al. 2003; Bischoff 2002). Thus, floristic diversity in agricultural landscapes also depends on the former and current land-use forms, intensities, patterns and dynamics present in these landscapes (Waldhardt et al. 2000; Cousins & Eriksson 2002).

In current grassland management regimes fertiliser application was low or absent. This is a typical feature of the Lahn-Dill Highlands, but is also found in other mountainous regions (e.g. Critchley et al. 2002). Therefore, the current management mainly comprises different cutting or grazing regimes, which were shown to exert no large impact on species richness. In contrast, Zechmeister et al. (2003) demonstrated the impact of current land-use practices on species richness along a strong gradient in land-use intensity, with a range of fertilisation levels between 0 and 168 kg N ha⁻¹ year⁻¹. The total species richness of these meadows differed significantly in response to the level of fertiliser application (below or above 90 kg N ha⁻¹ year⁻¹) and in response to mowing frequency (range from two to four cuttings per year). Studies of modern grassland management often investigate the influence of the cutting regime together with the level of fertilisation, because these are commonly connected in practice.

Nevertheless, it is important to recognise that mowing/grazing and fertilising are two fundamentally different types of impact on grassland vegetation.

In a subsequent analysis we asked about the relative importance of the management regime, the site conditions, the age of the grassland and regional-scale geomorphology on the floristic composition of grasslands. We evaluated the net effect of each determinant by adjusting for all other determinants. We expected management to have a major influence on the community composition. Other studies also stressed the importance of current management practices (e.g. Austrheim et al. 1999; Fischer & Wipf 2002; Zechmeister et al. 2003). Contrary to these studies and to our expectations, we found only relatively small effects of current management on floristic composition. Furthermore, grassland age was of little importance across all grassland sites. In contrast, the geomorphological subunit of the sampled grasslands significantly explained the highest amount of floristic variance of grassland sites, even after adjustment for all other determinants including site conditions. This can be interpreted as a strong influence of local species pools (Pärtel et al. 1996; Pärtel & Zobel, 1999) on floristic composition of grassland sites. We also found topography and soil chemical parameters to explain more of the variance than management. Vandvik and Birks (2002) found an even higher relative importance of site conditions in Norwegian upland grasslands in contrast to management.

Focussing on floristic composition of aboveground vegetation, the current management regime proved to be only moderately important. The different management types studied might have varied in respect to whether the sites were grazed or mown rather than in their intensity. The variability of site conditions, owing to the heterogeneity of the region, and only moderate variation in intensity of current grassland management are most likely responsible for the obtained relationships. We conclude that the heterogeneity of geomorphologic subunits may have had an effect on the development of different species pools in grassland vegetation of the region.

Seed bank diversity (Chapter 5)

The analysis of the seed bank, the established vegetation and edaphic factors in chapter 5 showed that current management is a main important factor influencing seed bank composition. This holds true even after adjusting for the overlying vegetation type and the edaphic factors. Differences in species identity and abundance between management types potentially imply differences in functional features. In our study, an effect of current

management on species composition was most obvious by an accumulation of ruderal species in the soil seed bank under pastures and silage meadows. This reflects the relatively high degree of disturbance by trampling and grazing and by frequent mowing in the respective management regimes. Ruderal strategy is connected with rapid growth and generative reproduction and thus the tolerance of disturbance and capacity of fast colonisation (pioneers) (Grime 1988). In contrast, hay meadows and meadow pastures are characterised by a higher proportion of the stress strategy, which probably reflects a lower degree of disturbance and a lower nutrient availability (Grime et al. 1988).

In our study, neither similarity of species composition between seed bank and aboveground vegetation nor quantitative seed bank traits, i.e. α -diversity and seed density, were significantly affected by current management. Other studies mostly found that intense management resulted in an increase of seed density due to a higher number of nutrient-demanding ruderal species and in a higher similarity between established vegetation and seed banks (e.g. Bekker et al. 1997; Matus et al. 2005). Here, however, differences in management intensity did not exceed a threshold beyond which phytodiversity would be reduced, i.e. losing typical mesic grassland species and gaining more widespread species.

