EFFECTS OF AGRICULTURAL MANAGEMENT AND MANIPULATED PLANT SPECIES COMPOSITION OF PERMANENT GRASSLAND ON PRODUCTIVITY AND SWARD STRUCTURE

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General Introduction

Introduction

The temperate grasslands in Europe are an important agricultural resource (Isselstein *et al.*, 2005) but also host a rich flora compared to other community types (Pärtel *et al.*, 2005). However, from 1960 onwards, changing land use practices including intensification and abandonment of grasslands led to a steep decline in grassland biodiversity (Herben & Huber-Sannwald, 2002; Plantureux *et al.*, 2005; Hopkins & Wilkins, 2006). Not only the species numbers were reduced due to nitrogen inputs combined with higher utilization frequency and the increasing use of a few specialized species (Swift & Anderson, 1994), but also the absolute area of grassland declined (Hopkins *et al.*, 2006). With beginning awareness of the consequences of biodiversity loss, numbers of scienctific studies that consider biodiversity and ecosystem functions increased rapidly from 1990 onwards (Loreau *et al.*, 2002). All kinds of ecosystems were analyzed, aquatic as well as terrestrial ones, including or excluding animals (Mittelbach *et al.*, 2001); but the plants and especially fast growing grasses and forbs were the objects studied the most (Diaz *et al.*, 2003; Balvanera *et al.*, 2006). A variety of relationships was found (Mittelbach *et al.*, 2001), but positive effects of biodiversity on ecosystem functioning dominated (Balvanera *et al.*, 2006; Quijas *et al.*, 2010). Of agricultural importance were especially the observed positive influences on productivity (e.g. Tilman *et al.*, 2001; Hector & Loreau, 2005; Kirwan *et al.*, 2007; Marquard *et al.*, 2009), stability (Tilman & Downing, 1994; Petchey *et al.*, 2002) and reduced invasibility (Frankow-Lindberg *et al.*, 2009). Several mechanisms for these relationships were discussed, including species complementary (Hooper & Vitousek, 1997; Cardinale *et al.*, 2007) and selection or sampling effects (Huston, 1997; Loreau & Hector, 2001). However, since the experimentally found relationships differed from observations in real world ecosystems (Jiang *et al.*, 2009), it was criticized that the experimental plant communities and especially the short duration of experiments do not reflect real world conditions (Lepš, 2004; Thompson *et al.*, 2005; Guo, 2007). Further, agricultural management has seldom be included into the experiments (Isselstein, 2005; Wrage *et al.*, 2011). This gap of knowledge can be filled by manipulating agriculturally managed grassland by removing several species or functional groups. Removal experiments are widely known (Fowler, 1981; Symstad &

Tilman, 2001; McLaren & Turkington, 2010) but have seldom been used in the context of the biodiversity–productiovity relationship (Diaz *et al.*, 2003).

To investigate the relationship between biodiversity and several ecosytem functions in permanent grassland under agicultural aspects, the Grassland management experiment (GrassMan) was set up in 2008 in the Solling Uplands (Germany). It was designed as interdisciplinary experiment with researchers from the fields of soil science, plant ecology, phytopathology, agroecology and grassland science working together.We used a new innovative approach to manipulate biodiversity in this experiment. Instead of seeding plots with different species richness, our starting point was a permanent grassland with a long history of agricultural use. The swards were manipulated by herbicide application against dicots and monocots, leaving us with three functionally different sward types: the untreated control, a dicot reduced sward without legumes and less than 10% of forbs and a monocot reduced sward in which the grass content was markedly reduced compared to the control sward. Since biodiversity–ecosystem function relationships depend on the environment they are tested in (Fridley, 2002; Fridley, 2003; Ma *et al.*, 2010; Bernhardt-Römermann *et al.*, 2011) the management intensity was varied via cutting regime and fertilization. This thesis concentrates on the agricultural aspects of biodiversity in managed grassland. The major aims were:

1. To test whether the method of manipulating established swards by herbicides creates a useful platform for biodiversity research (chapter 2)
2. To investigate the influences of species composition, functional diversity and biodiversity on yield and forage quality (chapter 3)
3. To analyze the sward architecture, the spatial distribution of leaf area and biomass in relation to functional diversity (chapter 4)

Experimental setup

Experimental area

The experimental site is located between Silberborn and Neuhaus, Solling Uplands, Germany (51°44' 53" N, 9°32' 42" E, 490 m a.s.l.) on historically documented permanent grassland which is managed by the experimental farm of the University of Goettingen at Relliehausen (Fig. 1). Mean annual temperature is 6.9 °C and mean annual rainfall amounts to 1028 mm (DWD 1960-1991, station Silberborn-

Holzminden, 440 m a.s.l.). The climate can be described as “montane sub-oceanic” with the precipitation being distributed almost evenly over the course of the year (Ellenberg *et al.*, 1986). The bedrock underneath the experimental area is, as in most parts of the Solling Uplands, middle Bunter, a Triassic sandstone formation (geological map of Prussia (1910); Hedemann, 1950)).

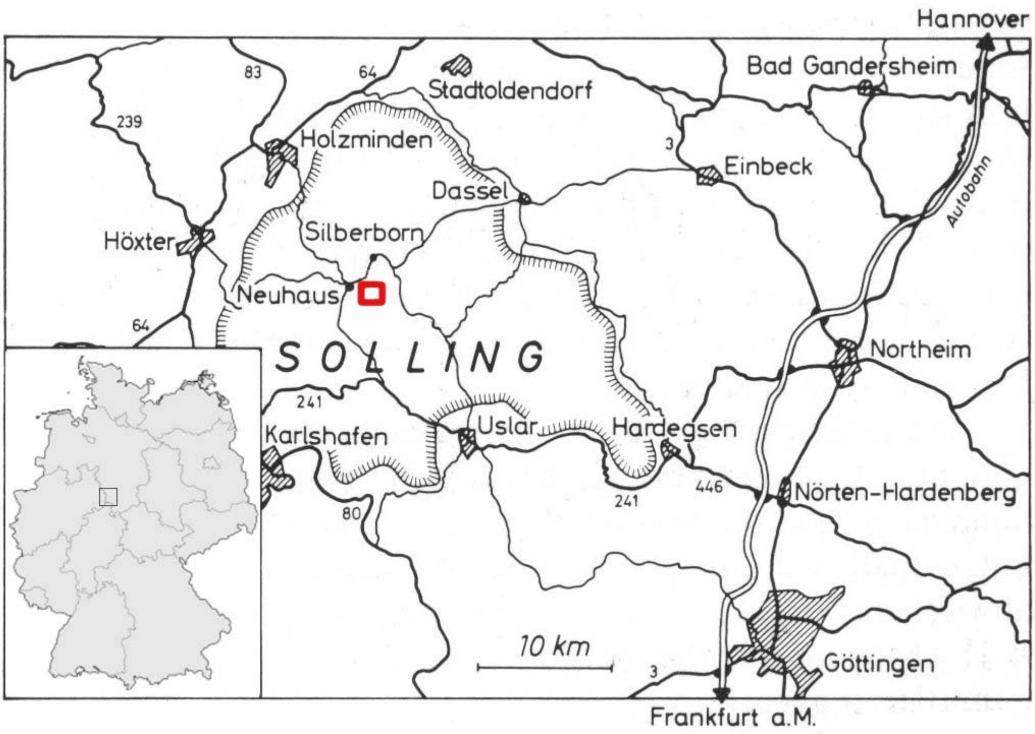

Fig. 1 Map of the experimental area □ in the Solling Uplands. Adapted from Ellenberg *et al.(1986)*, modified.

At least since 1896, the grassland was used regularly as pasture or for hay making (geological map of Prussia (1910) based on the topographic map of 1896), topographic maps of Neuhaus/Solling (1956; 1974; 1999, amendments in 2002). The first reference to the agricultural use of the area dates from 1783 (map Kurhannoversche Landesaufnahme (1783), map historical land use in Lower Saxony (2010)). The area was marked as bog, but already used as common rough grazing area. When the University of Goettingen took over the management of the farm in 1966, amelioration of the grassland started by application of fertilizer (80 kg N ha^{-1} yr^{-1}) and liming. Additionally, the sward was improved by sowing of high value forage species, but it was never ploughed. The grassland was used rather extensively as summer pasture for cattle (farm records Relliehausen). Its moderate fertilization was stopped in 2006, two years before the start of the experiment.

Experimental design

GrassMan is a three factorial experiment. Apart from the sward types, we varied the cutting frequency and the fertilization. Next to untreated control sward (Co), we established sward reduced in dicots (–Dic) and sward reduced in monocots (–Mon). The swards were manipulated by application of herbicides against dicots (Fluoroxypyr + Triclopyr and Mecoprop-P, 3 l ha^{-1} each) and monocots (Clethodim (0.5 l ha^{-1}) respectively, four weeks after the baseline harvest. The dying biomass was not removed to avoid any extra disturbance of the swards. The cutting regime comprised two levels, an intensive one with three harvests per year (mid of May, in line with the first silage cut in the Solling region, mid of July and mid of September) and an extensive one with just one cut per year in the mid of July (adapted to extensive use of grassland with just one late cut for hay). Whereas one half of the plots were left unfertilized the others were treated with 180 kg N ha^{-1} yr^{-1} (applied as calcium ammonium nitrate N27 in two equal doses in April and end of May) and 30 kg P ha^{-1} yr^{-1} plus 105 kg K ha^{-1} yr^{-1} in form of Thomaskali® (8% P_2O_5, 15% K_2O, 20% CaO), also applied at the end of May. Scheduled harvests and fertilization started in spring 2009. The combination of all factors and levels resulted in twelve treatments, which were replicated six times. To account for potential spatial gradients, the 72 experimental plots were arranged to form a Latin Rectangle with two columns forming one block (Fig. 2). The upper part was close to a forest border and the area was sloping gently (< 5% slope) towards the lower rows.

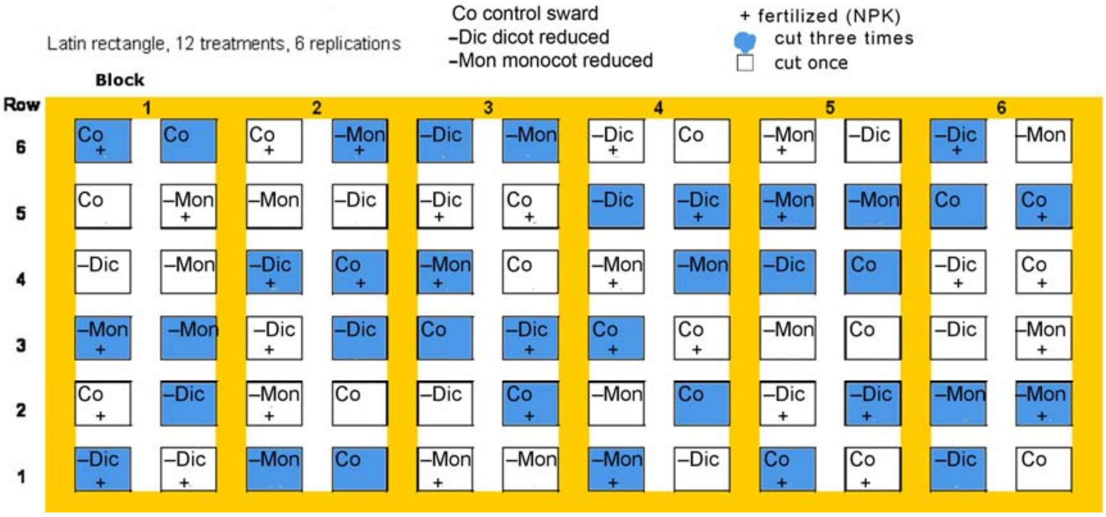

Fig. 2 Experimental setup and plot arrangement of the Grassland management experiment

Baseline data recording and processing

In April 2008, the 72 experimental plots (each 15 m by 15 m large) were aligned and marked. For determination of soil properties, mixed soil samples (9 subsamples per plot, each 20 cm deep) were taken, their pH measured in KCl before they were air dried and ground. Plant available phosphorus was determined by the resin method (Sibbesen, 1977; Bowman & Cole, 1978). It was extracted by resin bags, re-exchanged by NaCl and NaOH solutions and analyzed colometrically after blue-dyeing. Plant available potassium contents and effective ion exchange capacity (ECEC) were determined by percolating 2.5 g of soil with 100 ml 0.2 N $BaCl_2$ solution for 4 h and measuring K and concentrations of other soil ions by ICP-OES (Optima 3000 XL, Perkin Elmer). The C/N ratio of the soil was measured using a C/N elemental analyzer (Vario EL III, Elementar, Hanau, Germany).

After determination of the so called “minimum area” for phytosociological relevés by species-area curves as described by Dierschke (1994), we marked two nested squares (1 m^2 within 9 m^2) in each plot for repeated vegetation analysis. In June 2008, when most of the occuring grassland species were in bloom or already seeding, the dry biomass proportions of all species were estimated according to Klapp & Stählin (1936), to determine the phytosociological association of the experimental grassland. From 2009 onwards, these nested relevés were recorded twice per year (in May before the first harvest and in August) to monitor the changes induced by herbicide application and management. At the beginning of July 2008, the baseline harvest took place. All plots were cut to a height of 7 cm with a Haldrup® forage combine havester. The swards allocated to the three-cut-treatment were cut again at the end of October 2008. At all harvests, mixed samples of the forage of each plot were dried (60°C, 48 h) and ground to 1 mm. Their quality was analyzed by near infrared spectroscopy (NIRS, cf. chapter 3) and P and K contents were determined photometrically in a continuous flow analysator according to the VDLUFA method book volume I (Hoffman, 1991). The fertilized plots received 50 kg N ha^{-1} yr^{-1} in this first year.

