Shrub encroachment of temperate grasslands:

Effects on plant biodiversity and herbage production

Dissertation

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1 General Introduction

Over 40 % of the Earth’s land surface is grassland (White et al. 2000). With 52.5 million km² it represents the largest biome of the world, but only 20 % thereof are free of shrubs and wood. However, the agricultural interest in shrub encroached grassland in Central Europe is comparatively low.

In Central Europe, semi-natural grassland is considered to be one of the most important resources of biodiversity (Peet et al. 1983). At the same time, species-rich grasslands are threatened by changing land use and many of them have almost disappeared during the last decades. Due to the intensification of agricultural production grassland, sites were either ameliorated and fertilized resulting in highly productive but monotonous swards or, on very low productive sites, grassland management was ceased. Nowadays, abandonment of semi-natural grasslands from agricultural use is the major risk for grassland diversity, and recently, the interest in appropriate management systems has increased (Bruinenberg et al. 2002; Marriott et al. 2004; Pontes et al. 2007).

Abandonment as well as grazing at very low stocking rates induces processes of secondary succession with shrub encroachment as one major characteristic. In shrub-invaded grasslands, shrub species compete with grasses and forbs for light, water and nutrients, and they also affect the accessibility and utilization of herbage. Reduced light availability is regarded as a major cause of changing species composition (Tilman 1985) and has been linked to reduced biodiversity (Pausas & Austin 2001; Pykälä et al. 2005). In general, shrub encroachment is expected to have a negative effect on biodiversity. This is quite evident and has been proved for shrub encroachment of species-rich grasslands in long-term studies (Dierschke 2006; Galvanek & Leps 2008; Mitlacher et al. 2002). Contrary to this, we assume a benefit from low intensity shrub encroachment on the actual species richness due to increased habitat heterogeneity. In the present study, this concept has been tested witch respect to different spatial scales.

Semi-natural grasslands, as much as their highly diverse habitats, are a result of traditional extensive grassland management. Maintaining these species-rich grasslands requires continuous agricultural utilisation with respect to an appropriate management. For economic purposes, there is a need to optimize the management systems, to get maximal benefit. This implies a substantial knowledge of the forage potential of the swards. The influence of shrubs on herbage mass and parameters of herbage quality has hardly been ascertained. Measurements are required to make estimations on the forage potential of shrub encroached grasslands.

To prevent a further decline in biodiversity, farming systems have to be developed, which combine interests of agricultural production as well as biodiversity maintenance (Isselstein et al. 2005). Extensive grazing might offer these options and has been recommended (Dumont et al. 2007; Rook et al. 2004).

The present study focuses on shrub encroachment of temperate semi-natural grasslands. The effect of the presence of shrubs was studied on both, the biodiversity of the vegetation cover and on the forage potential of the sward.

1.1 References

Bruinenberg, M.H., Valk, H., Korevaar, H. & Struik, P.C. 2002. Factors affecting digestibility of temperate forages from seminatural grasslands: a review. Grass and Forage Science 57: 292-301.

Dierschke, H. 2006. Secondary progressive succession of an abandoned calcareous grassland - research on permanent plots 1987-2002. Hercynia N. F. 39: 223-245.

Dumont, B., Rook, A.J., Coran, C. & Röver, K.-U. 2007. Effects of livestock breed and grazing intensity on biodiversity and production in grazing systems. 2. Diet selection. Grass and Forage Science 62: 159-171.

Galvanek, D. & Leps, J. 2008. Changes of species richness pattern in mountain grasslands: abandonment versus restoration. Biodivers Conserv 17: 3241-3253.

Isselstein, J., Jeangros, B. & Pavlu, V. 2005. Agronomic aspects of biodiversity targeted management of temperate grasslands in Europe - A review. Agronomy Research 3: 139-151.

Marriott, C.A., Fothergill, M., Jeangros, B., Scotton, M. & Louault, F. 2004. Long-term impacts of extensification of grassland management on biodiversity and productivity in upland areas. A review. Agronomie 24: 447-462.

Mitlacher, K., Poschlod, P., Rosen, E. & Bakker, J.P. 2002. Restoration of wooded meadows - a comparative analysis along a chronosequence on Oland (Sweden). Appl Veg Sci 5: 63-73.

Pausas, J.G. & Austin, M.P. 2001. Patterns of plant species richness in relation to different environments: An appraisal. J Veg Sci 12: 153-166.

Peet, R.K., Glenn-Lewin, D.C. & Walker-Wolf, J.W. 1983. Prediction of man's impact on plant species diversity. In: Holzner, W., Werger, M.J.A. & Ikusima, I. (eds.) Man's impact on vegetation, pp. 41-54. Junk Publishers, The Hague, The Netherlands.

Pontes, L.S., Carrere, P., Andueza, D., Louault, F. & Soussana, J.F. 2007. Seasonal productivity and nutritive value of temperate grasses found in semi-natural pastures in Europe: responses to cutting frequency and N supply. Grass and Forage Science 62: 485-496.

Pykälä, J., Luoto, M., Heikkinen, R.K. & Kontula, T. 2005. Plant species richness and persistence of rare plants in abandoned semi-natural grasslands in northern Europe. Basic Appl Ecol 6: 25-33.

Rook, A.J., Dumont, B., Isselstein, J., Osoro, K., WallisDeVries, M.F., Parente, G. & Mills, J. 2004. Matching type of livestock to desired biodiversity outcomes in pastures - a review. Biological Conservation 119: 137-150.

Tilman, D. 1985. The Resource-Ratio Hypothesis of Plant Succession. Am Nat 125: 827-852.

White, R.P., Murray, S., Rohweder, M. & World Resources, I. 2000. Pilot analysis of global ecosystems : grassland ecosystems. World Resources Institute, Washington, DC.

2 Plant species richness in calcareous grasslands under different stages of shrub encroachment

2.1 Abstract

In the present study we examined the effect of shrub encroachment of temperate semi-natural grasslands on plant species diversity. We tested the hypothesis that an initial shrub invasion leads to enhanced habitat heterogeneity and thereby to a higher diversity. A descriptive correlative gradient analysis of shrub invaded grasslands and their species number of flowering plants was performed. Within 30 plots of different shrub encroachment a total of 203 plant species were recorded. The mean α-diversity (level of subplots), mean β1-diversity (level of plots) as well as the β2-diversity (level of shrub classes) have their highest values at medium shrub invaded sites. This finding is in line with our hypothesis of a hump-back relation between shrub encroachment and species diversity, and can be explained by the increase in habitat heterogeneity. However, Detrended Correspondence Analysis (DCA) emphasized the importance of the present vegetation composition for species richness. The dominance of highly competitive, clonal-growing grass species is accompanied by low diversity swards with a lower facilitation of shrub establishment.

Species accumulation curves highlight the benefit of shrub encroachment for γ-(landscape-) diversity. This result emphasises the importance of habitat heterogeneity on biodiversity and, therefore, on nature conservation.

2.2 Introduction

Calcareous grasslands as well as semi-natural temperate grasslands are strongly affected by abandonment of agricultural use. In consequence, woody plants invade the grassland and the typical species rich vegetation disappears (Dierschke 2006; Galvanek & Leps 2008). To preserve such habitats of high ecological value, continuing grassland management is required.

Shrub encroachment of semi-natural grasslands is commonly perceived as having a negative affect on biodiversity and on nature conservation in particular as rare species are threatened from extinction. This is something contradictory to conclusions of the mosaic concept of Duelli (Duelli 1992; 1997) or the habitat heterogeneity hypothesis in general (MacArthur & Wilson 1967). According to this, shrub invasion will lead to higher habitat heterogeneity and therefore to higher biodiversity. This perspective is driven by ecological thinking rather than conservation of rare species.

The presented work investigates the influence of shrub invasion on the species diversity of grasslands. The following hypothesis is proposed: An initial shrub invasion leads to enhanced habitat heterogeneity and thereby to a higher diversity. At later stages, that is after a certain degree of shrub encroachment, biodiversity will be depleted. At this point, shrub clearing is required.

In addition, more accurate information about the response of biodiversity to shrub encroachment of semi-natural grasslands will allow more effective measures to protect biodiversity.

2.3 Methods

2.3.1 Study area

The study area is situated in the north-east of Goettingen, Lower Saxony, Germany (51° 52'-51° 55' N, 10° 0' E; 300-375 m a.s.l). The area was used for military purposes from the early 19th century until 1993 and it, thus, passed the last century without agricultural intensification. Since 2004, it has been a nature reserve. Within an area of approximately 200 ha, there is a wide range of extensively managed or abandoned grasslands, ranging from rudimental semi-dry chalk grasslands (Gentiano–Koelerietum pyramidatae) and grasslands of the class Molinio-Arrhenatheretea (Lolio-Cynosuretum), to more or less unmanaged and shrub-invaded types linking to forest edges (Trifolion medii) and shrub vegetation (Prunetalia). The main woody species are *Crataegus spp.*, *Rosa canina*, *Fraxinus excelsior* and *Cornus sanguinea*. The soils are Cambisols with a small proportion Leptosol (Rendzina) on calcareous rock. The long-term mean annual temperature for the study area is 8.7 °C and the mean annual precipitation is 645 mm.

2.3.2 Experimental design and measurements

Within the predetermined geographical area, 30 plots (10 m x 10 m) were selected along a gradient of shrub cover (%), based on a time series of aerial photographs. Our aim was to represent a wide range of shrub encroachment from nearly shrub-free grasslands to sites with very dense shrub cover. As an extreme, we included one abandoned site that can be characterized as a pioneer forest on former calcareous grassland.

Because of different shrub height, we measured the intensity of shrub occurrence as a combination of percentage cover and maximum canopy height (cm) as follows:

$$Shrub\ index = \ln(1 + cover * canopy\ height)\ .$$

A shrub index of 8 therefore results from 15 % cover and 200 cm canopy height as well as 25 % cover and 120 cm canopy height. As the shrub index represents the shrub volume, it is a better indicator of the competition for light than shrub cover only. For single calculations plots were aggregated by ascending shrub index into 6 shrub classes, each containing 5 plots.

The botanical composition was measured in June. Within each plot, ten subplots of 1 m² were positioned randomly. For each subplot, the occurrence of vascular plants was listed (present-absent data). Abundance data at plot level arise from the present-absent data by calculating the frequency. The nomenclature follows Wisskirchen and Haeupler (1998). Phanerophyts (incl. *Rubus*) are included, if they extended into the space above the quadrate. In the case of *Ranunculus auricomus agg.*, *Ranunculus polyanthemos agg.*, *Rubus fruticosus agg.* and *Taraxacum sect. Ruderalia*, determination ended with species aggregates.

Ten soil samples (0-5 cm and 5-10 cm depth) were taken randomly and pooled per plot and analysed for pH, exchangeable phosphorus, magnesium and potassium (calcium ammonium acetate extraction).

2.3.3 Data analysis

The effect of shrub encroachment on species diversity was analysed by linear and nonparametric (loess) regression models as well as ordination techniques. Detrended Correspondence Analysis was used to expose the influence of vegetation composition on the dependency detected by the regression model. The analysis was performed on the log-transformed species abundance matrix with detrending by-segments and down-weighting of rare species using the statistic program Canoco (ter Braak & Smilauer 2002). Species richness was fitted by a Generalized Linear Model (GLM, quadratic degree) and visualised in the DCA-plot by isolines.

The hierarchical analysis of species diversity uses the additive model of species diversity (Lande 1996; Levins 1968; MacArthur et al. 1966). That is $\alpha + \beta = \gamma$, where α is within-community (within-subplot) diversity, β is among-community diversity and γ is the total species diversity. The β-diversity is subdivided into within-plot diversity ($\beta1$) and within-shrub class diversity ($\beta2$).

Species accumulation curves are calculated for single ordering of samples (ordered by shrub index) on the one hand and on the other hand as means of repeated resampling of all pooled samples (1000-fold resampling). The second is according to the sample-based rarefaction curve in terms of Gotelli et Colwell (2001). The 95 % confidence interval is the range which contains 95 % of the values.

Differences in species number per plot and subplot as well as differences in soil parameters between shrub classes were tested by analysis of variance (ANOVA).

Accumulation curves and ANOVA were computed using the statistic program R (R Development Core Team 2008).

2.4 Results

2.4.1 Shrub encroachment and vegetation composition

The vegetation in the present study covered a gradient of shrub encroachment from shrub-free grasslands to pioneer forest vegetation. The canopy height of the shrub vegetation was usually between 15 and 500 cm (pioneer forest with 1000 cm), and the canopy cover ranged from less than 1 % to nearly 100 %. The values of the calculated shrub index ranged from 0 to 11.4 with a mean of 6.4.

Caused by the wide gradient of shrub encroachment, the vegetation composition varied significantly between the plots. With further shrub encroachment, the number of woody species increased from 4.2 to 25.2 %, dominated by *Crataegus spp.*, *Rosa canina*, *Fraxinus excelsior* and *Cornus sanguinea*. The most frequent grass species were *Dactylis glomerata*, *Festuca rubra* and *Poa pratensis*. With more shrub encroachment, *Trisetum flavescens* and *Brachypodium pinnatum* became more abundant. The most frequent forbs were *Galium album*, *Plantago lanceolata*, *Veronica chamaedrys*, *Fragaria vesca* and *Taraxacum sect. Ruderalia*. With increasing shrub encroachment, there was a decrease in the ratio of grass species to forbs from 0.56 to 0.39, and a decrease in the proportion of the number of legume species from 0.157 to 0.046, averaged over shrub classes.

In Figure 1, the DCA biplot demonstrates the variability in vegetation composition. The length of the gradient for the first axis is 2.9 SD. The location of woody species in the plot suggests that the first axis represents the gradient of shrub occurrence. Shrubs and trees have relatively high values (>1.72), whereas typical species of mesophileous grasslands have values between -0.45 and 1.70 for the first axis. Calcareous grassland species have intermediate values, but are distinguished from mesophileous grassland species by a higher value for the second axis.

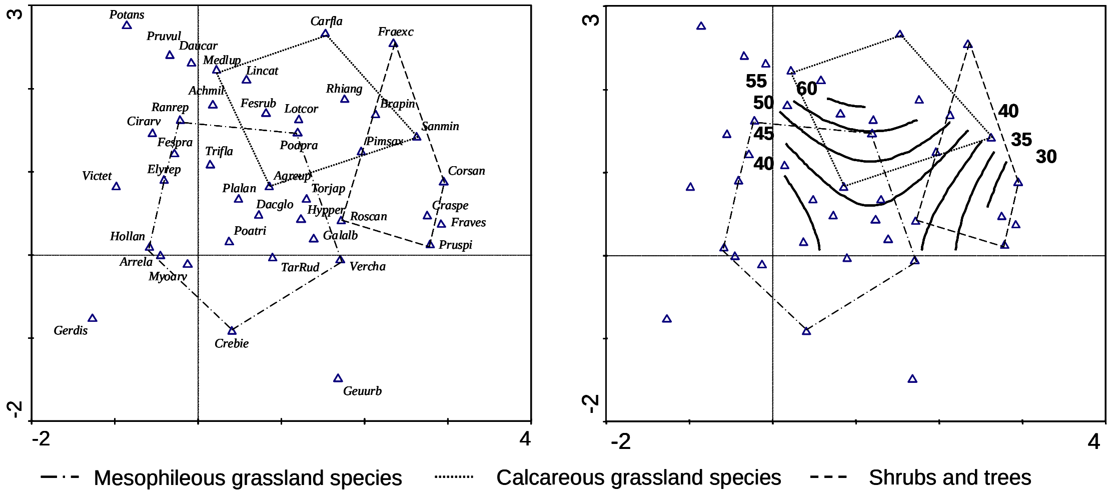

Figure 1 DCA ordination plots (axis 1 and 2) based on 30 samples of grassland vegetation. Plant species with highest fit are displayed and grouped by sociological behaviour. B: Isolines of similar species richness result from a fitted Generalized linear model (quadratic degree).