Some of the investigated sites underwent past changes in land-use from arable fields to grassland. Arable weeds were found to be almost lacking in aboveground vegetation. The past arable land use is reflected only by some relict arable weeds in the lower soil layer. Similar phenomena have been reported by other authors from European grasslands (e.g. Bekker et al. 1997; López-Mariño et al. 2000; Hölzel & Otte 2001).

By calculating the Seed Accumulation Index (SAI, Hölzel & Otte 2004) of grassland species, in chapter 5 a direct assessment of the potential of the seed bank in its contribution to the maintenance and restoration of species-rich grasslands was feasible. Our finding of a high proportion of grassland species present in the seed bank with low SAI values is in line with research of Bekker et al. (2000) suggesting that seed longevity of grassland plant species is low. We also found a remarkable amount of frequent grassland species with high seed accumulation. The latter have a lower risk of extinction, especially if these species are also present in the aboveground vegetation. Thus, irrespective of the management type, it is clear that only a limited proportion of characteristic grassland species is likely to re-establish from the seed bank after disappearing from the aboveground vegetation.

Population structure of Pimpinella saxifraga, Leontodon autumnalis, Sanguisorba officinalis
(Chapter 6)

For the conservation of species-rich semi-natural grasslands it is of major interest to evaluate the suitability of different management regimes for different species. In this context, a useful methodical approach is the investigation of plant population stage structure of perennial plants in relation to management. We studied the population stage structure of the model species *Pimpinella saxifraga*, *Leontodon autumnalis* and *Sanguisorba officinalis* in grasslands under the four different management regimes (see chapter 6). The results showed that viable populations of all three study species, as defined by relatively high numbers of seedlings and juveniles, occur under all management regimes. This means that there is neither a limitation for the maintenance of these species due to the timing of the first cut in spring, nor due to the choice between mowing and grazing. Under all studied management regimes the three studied model species exhibit the ability for successful vegetative regeneration, flowering and seed production during the second growth in late summer.

As indicated by significantly higher densities of seedlings and juveniles, especially meadow-pastures - in contrast to all other management regimes - enhanced seedling recruitment and early establishment. This is in line with other studies suggesting more suitable conditions for species establishment due to trampled gaps (e.g. Bullock et al. 1995; Lennartsson & Oostermeijer 2001). In contrast to such positive effects of low grazing intensity as applied in meadow-pastures of this study, negative effects of grazing intensity in heavily grazed fens were reported by Bühler & Schmid (2001). Destruction of flowering stalks by grazing cattle led to reduced seed set and lower seedling recruitment in populations of the perennial species *Succisa pratensis*. Once again, with respect to the three model species in our studies, management intensity of the studied regimes did not exceed levels beyond which population viability of these typical common grassland species might be affected.

Although the analysis of population stage structure of perennial plants only provided a short-term insight into demographic processes, the results of this study and several other studies showed that it is a useful tool to evaluate different management regimes (e.g. Bühler & Schmid 2001, Hegland et al. 2001; Bissels et al. 2004).

Synthesis

The basic hypothesis of this study - that the difference of management regimes has a major impact on phytodiversity of mesic grasslands - can only partly be confirmed in our study area. Differences in phytodiversity were only partly related to management. Specifically, neither the species richness of aboveground vegetation nor species richness of the seed bank were significantly affected by management. Floristic composition of aboveground vegetation was moderately affected by management, while soil chemical parameters, topography and local species pools of subregions were of higher importance. For the floristic composition of the seed bank management was a major important factor even after adjustment for aboveground vegetation and edaphic conditions. Furthermore, management influenced functional aspects of species present in the seed bank, such as components of C-S-R strategy. All management regimes supported viable populations of the perennial study species *Pimpinella saxifraga*, *Leontodon autumnalis* and *Sanguisorba officinalis*. Management regimes had significant effects on their population stage structure but accounted for less of the explained variance than differences between populations (i.e. sites). The main variables of influence were soil moisture, nutrient availability and litter coverage. For the obtained relationships the variability of site conditions, owing to the heterogeneity of the region, and only moderate variation in intensity of current grassland management are most likely responsible.