Univariate statistics (ANOVAs, linear contrasts to a reference level) were calculated in R, version 2.8.1-2.12.2 (R Development Core team, 2009-2011). For multiple comparison of means of several factor levels, Tukey's ‘Honest Significant Difference’ method (Miller, 1981; Yandell, 1997) was used with a confidence level of 0.95. For vegetation classification, the 9 m^2 relevés were sorted with the program Juice, version

7.0.42 (Tichý, 1999–2008). Diagnostic species were grouped according to Dierschke & Briemle (2002) and Neitzke *et al.* (2004). The same relevés were also used to calculate biodiversity indices - Shannon index, Gini-Simpson index and Shannon evenness (Dierschke, 1994; Jost *et al.*, 2010). To detect species patterns on the experimental area, we applied direct and indirect ordination methods (Canoco for Windows version 4.5 (ter Braak & Šmilauer, 1997–2004)) including the 9 m^2 relevés and all measured environmental variables. Visible correlations between single species and environmental variables were tested for significance by t-value biplots implemented in Canoco (ter Braak & Šmilauer, 2002), the significance of correlations of other variables (e.g. yield and row as continuous variable to ensure comparability to the ordination) was tested using ANOVAs and linear contrasts in R.

Baseline soil and vegetation

The soil of the experimental area is a haplic Cambisol (I. Hoeft & A. Keuter, unpublished data) with a pH (KCl) ranging fom 4.19 to 5.56 (D. Hertel, unpublished data). It is quite shallow (40-60 cm) and contains high amounts of stones. The C/N ratio for the soil was 12.6 ± 0.31. Plant available P showed the high variability typical for pastures (4.5 ± 3.7 mg P $(100\ g)^{-1}$ dry soil) (D. Hertel, unpublished), no spatial pattern in P contents was found. On the contrary, K contents (11.8 ± 3.3 mg exchangable K $(100\ g)^{-1}$) (D. Hertel, unpublished) showed a dependency on row with the highest K contents to be found in the row furthest from the forest edge (Fig. 3). These values of P and K were also mirrored in plant nutrient contents. We found a significant ($P < 0.001$, $R^2_{adj} = 0.28$, linear regression) decline in K contents with row (as continuous factor). This might be due to the shallower soils in higher row numbers, which reduced the absolute amounts of plant available K. Further, the cattle might have avoided these areas since there were higher amounts of weeds (*Juncus effusus, Deschampsia cespitosa*) but no indicator plants for nutrients inputs via cattle dung and urine (*Rumex obtusifolius*, *Urtica dioica*). Since lower utilisation frequency reduces K contents in plants (Voigtländer & Jacob, 1987), the areas with low K plant contents indicate a lower use intensity by cattle. Likewise, in a linear model for the yields of June 2008, with row and block as continuous factors, yields decreased significantly ($P < 0.001$) with row number, also depicted in Figure 4.

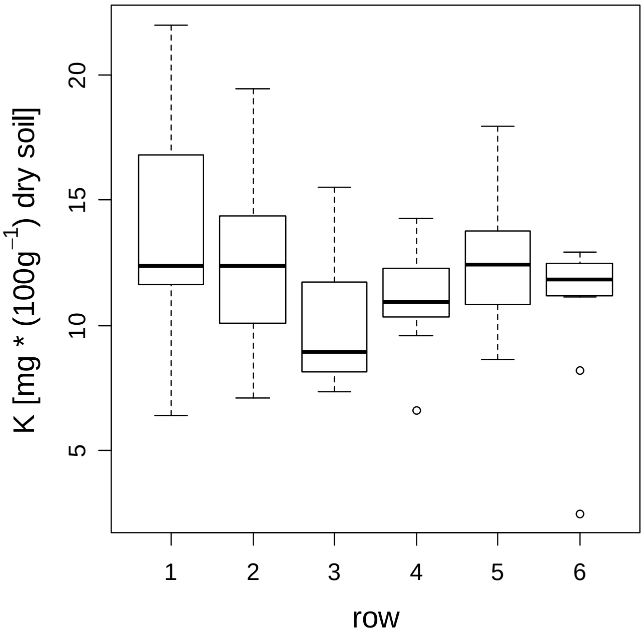

Fig. 3 Plant available K on the experimental area per row. A significant linear correlation between row as continuous variable and K content could not be detected.

Apart from the slightly worse soil conditions (slightly lower pH and shallower soil compared to the rows further downhill); plant composition might also have influenced yields. As shown in Figure 4, there were significantly higher proportions of *Festuca rubra* L. in the upper than in the lower part of the experimental area. For *Poa trivialis* L., *Dactylis glomerata* L. s.str., *Rumex obtusifolius* L. and *Achillea millefolium* L. it was the other way round. Along with this species turnover from comparatively small to taller species, the pH (P = 0.002) and the yield of the first cut (P < 0.001) decreased significantly with increasing row numbers. Apart from this main gradient, some other species were distributed in patches with palatable (e.g. *Trifolium repens* L., *Lolium perenne* L.) and unpalatable species (*Deschampsia cespitosa* (L.) P. BEAUV. s. str.).

Total species numbers did not differ significantly among rows or blocks. However, at the 9 m^2 scale of the relevés, there was a turnover in species composition in direction of the blocks, influencing biodiversity indices. Gini-Simpson, Shannon and Evenness increased, albeit not steadily, with increasing block numbers (P < 0.01 in ANOVA without (Shannon) and with arcsine transformation (Evenness, Simpson)). The lowest values for all indices were found in block 1, the highest in blocks 3 and 6.

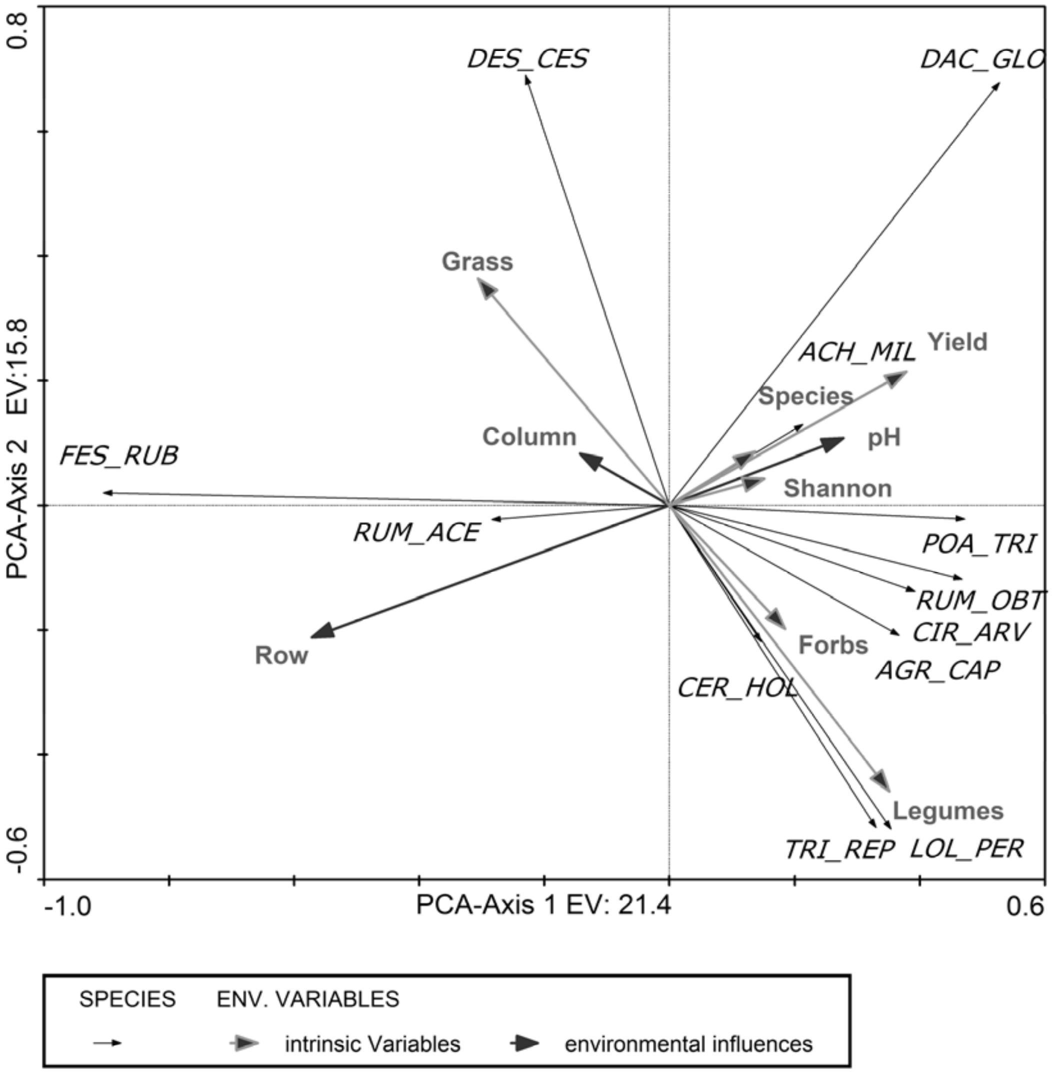

Fig. 4 PCA (species data log transformed) of the vegetation of the experimental area in June 2008. Included were all measured soil variables; only species and environmental variables with a fit > 5% are shown.

The current vegetation was classified as a nutrient poor, moderately wet Lolio perennis-Cynosuretum cristati (R. TX. 1937) with strong tendencies towards the Alchemillo-Cynosuretum Var. with *Cardamine pratensis / Lotus uliginosus* (MÜLL. ex GÖRS 1968) due to high amounts of red fescue (*Festuca rubra* L.) and bent grass (*Agrostis capillaris* L.). However, most of the diagnostic species of the latter plant community (which are also found in the Festuco-Cynosuretum (R. TX. ex BÜKER 1942)) are missing apart from *Alchemilla vulgaris agg.* (Appendix 1).

Above all, the experimental area is not perfectly homogeneous in terms of soil and vegetation characteristics. Since only some gradients lie in direction of the rows (pH, plant K content, amount of *Festuca rubra*, yield) or show a linear correlation with row number, it would be advisable to include rows and block as factors into all statistical models to also extract non linear environment induced patterns in the data. Care has to be taken if species specific traits or single species as explanatory variables are analyzed as some of them also vary in direction of the rows.

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Manipulating the species composition of permanent grasslands – a new approach to biodiversity experiments

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Abstract

The relationship between biodiversity and ecosystem functions of grasslands has received increasing attention in recent years. So far, experiments were mostly conducted in experimental grasslands. We used a different approach on permanent grassland by applying herbicides selective against either dicots or monocots. This allowed us to alter plant species composition and evenness and to obtain altered constellations of functional group abundances without deliberate introduction of new species or continued disturbance by weeding. The resulting swards were subjected to different management intensities in terms of cutting regime and fertilization. Compared to the baseline data before herbicide application, within one year, the combination of treatments, especially the herbicide application, led to a broad variety of swards with the herbicide treatment alone accounting for more than 25% of the variance in composition. We conclude that the application of specific herbicides is a method highly suitable for creating different sward types, because the swards differed significantly in species number, evenness and composition of functional groups without showing signs of disturbance, as neither the area of open soil nor the proportion of annual colonizer species increased.

Zusammenfassung

Die Diskussion um den Zusammenhang zwischen Artenvielfalt und Produktivität hat in den letzten Jahren immer mehr Aufmerksamkeit erfahren. Bis dato wurden die meisten Experimente auf experimentellem Grünland durchgeführt. Wir verwendeten einen anderen Ansatz auf Dauergrünland. Wir setzten Herbizide ein, die gegen Dikotyle bzw. Monokotyle wirken, was uns erlaubte, Artenzahl und Evenness zu verändern und eine neue Verteilung der funktionellen Gruppen zu erhalten, ohne bewusst neue Arten einzuführen und ohne die Grasnarbe durch regelmäßiges Jäten zu stören. Die so entstandenen Grasnarben wurden mit unterschiedlicher Intensität, in diesem Fall durch verschiedene Schnitt- und Düngekombinationen, bewirtschaftet.

Verglichen mit dem Zustand vor den Eingriffen führten die einzelnen Behandlungen, vor allem die Herbizidbehandlung, innerhalb eines Jahres zu unterschiedlichen Grasnarben, wobei die Herbizidbehandlung allein über 25% der Varianz der Vegetationszusammensetzung erklärte. Wir folgern, dass dieser Ansatz erfolgversprechend ist, weil die Grasnarben sich signifikant in Artenzahl, Evenness und Anteilen der funktionellen Gruppen unterschieden und die herbizid-behandelten Grasnarben keine Hinweise auf Störung zeigten, da weder der Anteil offener Bodenstellen noch die Zahl annueller Pionierarten zugenommen hatte.

Keywords: Removal experiment; Herbicide; Functional diversity; Monocot; Dicot

Introduction

During the past two decades, scientists have sought to disentangle the complex biodiversity–productivity relationship by biodiversity experiments (e.g. Naeem, Thompson, Lawler, Lawton, & Woodfin, 1994, Tilman, Wedin, & Knops, 1996; Loreau & Hector, 2001; Roscher, Schumacher, Baade, Wilcke, Gleixner et al., 2004; Kirwan, Lüscher, Sebastia, Finn, Collins et al., 2007) and observational studies (e.g. Kahmen, Perner, Audorff, Weisser, & Buchmann, 2005; Mouillot & Mouquet, 2006). Both approaches have advantages and shortcomings (Table 1).

As suggested by Diaz, Symstad, Chapin, Wardle, and Huenneke (2003), removal experiments combine most of the advantages of experiments and observational studies and may provide complementary knowledge on the relationship between biodiversity and ecosystem functioning. They allow for a set of defined environmental conditions, but start with natural plant communities that are manipulated by removing certain species or functional groups (Diaz et al., 2003). Removal can be either done by weeding (Fowler, 1981), which affects neighboring plants due to soil disturbance (McLellan, Fitter, & Law, 1995) or by herbicide application and clipping, leaving gaps which take some time to close again (McLaren & Turkington, 2010).

There have been removal experiments in grassland in the past, but they were focussing mainly on plant species interactions (e.g. Putwain & Harper, 1970; Fowler, 1981). Only a few were designed to analyze the productivity of the manipulated swards (Wardle, Bonner, Barker, Yeates, Nicholson et al., 1999; Symstad & Tilman, 2001).