Species codes: Achmil = *Achillea millefolium*, Agreup = *Agrimonia eupatoria*, Arrela = *Arrhenatherum elatius*, Brapin = *Brachypodium pinnatum*, Carfla = *Carex flacca*, Cirarv = *Cirsium arvense*, Corsan = *Cornus sanguinea*, Craspe = *Crataegus monogyna*, Crebie = *Crepis biennis*, Dacglo = *Dactylis glomerata*, Daucar = *Daucus carota*, Elyrep = *Elymus repens*, Fespra = *Festuca pratensis*, Fesrub = *Festuca rubra*, Fraves = *Fragaria vesca*, Fraexc = *Fraxinus excelsior*, Galalb = *Galium album*, Gerdis = *Geranium dissectum*, Geuurb = *Geum urbanum*, Hollan = *Holcus lanatus*, Hypper = *Hypericum perforatum*, Lincat = *Linum catharticum*, Lotcor = *Lotus corniculatus*, Medlup = *Medicago lupulina*, Myoarv = *Myosotis arvensis*, Pimsax = *Pimpinella saxifraga*, Plalan = *Plantago lanceolata*, Poapra = *Poa pratensis*, Poatriv = *Poa trivialis*, Potans = *Potentilla anserina*, Pruvul = *Prunella vulgaris*, Pruspi = *Prunus spinosa*, Ranrep = *Ranunculus repens*, Rhiang = *Rhinanthus angustifolius*, Roscan = *Rosa canina*, Sanmin = *Sanguisorba minor*, TarRud = *Taraxacum sect. Ruderalia*, Torjap = *Torilis japonica*, Trifla = *Trisetum flavescens*, Vercha = *Veronica chamaedrys*, Victet = *Vicia tetrasperma*.

2.4.2 Species diversity

The vegetation had relatively high numbers of vascular plant species at all examined spatial scales. In total, we found 203 vascular plant species. Number of species per plot ranged between 27 and 68 (mean = 44.5). Maximum recorded species number per square meter (subplot) was 41 (mean = 17).

Highest species diversity was found at medium shrub invaded sites. The mean α-diversity (level of subplots), mean β1-diversity (level of plots) as well as the β2-diversity (level of shrub classes) have its highest value at shrub class three (shrub index of 4.5 – 5.8). Differences in mean species numbers between shrub classes were, however, not significant (ANOVA, Table 1, Figure 2).

Table 1 Differences in species number per plot and subplot between shrub classes, ANOVA table.

	Df	Sum Sq	Mean Sq	F value	P
Species per plot					
Shrub class	5	570.27	114.05	1.105	0.3837
Residuals	24	2477.20	103.22		
Species per subplot					
Shrub class	5	295.01	59.00	2.056	0.1066
Residuals	24	688.76	28.70		

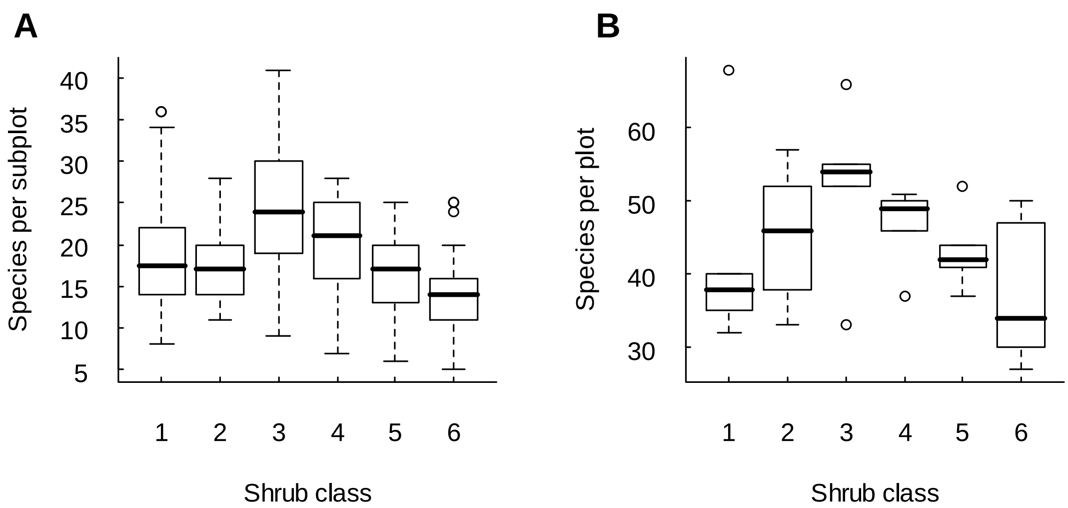

Figure 2 Number of vascular plant species (A) per subplot and (B) per plot according to increasing shrub encroachment (each shrub class contains 5 plots).

In the DCA, the species number was fitted by a generalized linear model (GLM) and visualized by isolines in the DCA biplot (Figure 1B). The highest species numbers were found at plots with intermediate values for the first axis and high values for the second. These plots are characterized by high proportions of calcareous grassland species.

To assess the effect of shrub encroached grassland sites on γ-diversity, species accumulation curves have been computed (Figure 3). The 'smoothed' curves represent the means of 1000-fold resampling of all pooled samples (sample-based rarefaction curve) with 95 % confidence interval. The solid lines are species accumulation curves for ordering of samples by shrub index. The species accumulation curve and the rarefaction curve are very similar, if samples are ordered by descending shrub index. If samples are ordered by ascending shrub index, the accumulation curve is close to or even lower than the 95 % confidence interval. This means the species accumulation curve and the sample-based rarefaction curve differ significantly by a probability value of 5 %. For instance, the ten samples with highest shrub index accounted for 35 additional species, whereas the theoretical rarefaction curve predicted only 18 additional species. This indicates a diversity benefit above average from the samples with high shrub index.

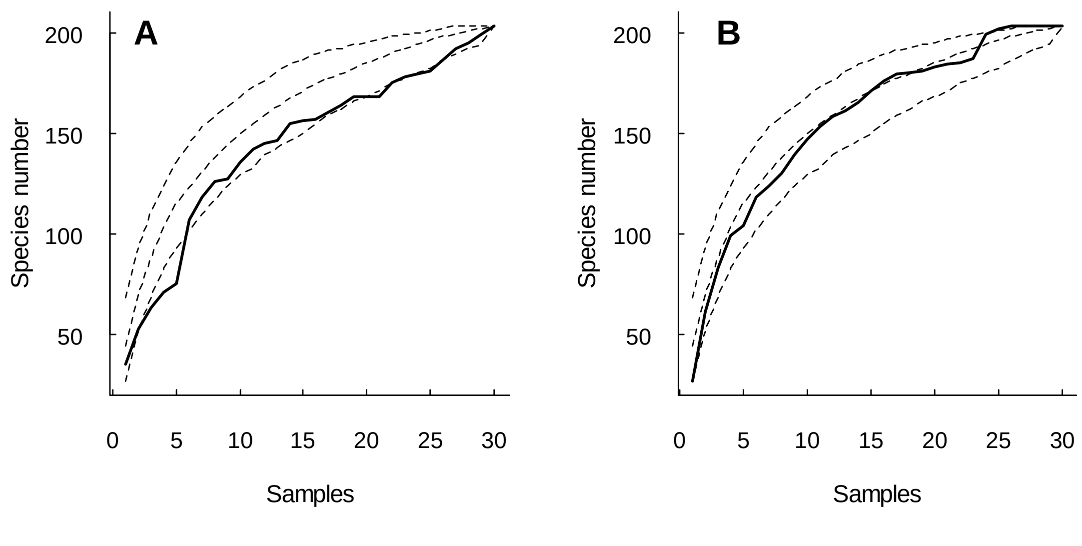

Figure 3 Species accumulation curves. Dashed lines are the expected species accumulation curves with 95 % confidence intervals, calculated by 1.000-fold resampling. Solid lines are the measured species accumulation curves with defined sample order. A: by ascending shrub index, B: by descending shrub index.

Soil parameters were measured to characterize the site conditions of the plots. No significant differences were found between them at the level of shrub classes for both, 0-5 cm and 5-10 cm soil depth (Table 2). In relation to the species richness we found a higher phosphorous content limiting the number of species per plot. Plots with more than 40 species had phosphorous contents below 2.55 g/100 g DM in the fraction of 0-5 cm depth. The phosphorous content was generally higher in the upper soil layer.

Table 2 Soil parameters pH, phosphorus (P), potassium (K) and magnesium (Mg) measured in 0-5 cm soil depth. Values are the mean and standard deviation averaged across shrub classes. Differences between the shrub classes were tested using ANOVA (α = 0.05).

Scrub class	pH	P (g/100 g DM)	K (g/100 g DM)	Mg (g/100 g DM)
1	6.58 ± 0.77	3.03 ± 2.10	18.62 ± 4.01	36.82 ± 23.53
2	6.92 ± 0.75	2.13 ± 1.47	22.70 ± 6.09	12.56 ± 1.30
3	6.84 ± 0.46	2.79 ± 2.81	19.92 ± 2.91	13.34 ± 3.98
4	6.78 ± 0.65	2.21 ± 1.43	21.32 ± 5.80	14.64 ± 2.04
5	6.64 ± 0.55	1.58 ± 0.66	26.22 ± 3.57	15.82 ± 3.97
6	6.10 ± 0.17	2.90 ± 1.99	26.20 ± 7.18	18.90 ± 9.65
Sign. (P)	0.33	0.78	0.13	not tested

2.5 Discussion

Due to the failure of agricultural intensification during the last century, the grasslands in the present study can be characterized as agriculturally unimproved, semi-natural grasslands. The vegetation had relatively high numbers of vascular plant species. The maximum of 41 species per m^{-2} corresponds to those of diverse calcareous grasslands (Kull & Zobel 1991). Highest numbers of plant species were found at medium shrub invaded sites, which is in line with our hypothesis of a hump-back relation between shrub encroachment and species diversity. A similar result has been reported from semi-natural grasslands in SW Finland (Pykälä et al. 2005). The authors found highest species richness with a tree cover of ca. 5 %. Further increasing cover of trees had a negative effect on species richness, which was mainly attributed to a reduced light availability. Pihlgren & Lennartsson (2008) analysed the effect of shrubs of *Rosa dumalis* on grassland plants in semi-natural pastures in Sweden. They found, that the net effect of shrubs in semi-natural grassland is neutral or positive rather than negative for most plant species. This means that the number of species which responded positively to shrubs were comparable to the number of species which had a negative response. Total species richness was, therefore, not significantly affected by the shrubs.

In the present study, strong influence on species richness could be attributed to the vegetation composition. In general, plots which were dominated by mesophileous grassland species were less diverse than plots with a higher abundance of calcareous grassland species. Calcareous grassland species are less competitive and better adapted to dry and nutrient poor conditions (stress tolerators) compared to mesophileous grassland species (Grime 2001). These species are often target species for nature conservation. A loss of those species during successional processes refers to the dominance of high competitive, usually clonal-growing, tall plants. In the present study, we found *Arrhenatherum elatius*, *Holcus lanatus*, *Elymus repens* and *Poa trivialis* characterizing plots with relatively low species numbers as well as low intensity of shrub encroachment. This can be explained by different pathways of succession. Shrub establishment and encroachment are not necessarily straightforward processes of grassland succession. Shrub establishment depends on several local factors like site history, availability of propagules and safe-sites for the seed germination. Dense swards of clonal-growing grass species and high litter depth impede the germination of shrub and tree species. The process of shrub establishment is highly subject to stochastic processes.

Several studies on calcareous grassland succession focus on the grass species *Brachypodium pinnatum*. It has been ascribed as an aggressive species of calcareous grasslands with increasing dominance and the ability to decrease species diversity during secondary succession (Bobbink & Willems 1987; Willems 2001). It is of some interest that the occurrence of *Brachypodium pinnatum* in the present study was related to more diverse vegetation.

The influence of shrub encroachment on γ-diversity was estimated using species accumulation curves. Our results show a considerable increase of total species richness (γ-diversity) due to the plots with a high shrub index. For the purpose of enhancing biodiversity, this seems to be a positive aspect of shrub encroachment. Nevertheless, we have no valid information about the γ-diversity of the whole study area, and how the selected grassland plots contribute to it. A current floristic mapping project detected more than 600 vascular plant species per 5.5 by 5.5 km^2 in this region (Garve 2007), which is more than three times the species we found. Our study is certainly a representative sample of the prevailing grassland vegetation of this area but lacks for other vegetation units particularly for the forest vegetation. The increase of species in our study could probably be compensated by other vegetation types.

The spatial distribution of the shrubs can be clumped (patchy) or more or less homogeneous. Border structures feature specialized biocoenosis and are known for their importance for nature conservation (Hondong et al. 1993; Kollmann & Poschlod 1997). Transition from grassland to wood forms fringe community types, of which Trifolio medii-Agrimonietum eupatoriae dominated in the present study. The patchier the structure of shrub encroachment is, the higher is the proportion of border structures, and the higher the potential value for nature conservation. This should be accounted for, if shrub encroachment of grassland is evaluated in further research.

From the present study, a general question arises. Shrub encroachment characterizes a phenological stage of succession. However, the extent of shrub establishment is neither a measure of succession nor a correlate to the time since abandonment. This is due to the different possible pathways and the stochastic character of succession. Therefore, the results of this study are not comparable with those of time series or long-term studies of grassland succession. It is evident that abandonment of species-rich grasslands will cause a decrease in species richness (Dierschke 2006; Galvanek & Leps 2008; Mitlacher et al. 2002). The finding of this study, that slight shrub encroachment benefits species diversity, was driven by the cross-sectional study design and the focus on broader spatial scales. Plots with shrub encroachment to a certain degree, were found to have highest species numbers. Furthermore, we found the γ-diversity of the studied grassland sites positively influenced by plots with higher shrub occurrence. The question how shrub vegetation in grasslands contributes to the total (landscape) species diversity could not finally be answered. Therefore, further research with a better control of environmental factors, or experimental studies are suggested.