Even though they have been applied for the least 25 years, current management types do not appear to cause severe constraints on the floristic composition and species-richness of the studied grassland sites. There is neither a limitation in the timing of the first cut nor in the choice between mowing and grazing. In particular, meadow-pastures with an intermediate disturbance impact on the plant biomass, the sward, and the topsoil exerted positive effects on phytodiversity: Meadow-pastures supported viable populations of the perennial study species, accounted for high species richness and showed mixed functional composition in seed banks. In accordance with findings of other authors (e.g. Cousins & Eriksson 2002; Vandvik & Birks 2002; Zechmeister et al. 2003; Pykälä 2005), the studies presented in this thesis show that a wide variety of low-intensity management options can be used in the maintenance of mesic grassland diversity in Europe.

8 Summary

This thesis evaluates the impact of land-use practices (management) on phytodiversity of mesic grasslands in a Central European sub-mountainous region (Lahn-Dill Highlands, Hesse, Germany). Evaluation of suitable management types is of crucial importance for the maintenance of species rich grasslands. The overall aim of the studies is to assess the relative impact of current management types (low-intensity grazing and mowing regimes) on three components of phytodiversity: the aboveground vegetation, the soil seed bank and the population structure of selected plant species. Furthermore, site conditions such as edaphic parameters and topography are considered.

In the *first study* the relative impact of management, site conditions, grassland age and regional scale geomorphology on aboveground vegetation of grasslands is quantified. The current management has relatively low impact on floristic composition. In contrast, soil chemical variables, together with topography, explain almost twice as much variation in floristic composition as does the current management. There is no evidence that the different management types exert a large impact on species richness.

The *second study* of soil seed banks in grasslands shows that the type of management has no significant impact on species richness and seed density of the seed bank, but significantly influences the floristic composition and functional characteristics. Irrespective of management type only a limited proportion of characteristic grassland species is likely to re-establish from the seed bank after disappearance from aboveground vegetation.

In the *third study* we investigated the population stage structure of three model species (*Pimpinella saxifraga*, *Leontodon autumnalis* and *Sanguisorba officinalis*) of grasslands with respect to management, site conditions and vegetation structure. The results show that viable populations of all three species may occur in all of the studied management types. The species respond differently to site conditions and vegetation structure and significant effects are stage-specific. The main variables of influence are soil moisture, nutrient availability and litter coverage.

The variability of site conditions, due to the heterogeneity of the region, and moderate variation in intensity of current grassland management are most likely responsible for the observed relationships. Finally, in accordance with other studies, our analyses show that there is a wide variety of low-intensity management options to contribute to the maintenance of phytodiversity in European mesic grasslands.

9 Zusammenfassung

Diese Arbeit untersucht den Einfluss von Landnutzungstypen (Management) auf die Phytodiversität mesophilen Grünlands in einer zentraleuropäischen Mittelgebirgsregion (Lahn-Dill-Bergland, Hessen, Deutschland). Die Evaluation geeigneter Nutzungstypen ist für die Erhaltung artenreichen Grünlands von entscheidender Bedeutung. Das übergeordnete Ziel der Studien ist die Untersuchung des relativen Einflusses von aktuellen Nutzungstypen (extensive Beweidungs- und Mahd-Regime) auf drei Komponenten der Phytodiversität: Oberirdische Vegetation, Bodensamenbank und Populationsstruktur ausgewählter Pflanzenarten. Weiterhin werden Standortbedingungen wie edaphische Parameter und Topographie berücksichtigt.

In der *ersten Studie* wird der relative Einfluss von Nutzungstypen, Standortbedingungen, Grünlandalter und regionaler Geomorphologie auf die oberirdische Vegetation der Grünlandflächen quantifiziert. Die aktuelle Nutzung hat relativ geringen Einfluss auf die floristische Zusammensetzung. Im Gegensatz dazu erklären bodenchemische Einflussgrößen und die Topographie zusammen fast zweimal soviel der Variation innerhalb der floristischen Zusammensetzung wie die aktuelle Nutzung. Es konnte nicht nachgewiesen werden, dass die unterschiedlichen Nutzungstypen großen Einfluss auf den Artenreichtum ausüben.

Die *zweite Studie* über die Bodensamenbanken des Grünlands zeigt, dass der Nutzungstyp keinen signifikanten Einfluss auf den Artenreichtum und die Dichte der Samen in der Samenbank hat. Die floristische Zusammensetzung und funktionelle Charakteristika werden jedoch signifikant beeinflusst. Unabhängig vom Nutzungstyp ist es nur für einen begrenzten Teil charakteristischer Grünlandarten wahrscheinlich sich nach Verschwinden aus der oberirdischen Vegetation aus der Samenbank zu reetablieren.