Table 1.Comparison of characteristics of experimental and observational studies of the biodiversity–productivity relationship.

Experimental	Observational
• Biodiversity clearly assigned and controlled (Diaz et al., 2003)	• No defined biodiversity levels
• Hypotheses can be tested (Esser, Lüttge, Beyschlag, Murata, Beierkuhnlein et al., 2006)	• Observations are not adequate for approval of theories (Esser et al., 2006)
• Investigation of single factors (Huston, 1997)	• Site and diversity confounded (Kahmen et al., 2005; Jiang, Wan, & Li, 2009)
	• Many co-varying factors (Mokany, Ash, & Roxburgh, 2008)
• Controlled environment (Diaz et al., 2003; Esser et al., 2006)	• Low control of external factors (Diaz et al., 2003)
	• Interactions of variables differ in each site, heterogeneity (Esser et al., 2006)
• No real world – composition, age structure and spatial distribution are artificial (Diaz et al., 2003; Lepš, 2004; Thompson, Askew, Grime, Dunnett, & Willis, 2005; Jiang et al., 2009)	• Real world, all ecosystem processes (Diaz et al., 2003)
• No dispersal/invasion allowed (Diaz et al., 2003)	
• Site preparations disturb soil microbes (Esser et al., 2006)	
• Soil organic matter levels too low compared to permanent grassland due to use of formerly arable fields (e.g. Roscher et al., 2004) or conversion of grassland (Hermle, Anken, Leifeld, & Weisskopf, 2008)	
• Set-up and management not comparable to agricultural situation (Isselstein, 2005)	• Can be combined with agricultural management
• Permanent disruption (weeding) (Huston, 1997)	• No disruption
• Often resricted to small, relatively fast growing herbaceous plants (Diaz et al., 2003)	• Species of all sizes, ages and functional types can be used (Diaz et al., 2003)
• No stable biodiversity–productivity relationship due to premature communities (Guo, 2007)	• Stabilization of biodiversity–productivity relationship over the course of succession can be observed (Guo, 2007)

Further, sward structure, an important determinant of plant growth and production processes (Laca & Lemaire, 2000), barely received attention in research on agriculturally managed permanent grassland (Sanderson, Soder, Brzezinski, Taube, Klement et al., 2006). In the Grassland Management Experiment (GrassMan), we used the approach of species removal by herbicides in agriculturally managed permanent grassland. To create a gradient of environmental conditions as suggested by Fridley (2001) and McLaren and Turkington (2010), the swards received four management treatments differing in cutting frequency and fertilization. No weeding or subsequent spraying of herbicides was used after the initial herbicide treatment, making biodiversity both a dependent (realized biodiversity) and independent variable (influencing ecosystem functions). The objective of this study was to test whether herbicide application is a useful tool to create initial swards of different species composition in established grassland vegetation as the largest effects on the remaining vegetation are to be expected at this time. We were also interested in herbicide influences on vertical biomass distribution as one aspect of sward structure, and gap colonization. We hypothesized that:

- herbicide application leads to swards differing in species composition, taxonomic diversity and relative abundances of functional groups;
- vertical biomass distribution is not affected;
- the decrease of herbicide-sensitive species is compensated by clonal growth of insensitive species, leading to no increase in the area of bare soil promoting annual species.

Material and Methods

Study area

The experimental site is located between Silberborn and Neuhaus, in the Solling Uplands, Central Germany (51°44' 53" N, 9°32' 42" E, 490 m a.s.l.), on a long–term permanent grassland. At least since 1896, this grassland was used regularly as pasture or for hay making (Geological Map of Prussia 1910 (based on the topographic inventory of 1896), topographic maps of Sievershausen and Neuhaus/Solling 1924, 1956 and 1974). The pasture has been improved by moderate fertilization (80 kg N ha^{-1} yr^{-1}), liming and overseeding with high value forage species, but it was never plowed (farm records Relliehausen) since 1966. The moderate fertilization was completely ceased two years before the start of the experiment.

The mean annual temperature is 6.9 °C and mean annual rainfall amounts to 1028 mm (DWD 1960–1991, station Silberborn–Holzminden, 440 m a.s.l.). The soil of the experimental area is a shallow (40–60 cm), stony haplic Cambisol (I. Hoeft & A. Keuter, unpublished) on middle Bunter (Triassic sandstone) (Hedemann, 1950). Before establishing the experiment, soil baseline data were collected as composite samples consisting of nine subsamples (0–20 cm) per plot. The $pH_{(KCl)}$ of the area was 4.6 ± 0.27. The plant available phosphorus (P) of the soil (extracted by resin bags from a soil–water solution (Sibbesen, 1977; Bowman & Cole, 1978), re–exchanged by NaCl and NaOH solutions and analyzed colometrically after blue-dyeing) amounted to 9.5 ± 7.5 mg P $(100\ g)^{-1}$, showing the large variation typical for pastures. The potassium (K) content (determined by percolating 2.5 g of soil with 100 ml

0.2 N $BaCl_2$ solution for 4 h and measuring K concentration by ICP-OES (Optima 3000 XL, Perkin Elmer)) was 23.5 ± 6.5 mg K $(100\ g)^{-1}$ and the C/N ratio 12.6 ± 0.31 (measured by C/N elemental analyzer (Vario EL III, Elementar, Hanau, Germany) (D. Hertel, unpublished data). The current vegetation was classified as a nutrient poor, moderately wet *Lolio-Cynosuretum* with high abundances of *Festuca rubra* and *Agrostis capillaris*.

Experimental design

The GrassMan experiment was established in 2008 as a three-factorial experiment with the factors sward type, utilization and nutrients (Table 2). To obtain three different levels of initial species richness, herbicides against dicots or monocots were mechanically applied each on one third of the experimental plots four weeks after the baseline harvest (Haldrup® forage combine harvester; cutting height 7 cm), which took place at the end of June 2008. A further harvest of the three-cut treatment followed at the end of October 2008. The fertilized plots (NPK treatment) received 50 kg N ha^{-1} in the first year. The full treatment with NPK fertilization and scheduled harvests (according to Table 2) started in spring 2009.

Table 2. Experimental factors and treatment levels of the GrassMan experiment. The acronyms of the different treatments are generated by combination of the factor level abbreviations in the order sward–utilization–nutrients, e.g. –Dic1x = dicot-reduced sward, cut once, no fertilization.

Factor	Level		Abbreviation
Sward type	1.1	Untreated control sward	**Co**
	1.2	Dicots reduced (herbicide treatment)[a]	**–Dic**
	1.3	Monocots reduced (herbicide treatment)[a]	**–Mon**
Utilization	2.1	Cut once (July)	**1**
	2.2	Cut three times (May, July, September)	**3**
Nutrients	3.1	No fertilization	**x**
	3.2	180/30/100 kg NPK ha^{-1} yr^{-1} [b]	**NPK**

[a] active ingredients against forbs: Fluoroxypyr+Triclopyr and Mecoprop-P (3l ha^{-1}) each, against grasses: Clethodim (0.5l ha^{-1}).

[b] N fertilizer: calcium ammonium nitrate N27, P&K fertilizer: Thomaskali® (8% P_2O_5, 15% K_2O, 20% CaO).

To account for potential spatial heterogeneity due to the location on a slope bordering a forest on the upper part, the experimental layout is a Latin rectangle design with six replicates (blocks), arranged in 6 rows and 12 columns with two columns forming one block. This leads to 72 experimental plots of 15 m × 15 m, (see Appendix 1). The whole area was fenced in October 2008 to exclude large wildlife, especially wild boars.

For sward monitoring, the initial sward composition of June 2008 was compared with the manipulated ones. After determination of the “minimum area” for phytosociological relevés by species-area curves (Dierschke, 1994), we marked two squares (9 m^2) in each plot with a 1 m^2 subplot in the center for investigating scale-dependent vegetation characteristics. Vegetation relevés and proportional yields for each species (Klapp & Stählin, 1936) were recorded on both scales two times per year (in May before the first harvest and in August) from 2009 onwards. In October 2008, just the proportions of functional groups (grasses, forbs, legumes) were recorded. Additionally, the area of bare soil and the cover of litter were estimated as a percentage. The 9 m^2 relevés were used to calculate Shannon index H' (loge), Gini-Simpson index and Shannon evenness ((H' /loge(n)) × 100; hereafter referred to as evenness) (Dierschke, 1994; Jost, DeVries, Walla, Greeney, Chao et al., 2010) of the vegetation.

Functional diversity was assessed by comparing proportions of the three functional groups grasses, forbs and legumes comparable to the classification used in the Jena experiment (Roscher et al., 2004) with further subdivisions into high- and low-yielding species following the classification of grasses in high- and low-yielding/tall and small species (Klapp, 1954, Klapp & Opitz von Boberfeld, 2006), which uses the growth height and the sensitivity to defoliation. It was adopted for legumes and forbs. For understanding the recolonisation after herbicide application, all species present were grouped according to their propagation traits (mainly vegetative by long stolons versus mainly by seeds). All traits needed for these classifications were based on Schrader & Kalthofen, 1974, Grime, Hodgson, & Hunt, 1988 and BiolFlor Version 1.1 (Klotz, Kühn, & Durka, 2002).

Data analysis

Univariate statistical analyses were conducted in R (R Development Core Team, 2009). Since we worked with spatially dependent subsamples, we compared the means of the response variables by linear mixed effects models with relative maximum likelihood estimation (REML) (nlme package, Pinheiro, Bates, DebRoy, Sarkar, & the R Core team, 2009) and linear contrasts with the treatment factors as explanatory variables. To account for the spatial variability of the experimental area, the rows and blocks of the Latin rectangle were included into the models as fixed effects. The best fitting models including only the significant predictive variables were obtained by comparison of the Akaike Information Criteria of the full and the reduced models (Zuur, Ieno, Walker, Saveliev, & Smith, 2009). To obtain homoscedacity and normal distribution of the residuals, the data were transformed according to the results of the boxcox analysis (MASS package in R, Venables & Ripley, 2002) as indicated in the results. Additionally, a part of the data was fitted in models including the "varIdent" variance structure (different variance per stratum), (nlme package Pinheiro et al. 2009). Ratios between grass and forb contents in the swards were analyzed with linear models with logit link and binomial error distribution (Zuur et al., 2009). In case of non-parametric data (% of open soil), we conducted the Kruskal–Wallis test. For multivariate statistics, we used Canoco for Windows version 4.5 (ter Braak & Šmilauer, 1997–2004) and applied log transformation to the species data. Visual correlations between variables of the PCA ordination diagram were tested for significance by linear regression and, in case of correlations between species and environmental variables, by *T*-value biplots ($\alpha = 5\%$) implemented in Canoco. Whether the single treatment factors explained any significant proportion of variance of the vegetation was analyzed by Monte Carlo permutation tests incorporating the spatial arrangement of the plots and subplots. Further, variance partitioning was conducted (Borcard, Legendre, & Drapeau, 1992) to quantify the amount of variance within the vegetation explained solely by the sward treatment, the management and the environment. If not stated otherwise, we used the default settings of Canoco. The β-diversity of the experimental area was measured as standard deviation of species turnover in DCA (Hill & Gauch, 1980). A standard deviation ≥ 4 indicates that within the data there are at least two relevés that have no species in common.

Results

In June 2008, prior to the start of the experiment, species numbers and biodiversity indices did not differ between the assigned treatments (Table 3). In May 2009, differences in sward composition between the treatments were distinct. Whereas the management (cutting regime and fertilization) alone hardly showed significant effects on the diversity of the sward, the herbicide-treated swards differed significantly from the control sward (Table 3). In the –Dic-plots, species number, Shannon index, evenness and Gini-Simpson index were significantly smaller than in the control plots.

The –Mon-treatment did not lead to larger indices compared to the control swards except for the plots cut three times.

Table 3. Means (geometric means for species numbers) and standard deviations (geometric deviations) of biodiversity indices in all 9 m^2 vegetation relevés before the application of herbicides (June 2008) and under full treatments, indicated by the treatment abbreviations (cf. Table 1), in May 2009.

	Species [per 9 m^2]	Shannon (H')	Evenness (J')	Gini-Simpson
	June 2008			
All plots	16±1	2.2±0.2	78.2±4.9	0.84±0.04
	May 2009			
Co1x	**16±1**	**2.1±0.2**	**77.5±4.6**	**0.82±0.05**
Co1NPK	18±1	2.3±0.1	81.9±3.5	0.87±0.03
Co3x	17±1	2.2±0.2	81.8±5.5	0.85±0.04
Co3NPK	16±1	2.2±0.2	79.5±7.2	0.83±0.06
–Dic1x	13±1***	1.7±0.2***	68.3±6.8**	0.71±0.06***
–Dic1NPK	12±1***	1.8±0.3***	73.7±11.3	0.76±0.11*
–Dic3x	13±1***	1.8±0.2***	70.1±6.9*	0.74±0.06***
–Dic3NPK	13±1***	1.8±0.3**	72.8±9.3	0.76±0.1*
–Mon1x	17±1	2.2±0.2	77.6±8.5	0.83±0.07
–Mon1NPK	17±1	2.2±0.2	78.1±6.1	0.83±0.05
–Mon3x	17±1	2.3±0.1*	83.5±4.1*	0.87±0.02
–Mon3NPK	17±1	2.3±0.2	82.4±4.4	0.87±0.03

Asterisks indicate significant differences from the control treatment **Co1x** in May 2009. *** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$. Response variable not transformed (Evenness, Shannon) or square root transformed (Simpson, species number).

In May 2009, the main gradient determining the distribution of species on the experimental area was the sward treatment (Fig. 1). The management did not have any significant effects. Only two grass species (*Agrostis capillaris* and *Lolium perenne*) profited significantly from the –Dic-treatment and increased their yield proportions. *Festuca rubra,* on the contrary, was not affected by the herbicide application at all. Its proportions in both of the sprayed sward types were more or less equal, indicated by a correlation close to zero in the species-environment table (ter Braak & Šmilauer, 2002). The most common forbs and legumes on the experimental area underwent the largest changes. Compared with their average yield proportion in the control plots, *Ranunculus repens, Rumex acetosa* and *Trifolium repens* were quite scarce in the –Dic-swards but had larger than average proportions in the –Mon-swards. This – albeit to a smaller extent – was also true for *Achillea millefolium, Cardamine pratensis* and *Taraxacum* Sect. *ruderalia* (Fig. 1).