2.6 References

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

Dierschke, H. 2006. Secondary progressive succession of an abandoned calcareous grassland - research on permanent plots 1987-2002. Hercynia N. F. 39: 223-245.

Duelli, P. 1997. Biodiversity evaluation in agricultural landscapes: An approach at two different scales. Agr Ecosyst Environ 62: 81-91.

Duelli, P. 1992. Mosaikkonzept und Inseltheorie in der Kulturlandschaft. Verhandlungen der Gesellschaft für Ökologie 21: 379-383.

Galvanek, D. & Leps, J. 2008. Changes of species richness pattern in mountain grasslands: abandonment versus restoration. Biodivers Conserv 17: 3241-3253.

Garve, E. 2007. Verbreitungsatlas der Farn- und Blütenpflanzen in Niedersachsen und Bremen. Nieders. Landesbetrieb für Wasserwirtschaft, Küsten- und Naturschutz, Hannover.

Gotelli, N.J. & Colwell, R.K. 2001. Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. Ecol Lett 4: 379-391.

Grime, J.P. 2001. Plant strategies, vegetation processes, and ecosystem properties. 2nd. Wiley, Chichester.

Hondong, H., Langner, S. & Coch, T. 1993. Untersuchungen zum Naturschutz an Waldrändern. Bristol-Schriftenreihe 2: 196 S.

Kollmann, J. & Poschlod, P. 1997. Population processes at the grassland-scrub interface. Phytocoenologia 27: 235-256.

Kull, K. & Zobel, M. 1991. High species richness in an Estonian wooded meadow. J Veg Sci 2: 715-718.

Lande, R. 1996. Statistics and partitioning of species diversity, and similarity among multiple communities. Oikos 76: 5-13.

Levins, R. 1968. Evolution in changing environments, some theoretical explorations. University Press, Princeton.

MacArthur, R.H., Recher, H. & Cody, M. 1966. On relation between habitat selection and species diversity. American Naturalist 100: 319-332.

MacArthur, R.H. & Wilson, E.O. 1967. The theory of island biogeography. Princeton University Press, Princeton.

Mitlacher, K., Poschlod, P., Rosen, E. & Bakker, J.P. 2002. Restoration of wooded meadows - a comparative analysis along a chronosequence on Oland (Sweden). Appl Veg Sci 5: 63-73.

Pihlgren, A. & Lennartsson, T. 2008. Shrub effects on herbs and grasses in semi-natural grasslands: positive, negative or neutral relationships? Grass and Forage Science 63: 9-21.

Pykälä, J., Luoto, M., Heikkinen, R.K. & Kontula, T. 2005. Plant species richness and persistence of rare plants in abandoned semi-natural grasslands in northern Europe. Basic Appl Ecol 6: 25-33.

R Development Core Team 2008. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

ter Braak, C.J.F. & Smilauer, P. 2002. CANOCO reference manual and CanoDraw for Windows user's guide: Software for canonical community ordination (version 4.5). Microcomputer Power, Ithaca NY, USA.

Willems, J.H. 2001. Problems, approaches, and, results in restoration of Dutch calcareous grassland during the last 30 years. Restor Ecol 9: 147-154.

Wisskirchen, R. & Haeupler, H. 1998. Standardliste der Farn- und Blütenpflanzen Deutschlands. In: Ulmer, Stuttgart.

3 Similarity between soil seed bank and aboveground vegetation with increasing shrub encroachment on extensively managed grasslands

3.1 Abstract

Question: We tested the hypothesis that shrub encroachment as a sign of secondary succession leads to a loss of similarity between vegetation and soil seed bank. We investigated whether plant functional types can be used to explain the differences in similarity.

Location: Extensively managed, shrub-encroached grasslands in Lower Saxony, Germany.

Methods: We performed a descriptive correlative gradient analysis of shrub invaded grasslands. Similarity between aboveground vegetation and corresponding soil seed banks were compared with respect to the degree of shrub encroachment and proportion of several plant functional types. We applied single linear models as well as Detrended Correspondence Analysis.

Results: Similarity between seed bank and aboveground vegetation (Jaccard's coefficient of community) ranged between 7.5 and 36.4 %. Highest similarity was found in intermediately shrub invaded grasslands (humpback relation). With changing vegetation composition from grassland to shrub and forest vegetation, the similarity decreased. The following plant functional types were positively correlated with Jaccard index: therophyte (life form), annual plants (life span), and proportion of forbs.

Conclusion: Seed bank-vegetation similarity is not linearly related with shrub encroachment in general. The present vegetation composition has a great influence on similarity and seems to be a better indicator for succession than shrub encroachment only. Plant functional traits can be used to detect characteristics predicting seed bank-vegetation similarity.

Nomenclature: Wisskirchen & Haeupler (1998)

3.2 Introduction

Soil seed banks have been widely discussed in the context of conservation and restoration of formerly species-rich vegetation. In particular, semi-natural grasslands have received great attention because of their importance for nature conservation. They are considered to belong to the most species-rich habitats in Europe while they are highly threatened by abandonment and shrub encroachment. However, the potential of soil seed banks for restoring such species-rich vegetation generally seems to be low (Bakker et al. 1996; Bekker et al. 1997; Bossuyt & Honnay 2008; Dutoit & Alard 1995; Grandin 2001; Hutchings & Booth 1996; Kalamees & Zobel 1997; Pärtel et al. 1998; Rosef 2008), with the exception of very early successional stages (Kiefer & Poschlod 1996) or certain species (Willems 1988).

Several studies have investigated the similarity between soil seed bank composition and aboveground vegetation in relation to environmental conditions such as salinity (Egan & Ungar 2000), altitude and topography (Peco et al. 1998), type and level of disturbance (Chang et al. 2001; Jutila 2003; Levassor et al. 1990; Osem et al. 2006; Peco et al. 1998) and primary or secondary succession (Bekker et al. 2000; Grandin 2001; Grandin & Rydin 1998; Milberg 1995). As Osem *et al.* (2006) noticed, results are sometimes contradictory and the relation between seed bank and aboveground vegetation is not clearly understood. It could be shown that the similarity between the seed bank and the aboveground vegetation decreases with continuing secondary succession (Falinska 1999; Grandin 2001; Kiirikki 1993; Matlack & Good 1990). In general, there are only weak seed bank-vegetation similarities in perennial grasslands because of the transient seed bank of most grassland species (Thompson et al. 1997).

In the present study, we tested the hypothesis that the seed bank-vegetation similarity decreases over a successional gradient in extensive grasslands using a shrub encroachment index as an indicator of successional stages. To find variables predicting the seed bank-vegetation similarity, we studied the influence of the present vegetation using a plant functional trait analysis.

3.3 Methods

3.3.1 Study site

The study site was the Kerstlingeroeder Feld, which is situated in the north-east of Goettingen, Lower Saxony, Germany (35°68’-70’R, 57°10’-14’H, 300-375 m a. s. l). Because of former military use, this site passed the last century without agricultural intensification. Since 2004, it has been a nature reserve. In an area of approximately 200 ha, there is a wide range of extensively managed or abandoned grasslands, leading from rudimental semi-dry chalk grasslands (Gentiano Koelerietum) and grasslands of the class Molinio Arrhenatheretea (Lolio-Cynosuretum), to more or less unmanaged and shrub-invaded types linking to forest edges (Trifolion medii) and shrub vegetation (Prunetalia). The main woody species are *Crataegus spp.*, *Rosa canina*, *Fraxinus* *excelsior* and *Cornus sanguinea*. The soils are Cambisol and to a small proportion Leptosol (Rendzina) on calcareous rock. The long-term mean annual temperature for the study area is 8.7 °C and the mean annual precipitation is 613 mm.

3.3.2 Experimental design

We performed a descriptive correlative gradient analysis with 30 plots (10 m x 10 m), systematically positioned within the predetermined geographical area. The intension was (1) to cover as much of the total variation in the species composition as possible and (2) to get a homogeneous gradient of shrub encroachment. The plots were selected by means of a time series of aerial photographs.

To measure the intensity of shrub occurrence, a shrub index was calculated based on the percentage cover and the canopy height (cm) of the shrubs:

$$Scrub\ index = \log(1 + cover * canopy\ height)$$

The shrub index represents a measure of the shrub volume, thus taking into account the competition for light more than shrub cover only. This reflects the finding that shrub encroachment is leading to a reduction of solar radiation, and light is regarded as an important factor influencing species diversity (Pausas & Austin 2001; Pykälä et al. 2005). Based on the shrub index, the plots were classified into six shrub classes with five plots per class.

3.3.3 Vegetation and seed bank sampling

Vegetation data was measured during June and July 2005 by recording the species present in 10 randomly distributed 1 m x 1 m quadrates per plot. Phanerophytes (incl. *Rubus spp.*) were included if they extended into the space above the quadrates. For statistical analyses, we used binary (presence-absence) data at the plot level.

To assess the soil seed bank composition, we collected soil samples in April 2006 before natural germination occured. Per plot, 20 soil cores (4 cm diameter, 4 cm depth) were taken randomly (i.e. approximately 1000 cm^3 soil per plot). The minimum soil depth to the chalk bedrock was about 5 cm, so we limited the sampling depth to 4 cm. The soil was washed and sieved according to the concentration method described by Ter Heerdt *et al.* (1996). The enriched soil was spread on sterilised substrate and placed in a greenhouse. Emerging seedlings were determined and counted over the following vegetation period until no further germination occurred.

The nomenclature of plant species was used according to Wisskirchen *et al.* (1998). In the case of *Ranunculus auricomus agg.*, *Ranunculus polyanthemos agg.*, *Rubus* *fruticosus agg.* and *Taraxacum sect. Ruderalia*, determination ended with species aggregates. Seedlings of *Poa pratensis*, *P. angustifolia*, and *P. trivialis* as well as *Agrostis gigantea* and *A. stolonifera* were pooled.

3.3.4 Plant functional types

Plant functional types (PFTs) are described as assemblages of species having certain plant functional attributes in common (Skarpe 1996). The use of PFTs instead of single plant species can be more efficient when searching for general processes or regulating mechanisms in ecological terms such as changes in vegetation composition due to management or succession. We used life form, life span, phytosociological unit as well as classification into woody plants, forbs and grasses (taxonomic group) to build PFTs. An overview is given in Table 3. The ecological data was extracted from the information system BiolFlor (Klotz et al. 2002). In case species were assigned to more than one functional group (e.g. therophyte and hemicryptophyte), we counted those species proportionally.

3.3.5 Data analysis

Similarity between seed bank and vegetation composition is calculated using the Jaccard index (Jaccard's coefficient of community) as an asymmetrical binary coefficient of similarity (Legendre & Legendre 1998). It is calculated as:

$$J(x1, x2) = \frac{a}{a+b+c}$$

where a is the number of species in common and b and c are the number of species occurring only at one site.

We applied linear models (single regression) with the Jaccard index as the response variable and shrub index and proportion of PFTs as the predictor variables. Percentage data were transformed using an arcsine-square root-function. Statistics were performed with the statistic program R (R Development Core Team 2008). Detrended Correspondence Analysis (DCA) as well as Canonical Correspondence Analysis (CCA) were calculated with the program Canoco (ter Braak & Smilauer 2002). Attribute plots with Jaccard index as response variables were generated using generalized linear models (GLM) with quadratic degree and default settings within CanocoDraw (ter Braak & Smilauer 2002).

Table 3 Plant functional traits and their attributes used to classify vegetation data. The proportion refers to the total number of species and is weighted in case of multiple entries.

Trait and attributes	Abbreviation	Number of species	Weighted proportion [%]
Phytosociological unit			
Weed communities	So1	53	17.3
Shrubs and deciduous forests	So2	104	35.0
Dry and semi-dry grasslands	So3	74	16.4
Commercially used grasslands	So4	117	31.3
Life form			
Therophyte	LF1	45	16.1
Geophyte	LF2	19	6.6
Hemicryptophyte	LF3	155	60.2
Chamaephyte	LF4	9	2.9
Phanerophyte	LF5	34	14.2
Life span			
pluriennial	LS1	195	78.1
biennial	LS2	26	6.3
annual	LS3	44	15.6
Taxonomic group			
Woody plants	G0	33	13.8
Legumes	G1	21	8.8
Forbs excl. Legumes	G2	116	57.3
Graminaceous plants	G3	15	6.3
Grasses	G4	33	13.8

3.4 Results

A total of 3487 seedlings germinated from the soil samples, which corresponds to a mean seed density of 4625 seeds m^{-2} (minimum: 796, maximum: 12412). The most abundant species in the seed bank were *Hypericum perforatum* (20 % of the seedlings), *Poa pratensis/trivialis* (16 %), *Centaurium erythraea* (5.1 %) and *Epilobium tetragonum* (4.2 %). The first two species were also frequent in the aboveground vegetation (H. perforatum 0.25, P. pratensis/trivialis 0.96 of the recorded subplots), whereas the latter two were rare and even absent in some of the plots (*C. erythraea* 0.01, *E. tetragonum* 0.04 of the subplots) (Table 4). In total, we found 241 plant species, 38 of which were found exclusively in the soil seed bank, 119 exclusively in the aboveground vegetation, and 84 species in both seed bank and vegetation. The similarity between the soil seed bank and the aboveground vegetation (Jaccard index) ranged between 7.4 and 36.4 % and reached its maximum at intermediately shrub invaded grasslands. This relation could be described by a second order polynomial (Figure 4).

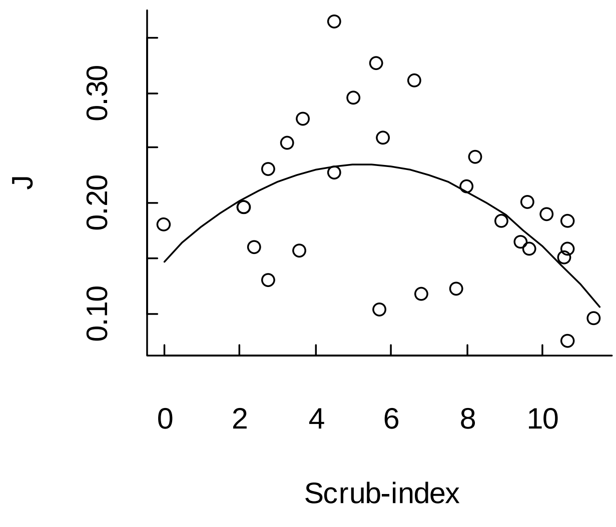

Figure 4 Similarity in species composition (Jaccard index) between soil seed bank and aboveground vegetation in different shrub invaded grasslands (high values correspond to a high degree of shrub encroachment), $J = -0.0033\ x^2 + 0.034\ x + 0.148$, $R^2 = 0.28$, $p = 0.011$.

Table 4 Most frequent species in the soil seed bank: the number of seedlings in total (30 plots, 7540 cm²) and per shrub class (5 plots, 1257 cm²) and their frequency of occurrence in the grassland vegetation (counts per subplots).