In der *dritten Studie* untersuchten wir die Stadienstruktur der Populationen dreier Modellarten des Grünlands (*Pimpinella saxifraga*, *Leontodon autumnalis* and *Sanguisorba officinalis*) im Bezug auf Nutzung, Standortbedingungen und Vegetationsstruktur. Die Ergebnisse zeigen, dass überlebensfähige Populationen aller drei Arten in allen untersuchten Nutzungstypen auftreten können. Die Arten reagieren unterschiedlich auf Standortbedingungen und Vegetationsstruktur und signifikante Effekte sind Stadien-spezifisch. Die hauptsächlichen Einflussgrößen sind Bodenfeuchte, Nährstoffverfügbarkeit und Streubedeckung.

Aufgrund der Heterogenität der Region ist die Variabilität der Standortbedingungen und eine nur mäßige Variation in der Intensität der aktuellen Nutzungstypen sehr wahrscheinlich für die beobachteten Verhältnisse verantwortlich. Übereinstimmend mit anderen Studien zeigen

unsere Analysen schließlich auf, dass es eine große Vielfalt an Optionen nicht-intensiver Nutzung gibt, die zur Erhaltung der Phytodiversität mesischen Grünlands in Europa beitragen können.

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Acknowledgements

First of all, I want to thank Prof. Dr. Dr. Annette Otte and PD Dr. Rainer Waldhardt for giving me the opportunity to pursue my doctoral studies on such an interesting and wide variety of topics. They provided me with helpful advice and gave me enough freedom to address interesting topics. My thanks go also to Prof. Dr. Gerd Esser for his willingness to take over the task of the second referee.

PD Dr. Rainer Waldhardt helped me in particular with his quick feedback and proof readings. He was always approachable for profound discussions. I also appreciate the help of my colleagues Dr. Tobias W. Donath, Dr. Lutz Eckstein and Dr. Dietmar Simmering who gave me statistic advice and revised the papers with many valuable comments and suggestion for linguistic improvements. We had fruitful discussions that helped to enhance the present work. I particularly appreciate the help of PD Dr. Norbert Hölzel including many inspiring discussions and suggestions on all topics of the grassland studies. His willingness to share his knowledge made me always get ahead. Furthermore, I want to thank all the editors and referees of the papers comprised in this thesis. Dr. Stephanie Bissels gave advice for the population biological study and Birgit Reger supported me with help on GIS and the production of nice maps and figures. Jan Thiele helped me with interpretation of aerial images. For their statistical help I also thank Dr. Jutta Ahlemeyer and Dr. Klemens Ekschmitt from the Division for Biometry and Population Genetics. It was a pleasure to work with Josef Scholz vom Hofe who was a great support in the large filed work including setting up experiments, collection of data and motivational aspects (the early bird...).

Oliver Ginzler helped me very much to collect vegetation field data, it was a pleasure to work with him. Thanks go also to Christiane Lenz-Kuhl and Walter Mayrink for their help in data collection. Furthermore, I want to express my appreciation to the land owners that supplied me with information and allowed me to use their fields. For funding the collaborative reseach center 'Land Use Options for Peripheral Regions' (SFB 299), I thank the German Research Foundation (DFG). Prof. Dr. Rüdiger Wittig and his team from the Division of Geobotany and Ecology, Johann Wolfgang Goethe-University Frankfurt, provided a kind basis to finish my Ph. D.

For constructive comments and proof-reading parts of this thesis, many thanks go to Dr. Tobias W. Donath, Dr. Ute Becker, Dr. Rod Snowdon and my brother Benjamin Wellstein. I wish to express my gratitude to all my colleagues at the Division of Landscape Ecology and Landscape Planning for sharing their scientific and their human enthusiasm with me: ideals of humanism! Not to forget, the legendary coffee-breaks! Last but not least, I thank my family for their important support and my friends who kept me to keep on climbing mountains and to master other special challenges.

Erklärung

Ich erkläre: Ich habe die vorgelegte Dissertation selbständig und ohne unerlaubte fremde Hilfe und nur mit den Hilfen angefertigt, die ich in der Dissertation angeben habe.

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