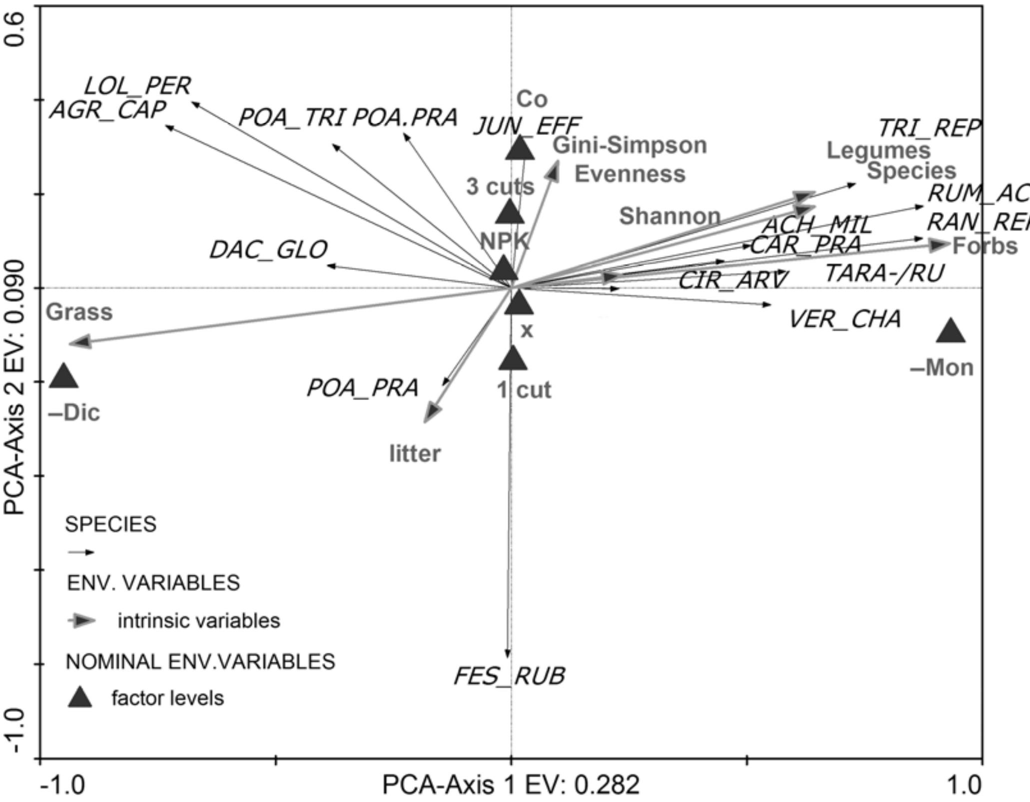

Fig. 1. Ordination diagram based on partial PCA (environmental influences (row, column, date) as covariables) with species, treatment and intrinsic variables, May 2009. Included are species with a fit of > 5%. Only sward types explained significant ($P < 0.05$) conditional proportions of variance as analyzed by Monte Carlo permutation tests. Abbr. of species names: Ach_mil: *Achillea millefolium*, Agr_cap: *Agrostis capillaris*, Car_pra: *Cardamine pratensis*, Cir_arv: *Cirsium arvense*, Dac_glo: *Dactylis glomerata*, Jun_eff: *Juncus effusus*, Lol_per: *Lolium perenne*, Poa_pra: *Poa pratensis*, Poa.pra: *P. humilis* + *P. pratensis* aggregated, Poa_tri: *P. trivialis*, Ran_rep: *Ranunculus repens*, Rum_ace: *Rumex acetosa*, Tara-/Ru: *Taraxacum* Sect. *Ruderalia*, Tri_rep: *Trifolium repens*, Ver_cha: *Veronica chamaedrys*. Instrinsic variables: Grass/Forbs/Legumes: yield proportions in %, species: no. of species per relevé, litter: % of soil covered by dead plant material. Factor levels: for abbreviations of factor levels please refer to Table 2.

Table 4. Variance partitioning and β-Diversity of the vegetation data before (June 2008) and after the start of the experiment. Fraction sward type: the three sward types Control, –Dic and –Mon, fraction management: fertilization and cutting frequency, fraction environment: spatial grid, date and disturbance (open soil). Asterisks indicate significant proportions of variance explained solely by a fraction (*$P < 0.05$, **$P < 0.01$).

Explained variance [%]	Sward type	Manage-ment	Environ-ment	Undet.	β-Diversity SD units (DCA)
June 2008	0.1	2.1	14.0	84.1	1.4
May 2009	26.5**	2.8**	11.9**	58.8	1.96
August 2009	21.0**	5.5**	11.2	62.1	2.18

The Shannon index and species richness significantly ($P < 0.001$) increased with increasing forb and legume proportion (Fig. 1). Evenness and Gini-Simpson index did not show a significant correlation with the first ordination axis and the grass and forb proportion gradient. However, there was a negative correlation with litter cover ($P < 0.001$).

In June 2008, before the establishment of the treatments, neither the assigned treatments nor the spatial variation explained a significant part of the variation within the vegetation (Table 4); most of the variation remained unaccounted for by the variables recorded. In May 2009, more than a quarter of the variation was solely due to the herbicide treatment of the sward, with management gaining in importance towards August 2009. The β-diversity of the experimental area even increased during the second year of the experiment (Table 4).

Table 5. Means (medians for legumes) and standard deviations (median deviation) of the estimated yield proportions (9 m^2) in different growth height classes before (June 2008) and after (May 2009) the herbicide treatment. For treatment abbreviations see Table 2.

	Grasses [%]			Forbs [%]		Legumes [%]		All species [%]	
Treatment	Total	Tall	Small	Total	Tall	Small	*T. repens*	Tall	Small
				June 2008					
All plots	76±7	9±8	66±8	22±6	12±3	10±3	2±1	21±8	78±8
				May 2009					
Co1x	**76±6**	**17±9**	**59±11**	**21±5**	**9±2**	**12±3**	**3±2**	**25±10**	**74±11**
Co1NPK	68±5*	11±4	57±5	31±5**	12±3*	20±2**	1±0*	23±4	77±4
Co3x	73±7	12±4	61±7	23±5	10±2	13±2	4±1	22±4	78±4
Co3NPK	70±7	8±4*	62±8	27±6*	14±2**	14±4	3±1	22±5	78±5
–Dic1x	93±3***	11±4	82±6***	7±3***	2±1***	5±3***	0±0***	13±4**	87±4*
–Dic1NPK	93±4***	12±6	82±12***	7±4***	2±1***	4±3***	0±0***	14±7*	86±10*
–Dic3x	91±7***	8±3*	83±8***	9±7***	3±2***	7±4**	0±0***	10±4***	90±4***
–Dic3NPK	91±5***	14±7	77±10***	9±5***	3±2***	6±3***	0±0***	17±8	83±8
–Mon1x	46±14***	6±5**	40±12***	49±12***	17±4***	32±6***	7±2	23±7	78±7
–Mon1NPK	47±10***	8±7*	40±11***	49±9***	18±6***	31±5***	4±1	26±9	74±9
–Mon3x	40±7***	4±3***	35±6***	53±7***	20±3***	33±6***	9±1**	24±4	75±4
–Mon3NPK	44±10***	7±5*	37±11***	52±9***	21±4***	31±5***	5±2	28±7	72±7

Asterisks indicate significant differences from the control sward of May 2009 (***$P < 0.001$, **$P < 0.01$, *$P < 0.05$). Response variables were either not transformed (legumes) or arcsine (grass total) or square root transformed (all others). The models for legumes and all species were fitted in a linear mixed effects model with one variance term per sward type (legumes) and per sward × nutrient combination (all species).

The composition of functional groups of the swards was influenced by management intensity as well as herbicide application (Table 5). The –Dic-treatment almost completely eliminated the legumes and spared only about 8% of the forbs. The –Mon-treatment reduced the grasses from 80% to about 45% cover. Fertilization favoured forbs on at the expenses of grasses and legumes in the control plots. Furthermore, there was a significant interaction between herbicide treatment and fertilization

($P < 0.05$ for forb contents). Legume proportions (almost 100% *T. repens*) significantly increased in the –Mon-plots cut three times.

The structural diversity differed among the swards (Table 5). In the –Dic-swards, the ratio between tall and short species shifted significantly towards the shorter species ($P < 0.001$), as tall grasses did not expand in the –Dic, but forbs spread in the –Mon-swards, irrespective of their height class.

Herbicide application did not cause any visible increase in open soil patches. There was a significant seasonal fluctuation of bare soil patches within the control sward (median and median deviation in June 08: $3.5 \pm 1.5\%$ of open soil, October 08: $0.5 \pm 0.5\%$, May 09: $3 \pm 3\%$, August 09: $2.5 \pm 2.5\%$, $P < 0.001$). Among the three sward types, the amount of open soil did not differ between the measurement events ($P > 0.4$ for October, May and August).

Table 6. Means (medians for legumes) and standard deviations (median deviations) of the estimated yield proportions (9 m^2) of main propagation types of grasses, forbs and legumes before (June 2008) and after (May 2009) the herbicide treatment as indicated by treatment abbreviations (cf. Table 2).

	Grass [%]		Forbs [%]		Legumes [%]	Total [%]	
Treatment	Stolons	Seeds	Stolons	Seeds	*T. repens*	Stolons	Seeds
			June 2008				
All plots	43±10	33±10	9±3	12±3	2±1	55±10	45±10
			May 2009				
Co1x	**53±11**	**22±9**	**11±2**	**10±1**	**3±2**	**67±9**	**32±9**
Co1NPK	49±6	18±6	17±2**	15±2**	1±0*	67±6	33±6
Co3x	55±8	18±6	11±3	12±1	4±1	70±6	30±6
Co3NPK	52±8	17±6	12±4	15±4**	3±1	67±5	32±5
–Dic1x	70±6***	23±7	4±2**	3±1***	0±0***	74±6	26±6
–Dic1NPK	69±9***	24±4	3±2***	3±2***	0±0***	73±7	27±5
–Dic3x	73±9***	17±6	6±5**	3±2***	0±0***	79±7**	21±7*
–Dic3NPK	70±6***	21±4	4±2***	4±2***	0±0***	74±5	26±5
–Mon1x	39±12**	5±2***	32±8***	18±4***	7±2	78±5	22±5
–Mon1NPK	38±11***	9±6***	27±6***	22±3***	4±1	69±7	31±6
–Mon3x	33±6***	6±3***	29±4***	24±4***	9±1**	70±5	30±5
–Mon3NPK	35±10***	9±3***	28±6***	24±4***	5±2	67±3	33±3

Asterisks indicate significant differences of the proportion of the propagation groups from the control sward of May 2009 (***$P < 0.001$, **$P < 0.01$, *$P < 0.05$). We used no (legumes and grass stolons), square root (grass seeds, forbs, total seeds) and arcsine transformation (total stolons) of the response variable. Some models were fitted with one variance term per sward type (legumes, forb seeds), per treatment (forb stolons), per utilization (grass seeds, total stolons) or per utilization × sward combination (total seeds).

The proportion of annual species did not increase from 2008 to 2009 in any treatment (data not shown). In the –Dic-sward, only the grasses growing as matrices with stolons (e.g. *A. capillaris, F. rubra, Poa trivialis, Holcus mollis*) gained significantly more space (Table 6). Since the proportion of seed-propagated tuft grasses hardly increased, the ratio of matrix to tuft grasses changed from June 2008 to May 2009 ($P = 0.018$). Both propagation types of forbs were affected by the herbicide in equal measure, their ratio did not change. In the –Mon-swards, both types of forbs expanded after the herbicide application, although the forbs with stolons gained more space than the ones with mainly generative propagation, leading to a changing ratio ($P = 0.004$). The –Mon-treatment reduced the proportions of tuft grasses more than those of sward grasses ($P < 0.001$). Legumes only expanded significantly in the –Mon3x sward.

Discussion

In this study, the change of composition and functional diversity of an established grassland sward by herbicide application was investigated to assess the usefulness of this approach for biodiversity experiments. Herbicides against dicots clearly reduced species number, Shannon and Gini-Simpson indices and partly sward evenness (Table 3). In the –Mon-treatments, diversity indices even increased in some cases since the composition of the swards became more even. The resulting gradient was one in composition and functional diversity rather than species richness, supporting our first hypothesis. The range of proportions of functional groups did not exceed the bounds characteristic for semi-natural grasslands in upland areas. Baumont, Andueza, Vuattoux, Picard and Michaud (2010), who wanted to test the model by Jouven, Carrère and Baumont (2006) predicting the dynamics of herbage biomass in managed permanent grasslands on contrasting semi-natural grasslands, chose grasslands similar in composition to ours with 86%, 68% and 39% grass cover for their experiment. Hence, due to the graded sensitivity of some grass species to herbicides, especially the insensitivity of *F. rubra,* the herbicide treated swards are still comparable to semi-natural swards found elsewhere in Europe. For future experiments, a wider range of herbicides adapted to the local species pool should be tested along with the persistence of the herbicide effects. In a pasture experiment on manipulated grassland comprising untreated swards and swards with reduced forb contents grazed by sheep and cattle (Seither, Petersen, Wrage & Isselstein, 2010), the herbicide effects on forbs lasted for three years until reapplication of herbicides was considered necessary (personal observation and farm records Relliehausen 2006-2009).