	Number of seedlings							Frequency of occurrence in the vegetation						
		Shrub class							Shrub class					
	total	1	2	3	4	5	6	total	1	2	3	4	5	6
Hypericum perforatum	692	10	19	230	219	104	110	0.25	0.26	0.06	0.40	0.32	0.36	0.10
Poa pratensis/trivialis	556	76	61	133	138	75	73	0.96	0.88	1.00	1.16	0.94	0.96	0.80
Centaurium erythraea	179	41	0	68	23	9	38	0.01	0.04	0.02	0.00	0.00	0.00	0.00
Epilobium tetragonum	145	2	14	98	4	15	12	0.04	0.00	0.14	0.12	0.00	0.00	0.00
Campanula rotundifolia	131	0	14	2	85	27	3	0.02	0.00	0.02	0.00	0.04	0.06	0.00
Agrostis capillaris	117	97	0	3	0	16	1	0.06	0.12	0.00	0.08	0.04	0.08	0.02
Holcus lanatus	116	56	44	9	6	1	0	0.28	0.72	0.34	0.34	0.24	0.00	0.02
Juncus inflexus	104	13	66	7	1	16	1	0.01	0.00	0.08	0.00	0.00	0.00	0.00
Plantago lanceolata	97	27	1	41	7	20	1	0.39	0.82	0.16	0.48	0.56	0.24	0.06
Trifolium campestre	92	29	20	29	11	2	1	0.10	0.00	0.18	0.34	0.04	0.04	0.02
Prunus spinosa	82	12	18	12	13	18	9	0.18	0.00	0.16	0.08	0.42	0.28	0.14
Ranunculus repens	74	31	1	15	5	20	2	0.21	0.24	0.14	0.26	0.30	0.16	0.14
Agrostis gigantea/stolonifera	69	32	3	8	6	18	2	0.09	0.38	0.04	0.04	0.04	0.00	0.02
Carex flacca	67	2	12	22	1	25	5	0.21	0.40	0.32	0.18	0.18	0.10	0.08
Deschampsia cespitosa	66	0	1	59	0	0	6	0.11	0.12	0.20	0.14	0.06	0.02	0.14
Veronica serpyllifolia	62	43	0	7	7	4	1	0.03	0.02	0.02	0.14	0.00	0.00	0.00
Leucanthemum vulgare	45	7	3	14	11	2	8	0.12	0.20	0.16	0.18	0.10	0.02	0.04
Medicago lupulina	39	4	8	7	3	14	3	0.22	0.14	0.44	0.36	0.26	0.12	0.00
Daucus carota	37	0	12	17	6	2	0	0.18	0.08	0.46	0.42	0.06	0.08	0.00
Sanguisorba minor	34	0	1	5	9	17	2	0.20	0.00	0.24	0.28	0.34	0.34	0.02

Focussing on plant functional types, we found strong differences between the aboveground vegetation and the soil seed bank with shrub encroachment. While the vegetation composition showed clear responses to shrub encroachment in several PFTs, the soil seed bank composition remained more or less stable (Figure 5). With increasing shrub encroachment, the percentage of grassland and weedy species decreased from 0.44 and 0.15 to 0.22 and 0.05, respectively, whereas shrub species and those of deciduous forests increased from 0.20 to 0.62 in the vegetation. Again, the percentage of hemicryptophytes and therophytes decreased (from 0.72 and 0.13 to 0.59 and 0.07, respectively), benefiting phanerophytes (which increased from 0.05 to 0.25). Accordingly, we found less herbaceous and more woody species with shrub encroachment. Focussing on life span, there was a decrease of annual species in the vegetation (similar to the decrease of therophytes) but no clear trend in the proportion of annual species in the seed bank (Figure 5).

The proportions of plant functional types in the vegetation were tested to predict seed bank-vegetation similarity using linear regression models. A high explanatory power had the proportion of forbs ($R^2 = 0.47$), therophytes ($R^2 = 0.44$) and annual species, respectively. They were all positively correlated with Jaccard index. Within the phytosociological units we found a positive influence of species of weed communities ($R^2 = 0.27$) and a negative influence of species of shrubs and deciduous forests ($R^2 = 0.27$) on seed bank-vegetation similarity.

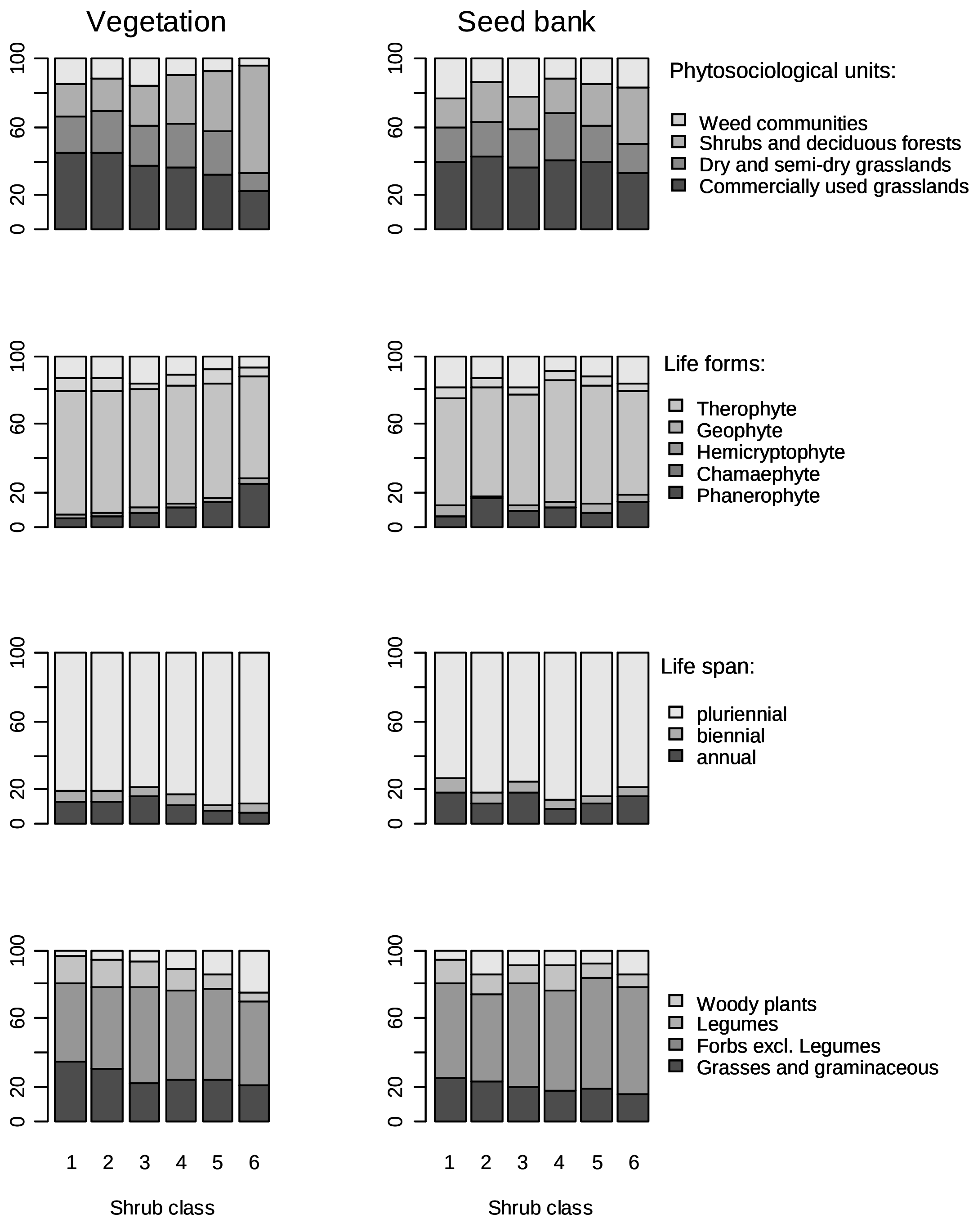

Figure 5 Species composition of aboveground vegetation (left) and soil seed bank (right) depending on shrub encroachment (a higher shrub class corresponds to a higher degree of shrub encroachment). Displayed are percentages of plant species differentiated into phytosociological units, life forms, life span and taxonomic groups.

Canonical Correspondence Analysis shows the alignment of the plots by their vegetation composition constrained by the proportion of PFTs (Figure 6). The significant PFTs were therophyte (LF1), hemicryptophyte (LF3), graminaceous plants (G3), grasses (G4) and the phytosociological units shrubs and deciduous forests (So2) and dry and semi-dry grasslands (So3). The first CCA-axis obviously represents a gradient of shrub encroachment, which is confirmed by the positive correlation with the PFT shrubs and deciduous forests. A fitted model with Jaccard index as response variable (GLM, quadratic degree) showed lowest seed bank-vegetation similarity with high values for the first CCA-axis (Figure 6). This indicates that a higher proportion of species of the PFT shrubs and deciduous forests lead to a lower seed bank-vegetation similarity. In addition, higher proportions of therophytes, hemicryptophytes as well as grasses lead to higher seed bank-vegetation similarity. The results of the CCA corresponded to those of single linear regression models but provided a better overview of the measured variables in condensed form.

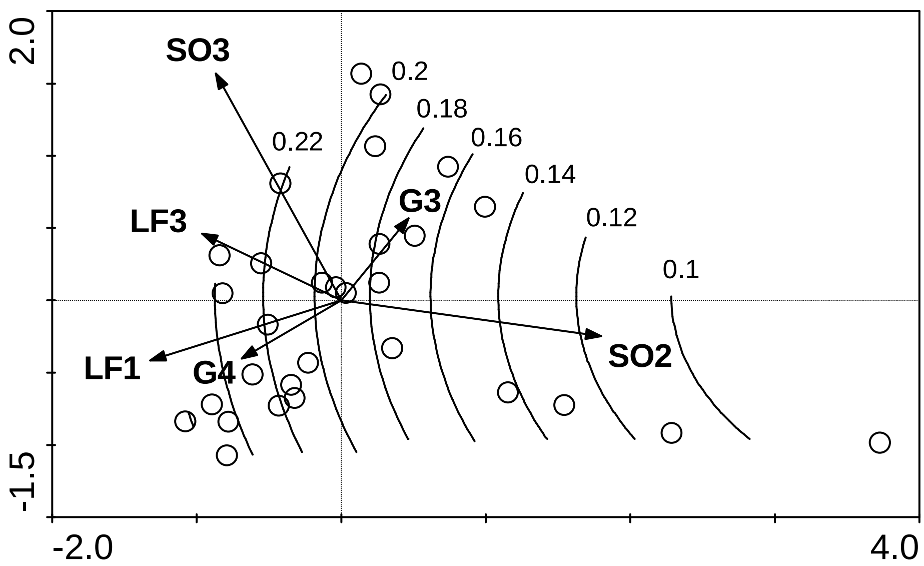

Figure 6 Ordination plot (CCA, 1. and 2. axis) of vegetation data. Arrows represent the proportion of plant functional types (for abbreviations see Table 3), curved lines are the visualization of a fitted model with Jaccard Index (similarity between the vegetation and the soil seed bank) as response variables (GLM, quadratic degree).

3.5 Discussion

Contrary to expectations, our results showed a humpback relation between seed bank-vegetation similarity and shrub encroachment. Highest similarity occurred at medium shrub invaded grasslands. So far, several studies found a decreasing seed bank-vegetation similarity with increasing secondary succession (Falinska 1999; Grandin 2001; Kiirikki 1993; Matlack & Good 1990; McGee & Feller 1993; Pierce & Cowling 1991). On the contrary, similarity increased during primary succession (Grandin & Rydin 1998). In general, lowest similarity should occur where vegetation composition has changed substantially in the recent past. This is true when the vegetation has passed a series of compositionally different successional stages. There could be two reasons for the humpbacked relation we observed. First, there might be different levels of disturbance in grasslands with different shrub invasion. In general, succession can be viewed as a gradient from disturbance-adapted to stress-tolerant vegetation (Davies & Waite 1998; Grime 1977), and a higher level of disturbance is leading to a higher similarity caused by increased generative reproduction. Secondly, we used shrub encroachment as a measure of succession. It is, however, a hypothetic successional gradient, where later successional stages need not necessarily pass the earlier ones. This may influence the observed relation for seed bank-vegetation similarity. Nevertheless, shrub encroachment is one of the most characteristic results of secondary succession in grasslands and can be seen as an important biotic as well as environmental factor influencing vegetation composition. It affects vegetation composition primarily by competition for light, but also by competition for nutrients and water (Pykälä et al. 2005; Tilman 1985).

Calculated seed bank-vegetation similarity depends on the proportion of shared as well as the ratio of the number of species. The maximum of the Jaccard index is defined as:

$$J\max = A/B$$

where A and B are the numbers of species and A $\leq$ B. In agreement with other studies, we found the seed bank less diverse than the corresponding vegetation. A decline in the number of seed bank species, with constant numbers of species in the vegetation, limits the calculated similarity. In our investigation, there was no significant effect of the ratio of the number of species on the similarity, but it should be accounted for if high similarities are expected.

Several plant functional types have been discussed in the context of seed bank-vegetation analyses, including life span (perennial-annual ratio) (Peco et al. 1998), seed mass (Donelan & Thompson 1980; Grandin & Rydin 1998), strategy type *sensu* Grime (Pellissier et al. 2004) and seed longevity. Annual plants produce mostly high amounts of small seeds and they often form a persistent seed bank. Furthermore, they are often linked to the strategy type R (ruderals). Accordingly, we found a positive correlation between proportion of annual plants (which is similar to the life form therophyte) and seed bank-vegetation similarity. Peco *et al.* (1998) pointed out a similar result, as they found the ratio of number of perennial species and number of annual species able to predict the seed bank-vegetation similarity. In contrast, they could proof this result only for autumn collected and not for spring collected seed bank samples. This was attributed to the loss of seeds over the winter period. Nevertheless, life span (annual) is probably a good indicator for seed bank-vegetation similarity.

We also tested the plant functional type life form, phytosociological unit and taxonomic group for correlations with seed bank-vegetation similarity. Due to the gradient of shrub encroachment in the present study, there was a high variability in the proportion of the PFTs concerning shrubs: phanerophytes (life form), woody plants, shrubs and deciduous forests (phytosociological unit). To avoid autocorrelations, we used single regressions as well as CCA with forward selection of the variables to explain the seed bank-vegetation similarity. Besides the life span (annual and pluriennial), we found well fitted models with the proportion of forbs and therophytes as explanatory variables. They were positively correlated with the Jaccard index. The high influence of the proportion of forbs might be explained by their tendency to have persistent seeds (Peco et al. 1998) as well as by the negative correlation between the proportion of forbs and the proportion of woody plants. Woody species, especially trees and shrubs, are often found to be little represented or absent from the soil seed bank (Brown & Oosterhuis 1981; Davies & Waite 1998; Donelan & Thompson 1980; Thompson et al. 1997; Warr et al. 1994).