The second hypothesis was partly supported by our data. Only the –Mon-swards showed structural redundancy compared with the control swards. In the –Dic-swards, possibly recruitment limitation, also encountered by Symstad and Tilman (2001), prevented the taller grasses (most of them seed propagating tuft grasses) from occupying available space. Altogether, the recolonization after herbicide application was faster than in experiments by Fowler (1981), Symstad and Tilman (2001; 1 year) and McLaren and Turkington (2010; 4 years), since the former experiments underwent additional weeding and in the latter, the environmental conditions in the tundra hindered fast expansion of remaining vegetation. As stated in our third hypothesis, the available space was quickly filled up by mainly vegetative growth of the neighbouring species. The high expansion rate of forbs spread by seeds was mainly due to *Rumex acetosa*, which propagates not only by seeds but, to a lesser extent, also by short rhizomes (Grime et al., 1988).

The safety of the herbicides concerning harmful effects on soil fauna had been thoroughly tested before approval according to the Council Directive 91/414/EEC (European Economic Community). Removal of dead plant material from the system would have meant a substantial export of nutrients (Oelmann, Kreutziger, Temperton, Buchmann, Roscher et al., 2007), so we decided to keep the nutrient balance constant among the treated and untreated swards. In the harvest in October 2008, none of the treated swards had gained advantage from the decaying plant material; their yields were not higher, sometimes even significantly lower than those of the control swards (data not presented). We did not analyze the effects of added plant material on the soil decomposer food web. However, since Wardle et al. (1999) found out that plant removal has much stronger effects on the food web than different inputs of biomass, we are confident, that the plant residuals did not induce substantial changes within the food web below the treated swards.

The nitrate concentration in soil water, one of the rather sensitive soil parameters, did not differ between control and treated swards in the two consecutive springs of 2009–2010 (I. Hoeft & A. Keuter, unpublished), indicating no herbicide-induced effects in the first spring after the herbicide treatment. In conclusion, our experiment showed the potential of mechanically applied herbicides as a means for the successful establishment of swards differing in floristic composition, creating a platform for biodiversity–productivity experiments under realistic conditions comprising agriculturally relevant scales and methods.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.baae.2011.10.003.

In this thesis, for the supplementary data, see Fig. 2 in the general introduction.

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Sward effects on forage yield and quality beyond 10 species per squaremeter

Abstract

So far, most experiments investigating ecosystem services, environmental or agricultural benefits of plant diversity in grassland have dealt with sown grassland that showed diversity effects, whereas permanent grassland is poorly examined. In a removal experiment in the Solling Uplands (Germany), the biodiversity of permanent grassland has been manipulated by herbicides to obtain either relatively pure grass swards or swards with comparatively large amounts of forbs and legumes, on top of untreated control swards. These sward types, still hosting on average more than 10 species per m^2, were examined under a gradient in management intensity, regulated by both cutting regime and fertilizer supply. The objective of this study was to reveal which sward characteristics, namely biodiversity (expressed in terms of different biodiversity indices), functional diversity (proportions of functional groups, division into tall and small species) and species composition, had an influence on agricultural yield and forage quality (crude protein, water soluble carbohydrates and fiber content). Yield was not influenced by species number. It was only influenced by functional sward characteristics; the growth form of the dominant species determined the yield in fertilized plots. For variation in forage quality, all analyzed sward characteristics were important, although management had a much larger influence than vegetation.

Keywords: biodiversity, functional groups, forage production, nutritive value, monocots, dicots

Introduction

The relationship between biodiversity and ecosystem functions has been in the focus of scientific interest for more than two decades now. As summarized by Schläpfer and Schmid (1999), Mittelbach *et al.* (2001), Balvanera *et al.* (2006) and Quijas *et al.* (2010), the main focus in observational studies and experiments lay on the biodiversity-productivity relationship, but also stability and nutrient retention and utilization were common ecosystem functions to be analyzed. In most studies, the explanatory variable was species richness, other measures of biodiversity have been used seldomly (Chalcraft *et al.,* 2009). Forage quality, an important agricultural aspect with a century of scientific research history (Hopkins & Wilkins, 2006), has rarely been investigated in the context of biodiversity research as pointed out by Duru et al. (2008) and Andueza *et al.* (2010). Merely single species, most of them grasses, have been analyzed in this context (e.g. Frame, 1991; Wilman & Riley, 1993; Deak *et al.*, 2007; Čop *et al.*, 2009). Only recently, with the possibility to use the forage of extensive grasslands as biofuels, scientific interest in quality analyses of semi-natural mixed swards increased (e.g. Tilman *et al.*, 2006; Tonn *et al.*, 2010; Mangan *et al.*, 2011)**.**

As for the results of the biodiversity–productivity research, a wide variety of forms of relationships were found (hump shaped, (linear) positive and negative as well as no relation at all), with positive relationships between biodiversity and ecosystem function dominating in experiments (Quijas *et al.*, 2010). Most of these experiments were planned from an ecological point of view and lack applicability to agricultural systems (Isselstein, 2005; Wrage *et al.*, 2011). Some were designed as agronomic experiments, but likewise used sown species mixtures (e.g. Kirwan *et al.* (2007), Frankow-Lindberg *et al.* (2009) and Mangan *et al.* (2011)).The use of immature, seeded and sometimes weeded communities for field experiments does not reflect real world conditions (Lepš, 2004; Thompson *et al.*, 2005; Jiang *et al.*, 2009) and may be one reason for the discrepancy between relationships in observational studies and those found in experiments (Mittelbach *et al.*, 2001; Jiang *et al.*, 2009). Further, the site preparations disturb soil microbes (Esser *et al.*, 2006) and reduce soil organic matter contents if grassland has to be converted to set up the experiment (Hermle *et al.*, 2008). In case of use of former arable fields e.g. as in Roscher *et al.* (2004), the soil organic matter content is generally smaller than in permanent grasslands. Since on average 30% of the farmland in Europe is permanent grassland (Osterburg *et al.* 2007, Eurostat 2011, own calculations), experiments aiming to transfer their results into the real world should use permanent grassland rather than sown plant communities. Especially the species numbers should be adapted, since apart from lay farming systems, even the intensively managed grasslands in Europe have on average at least 6 species per m^2 (Pywell *et al.*, 2007), or 15 per 20 m^2 (Kleijn *et al.*, 2001). Sanderson *et al.* (2004) mention an average number of 10-60 species per 100 m^2 on grazing lands in Europe. So species numbers in European grasslands only cover the upper part of the species richness gradient commonly used in experiments starting with monocultures via 2, 4, 8 up to 32 or 64 species (Esser *et al.*, 2006). At species numbers beyond 10 however, diversity effects driven by resource partitioning and facilitation, so called complementary effects (Tilman *et al.*, 2001) should be of less importance, shown in a flattening of diversity–ecosystem function graphs at higher species numbers (e.g. in Tilman *et al.*, 1997; Tilman *et al.*, 2001). Even at low species numbers, the functional diversity is a much better determinant for ecosystem functioning than species richness, although richness still explains a significant part of biomass variation on its own (Tilman *et al.*, 1997). A method for manipulating biodiversity or functional diversity in permanent grasslands at higher species richness levels are removal experiments, where a part of the vegetation (species, functional groups) is removed manually or by the use of herbicides, still leaving several species behind (Diaz *et al.*, 2003; McLaren & Turkington, 2010; Petersen *et al.*, 2012).

In this paper, we report first results from the grassland management experiment (GrassMan), an experiment on managed permanent grassland manipulated by herbicides to vary species composition and functional diversity in the swards (Petersen *et al.*, 2012). To create a gradient of environmental conditions as suggested by Fridley (2001) and McLaren & Turkington (2010), the swards received four management treatments. No weeding or additional spraying of herbicides was used, so we can consider biodiversity as both a dependent (realized biodiversity) and independent variable (influencing ecosystem functions). We monitored the biodiversity and functional group diversity of the manipulated grass swards by means of vegetation relevés. We hypothesized that at a given species richness beyond 10 per m^2 yield and forage quality are determined by functional group identity rather than by biodiversity.

Material and Methods

Site and experimental design

The experimental site is located between Silberborn and Neuhaus, in the Solling Uplands, Germany (51°44' 53" N, 9°32' 42" E, 490 m a.s.l.) on a long-term permanent grassland managed by the experimental farm of the University of Goettingen at Relliehausen since 1966. The mean annual temperature is 6.9°C and mean annual rainfall amounts to 1028 mm (DWD 1960-1991, station Silberborn-Holzminden, 440 m a.s.l.). The soil of the experimental area was determined as a shallow (40-60 cm), stony haplic Cambisol (I. Hoeft and A. Keuter, unpublished) on middle Bunter (Triassic sandstone) (Hedemann, 1950). The grassland had been used as summer pasture for cattle and received an annual fertilization of 80 kg N ha^{-1} yr^{-1} until two years prior to the start of the experiment. Its vegetation was classified as a nutrient poor, moderately wet Lolio-Cynosuretum with high abundances of *Festuca rubra* and *Agrostis capillaris*.

Tab. 1 Experimental factors and treatment levels of the GrassMan experiment. The acronyms of the different treatments are generated by combination of the factor level abbreviations in the order sward-utilization-nutrients, e.g. –Dic1x = dicot-reduced sward, cut once, no fertilization.

Factor	Level		
Sward type	1.1	untreated control sward	**Co**
	1.2	dicots reduced	**–Dic**
	1.3	monocots reduced	**–Mon**
Utilization	2.1	cut once (July)	**1**
	2.2	cut three times (May, July, September)	**3**
Fertilization	3.1	no fertilization	**x**
	3.2	180/30/100 kg NPK ha^{-1} yr^{-1} *	**NPK**

* N fertilizer: *calcium ammonium nitrate N27,* P&K fertilizer: *Thomaskali® (8% P_2O_5, 15% K_2O, 20% CaO)*

The GrassMan experiment was set up in summer 2008. It is a three-factorial experiment incorporationg the factors sward type, utilization and fertilization (Table 1). It has got six replicates resulting in 72 experimental plots, each 15 m by 15 m large. To account for potential spatial heterogeneity due to the location on a shallow slope bordering a forest on the upper part, the experimental layout is a Latin rectangle design with the six replicates (blocks) arranged in 6 rows and 12 columns, two columns forming one block.

To obtain three different levels of species composition or sward types, namely the control (the untreated original sward (Co)), dicot reduced (–Dic) and monocot reduced (–Mon) sward, herbicides against dicots (active ingredients Fluoroxypyr +Triclopyr and Mecoprop-P; 3 l ha^{-1} each) and monocots (Clethodim 0.5 l ha^{-1}) were applied each on a third of the experimental plots. The dead plant material was not removed. The herbicide application followed four weeks after the first harvest of the whole area, at the end of July 2008. By October 2008, the remaining vegetation in the treated plots had expanded, but the new swards were not as dense as the control sward yet. In spring 2009, three initially distinct sward types had developed on the experimental area. They differed in species numbers and composition, biodiversity levels and functional group composition (Petersen *et al.*, 2012). The fertilized plots (NPK treatment) received 50 kg N ha^{-1} in 2008 and the plots of the 3 times cut treatment were harvested a second time at the end of October that year. The full treatment with NPK fertilization (90 kg N ha^{-1} at the end of April, the remaining N, P and K at the end of May) and scheduled harvests did not start until spring 2009.

Measurements

Biodiversity and functional diversity were monitored by means of vegetation relevés on permanent sub-plots estimating the dry matter yield proportions of each species according to Klapp and Stählin (1936). Two 9 m^2 large sub-plots per plot, each with an additional 1 m^2 plot in its center, were recorded twice a year at the beginning of May before the first and in mid-August four weeks after the second harvest. They were used to calculate Shannon index, Gini-Simpson index and Shannon evenness (Dierschke, 1994; Jost *et al.*, 2010) of the vegetation. The yield proportions of the species occuring in at least a third of the plots with proportions larger than 5% were included in the statistical analyses as factor “species identity” (ID). Additionally, the mass proportions of grasses, forbs and legumes and the amount of dead plant material were determined by the sorting of subsamples of each plot taken at harvest. Another functional grouping comprised the three functional groups grasses, forbs and legumes comparable to the classification used by Roscher *et al.* (2004) with further subdivisions into species with tall and small stature. The subdivision closely follows the classification of grasses in tall and short growing/high and low yielding species according to Klapp (1954) and Klapp and Opitz von Boberfeld (2006) which does not only use the growth height and stature but also the sensitivity to defoliation. It was adopted for legumes and forbs. Relative growth rate measured by Grime *et al.* (1988) was not included in this classification since almost all common species had the same growth rate (1–1.4 g g^{-1}week^{-1}). The only fast growing species *Urtica dioica* and *Holcus lanatus* were not present in large amounts on the experimental area. All traits needed for this classification were acquired from Schrader and Kalthofen (1974), Grime *et al.* (1988), Dierschke & Briemle (2002) and the database BiolFlor Version 1.1. (Klotz *et al.*, 2002).

The dry matter (DM) yield per hectare was projected from the average yield of two 1.50 × 15 m stripes of each plot, harvested with a Haldrup® forage combine harvester (cutting height 7 cm). For forage quality analyses, mixed herbage samples per harvested plot were taken and dried at 60°C (for 48 hours) in a forced-air oven. The material was then ground to pass through a 1 mm screen. We estimated crude protein (CP), water soluble carbohydrates (WSC), neutral detergent fiber (NDF) and acid detergent fiber (ADF) contents by near-infrared reflectance spectroscopy (NIRS). The spectra were analyzed using the large dataset of calibration samples from different types of grasslands by the Institute VDLUFA Qualitätssicherung NIRS GmbH, Kassel, Germany. As described in Kesting *et al.* (2009), samples showing a lack of accurancy (H value exceeding 3) were excluded from further statistical analyses (1 out of 144 samples). For calculation of energy content (metabolisable energy, ME) of the forages, we determined the dry ash content by incinerating samples of the ground material in a muffle furnace (550°C) for 5 hours. ME was calculated according to the equation by GfE, Gesellschaft für Ernährungsphysiologie (2008) incorporating among others crude ash, crude protein, crude fat and ADF contents.

Statistical Analyses

Univariate statistical analyses were conducted with R (version 2.12.2) (R Development Core Team, 2011). Anovas, linear contrasts and linear models (lm) were used to compare the importance of treatment factors and diversity of the measured parameters as well as their means. For comparison of means of all treatments, Tukey's ‘Honest Significant Difference’ method (Miller, 1981; Yandell, 1997) was used with a confidence level of 0.95. To take into account the environmental heterogeneity and its influence on forage yield and quality, the rows and blocks of the experimental area were added to the models first of all factors. The best fitting models including only row, block and the significant independent predictive variables and interactions were obtained by comparison of the Akaike Information Criteria of the full and the reduced models (Zuur *et al.*, 2009). The collinearity of continuous variables like forb and grass content, individual species yield proportions and biodiversity indices was checked beforehand in a special version of the pairs plot following Zuur *et al.* (2009). If vegetation characteristics like species number, proportion of tall species, amounts of legumes etc. were included, the factor sward type was excluded from the models since it was strongly correlated with all the vegetation characteristics. To obtain homoscedacity and normal distribution of the residuals, the data were fitted in general least square (gls) models including the “varIdent” variance structure (different variance per stratum, nlme package Pinheiro & Bates 2009) if necessary. Additionally, a part of the data was transformed according to the results of the boxcox analysis

(MASS package in R, (Venables & Ripley, 2002) as indicated in the results. The spatial and temporal stability of yields was determined by calculation of the coefficient of variation (CV) across the Latin rectangle and the three harvests in 2009 as suggested in Serrano *et al.* (2011). To analyze the influence of management and vegetation characteristics on forage quality as a whole, all NIRS-measured quality parameters were included in an ordination as dependent variables (they took the place of the "species" in ordination of vegetation relevés), whereas management (fertilization and utilization frequency) and vegetation characteristics (sward type, proportions of functional groups or tall and small grasses, forbs and legumes, species ID) represented the independent, "environmental" variables. Since the spatial distribution of several species depended on rows and blocks of the Latin rectangle, these two spatial variables were excluded from direct ordinations. The program Canoco for Windows version 4.5 (ter Braak & Šmilauer, 1997–2004) was used for principal component analysis (PCA) and redundancy analysis (RDA) including Monte Carlo permutation tests for assessing importance and significance of the environmental variables (ter Braak & Šmilauer, 2002). We used the variance partitioning procedure (Borcard *et al.*, 1992; Vandvik & Birks, 2002) to quantify the proportions of variance in quality explained by management, vegetation characteristics or environmental influences (date, percentage of open soil, position within the Latin rectangle).

Results

The twelve treatments resulted in widely spread annual yields ranging from an average of 550 g m^{-2} (–Mon3x) up to 1220 g m^{-2} in the Co3NPK treatment. In none of the four management types, the yields differed significantly among the three sward types. In the plots without fertilization cut three times, the –Mon-swards tended to have larger yields, but the yield increase due to fertilization was significantly smaller than in the control swards (interaction fertilization × sward type –Mon, $P = 0.019$). In the fertilized swards cut only once, the –Dic-swards tended to produce more forage. The untreated control swards gained most from the most intensive treatment with fertilization and three cuts. Responsible for yield differences in overall yields 2009 were mainly the management in terms of fertilization and utilization frequency (Table 2).

Tab. 2 Importance of the experimental factors in explaining the differences in annual yield 2009. ANOVA including spatial effects (row + block).

Factors	df	Sum Sq	Mean Sq	*F* value	*P* (>*F*)	% Var expl.
Sward type	2	135.9	67.9	0.4546	0.637	0.28
Fertilization	1	27670.1	27670.1	185.1709	<0.001	58.5
Utilization	1	5859.4	5859.4	39.2114	<0.001	10.4
Fertilization x Utilization	1	4825.1	4825.1	32.2903	<0.001	8.6

However, the influence of the treatment factors on single yields was not constant as shown in Table 3. During the course of the year 2009, fertilization gained in importance, whereas the sward type did not explain significant amounts of yield variation apart from the very first cut after herbicide application in October 2008.

Tab. 3 Proportion of variation in single yields 2008-2009 explained by the experimental factors (%). June 2008 is the baseline yield without any experimental treatments. Anova based on gls estimation allowing for different variances per utilization (June 2008), per nutrient level (July 2009, July 1 cut) or per sward (Sept 2009) or based on lm with transformation of the response variable. Response variable raised to the power of 0.25, (Oct 2008, May 2009), or 0.5 (July 3 cuts, total 2009). *** $P < 0.001$, ‘ $P < 0.1$

	June 08	Oct 08	May 09	July 09	Sept 09	ges 2009	July 1cut	July 3cuts
Sward type	1.7	26.6***	7.2	1.1	0.4	0.3	1.7	2.1
Utilization	0.5			37.4***		58.5***		
Fertilization	0	23.1***	32.0***	39.3***	77.7***	10.4***	50.9***	77.3***
Use x Fert				1.0’		8.6***		
Sw x Fert								2.7'

We found no significant relationship between species richness, Evenness, Shannon and Gini-Simpson Index and yield within the four management groups (exemplary data shown in Figure 1 a and b). Evenness and Gini-Simpson index only explained a significant part ($P < 0.05$) of yield variation if added into the linear model before the factors utilization and fertilization, since they were correlated with these factors. Likewise, the proportions of grasses, forbs and legumes showed no significant correlation with total yield 2009 (exemplary data shown in Figure 1 c and d). The variance explained by the linear models did not differ regardless of whether one of the functional groups or the sward type was included.

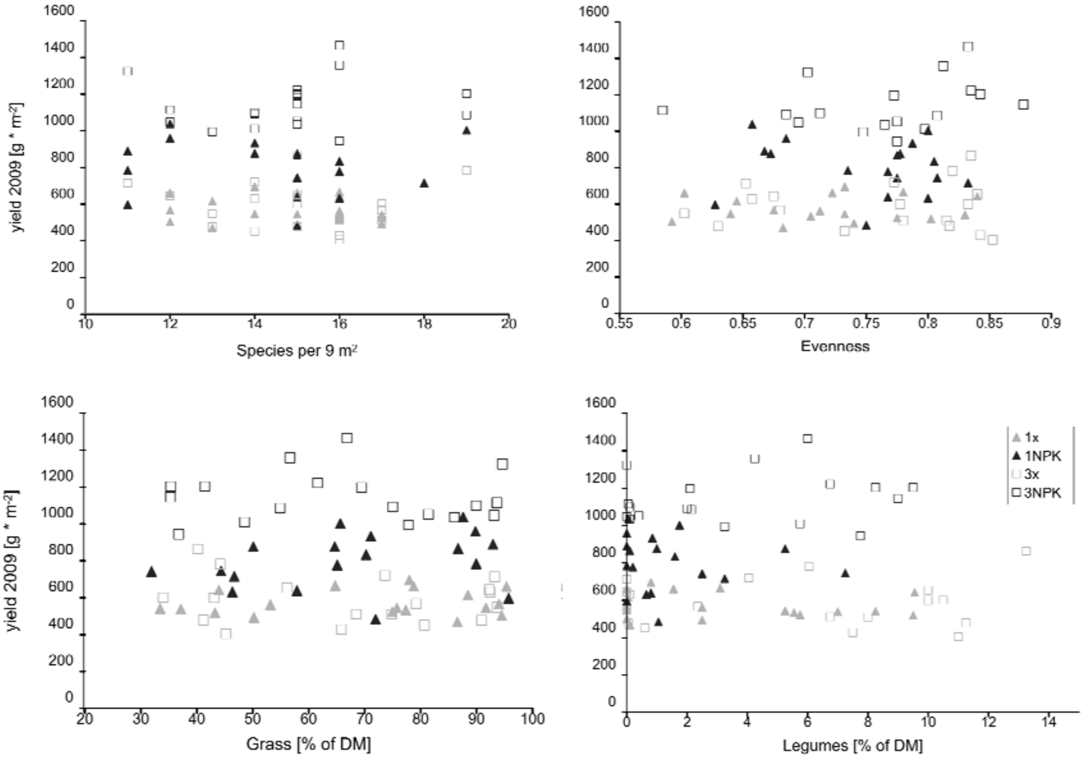

Fig. 1 Relationships between total yield 2009 and biodiversity (a, b) and proportions of functional groups (c, d) under the four management regimes (legend: middle right). None of the correlations between yield and independent variable within one management group was significant.

However, using the finer division into tall and small grasses, forbs and legumes, we found significant effects on yield in May 2009 (Figure 2), when we had recorded both vegetation and yield data. A larger proportion of tall grasses (Figure 2 a) or tall species altogether (data not shown) increased yields in May 2009 significantly - but only in the fertilized plots. The number of tall species or grasses was irrelevant; we found no significant correlation between these numbers and yield. The more small species were present, the less forage was harvested on NPK-plots. This trend was also visible in the yield × species ID correlation (data not shown). *Achillea millefolium* (classified as a tall forb) showed a tendancy to increase yield in fertilized plots, whereas *Agrostis capillaris* (a small grass) seemed to decrease yield in fertilized plots when it was present in large amounts. However, the correlations were not significant at the 5% level and all other frequent species showed no visible correlation with yield at all. The variability in yield at the experimental area was best explained by a linear model containing the amounts of tall grasses, small species, the factor fertilization and all interaction terms ($R^2_{adj} = 0.529$, $P < 0.001$). Still, the fertilization alone (excluding interactions with vegetation) accounted for 21.3% of all variation in yield.

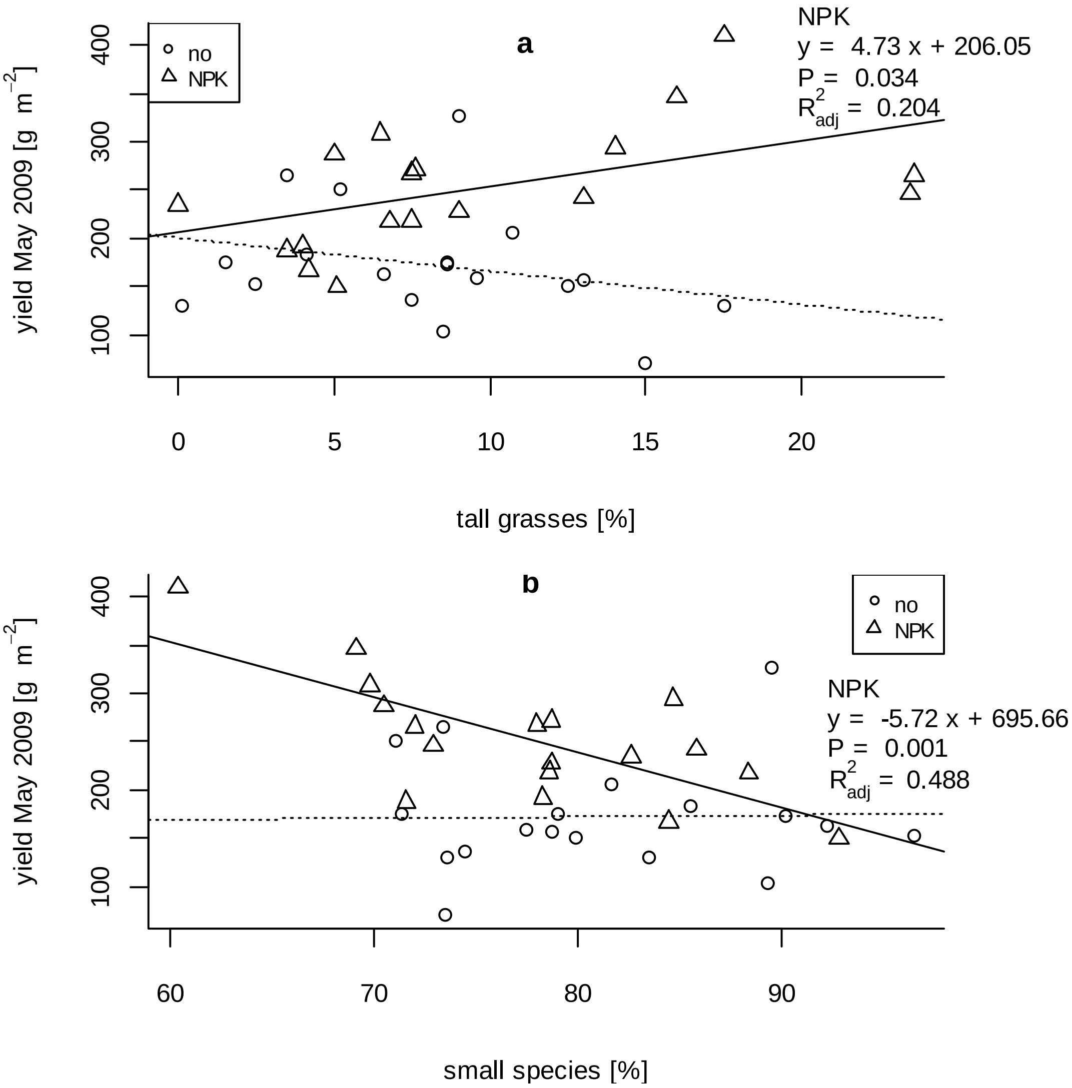

Fig. 2 Yield May 2009 dependent on tall grasses (a) and proportion of small species (b) grouped by nutrient regime with regression lines. Only equations of significant regressions are shown. Linear model including a significant interaction between nutrients and tall grasses (*P* = 0.032) and nutrients and small species (*P* = 0.017), response variable untransformed.

Tab. 4 Spatial variability (coefficient of variation in %) of yields per harvest date 2009, n = 6. For treatment abbreviations please refer to Table 1.

treatment	May	July	Sept
Co1x		12.95	
Co1NPK		24.6	
Co3x	27.36	15.7	43.19
Co3NPK	27.06	23.13	13.19
–Dic1x		12.62	
–Dic1NPK		17.85	
–Dic3x	40.62	23.68	30.1
–Dic3NPK	20.94	12.83	13.13
–Mon1x		9.23	
–Mon1NPK		12.5	
–Mon3x	30.28	32.16	29.66
–Mon3NPK	26.64	5.89	10.56

The spatial variation, i.e. the range of yields found in the six replicates of each treatment at a given harvest date showed no consistent pattern with sward type, fertilization or harvest date (Table 4). Only in September, all unfertilized plots showed a higher variation than the fertilized ones. The yield variation among the single harvest dates in 2009 was smallest in the –Mon-swards (Table 5).