In addition, the CCA pointed out the negative effect of species of the sociological unit shrubs and deciduous forests and the positive effect of therophytes, hemicryptophytes and grass species on the seed bank-vegetation similarity. While a predominance of grass species and hemicryptophytes is characteristic of grassland vegetation, the first CCA axis can be regarded as a gradient of decreasing seed bank-vegetation similarity from grassland to shrub and forest vegetation. The change in vegetation composition is obviously a better indicator for succession than the establishment of shrubs and trees only.

In summary, we could not verify the hypothesis that seed bank-vegetation similarity decreases with shrub encroachment. However, we found evidence for decreasing similarity with changing vegetation composition from grassland to shrub and forest vegetation. Furthermore, the proportion of the PFTs therophyte (life form), annual plants (life span) and forbs seem to be useful as predictors of seed bank-vegetation similarities in shrub-encroached grassland.

3.6 References

Bakker, J.P., Bakker, E.S., Rosen, E., Verweij, G.L. & Bekker, R.M. 1996. Soil seed bank composition along a gradient from dry alvar grassland to Juniperus shrubland. J Veg Sci 7: 165-176.

Bekker, R.M., Verweij, G.L., Bakker, J.P. & Fresco, L.F.M. 2000. Soil seed bank dynamics in hayfield succession. J Ecol 88: 594-607.

Bekker, R.M., Verweij, G.L., Smith, R.E.N., Reine, R., Bakker, J.P. & Schneider, S. 1997. Soil seed banks in European grasslands: does land use affect regeneration perspectives? Journal of Applied Ecology 34: 1293-1310.

Bossuyt, B. & Honnay, O. 2008. Can the seed bank be used for ecological restoration? An overview of seed bank characteristics in European communities. J Veg Sci 19: 875-884.

Brown, A.H.F. & Oosterhuis, L. 1981. The role of buried seed in coppicewoods. Biological Conservation 21: 19-38.

Chang, E.R., Jefferies, R.L. & Carleton, T.J. 2001. Relationship between vegetation and soil seed banks in an arctic coastal marsh. J Ecol 89: 367-384.

Davies, A. & Waite, S. 1998. The persistence of calcareous grassland species in the soil seed bank under developing and established scrub. Plant Ecol 136: 27-39.

Donelan, M. & Thompson, K. 1980. Distribution of buried viable seeds along a successional series. Biological Conservation 17: 297-311.

Dutoit, T. & Alard, D. 1995. Permanent seed banks in chalk grassland under various management regimes - their role in the restoration of species-rich plant-communities. Biodivers Conserv 4: 939-950.

Egan, T.P. & Ungar, I.A. 2000. Similarity between seed banks and above-ground vegetation along a salinity gradient. J Veg Sci 11: 189-194.

Falinska, K. 1999. Seed bank dynamics in abandoned meadows during a 20-year period in the Bialowieza National Park. J Ecol 87: 461-475.

Grandin, U. 2001. Short-term and long-term variation in seed bank/vegetation relations along an environmental and successional gradient. Ecography 24: 731-741.

Grandin, U. & Rydin, H. 1998. Attributes of the seed bank after a century of primary succession on islands in Lake Hjalmaren, Sweden. J Ecol 86: 293-303.

Grime, J.P. 1977. Evidence for existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. Am Nat 111: 1169-1194.

Hutchings, M.J. & Booth, K.D. 1996. Studies on the feasibility of re-creating chalk grassland vegetation on ex-arable land. 1. The potential roles of the seed bank and the seed rain. Journal of Applied Ecology 33: 1171-1181.

Jutila, H.M. 2003. Germination in Baltic coastal wetland meadows: similarities and differences between vegetation and seed bank. Plant Ecol 166: 275-293.

Kalamees, R. & Zobel, M. 1997. The seed bank in an Estonian calcareous grassland: Comparison of different successional stages. Folia Geobot Phytotx 32: 1-14.

Kiefer, S. & Poschlod, P. 1996. Restoration of fallow of afforested calcareous grasslands by clear-cutting. In: Settele, J., Margules, C.R., Poschlod, P. & Henle, K. (eds.) Species survival in fragmented landscapes., pp. 209–218. Kluwer, Dordrecht.

Kiirikki, M. 1993. Seed bank and vegetation succession in abandoned fields in Karkali-Nature-Reserve, southern Finland. Ann Bot Fenn 30: 139-152.

Klotz, S., Kühn, I. & Durka, W. 2002. BIOLFLOR - Eine Datenbank zu biologisch-ökologischen Merkmalen der Gefäßpflanzen in Deutschland. In: Schriftenreihe für Vegetationskunde, Bundesamt für Naturschutz, Bonn.

Legendre, P. & Legendre, L. 1998. Numerical ecology. 2nd English. Elsevier, Amsterdam ; New York.

Levassor, C., Ortega, M. & Peco, B. 1990. Seed bank dynamics of mediterranean pastures subjected to mechanical disturbance. J Veg Sci 1: 339-344.

Matlack, G.R. & Good, R.E. 1990. Spatial heterogeneity in the soil seed bank of a mature coastal-plain forest. B Torrey Bot Club 117: 143-152.

McGee, A. & Feller, M.C. 1993. Seed banks of forested and disturbed soils in southwestern British-Columbia. Can J Bot 71: 1574-1583.

Milberg, P. 1995. Soil seed bank after 18 years of succession from grassland to forest. Oikos 72: 3-13.

Osem, Y., Perevolotsky, A. & Kigel, J. 2006. Similarity between seed bank and vegetation in a semi-arid annual plant community: The role of productivity and grazing. J Veg Sci 17: 29-36.

Pärtel, M., Kalamees, R., Zobel, M. & Rosen, E. 1998. Restoration of species-rich limestone grassland communities from overgrown land: the importance of propagule availability. Ecol Eng 10: 275-286.

Pausas, J.G. & Austin, M.P. 2001. Patterns of plant species richness in relation to different environments: An appraisal. J Veg Sci 12: 153-166.

Peco, B., Ortega, M. & Levassor, C. 1998. Similarity between seed bank and vegetation in mediterranean grassland: a predictive model. J Veg Sci 9: 815-828.

Pellissier, V., Gallet, S. & Roze, F. 2004. Comparison of the vegetation and seed bank on hedge banks of different ages in Brittany, France. Environ Manage 34: 52-61.

Pierce, S.M. & Cowling, R.M. 1991. Dynamics of soil-stored seed banks of six shrubs in fire-prone dune fynbos. J Ecol 79: 731-747.

Pykälä, J., Luoto, M., Heikkinen, R.K. & Kontula, T. 2005. Plant species richness and persistence of rare plants in abandoned semi-natural grasslands in northern Europe. Basic Appl Ecol 6: 25-33.

R Development Core Team 2008. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Rosef, L. 2008. Germinable soil seed banks in abandoned grasslands in central and western Norway and their significance for restoration. Appl Veg Sci 11: 223-U234.

Skarpe, C. 1996. Plant functional types and climate in a southern African savanna. J Veg Sci 7: 397-404.

ter Braak, C.J.F. & Smilauer, P. 2002. CANOCO reference manual and CanoDraw for Windows user's guide: Software for canonical community ordination (version 4.5). Microcomputer Power, Ithaca NY, USA.

Ter Heerdt, G.N.J., Verweij, G.L., Bekker, R.M. & Bakker, J.P. 1996. An improved method for seed-bank analysis: Seedling emergence after removing the soil by sieving. Funct Ecol 10: 144-151.

Thompson, K., Bakker, J.P. & Bekker, R.M. 1997. The soil seed banks of North West Europe. Methodology, density and longevity. Cambridge Univ. Press, Cambridge.

Tilman, D. 1985. The Resource-Ratio Hypothesis of Plant Succession. Am Nat 125: 827-852.

Warr, S.J., Kent, M. & Thompson, K. 1994. Seed bank composition and variability in five woodlands in south-west England. J Biogeogr 21: 151-168.

Willems, J.H. 1988. Soil seed bank and regeneration of a Calluna vulgaris community after forest clearing. Acta Bot Neerl 37: 313-320.

Wisskirchen, R. & Haeupler, H. 1998. Standardliste der Farn- und Blütenpflanzen Deutschlands. In: Ulmer, Stuttgart.

4 Herbage mass and nutritive value of herbage of extensively managed temperate grasslands along a gradient of shrub encroachment[1]

4.1 Abstract

Semi-natural grasslands often serve as important reserves of biodiversity. In Europe extensive grazing by livestock is considered an appropriate management to conserve biodiversity value and to limit shrub encroachment. However, little is known about the influence of shrubs on agronomic values. A gradient analysis of shrub-invaded temperate grasslands (from shrub-free to pioneer forest) in Germany was carried out to test the hypothesis that herbage mass and variables describing nutritive value of herbage decrease with increasing shrub encroachment. The herbage mass of dry matter (DM), variables describing the nutritive value of herbage, composition of the vegetation and mean of Ellenberg's indicator values were analysed with respect to the extent of shrubs. There was a reduction of herbage mass of DM from 3570 to 210 kg ha^{-1} with increasing shrub encroachment. Metabolizable energy concentration of herbage ranged from 8.9 to 10.2 MJ kg^{-1} DM and crude protein concentration from 72 to 171 g kg^{-1} DM, both measures being positively correlated with shrub occurrence. Increasing shrub occurrence was associated with a decrease in water-soluble carbohydrates concentration (from 151 to 31 g kg^{-1}) and a reduction in the indicator 'forage value'. The results indicate a potentially large agronomic value for shrub-encroached temperate grasslands.

4.2 Introduction

In Europe species-rich grasslands are of high conservation interest but are often invaded by shrubs, and many are threatened by under-utilization and abandonment which contribute to further shrub encroachment. Extensive grazing has been suggested as a means for conserving these species-rich grasslands (Dumont et al. 2007; Rook et al. 2004). In a global context, shrub lands play an important role in supporting the nutrition of grazing livestock. Little is known about shrub-invaded temperate grasslands and their value, and their potential use for livestock production in Central Europe. Reasons for this could be a low interest in their agronomic use and a general decrease in the numbers of small ruminants available to graze these grasslands. Interest in species-rich semi-

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natural grassland and its utilization for livestock production, however, has recently increased (Bruinenberg et al. 2002; Marriott et al. 2004; Pontes et al. 2007).

In shrub-invaded grasslands, shrub species compete with grasses and forbs for the resources of light, water and nutrients, and they also affect the utilization of herbage. Since shrubs function as refuges for plants from grazing, their effect on the sward can be either positive or negative (Pihlgren & Lennartsson 2008). Several studies have described the relationships between shrub cover, herbage mass and nutritive value of herbage in the Mediterranean region (Papachristou et al. 1997; Platis & Papanastasis 2003; Zarovali et al. 2007). In situations affected by shrub encroachment, a sharp reduction in herbage mass and a decrease in the nutritive value of herbage have been usually been found.

In this paper, the herbage mass, and nutritive value of herbage, in relation to shrub encroachment were studied at a site in northern Germany. The hypothesis tested was that both herbage production and the nutritive value of herbage would decrease with shrub encroachment.

4.3 Materials and Methods

4.3.1 Study area

The study area was the Kerstlingeroeder Feld, which is situated in the north-east of Goettingen, Lower Saxony, Germany (51° 52'-51° 55' N, 10° 0' E; 300-375 m a.s.l). The area was used for military purposes from the early 19th century until 1993 and it, thus, passed the last century without agricultural intensification. Since 2004, it has been a nature reserve. Within an area of approximately 200 ha, there is a wide range of extensively managed or abandoned grasslands, ranging from rudimental semi-dry chalk grasslands (Gentiano–Koelerietum pyramidatae) and grasslands of the class Molinio-Arrhenatheretea (Lolio-Cynosuretum), to more or less unmanaged and shrub-invaded types linking to forest edges (Trifolion medii) and shrub vegetation (Prunetalia). The main woody species are *Crataegus* spp., *Rosa canina*, *Fraxinus excelsior* and *Cornus sanguinea*. The soils are Cambisols with a small proportion Leptosol (Rendzina) on calcareous rock. The long-term mean annual temperature for the study area is 8.7 °C and the mean annual precipitation is 645 mm.

4.3.2 Experimental design and measurements

Within the predetermined geographical area, 30 homogeneous plots (10 m x 10 m) were selected along a gradient of shrub cover (expressed as % cover), based on a time series of aerial photographs. The aim was to represent a wide range of shrub encroachment from grasslands that were nearly shrub-free to sites with very dense shrub cover. One abandoned site, which can be characterized as a pioneer forest on former calcareous grassland, was also included.

Because of differences in shrub height, the intensity of shrub occurrence was measured as a shrub index, based on a combination of percentage cover and maximum canopy height (cm), as follows:

Shrub index = ln (1 + cover x canopy height).

As the shrub index represents a measure of the shrub volume, this was considered to be a better indicator of the competition for light than shrub cover alone.

Herbage samples were harvested at the end of June 2005, at the time of the maximum herbage mass. For reasons of nature conservation, all plots were not grazed until the first week of July. Four randomly placed 1 m x 1 m quadrats were harvested per plot. The herbage was cut to ground level using hand-scissors and subsequently dried to constant weight for 24 h at 60 °C. After determining the dry matter (DM) content of the herbage, the material was ground to pass a 1-mm screen.

Measurements of nutritive value were estimated using near infrared reflectance spectroscopy (NIRS). The spectra were analysed using a large dataset of calibration samples by the Institute VDLUFA Qualitätssicherung NIRS GmbH, Kassel, Germany. The calibration has been validated for a wide range of intensively as well as extensively managed grassland types. In the present study, samples from just one plot (pioneer forest) exceeded a critical H value of 6, indicating a lack of accuracy. The remaining samples had a mean H value of 2.68. The following variables were estimated: crude protein, crude fibre, acid-detergent fibre, crude lipids and water-soluble carbohydrates concentrations. The ash concentration was determined by combusting 1 g of the dried material for 8 h at 550°C.

Metabolizable energy concentration was calculated according to Potthast *et al.* (1997), and estimation of organic matter digestibility following the method of Menke and Steingass (1987).

The botanical composition of the vegetation was determined before cutting the herbage. For each 10 m x 10 m plot, the occurrence of vascular plant species was listed (presence-absence data), and the three dominant species were recorded. The species nomenclature followed Wisskirchen and Haeupler (1998).

4.3.3 Data analysis

The data on the herbage mass of DM and variables describing the nutritive value of herbage from the sub-plots of 1 m x 1 m were used to derive mean values for each plot. Using single linear regressions, the influence of shrub index on the herbage mass of DM and the variables describing the nutritive value of herbage were tested. Tests for homogeneity of variance (Levene’s test) and normality of the residuals (Shapiro-Wilk test) demonstrated that there was no need for transformation of the data although the shrub index was subjected to a log-transformation.

Ellenberg’s indicator values for light, temperature, soil moisture, pH and soil nitrogen (Ellenberg et al. 2001), as well as indicator values for the ‘forage value’ of grassland species (Briemle et al. 2002), were used to calculate mean indicator values per plot. The ‘forage value’ is one of a set of indicator values of grassland utilization for vascular plant species similar to those of Ellenberg. It is based on nutrient concentrations, and the preference for a species to be grazed over space and time, and it is available for 661 species. The mean of Ellenberg’s indicator values was calculated using all species present without weighting, whereas the mean ‘forage value’ was weighted by the dry-weight percentages of the species. The dry-weight percentages were estimated according to the dry-weight-rank method (Mannetje & Haydock 1963). Using this method, estimates are made for a number of subplots (10 in the present study) of the number of times a species occupies the first, second or third place in terms of its contribution on a dry weight basis. Subsequently, the proportion of first, second or third rank per species is multiplied by 70.2, 21.1 or 8.7, respectively and values added for dry weight percentages of these species. The method has previously been tested successfully against the hand seperation method for different types of pastures (Jones & Hargreaves 1979; Mannetje & Haydock 1963; Scott 1993). Averaged indicator values per plot were compared with crude protein, water-soluble carbohydrate and metabolizable energy (ME) concentrations by calculating Pearson’s correlation coefficients.

Statistic analyses was performed using the statistics program R (R Development Core Team 2007).

4.4 Results

4.4.1 Shrub encroachment and vegetation composition

The shrub cover ranged from less than 1 % to nearly 100 %. The canopy height was usually between 15 cm and 500 cm, with one plot being shrub-free and one plot (pioneer forest) having a canopy height of 1000 cm. The values of the shrub index ranged from 0 to 11.4 with a mean of 6.4. The values for shrub encroachment per plot are summarized in Table 5.

The change in vegetation composition was dominated by the occurrence of woody species, especially *Crataegus spp.*, *R. canina*, *F. excelsior* and *C. sanguinea.* The percentage of the number of woody species increased from 4.2 % to 25.2 %, averaged per five plots ordered by shrub index. The most frequent grass species were *Dactylis glomerata*, *Festuca rubra* and *Poa pratensis*. In plots that had a greater proportion of shrub encroachment, the grasses, *Trisetum flavescens* and *Brachypodium pinnatum*, became more abundant. The most frequent forbs were *Galium album*, *Plantago lanceolata*, *Veronica chamaedrys*, *Fragaria vesca* and *Taraxacum sect. Ruderalia*. There was a decrease in the ratio of grass species:forbs from 0.56 to 0.39, and a decrease in the proportion of legume species from 0.157 to 0.046 with increasing shrub encroachment.

Table 5 Shrub cover, shrub canopy height and shrub index, estimated from cover and canopy height of shrubs, for the 30 10 m x 10 m plots from extensively managed grasslands used in the study.

Plot	Shrub cover (%)						Canopy height (cm)	Shrub index
	0-1	1-5	5-25	25-50	50-75	75-100		
1		x					30	4.51
2						x	500	10.69
3						x	500	10.69
4		x					50	5.02
5			x				50	6.62
6		x					90	5.60
7	x						30	2.77
8					x		200	9.43
9						x	1000	11.38
10		x					110	5.80
11			x				250	8.23
12					x		400	10.13
13					x		250	9.66
14	x						70	3.58
15		x					30	4.51
16				x			60	7.72
17				x			400	9.62
18						x	450	10.58
19	x						15	2.14
20	x						15	2.14
21	x						20	2.40
22	x						0	0.00
23	x						30	2.77
24						x	500	10.69
25		x					100	5.71
26	x						80	3.71
27		x					300	6.80
28	x						50	3.26
29			x				200	8.01
30				x			200	8.92

4.4.2 *Herbage mass and variables describing the nutritive value of the herbage*

The herbage mass of DM ranged from 3570 kg ha^{-1} on very open stands to 210 kg ha^{-1} on very dense shrub stands (Table 6). In general, the herbage mass of DM was reduced with increasing shrub encroachment. The influence of the shrub index (X) on the herbage mass of DM (Y, kg DM ha^{-1}) was significant and could be described by a linear regression:

$Y = 2987 - 214 X$, $r^2 = 0.50$, $P < 0.001$ Equation 1

Table 6 summarizes the variation for a range of measures of nutritive value of herbage. In particular, the concentrations of water-soluble carbohydrate (31 to 151 g kg^{-1} DM) and crude protein (72 to 171 g kg^{-1} DM) varied considerably. Values for the concentration of ME ranged from 8.9 to 10.2 MJ kg^{-1} DM. Significant linear regressions of variables of the nutritive value of herbage and shrub index are shown in Figure **7**. Crude protein and crude lipid concentrations of herbage were highly positively correlated with shrub index. Concentration of ME, which is strongly influenced by crude protein and crude fibre concentrations, were also highly positively correlated with the shrub index. On the other hand, water-soluble carbohydrate concentrations were negatively correlated with the shrub index. Organic matter digestibility was not significantly affected by shrub occurrence.

Table 6 Mean values and variation for herbage mass of dry matter (DM), and estimated concentrations of metabolizable energy (ME) and organic matter digestibility (OMD), and variables describing the nutritive value of herbage: concentrations of crude protein (CP), crude fibre (CF), crude lipid (CL), acid-detergent fibre (ADF) and water-soluble carbohydrates (WSC).

	Herbage mass (kg DM ha^{-1})	ME (MJ kg DM^{-1})	OMD	CP (g kg^{-1} DM)	CF (g kg^{-1} DM)	CL (g kg^{-1} DM)	ADF (g kg^{-1} DM)	WSC (g kg^{-1} DM)
Mean	1629	9.6	0.624	117	261	28	295	81
s.d. of mean	1009	0.3	0.002	27	42	4	30	32
Minimum	209	8.9	0.590	72	176	17	238	31
Maximum	3575	10.2	0.659	171	337	35	348	151
CV (%)	62.0	3.1	3.2	228	162	152	101	392

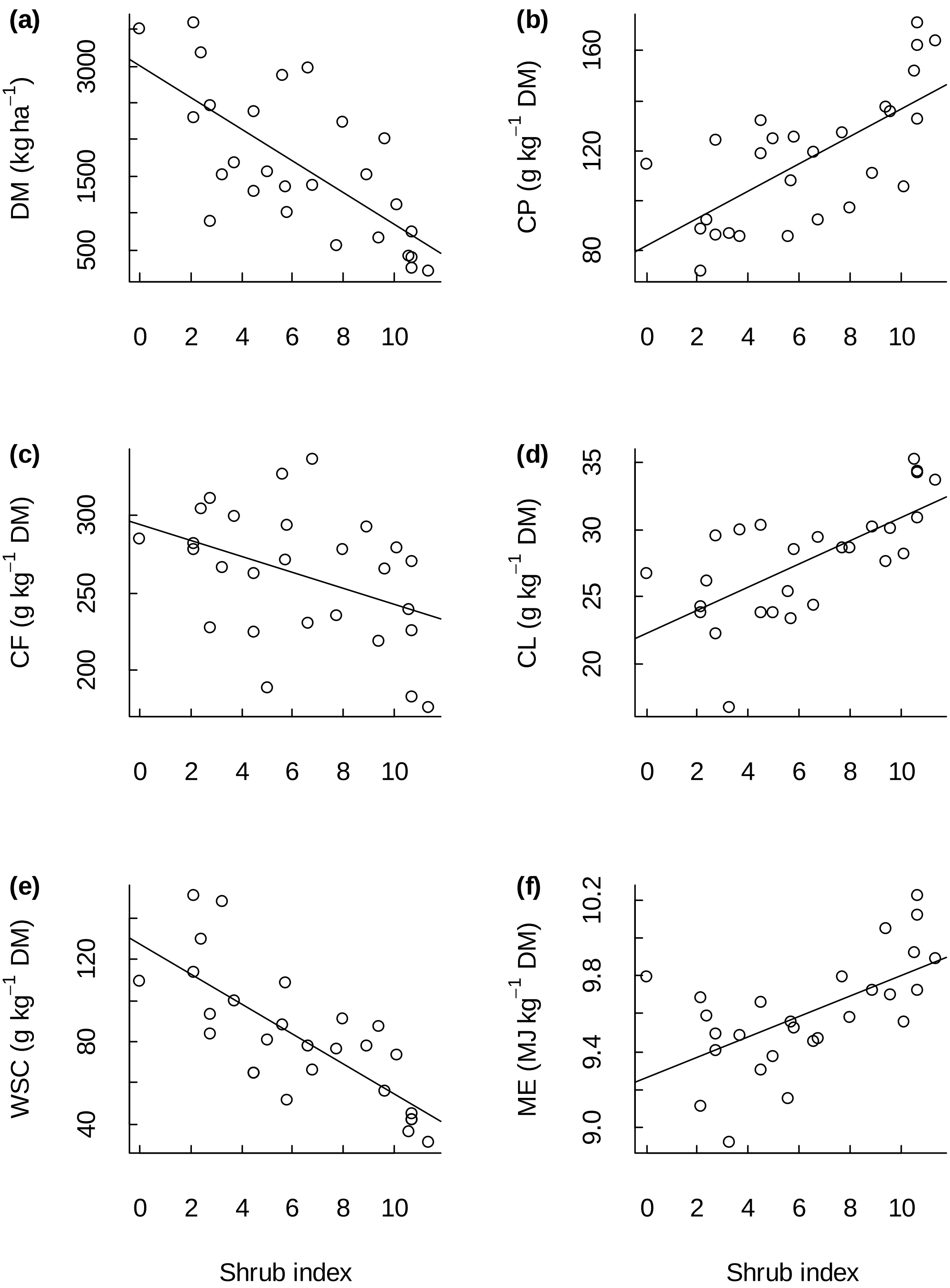

Figure 7 Linear regression models describing the relationship between shrub encroachment (shrub index) and (a) herbage mass of dry matter (DM; R2 = 0.50, P<0.001) and variables describing nutritive value: concentrations of (b) crude protein (CP; R2 = 0.47, P<0.001), (c) crude fibre (CF; R2 = 0.17, P<0.05), (d) crude lipid (CL; R2 = 0.46, P<0.001), (e) water-soluble carbohydrates (WSC; R2 = 0.58, P<0.001) and (f) metabolizable energy (ME, R2 = 0.35, P<0.01).

4.4.3 *Indicator values*

The largest variation in indicator values for species was found for nitrogen and 'forage value' (Table 7). The lowest variation was for the indicator value of temperature, which ranged from 5.3 to 5.7. In general, there was little effect of shrub index on the indicator values. Only the 'forage value' was negatively correlated with shrub index ($r = -0.58$, $P < 0.05$), and the indicator value for light was much lower in very dense shrub stands compared with low and medium shrub-invaded sites (no linear relationship).

Significant correlations between indicator values and variables describing the nutritive value of the herbage are summarized in Table 8. Crude protein and ME concentrations were both negatively correlated with indicator values for light, temperature and 'forage value'. Positive correlations were found between the concentration of water-soluble carbohydrates and indicator values for light and 'forage value'. The other indicator values showed no trends with either increasing shrub encroachment or variables describing the nutritive value of the herbage.

Table 7 Ellenberg's indicator values (Ellenberg et al. 2001) for light (L), temperature (T), moisture (M), pH, nitrogen (N) and 'forage value' of grassland species (FV) according to Briemle *et al.* (2002) Values are the mean of species in each plot averaged across all plots.

	Indicator values					
	L	T	M	pH	N	FV
Minimum	5.67	5.35	3.95	6.45	3.21	2.00
Maximum	7.14	5.71	5.55	7.39	6.13	7.66
Mean	6.74	5.53	4.80	6.95	4.73	5.01
s.d. of mean	0.37	0.10	0.38	0.27	0.67	1.53

Table 8 Pearson correlation between concentrations of crude protein (CP), water-soluble carbohydrates (WSC) and metabolizable energy (ME) and mean species indicator values for light (L), temperature (T), moisture (M), reaction (R), nitrogen (N) and 'forage value' of grassland species (FV).

	CP	WSC	ME	FV
L	-0.58 *	0.56 *	-0.45 *	0.55 *
T	-0.38 *	0.19	-0.51 *	0.66 *
M	-0.11	0.24	-0.18	0.14
R	0.17	-0.29	0.15	-0.20
N	0.26	-0.26	0.15	-0.05
FV	-0.48 *	0.47 *	-0.38 *	-

* Significance at $\alpha = 0.05$

4.5 Discussion

In this study, the effect of shrub encroachment on the agronomic value of extensive grassland was investigated for a site in Central Europe. The decision to use shrub index instead of canopy cover was based on the effect that shrub height has on the amount of shade. The effect depends on the morphology of the shrub, especially the orientation and vertical distribution of leaves. In the present study, the shrub cover and canopy height were highly correlated ($r = 0.81$). However, there is no disadvantage in measuring both traits as this provides a more general description of shrub encroachment and allows comparison with other studies.

The results showed a large variability between plots with regard to shrub index, herbage mass, variables describing the nutritive value of the herbage and the indicator values. In line with the first hypothesis, a decrease in herbage mass with increasing shrub encroachment was found. The hypothesis that there was a decrease in variables describing the nutritive value of the herbage with increasing shrub encroachment, however, was rejected. While some variables describing the nutritive value of herbage were positively related to the presence of shrubs, the indicator value for 'forage value' was negatively related to the presence of shrubs.

In the following sections the influence of shrub encroachment is considered firstly in terms of its effects on herbage mass, then on variables describing the nutritive value of the herbage and finally in relation to species indicator values.

4.5.1 Herbage mass

The maximum value of herbage mass of DM of 3500 kg ha^{-1} was from unfertilized semi-natural grassland, which is about 0.30 to 0.45 of the herbage mass that might be expected from ungrazed agriculturally improved and intensively managed grasslands (Hopkins et al. 1990; Tallowin & Jefferson 1999). In this comparison with published results on herbage mass values, it was assumed that the herbage mass from a single cut at peak herbage mass represents about 0.70 of the annual DM production of herbage (Tallowin & Jefferson 1999).

The negative effect of shrub encroachment on herbage mass of DM is in line with results from Mediterranean grasslands in Greece (Papachristou et al. 1997; Platis & Papanastasis 2003; Zarovali et al. 2007) as well as temperate silvopastoral systems in pine forests in the Black Hills, USA (Pase 1958) and Galicia (Garcia et al. 1999).

In line with Zarovali *et al.* (2007), the main effect on herbage mass of DM is from competition for light, at least for medium and highly shrub-invaded sites. Besides reducing assimilation, reduced light availability also influences vegetation composition and species diversity (Pausas & Austin 2001; Pykälä et al. 2005). This aspect is discussed below.

4.5.2 Variables describing the nutritive value of the herbage

Results from the present study showed different effects on variables describing the nutritive value of herbage in response to shrub encroachment. While crude protein and crude lipid concentrations in the herbage, as well as its ME concentration, increased with increased shrub encroachment, the concentration of water-soluble carbohydrates decreased. These findings differ from those of other studies which have reported a negative relationship between nutritive value of herbage and shrub cover (Yiakoulaki & Nastis 1995; Zarovali et al. 2007). Zarovali *et al.* (2007) attributed the higher crude protein concentration in the open shrub cover type to a larger proportion of legume species in the herbage. In the present study, a larger proportion of legume species was also found in the open stands. However, as these data were based on species numbers, no conclusion about the herbage mass of legumes and their contribution to the nutritive value of the herbage could be drawn. The decrease in the number of legume species in shrub-invaded stands coincided with an increase in the number of forb species compared to grass species, which may also have increased the crude protein concentration of herbage.