Fertilization also added a significant amount of variation to the yields per harvest (linear contrasts, $P < 0.05$).

Tab. 5 Temporal variability of yields (CV of the three harvests per plot) on plots cut 3 times in 2009. Means ± SD of coefficients of variation per treatment, n=6. Different letters indicate significant differences among treatments at the 0.95 confidence level according to Tukey's mean separation (response variable arcsine transformed). For treatment abbreviations see Table 1.

treatment	**CV [%]**
Co3x	33.03 ± 8.32 ^{ab}
Co3NPK	45.67 ± 13.43 ^{a}
–Dic3x	31.44 ± 7.52 ^{ab}
–Dic3NPK	39.18 ± 6.18 ^{ab}
–Mon3x	25.66 ± 11.98 ^{b}
–Mon3NPK	27.97 ± 6.33 ^{b}

The energy content of the forages at the first and third harvests (May: 11.55 ± 0.17 MJ (kg DM)$^{-1}$, Sept: 11.55 ± 0.18 MJ (kg DM)$^{-1}$) was not influenced by any of the treatment factors. At the second harvest in July, the cutting regime (1 cut regime 10.63 ± 0.21 MJ (kg DM)$^{-1}$, 3 cut regime 11.12 ± 0.11 MJ (kg DM)$^{-1}$) was responsible for most of the variation in energy content (Anova including one variance term per utilization type, $P < 0.001$, data not shown). However, in unfertilized plots, the forage samples from the –Mon-swards had significantly lower energy contents than those from the other two sward types (linear contrasts in lm including one variance term per utilization type, $P = 0.005$). This distinction was not visible in fertilized plots (significant interaction sward type –Mon × fertilization, $P = 0.014$). For all four analyzed forage quality parameters (CP, WSC, NDF, ADF), we found significant sward effects at different harvest dates (Figure 3). However, these effects were not consistent across the fertilization levels; we found significant interactions between sward type and fertilization (Figure 3 a-d). When comparing the forage quality of the first growth cycles (i.e. forages cut in May and the ones cut for the first time in July), we detected, apart from a general loss of quality due to senescence of the sward, a significant time × sward interaction. From May to July, the swards rich in forbs increased in ADF contents significantly more ($P = 0.043$) than the other swards.

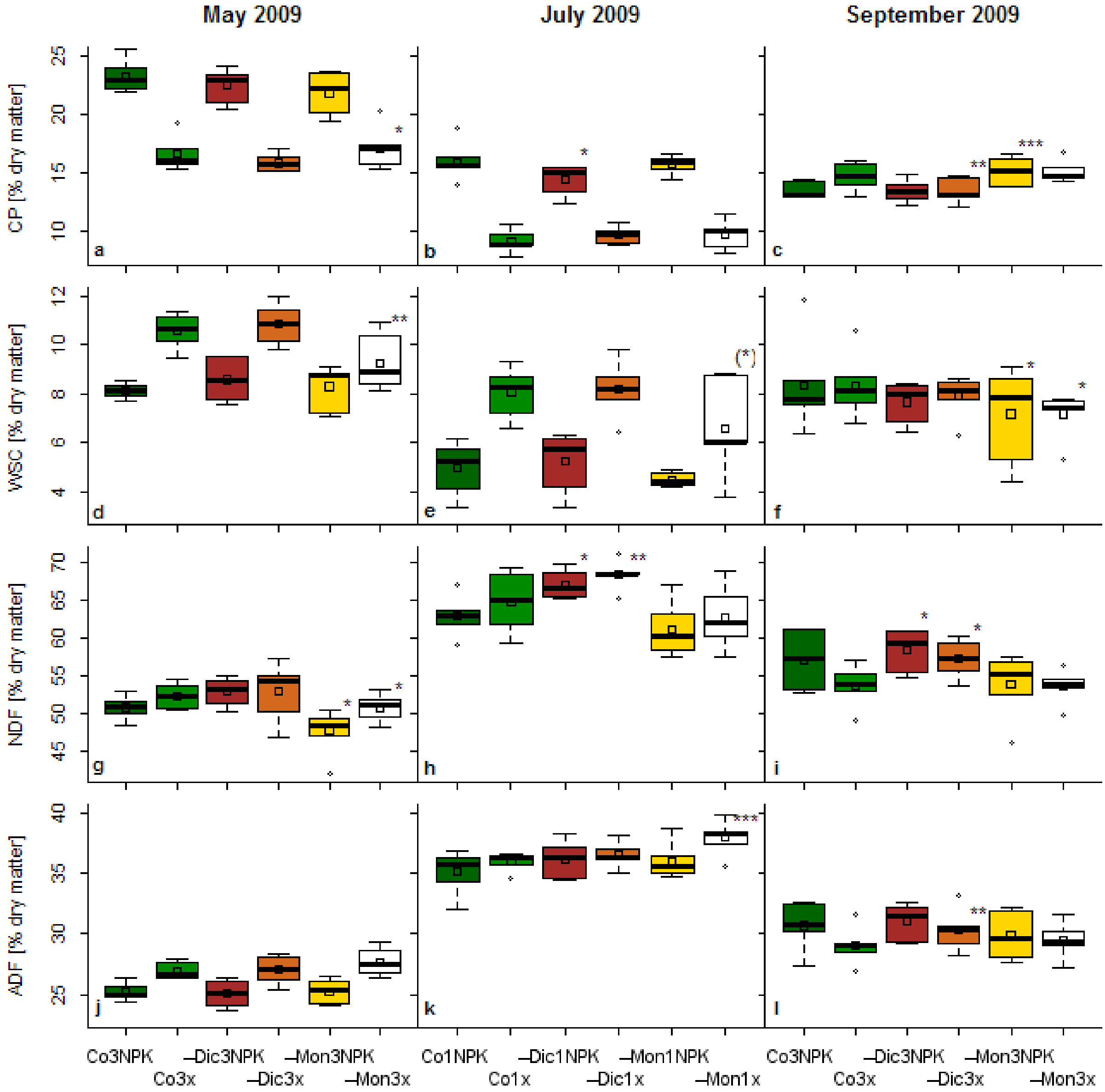

Fig. 3 Box and whisker plots showing the four quartiles, the medians (calculation of outliers by the default method in R) and the means (□) of selected forage quality characteristics in the six different sward type × nutrient combinations at each of the three harvests. Second cut (July) of the 3 cut treatment not presented. Asterisks denote significant differences from the control sward of the same nutrient level (*** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$, (*) $P = 0.0506$). Linear contrasts in linear models; either models with different variances per nutrient level (July ADF, Sept CP) or sward type (Sept WSC) or response variable either squareroot (July NDF) or not transformed (all others). For abbreviations of treatments please refer to Table 1.

The indirect ordination (PCA) of the quality parameters showed the same main gradients determining forage quality as the direct one (RDA) (Figure 4). The cutting regime, or rather the age of the swards at harvest, explained most of the variation (57%, $P < 0.010$, Monte Carlo permutation test) in forage quality in our experiment, influencing especially the fiber contents. The variation in sugar and protein contents made up the second gradient of forage quality variation. It was mainly determined by the fertilization regime, which explained 12% of the total variation ($P < 0.010$). After accounting for management influences, only forbs, the three species *Rumex acetosa, Trifolium repens* and *Achillea millefolium*, the amount of tall forbs or the sward type – Mon (not included in the ordination diagram in Figure 4) explained significant ($P < 0.050$, Monte Carlo permutation test) conditional proportions of the remaining variance if added as separate groups to the ordination model.

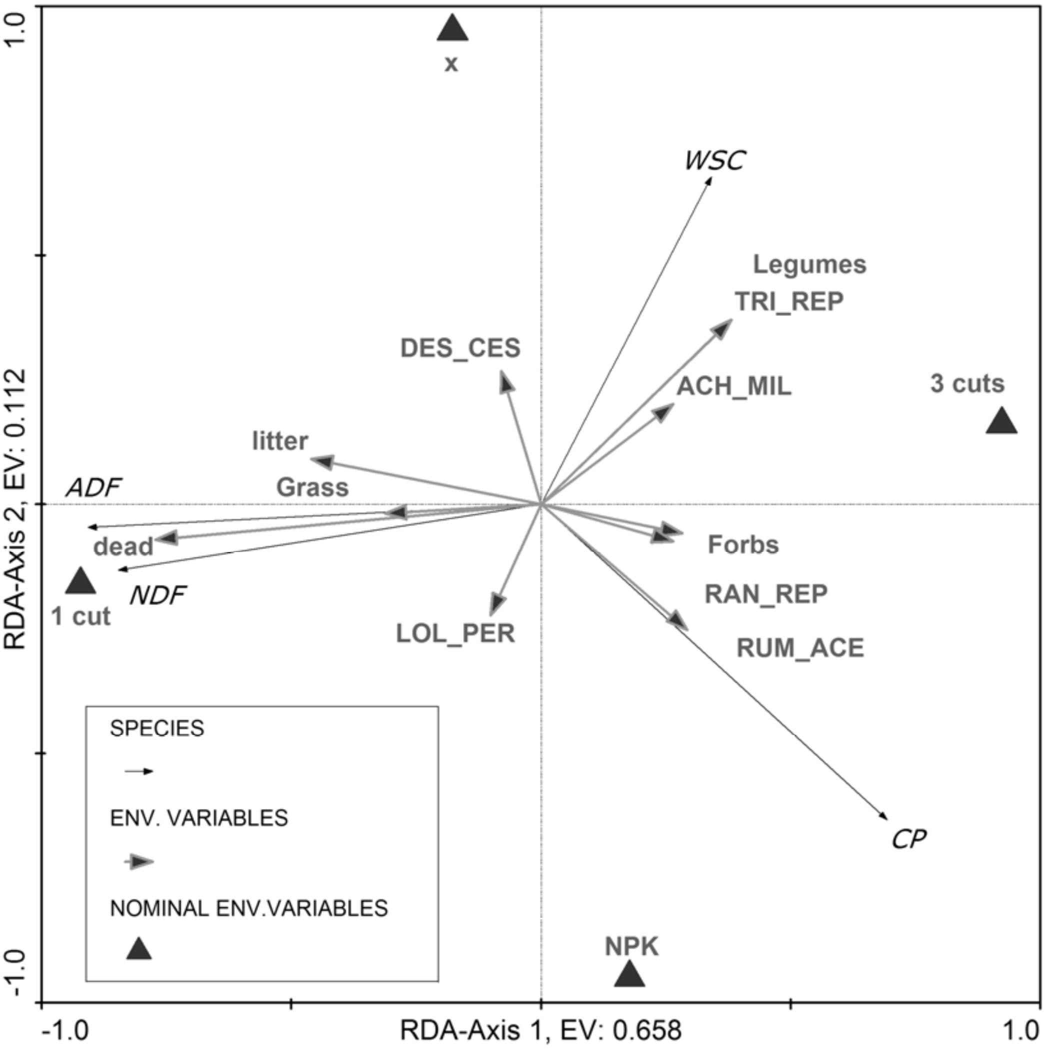

Fig. 4 Redundancy analysis (RDA) with forage quality characteristics (means of CP, WSC, ADF, NDF of all harvests 2009, untransformed) as dependent variables ("species") and vegetation characteristics (instead of sward types) and management treatments (cf. Table 1) as explanatory variables ("Env. Variables"). Included are environmental variables with a correlation with the 1st and 2nd ordination axis < -0.2 and > 0.2.
Abbr. of species names: Ach_mil: Achillea millefolium, Des_ces: Deschampsia cespitosa, Lol_per: Lolium perenne, Ran_rep: Ranunculus repens, Rum_ace: Rumex acetosa, Tri_rep: Trifolium repens. Explanatory variables: Grass/Forbs/Legumes: yield proportions in %, litter: % of soil covered by dead plant material, dead: proportion of dead plant material found in sorted samples in %.

The remaining species and functional groups shown in Figure 4 only accounted for significant parts of the remaining variation (after extracting the influences of management) if added as single extra independent variables. Only the variable dead material in forage samples did not explain any extra variation, since it was highly correlated with cutting regime. Biodiversity per se (species number, biodiversity indices) was not included into the variance partitioning since the indices had shown a far too small variance in PCA. Additionally, the number of species was dependant on forb content. The results of the variance partitioning (Table 6) emphasized the influence of management on forage quality. Just a small part (up to 8.6%) of variation in forage quality was solely due to sward characteristics.

Tab. 6 Variance partitioning of average forage quality parameter data (CP, WSC, ADF, NDF) of the three harvests in 2009. Fraction ‘management’: cutting frequency and fertilization, fraction ‘vegetation’: either vegetation in terms of species abundances, or proportions of functional groups or proportions of tall and small growing grasses (G), forbs (F) and legumes (L), (averages of the two vegetation recordings), fraction ‘environment’: spatial heterogeneity (rows and columns of the experimental area), disturbance (% of open soil), amount of litter and amount of dead plant material in forage. Res. Var. = Residual variance

	fraction Vegetation consists of	**Management**	**Vegetation**	**Environment**	**Res. Var.**
marginal variance [%] (each fraction as single explaining variable)	*Species*	69.4*	32.2*	48.1**	
	Grass-Forb-Legume		18.9*		
	tall-small G-F-L		32.1**		
conditional variance [%] (each fraction added to model after the two others)	*Species*	15.2**	5.1*	1.9	15.6
	Grass-Forb-Legume	23.0*	7.4*	2.2	18.9
	tall-small G-F-L	19.4**	8.6**	3.4*	17.9

Discussion

The main objective of this study was to investigate the effects of sward characteristics on forage yield and quality in managed permanent grassland under different management regimes. We hardly found any influences of biodiversity or botanical composition on yield in this experiment, most of the yield variation was due to management. This may be due to the comparatively narrow range of species in the different sward types and intermediate species number (Schläpfer *et al.*, 1999) analyzed here. As Schwartz *et al.* (2000) and Waide *et al.* (1999) point out, most of the ecosystem processes are saturating at low species numbers and Wrage *et al.* (2011) reported in their review on studies on phytodiversity in agriculturally managed grassland that the strongest effects were found at species numbers from one to two or four. So with the narrow range of species in the GrassMan experiment, combined with intermediate species numbers comparable to managed grassland in temperate European regions, we seem to have analyzed a part of the biodiversity–productivity–function with a relatively low rate of change. Hence we found no effects, or the existing effects were too small compared to the variability in our treatments as it is the case in experiments with no controlled environments (Balvanera *et al.*, 2006). The sward effect found in October 2008 cannot be counted as biodiversity effect, since both treated swards had lower yields than the control sward, indicating the ongoing recovery process after the herbicide application. By May 2009 however, the treated swards had fully recovered (Petersen *et al.*, 2012). In other removal experiments (e.g. Fowler, 1981; Symstad & Tilman, 2001; McLaren *et al.*, 2010) it took a year or more for the remaining vegetation to regrow to full cover after the removal had taken place.