The higher crude protein concentrations of herbage, associated with higher shrub cover, were considered to be due not only to the change in vegetation composition but also to physiological processes. The concentration of water-soluble carbohydrates in herbage in the present study decreased with increasing shrub index. This was probably caused by lower light availability. Furthermore, the assimilation of carbohydrate is usually more limited by availability of light than is nitrogen uptake. As a result, nitrogen metabolites can accumulate. This might further depend on climatic conditions, in particular solar radiation, which would explain the difference between this study and those of Mediterranean grasslands.

Besides the crude protein concentration, other important variables are organic matter digestibility and fibre concentration. In this study, organic matter digestibility showed no response to shrub encroachment whereas the crude fibre concentration tended to decrease slightly with increasing shrub encroachment, which can be attributed to the lower ratio of grass species:forbs.

To discriminate between the effects of vegetation composition and shrub encroachment on the nutritive value of herbage, the herbage mass of grass, forbs and legumes species needed to be measured. The dry-weight rank method gives satisfactory results for the dominant species but is not precise enough for this discrimination.

4.5.3 Indicator values

Traits of vegetation composition are reflected in the average values for species indicators. Ellenberg's indicator value for light decreased but only at very dense shrub stands. All other Ellenberg indicator values showed no response to shrub encroachment. Three factors may have led to this result: (i) a relatively small influence of shrubs on edaphic parameters, (ii) a time lag between changing environmental conditions and the response by grassland species, and (iii) an effect of scale. A change in soil variables was reported by Zarovali *et al.* (2007) who suggested there is a greater decomposition rate of organic matter as a result of environmental amelioration caused by shrubs. Other studies have found a shift in nutrient concentrations (especially phosphorus) under *Eucalyptus* trees in Australian pastures (Graham et al. 2004; Prober et al. 2002). More generally, invasion of grasslands by woody plants has been discussed in terms of carbon and nitrogen cycles at the level of the ecosystem (Liao et al. 2006; McLaren et al. 2008).

Encroachment by woody plants has been found to be important for terrestrial carbon sequestration (Houghton 2003; Jackson et al. 2002; Pacala et al. 2001). However, in this study the effect on soil properties seems to be insufficient to be reflected in mean species indicator values for nitrogen and pH. Similarly, no effect of shrubs on indicator values was found for temperature and humidity.

Many grassland species grow under or in close proximity to shrubs. This can lead to increases in species numbers at the beginning of shrub encroachment, a situation in which grassland species as well as shade-tolerant species are supported (Pykälä et al. 2005). In addition, some species growing under shrubs are favoured more by the protection from grazers than the effect of abiotic conditions. Pihlgren and Lennartsson (2008) attributed a positive effect on vegetation height and the ability of reproduction of grasses and forbs to the functioning of shrubs as grazing refuges. The patchy structure of shrub-encroached sites increases heterogeneity, which enables grassland species to survive in spatially distinct areas. The measured effect on vegetation composition is therefore scale-dependent. The plot size of 10 m x 10 m, which was used in this study, may be too large to detect effects on species in the direct neighbourhood of shrubs.

The indicator 'forage value' showed a negative response to shrub encroachment. This finding is in line with the hypothesis of decreasing nutritive value of herbage with increasing shrub cover but it is contrary to the results on the nutritive value of herbage found in this study. The indicator 'forage value' is based on a wider set of measurements than the variables used to describe nutritive value in this study. Only weak correlations were found between 'forage value' and crude protein, water-soluble carbohydrates and ME concentrations. The nutritive value of forage from semi-natural grasslands is not well described by the chemical composition, as equations are mainly derived from the analysis of forage dominated by *Lolium perenne* (Bruinenberg et al. 2002). Herbage from semi-natural grasslands may have relatively high feeding values, if large proportions of dicotyledonous species are present. Low stocking rates, which allow selective grazing, will further increase the nutritive value of the ingested herbage (Isselstein et al. 2007). Also, Pontes *et al.* (2007) found that some grass species of semi-natural grasslands have a nutritive value that is comparable to that of species selected for high yields.

The species involved in estimating the indicator 'forage value' in the present study were estimated according to the dry-weight rank method ('t Mannetje & Haydock 1963). This has been developed on sub-tropical pastures but has been validated in a large number of grasslands comprising different species and different species composition (Jones & Hargreaves 1979; Scott 1993). However, the method needs to be improved for application to semi-natural European grasslands. The main disadvantage in its use in such grasslands is the greater diversity and more complex manner of species dominance. In the present study, there were often more than three dominant species with small differences in abundance and, therefore, the number of weighted species should be increased or adapted. Furthermore, 'forage value' has not been described for all species growing in extensive grassland. In this study, there were 63 out of 202 plant species without a published indicator value for 'forage value'. While the use of indicator values would provide some advantage over expensive and time-consuming analyses, further investigation is recommended to improve the method and its predictive value.

4.6 Conclusions

There was a sharp reduction in herbage production mass of DM with increasing shrub encroachment. There was also an increase in crude protein, crude lipid and ME concentrations and a decrease in water-soluble carbohydrates concentration with increasing shrub encroachment.

In contrast to the variables describing the nutritive value of herbage, the indicator, 'forage value', declined as a consequence of shrub encroachment. This was probably due to the broader range of variables other than chemical composition, used to estimate 'forage value'. The accuracy of this indicator, however, could be improved for extensive grassland by using more than three dominant species per subplot within the dry-weight rank method or by directly determining the dry-weight percentages. 'Forage value' also needs to be described for more species. Ellenberg's indicator values for species showed no response to shrub encroachment which was attributed mainly to the effect of scale of measurement.

4.7 References

Briemle, G., Nitsche, S. & Nitsche, L. 2002. Nutzungswertzahlen für Gefäßpflanzen des Grünlandes. In: Klotz, S., Kühn, I. & Durka, W. (eds.) BIOLFLOR - eine Datenbank mit biologisch-ökologischen Merkmalen zur Flora von Deutschland, pp. 203-225. Bundesamt für Naturschutz, Bonn.

Bruinenberg, M.H., Valk, H., Korevaar, H. & Struik, P.C. 2002. Factors affecting digestibility of temperate forages from seminatural grasslands: a review. Grass and Forage Science 57: 292-301.

Dumont, B., Rook, A.J., Coran, C. & Röver, K.-U. 2007. Effects of livestock breed and grazing intensity on biodiversity and production in grazing systems. 2. Diet selection. Grass and Forage Science 62: 159-171.

Ellenberg, H., Weber, H.E., Düll, R., Wirth, V. & Werner, W. 2001. Zeigerwerte von Pflanzen in Mitteleuropa. Goltze, Göttingen.

Garcia, A., Rozados, M.J., Silva-Panto, F.J. & Lindner, R. 1999. Evaluation of natural populations of Dactylis glomerata for grazing under pinewoods. Grassland Science in Europe 4: 167-169.

Graham, S., Wilson, B.R., Reid, N. & Jones, H. 2004. Scattered paddock trees, litter chemistry, and surface soil properties in pastures of the New England Tablelands, New South Wales. Aust J Soil Res 42: 905-912.

Hopkins, A., Gilbey, J., Dibb, C., Bowling, P.J. & Murray, P.J. 1990. Response of Permanent and Reseeded Grassland to Fertilizer Nitrogen .1. Herbage Production and Herbage Quality. Grass and Forage Science 45: 43-55.

Houghton, R.A. 2003. Revised estimates of the annual net flux of carbon to the atmosphere from changes in land use and land management 1850-2000. Tellus B 55: 378-390.

Isselstein, J., Griffith, B.A., Pradel, P. & Venerus, S. 2007. Effects of livestock breed and grazing intensity on biodiversity and production in grazing systems. 1. Nutritive value of herbage and livestock performance. Grass and Forage Science 62: 145-158.

Jackson, R.B., Banner, J.L., Jobbagy, E.G., Pockman, W.T. & Wall, D.H. 2002. Ecosystem carbon loss with woody plant invasion of grasslands. Nature 418: 623-626.

Jones, R.M. & Hargreaves, J.N.G. 1979. Improvements to the Dry-Weight-Rank Method for Measuring Botanical Composition. Grass and Forage Science 34: 181-189.

Liao, J.D., Boutton, T.W. & Jastrow, J.D. 2006. Storage and dynamics of carbon and nitrogen in soil physical fractions following woody plant invasion of grassland. Soil Biol Biochem 38: 3184-3196.

Mannetje, L.t. & Haydock, K.P. 1963. The dry-weight-rank method for the botanical analysis of pasture. J Brit Grassland Soc 18: 268-275.

Marriott, C.A., Fothergill, M., Jeangros, B., Scotton, M. & Louault, F. 2004. Long-term impacts of extensification of grassland management on biodiversity and productivity in upland areas. A review. Agronomie 24: 447-462.

McLaren, M.P., Moore-Kucera, J., Martens, D.A., van Haren, J. & Marsh, S.E. 2008. Soil carbon and nitrogen in relation to shrub size and death in a semi-arid grassland. Geoderma 145: 60-68.

Menke, K.H. & Steingass, H. 1987. Schätzung des energetischen Futterwertes aus der in vitro mit Pansensaft bestimmten Gasbildung und der chemischen Analyse. II. Regressionsgleichungen. Übers. Tierernährung 15: 59-99.

Pacala, S.W., Hurtt, G.C., Baker, D., Peylin, P., Houghton, R.A., Birdsey, R.A., Heath, L., Sundquist, E.T., Stallard, R.F., Ciais, P., Moorcroft, P., Caspersen, J.P., Shevliakova, E., Moore, B., Kohlmaier, G., Holland, E., Gloor, M., Harmon, M.E., Fan, S.M., Sarmiento, J.L., Goodale, C.L., Schimel, D. & Field, C.B. 2001. Consistent land- and atmosphere-based US carbon sink estimates. Science 292: 2316-2320.

Papachristou, T.G., Platis, P.D. & Papanastasis, V.P. 1997. Forage production and small ruminant grazing responses in Mediterranean shrublands as influenced by the reduction of shrub cover. Agroforest Syst 35: 225-238.

Pase, C.P. 1958. Herbage production and composition under immature Ponderosa Pine stands in the Black Hills. Journal of Range Management 11: 238-243.

Pausas, J.G. & Austin, M.P. 2001. Patterns of plant species richness in relation to different environments: An appraisal. J Veg Sci 12: 153-166.

Pihlgren, A. & Lennartsson, T. 2008. Shrub effects on herbs and grasses in semi-natural grasslands: positive, negative or neutral relationships? Grass and Forage Science 63: 9-21.

Platis, P.D. & Papanastasis, V.P. 2003. Relationship between shrub cover and available forage in Mediterranean shrublands. Agroforest Syst 57: 57-65.

Pontes, L.S., Carrere, P., Andueza, D., Louault, F. & Soussana, J.F. 2007. Seasonal productivity and nutritive value of temperate grasses found in semi-natural pastures in Europe: responses to cutting frequency and N supply. Grass and Forage Science 62: 485-496.

Potthast, V., Haverkamp, R. & Rodehutscord, M. 1997. Ableitung von Formeln zur Schätzung des Energiegehaltes von Grasprodukten unter Verwendung von in-vitro-Parametern (Gasbildung, Cellulase-Löslichkeit). Das Wirtschaftseigene Futter 43: 205-216.

Prober, S.M., Lunt, I.D. & Thiele, K.R. 2002. Determining reference conditions for management and restoration of temperate grassy woodlands: relationships among trees, topsoils and understorey flora in little-grazed remnants. Aust J Bot 50: 687-697.

Pykälä, J., Luoto, M., Heikkinen, R.K. & Kontula, T. 2005. Plant species richness and persistence of rare plants in abandoned semi-natural grasslands in northern Europe. Basic Appl Ecol 6: 25-33.

R Development Core Team 2007. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Rook, A.J., Dumont, B., Isselstein, J., Osoro, K., WallisDeVries, M.F., Parente, G. & Mills, J. 2004. Matching type of livestock to desired biodiversity outcomes in pastures - a review. Biological Conservation 119: 137-150.

Scott, D. 1993. Constancy in pasture composition? In: Proceedings of the XVII International Grassland Congress, pp. 1604-1606. New Zealand Grassland Association, Palmerston North, New Zealand.

Tallowin, J.R.B. & Jefferson, R.G. 1999. Hay production from lowland semi-natural grasslands: a review of implications for ruminant livestock systems. Grass and Forage Science 54: 99-115.

Wisskirchen, R. & Haeupler, H. 1998. Standardliste der Farn- und Blütenpflanzen Deutschlands. In: Ulmer, Stuttgart.

Yiakoulaki, M.D. & Nastis, A.S. 1995. Intake by goats grazing Kermes Oak shrublands with varying cover in Northern Greece. Small Ruminant Res 17: 223-228.

Zarovali, M.P., Yiakoulaki, M.D. & Papanastasis, V.P. 2007. Effects of shrub encroachment on herbage production and nutritive value in semi-arid Mediterranean grasslands. Grass and Forage Science 62: 355-363.

5 General Discussion

In the context of temperate semi-natural grassland, which on the one hand represents an important resource of biodiversity and on the other hand is highly threatened by abandonment, this study was conducted to provide information on the effects of shrub encroachment on both, the species diversity of the vegetation and the forage potential of the sward. Results of the present study should give information to answer the following questions: How is species diversity of semi-natural grasslands related to shrub occurrence? How is the soil seed bank, which can be important for restoring species-rich grasslands, influenced by the shrubs? And what are the effects of shrub encroachment on agronomic values in terms of herbage mass and nutritive value of herbage? Such information is required to develop farming systems, which combine interests of agricultural production and biodiversity maintenance (Isselstein et al. 2005).

Our hierarchical analysis of species diversity pointed out the importance of shrub encroached sites for the actual species richness of the study area. The highest numbers of vascular plant species were found at medium shrub invaded sites, which is in line with our hypothesis of a hump-back relation between shrub encroachment and species diversity. Similar results have been reported from semi-natural grasslands in Sweden and Finland (Pihlgren & Lennartsson 2008; Pykälä et al. 2005). Referring to the landscape (γ-) diversity, our results also show a positive effect of shrub encroached sites on species diversity, whereas this effect is restricted to the studied grassland vegetation and could probably be compensated by other vegetation types.

The soil seed bank was studied in consideration of the similarity between the seed bank and the aboveground vegetation (seed bank-vegetation similarity). Contrary to expectations, our results show no linear relation between seed bank-vegetation similarity. Highest similarity was found at medium shrub invaded sites. The interpretation of the data using plant functional types pointed out a positive effect of the proportion of annuals (therophytes), forbs, hemicryptophytes and grass species as well as a negative effect of species of shrubs and deciduous forests on the seed bank-vegetation similarity. This suggests increasing seed bank-vegetation similarity with changing vegetation composition from grassland to shrub and forest vegetation. This would be in line with several studies, which found a decreasing seed bank-vegetation similarity with increasing secondary succession (Falinska 1999; Grandin 2001; Kiirikki 1993).

The present study focuses on shrub encroachment of grasslands as a current state. As shrub encroachment characterizes a phenological stage of succession, it is no measure of it. This is due to different possible pathways and stochasticity of succession. Therefore, the results of this study are not comparable with those of grassland successions in the strict sense. Using ordination techniques and the knowledge about plant functional traits, it was possible to differentiate the gradient of shrub occurrence with respect to the vegetation composition. This step allows conclusions on a hypothetical pathway of succession. The pathway can be regarded as a gradient from grassland to shrub and forest vegetation, characterized by its typical composition of plant functional types. However, the aim of this study was to analyse the actual situation of a defined area of semi-natural grasslands rather than the processes behind it. Furthermore it is evident, that abandonment of species-rich grasslands will cause a decrease in species richness (Dierschke 2006; Galvanek & Leps 2008; Mitlacher et al. 2002).

Our results concerning the forage potential of shrub encroached grasslands showed (1) a sharp reduction in herbage production mass of DM, (2) an increase in crude protein, crude lipid and metabolizable energy concentrations, and (3) a decrease in water-soluble carbohydrates concentration with increasing shrub encroachment. The negative effect of the shrubs on herbage mass is in line with our hypothesis and corresponds to studies from Mediterranean grasslands (Papachristou et al. 1997; Platis & Papanastasis 2003; Zarovali et al. 2007) as well as temperate silvopastoral systems (Garcia et al. 1999; Pase 1958). The main effect on herbage mass can be attributed to the reduced light availability. The respond of the variables describing the nutritive value of herbage on the shrubs was unexpected and differs from those of other studies which have reported a negative relationship between nutritive value of herbage and shrub cover (Yiakoulaki & Nastis 1995; Zarovali et al. 2007). The higher crude protein and ME concentrations of herbage, associated with higher shrub cover, could be an effect of both, physiological processes (dependent on light availability) and the vegetation composition. The proportion of legume species, forbs or highly palatable plants has a considerable influence on the nutritive value of herbage. To assess the effect of the vegetation composition, we used the dry-weight rank method (Mannetje & Haydock 1963) to estimate the dry-weight percentages of single species. However, this method was not precise enough, to give satisfactory results.

To conclude, the establishment of shrubs in semi-natural grasslands can enhance the habitat heterogeneity and, therefore, the species diversity. Further shrub encroachment negatively affects the herbage mass and the utilisation of herbage, and will finally result in a serious decrease of species richness. The nutritive value of herbage is not negatively affected by shrubs, which indicates a potentially large agronomic value for shrub-encroached temperate grasslands.

5.1 References

Dierschke, H. 2006. Secondary progressive succession of an abandoned calcareous grassland - research on permanent plots 1987-2002. Hercynia N. F. 39: 223-245.

Falinska, K. 1999. Seed bank dynamics in abandoned meadows during a 20-year period in the Bialowieza National Park. J Ecol 87: 461-475.

Galvanek, D. & Leps, J. 2008. Changes of species richness pattern in mountain grasslands: abandonment versus restoration. Biodivers Conserv 17: 3241-3253.

Garcia, A., Rozados, M.J., Silva-Panto, F.J. & Lindner, R. 1999. Evaluation of natural populations of Dactylis glomerata for grazing under pinewoods. Grassland Science in Europe 4: 167-169.

Grandin, U. 2001. Short-term and long-term variation in seed bank/vegetation relations along an environmental and successional gradient. Ecography 24: 731-741.

Isselstein, J., Jeangros, B. & Pavlu, V. 2005. Agronomic aspects of biodiversity targeted management of temperate grasslands in Europe - A review. Agronomy Research 3: 139-151.

Kiirikki, M. 1993. Seed bank and vegetation succession in abandoned fields in Karkali-Nature-Reserve, southern Finland. Ann Bot Fenn 30: 139-152.

Mannetje, L.t. & Haydock, K.P. 1963. The dry-weight-rank method for the botanical analysis of pasture. J Brit Grassland Soc 18: 268-275.

Mitlacher, K., Poschlod, P., Rosen, E. & Bakker, J.P. 2002. Restoration of wooded meadows - a comparative analysis along a chronosequence on Oland (Sweden). Appl Veg Sci 5: 63-73.

Papachristou, T.G., Platis, P.D. & Papanastasis, V.P. 1997. Forage production and small ruminant grazing responses in Mediterranean shrublands as influenced by the reduction of shrub cover. Agroforest Syst 35: 225-238.

Pase, C.P. 1958. Herbage production and composition under immature Ponderosa Pine stands in the Black Hills. Journal of Range Management 11: 238-243.

Pihlgren, A. & Lennartsson, T. 2008. Shrub effects on herbs and grasses in semi-natural grasslands: positive, negative or neutral relationships? Grass and Forage Science 63: 9-21.

Platis, P.D. & Papanastasis, V.P. 2003. Relationship between shrub cover and available forage in Mediterranean shrublands. Agroforest Syst 57: 57-65.

Pykälä, J., Luoto, M., Heikkinen, R.K. & Kontula, T. 2005. Plant species richness and persistence of rare plants in abandoned semi-natural grasslands in northern Europe. Basic Appl Ecol 6: 25-33.

Yiakoulaki, M.D. & Nastis, A.S. 1995. Intake by goats grazing Kermes Oak shrublands with varying cover in Northern Greece. Small Ruminant Res 17: 223-228.

Zarovali, M.P., Yiakoulaki, M.D. & Papanastasis, V.P. 2007. Effects of shrub encroachment on herbage production and nutritive value in semi-arid Mediterranean grasslands. Grass and Forage Science 62: 355-363.

6 Summary

In Europe, semi-natural grasslands are an important resource of biodiversity and are, therefore, of high conservation interest. They are often invaded by shrubs, and they are threatened by under-utilization or abandonment which leads to further shrub encroachment.

A gradient analysis of shrub-invaded temperate grasslands (from shrub-free to pioneer forest) in Germany was carried out to study the effect of shrub encroachment on plant biodiversity, herbage mass and nutritive value of herbage, as well as the effect on seed bank-vegetation similarity. The latter was driven by the question of the role of the soil seed bank for ecological restoration (Bossuyt & Honnay 2008).

Our hypotheses are: (1) An initial shrub invasion leads to enhanced habitat diversity and according to the habitat heterogeneity hypothesis (MacArthur & Wilson 1967) thereby to higher species diversity. (2) Shrub encroachment leads to a loss of similarity between vegetation and soil seed bank. (3) Herbage mass and variables describing nutritive value of herbage decrease with increasing shrub encroachment.

The selected 30 plots (10 m x 10 m) covered a wide gradient of shrub encroachment. Canopy height of the shrubs was between 15 and 500 (1000) cm, and the canopy cover ranged from less than 1 % to nearly 100 %. We recorded a total of 203 vascular plant species in the vegetation. Number of species per plot ranged between 27 and 68 (mean = 44.5), maximum species number per square meter was 41. Highest species diversity was found at medium shrub invaded sites, which is in line with our hypothesis of a hump-back relation between shrub encroachment and plant biodiversity.

Similarity between seed bank and aboveground vegetation (Jaccard's coefficient of community) ranged between 7.5 and 36.4 %. Highest similarity was found in intermediate shrub invaded grasslands. We have to reject our hypothesis of decreasing seed bank-vegetation similarity with increasing shrub encroachment, but we found evidence for decreasing similarity with changing vegetation composition from grassland to shrub and forest vegetation. The following plant functional types were positively correlated with Jaccard index: therophytes (life form), annual plants (life span), and proportion of forbs.

We found a reduction of herbage mass of DM from 3570 to 210 kg ha^{-1} with increasing shrub encroachment. Metabolizable energy concentration of herbage ranged from 8.9 to 10.2 MJ kg^{-1} DM and crude protein concentration from 72 to 171 g kg^{-1} DM, both measures being positively correlated with shrub occurrence. Increasing shrub

occurrence was associated with a decrease in water-soluble carbohydrates concentration (from 151 to 31 g kg^{-1} DM) and a reduction in the indicator ‘forage value’. The results are in line with our hypothesis of decreasing herbage mass, but are contradictory to the hypothesis of decreasing nutritive value of herbage with increasing shrub encroachment. Our results emphasise the importance of semi-natural grasslands as a resource of biodiversity. Conserving these grasslands is closely connected to continuous agricultural use. Our results indicate a potentially large agronomic value for shrub-encroached temperate grasslands and suggest its utilization for livestock production.

7 Zusammenfassung

Halb-natürliches Grünland stellt in Europa eine wichtige Ressource von Biodiversität dar und ist deshalb von besonderem Interesse für den Naturschutz. Häufig kommt es zur Ansiedelung von Gehölzen. Viele der Flächen sind zudem durch Unternutzung bzw. Nutzungsaufgabe bedroht, was eine weitere Verbuschung fördert.

In dieser Arbeit wurden der Einfluss der Verbuschung auf die Pflanzendiversität, den Ertrag und Futterwert des Aufwuchses sowie auf die Ähnlichkeit zwischen Samenbank und Vegetation untersucht. Hierzu wurde eine Gradientenanalyse von verbuschtem Grünland (von gehölzfreier Vegetation bis Pionierforst) in Deutschland durchgeführt.

Folgende Hypothesen wurden getestet: (1) Eine initiale Verbuschung führt zu einer erhöhten Habitatheterogenität und damit, im Sinne der Habitat-Heterogenität-Hypothese (MacArthur & Wilson 1967) zu einer höheren Artendiversität. (2) Verbuschung führt zu einer geringeren Ähnlichkeit zwischen Samenbank und Vegetation. (3) Der Ertrag und Futterwert des Aufwuchses nimmt mit steigender Verbuschung ab.

Die ausgewählten 30 Plots (10 m x 10 m) umfassten einen weiten Verbuschungsgradienten. Die Strauchschicht hatte eine Höhe zwischen 15 und 500 (1000) cm, mit einem Deckungsgrad von weniger als 1 % bis fast 100 %. Insgesamt wurden 203 Gefäßpflanzenarten in der Vegetation festgestellt. Die Artenzahl pro Plot betrug zwischen 27 und 68 (Mittelwert = 44.5), die maximale Artenzahl pro Quadratmeter war 41. Die höchsten Artenzahlen wurden auf Flächen mittlerer Verbuschung registriert. Dies entspricht der Hypothese einer „hump-back“ Relation zwischen Verbuschung und Pflanzendiversität.

Die Ähnlichkeit zwischen der Samenbank und oberirdischer Vegetation (Jaccard-Index) betrug zwischen 7.5 und 36.4 %. Die höchste Ähnlichkeit wurde auf mittleren verbuschten Flächen festgestellt. Die Hypothese einer abnehmenden Ähnlichkeit mit steigender Verbuschung muss demnach verworfen werden, jedoch nahm die Ähnlichkeit mit der Vegetationsänderung von Grasland zu Gebüsch- und Waldvegetation ab. Die folgenden funktionellen Gruppen waren positiv mit dem Jaccard-Index korreliert: Therophyten (Lebensform), einjährige Pflanzen (Lebensdauer) und Anteil krautiger Pflanzen.

Mit zunehmender Verbuschung nahm der Trockenmasseertrag des Aufwuchses von 3570 auf 210 kg ha^{-1} ab. Der Energiegehalt lag zwischen 8.9 und 10.2 MJ kg^{-1} TM, und für die Rohproteinkonzentration wurden Werte zwischen 72 bis 171 g kg^{-1} TM gemessen. Beide Parameter waren positiv mit dem Verbuschungsgrad korreliert.

Weiterhin war eine stärkere Verbuschung mit einer Abnahme der wasserlöslichen Kohlenhydratkonzentration (von 151 auf 31 g kg^{-1} TM) und einer Abnahme des Indikatorwertes „Futterwert“ verbunden. Die Ergebnisse bestätigen die Hypothese der Ertragsminderung, stehen jedoch im Gegensatz zu der Hypothese einer generellen Abnahme des Futterwertes mit zunehmender Verbuschung.

Die Ergebnisse der vorliegenden Arbeit betonen die Bedeutung von halb-natürlichem Grünland als Ressource von Biodiversität. Die Erhaltung dieses Grünlandes ist eng an die Aufrechterhaltung landwirtschaftlicher Nutzung geknüpft. Die Ergebnisse weisen auf einen potentiell hohen landwirtschaftlichen Wert von verbuschtem Grünland hin und können die Nutzung solcher Flächen für die Tierproduktion empfehlen.

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List of Publications

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Stroh, H.-G., Kesting, S. & Isselstein, J. (2009): Pflanzliche Artenvielfalt im heutigen Wirtschaftsgrünland – Ein Vergleich von Weiden, Mähweiden und Wiesen. *Mitteilungen der Arbeitsgemeinschaft Grünland und Futterbau* 21: 240-244.

Kesting, S. & Isselstein, J. (2008): Die Verbuschung artenreichen Grünlands aus agronomischer und ökologischer Sicht. *Mitteilungen der Gesellschaft für Pflanzenbauwissenschaften* 20: 333-336.

Kesting, S., Wrage, N., Schellberg, J. & Isselstein, J. (2007): Schafbeweidung oder Mulchen? Ergebnisse eines langjährigen Landschaftspflegeversuches auf Grünland. *Mitteilungen der Gesellschaft für Pflanzenbauwissenschaften* 19: 148-149.

Kesting, S. & Isselstein, J. (2007): Einfluß der Verbuschung auf Ertrag und Futterqualität des Pflanzenaufwuchses im Grünland. *Mitteilungen der Arbeitsgemeinschaft Grünland und Futterbau* 8: 67-70.

Faramarzi, M., Kesting, S., Wrage, N. & Isselstein, J. (2007): Biodiversity and plant-environmental interaction in semi-arid rangeland in Western Iran. *Mitteilungen der Arbeitsgemeinschaft Grünland und Futterbau* 8: 254-257.

Müller, J., Seidel, K., Kayser, M. & Kesting, S. (2006): Nährstoffmanagement in geschützten Grünlandarealen am Beispiel eines Niedermoorgebietes mit dem Vorrang Wiesenvogelschutz. *Mitteilungen der Gesellschaft für Pflanzenbauwissenschaften* 18: 302-303.

Kesting, S., Isselstein, J. (2006): Habitat-Heterogenität-Hypothese getestet an einem Sukzessionsgradienten des Grünlands. *Mitteilungen der Arbeitsgemeinschaft Grünland und Futterbau* 7: 191-194.

Kesting, S., Hoffmann, M. H. (2000): Type specimens of the Apocynaceae, Asclepiadaceae, Gentianaceae, Loganiaceae and Menyanthaceae in the Herbarium of the Martin-Luther-University Halle-Wittenberg (HAL). Schlechtendalia 5: 11-17.

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