In a review of observational studies, representing real world conditions, Mittelbach *et al.* (2001) and Waide *et al.* (1999) found the hump shaped biodiversity-productivity relationship as the most common pattern at local scale (< 20 km). As in other observational studies (Jiang *et al.*, 2009), the abundance of the dominant species along with their special traits (here *Agrostis capillaris* and *Festuca rubra* as low to medium yielding grasses) may have influenced yields more than the biodiversity per se. This is consistent with the findings of Mokany *et al.* (2008), who showed that not the “diversity” (Tilman, 1997) but rather the “mass ratio” (Grime, 1998) hypothesis better explained ecosystem process variation in natural communities. Thus, the more tall grasses were present in the plots the higher yields we got in the first cut, supporting our hypothesis. However, as Bernhardt-Römermann *et al.* (2011) also reported, the effects of functional diversity on ecosystem functions depend on management, so the effects of growth characteristics were only visible in fertilized plots. The faster growing tall grasses gained more biomass from the fertilization than the smaller species.

The increased spatial yield variation on the unfertilized plots in September 2009 (Table 4) might be due to the different mineralization rates at the different experimental plots. At this rather intensive utilization without fertilization, the soil might not be able to supply enough nutrients for the third cut, at least not in all plots of the experimental area. This lack of soil-provided nutrients was also observed by Bernhard-Römermann *et al.* (2011) on intensively used plots, albeit at a higher cutting frequency since their experiment was situated on fertile loam. The lower variability of the –Mon-swards originated in the small yield differences between the first and second cut. In spring, these swards rich in forbs had in tendency slightly lager yields than the other swards. However, in summer, the control and grass-rich swards yielded more than the –Mon-swards. Since species in the reproductive stage have much higher growth rates than during the vegetative stage (Menzi *et al.*, 1991; Ansquer *et al.*, 2009), the –Mon-swards, consisting for a large part of *Rumex acetosa* and *Ranunculus repens* already in bloom, had a little head start in May when the rest of the swards was still in the vegetative growth phase. In May, the most abundant grass species *Festuca rubra* and *Poa* sp. had just started stem elongation and were not in full bloom till the second harvest, joined by *Agrostis capillaris*, one of the latest flowering grasses on the experimental area.

Since the energy content of forages depends on all cell contents (protein, carbohydrates and fats) and the fiber content determining their digestibility (Voigtländer & Jacob, 1987), one can explain the equal energy contents in fertilized vs unfertilized swards by their contrasting contents of CP and WSC in May and July (Figure 3 a, b, d, e). Low CP contents in unfertilized swards were compensated for by higher WSC proportions and vice versa. In September, CP and WSC did not differ among the fertilization treatments, leading to equal energy contents again. The senescence of the swards combined with higher amounts of structural tissue (= higher amounts of dead plant material, see Figure 4) reduced forage quality in terms of digestibility (Duru *et al.*, 2008) in the swards of the 1 cut regime. The –Mon-sward contained less energy due to increased levels of ADF and decreased levels of WSC (Figure 3). This is consistent with Andueza *et al.* (2010), who found that high amounts (> 20%) of forbs have a great influence on forage quality and that forbs generally degenerate faster than grasses over the course of the seasons. For the summer regrowth, Bruinenberg *et al.* (2002) reported higher digestibility in forb species than in grass species. This is comparable with our results. The –Dic-swards had higher NDF and ADF contents than the –Mon-swards in the second (data not shown) and third cut (Figure 3 i, l), whereas the CP contents were highest in the –Mon-swards. However, there may be other crucial factors influencing forage quality far more than sward composition. Especially the cutting date and along with it the phenological development of the swards can be responsible for the largest changes in quality (van Soest *et al.*, 1978; Bruinenberg *et al.*, 2002; Čop *et al.*, 2009; Bochi-Brum *et al.*, 2011). This is due to a declining leaf:stem ratio as the grasses start their generative growth (Duru *et al.*, 2008). Further, the accumulated biomass needs to be supported by structural tissues. Contents of soluble carbohydrates, mainly found in the leaf tissue, are in decline, reducing digestibility. This is also mirrored in our data. The forage of the late first cut in July, had the highest NDF and ADF contents (Figure 3 h, k). The high ADF contents in the –Mon1x swards could be due to higher proportions of fruiting *Rumex acetosa*, *Ranunculus repens* and red fescue. The other sward types hosted larger amounts of *Agrostis capillaris* still in bloom. In the redundancy analysis, most variation in forage quality of the whole year 2009 was explained by management (Table 6). The high influence of the environment was due to a redundancy with cutting regime; a late cut means a lot of dead plant material in the forage, which we had included as one factor in the environmental fraction since the senescence of the sward is also influenced by weather conditions during spring and summer (van Soest *et al.*, 1978). As also reported by Čop *et al.* (2009), who analyzed the quality of forages by means of ordination as well, the main gradient in our redundancy analysis was the contrast in fiber contents induced by different cutting dates. The CP content as the second largest gradient showed a much smaller variability. Just in the third ordination axis the sward characteristics were the determining factors but they explained hardly anything (eigenvalue: 0.046) of the remaining variation in forage quality.

To sum up, the manipulated swards in the GrassMan experiment reacted similarly to untreated swards analyzed in observational studies. Yield was mainly influenced by fertilization and cutting regime, merely trait-based sward characteristics could be used to predict patterns in yield, supporting the mass-ratio hypothesis. Forage quality was strongly influenced by phenological development of the sward, which hardly differed among our three sward types since they all belonged to the same plant community and had the same set of early and late flowering species, albeit in different proportions. Just at single harvest dates, the influences of forbs and grasses on quality characteristics were visible, most of the time relatively small compared with fertilization effects. As we suggested, biodiversity per se did not have significant influences on forage yield and quality in our study. At species richness levels beyond 10 species per m^2, the effects of sward characteristics were less pronounced than at low species numbers where niche space is still available favouring complementary effects and facilitation (Loreau & Hector, 2001; Roscher *et al.*, 2004). The “sampling” or “selection effect” (Huston, 1997; Loreau *et al.*, 2001) should not play a role in agricultural grasslands since they already contain productive species, often optimized by breeding. However, as discussed by White *et al.* (2004) and Isbell *et al.* (2011), sward effects even at higher species numbers can still be of importance if considering different contexts and thus expanding the available niche space by including greater spatio–temporal scales. Especially climatic fluctuations between years might strengthen sward effects on ecosystem functions.

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Vertical structure and leaf area index in swards of different functional composition

Abstract

Sward architecture and yield formation in swards of different functional and species composition have not been widely studied. In a removal experiment on permanent grassland comprising three functionally different sward types (untreated control, dicot reduced, monocot reduced) in the Solling Uplands (Germany) we studied the vertical structure, leaf area and dead tissue in contrasting fertilization and cutting regimes. The main focus lay on structural differences due to the special morphological characteristics in grasses and dicots, rather than on management influences on sward structure. Additionally to the functional diversity, species richness was also varied within the limits of agriculturally managed grasslands. Biomass and leaf area did not increase with species numbers. Dicot reduced swards had a higher leaf area, but also higher amounts of dead plant material than monocot reduced swards. Control swards with an intermediate grass–dicot ratio mediated between the other sward types and were not distinct from any of them. Total biomass was lower in monocot reduced swards but due to a different spatial arrangement of biomass, the harvestable yields did not differ between the structurally different swards.

Keywords: sward architecture, LAI, monocots, dicots

Introduction

Plant architecture, the arrangement of plant components in space, is quite diverse in grasslands, despite their relatively low canopy height compared to woody vegetation (Körner, 1994). There are not only species with horizontally arranged leaves and species with steep angled leaves; there are also small and tall species adding up to several distinct growth forms (Liira & Zobel, 2000). The widely used classification of grassland species into graminoids (more vertically arranged leaves) and dicotyledonous species (horizontal leaves) also takes this fact into account. These groups do not only differ in their visual appearance, their leaves also differ in N contents and photosynthetic nitrogen use efficiency (Kahmen *et al.*, 2006). Plants with horizontally arranged leaves absorb more light, have higher leave nitrogen contents (Anten *et al.*, 1995; Tjoelker *et al.*, 2005) and allocate more of the photosynthates to their root system (Körner, 1994). On the contrary, graminoids have a higher leaf area index (leaf area per gound area unit, LAI), the self-shading is reduced due to steep leaf angles and the leaves contain less nitrogen. They have a higher photosynthetic nitrogen use efficiency and allocate more of the photosynthates to above ground biomass than dicots. Consequently, a higher LAI is found in grass-rich swards compared to forb rich ones.

The sward architecture exerts a strong influence on biodiversity due to its impact on light availability (Mitchley & Willems, 1995). Some research has been done on the sward architecture of semi-natural grasslands. The vertical distribution of biomass and leaf area index (LAI) has been found to depend on management regime (pasture versus one late cut, Mitchley & Willems (1995)), nutrient and moisture status of the soil (Werger *et al.*, 1986) and light and nutrient availability (Liira *et al.*, 2000). Most of these studies included some kind of classification according to the growth from of the different plants (e.g. Liira *et al.*, 2000). Further, research on the LAI of single species has been conducted (Sheehy & Cooper, 1973; Sheehy & Peacock, 1977; Cheng *et al.*, 2009). Along with the increasing number of biodiversity–functionality experiments during the last decades, sward structure and LAI were also correlated to species richness. Spehn *et al.* (2000), Fridley (2003), Lorentzen *et al.* (2008) and Vojtech *et al.* (2008) all found a positive effect of species richness on LAI and biomass, indicating that ressource partitioning of light and above ground space might be possible, especially in environments, where nutrients are not limiting. However, they used seeded, experimental plant communities and the applicability of results from these plant communities on real world ecosystems is currently debated (Schmid, 2002; Thompson *et al.*, 2005; Hector *et al.*, 2007; Mokany *et al.*, 2008; Jiang *et al.*, 2009). Further, most of the experiments are not managed according to agricultural principles whereas a large part of the European grasslands are managed grasslands (Wrage *et al.*, 2011). The species richness range of typical agricultural grasslands in Europe, which lies between 7/m^2 (intensively managed grassland analyzed by Pywell *et al.* (2007)) and 15 per 20 m^2 as reported by Kleijn *et al.* (2001), is not covered adequately by the logarithmic scale of species richness often used in biodiversity experiments (e.g. Spehn *et al.*, 2000; Roscher *et al.*, 2004; Vojtech *et al.*, 2008; Nyfeler *et al.*, 2009). A solution to this problem, or rather a reasonal complement to biodiversity experiments, are removal experiments, where one part of the vegetation (most of the time one or several functional groups) is removed manually or by herbicide application (Diaz *et al.*, 2003; McLaren & Turkington, 2010; Petersen *et al.*, 2012).

In 2008, we set up a removal experiment and manipulated permanent grassland by herbicide application (Petersen *et al.*, 2012). With our experiment, we tried to fill this gap between low (< 10) and high (> 30) species numbers. In the first year after the setup the swards had a species richness ranging from 9–16/m^2 or 14–21 per 16 m^2 respectively. At these intermediate species numbers, we found no effects of species richness on yield, merely functional diversity or trait based sward characteristics were able to explain observed patterns in yield (Petersen *et al.*, 2010, cf. chapter 3). Since the swards still host plants of different growth forms, we might find influences on sward structure due to the functional differences between the swards. For yield formation, these differences should be redundant, otherwise they would have affected yield in our experiment. Or, as Falster & Westoby (2003, l. 6-7) put it:"Are coexisting architectures just alternative ways to achieve similar overall outcomes?" We hypothesise that biomass, leaf area and their vertical distribution are dependant on the functional composition (proportions of functional groups) of the sward. Likewise, the texture of the swards, more precisely, the amount of dead plant material is influenced by the functional composition. Further, species richness has no impact on total LAI and biomass values.

Material and methods

Biodiversity experiment

The Grassland management experiment (GrassMan) is a biodiversity experiment managed according to agricultral principles. It was established in 2008 on permanent grassland between Silberborn and Neuhaus in the Solling Uplands, Germany (51°44' 53" N, 9°32' 42" E, 490 m a.s.l.). Prior to the setup of the experiment, the grassland had been used as summer pasture for cattle. The area has a mean annual temperature of 6.9°C and mean annual precipitation of 1028 mm (DWD 1960-1991, station Silberborn-Holzminden, 440 m a.s.l.). The soiltype of the experimenterial area was classified as haplic cambisol (I. Hoeft & A. Keuter, unpublished); its vegetation was a nutrient poor *Lolio-Cynosuretum*.

GrassMan is a three factorial experiment (Tab. 1). The three sward types were obtained by herbicide application against dicotyledonous and monocotyledonous species respectively. For harvesting we used a Haldrup® forage combine havester with a cutting height of 7 cm.

Tab. 1 Experimental factors and treatment levels of the GrassMan experiment. The acronyms of the different treatments are generated by combination of the factor level abbreviations in the order sward-utilization-nutrients, e.g. –Dic1x = dicot-reduced sward, cut once, no fertilization.

Factor	Level		
Sward type	1.1	untreated control sward	**Co**
	1.2	dicots reduced	**–Dic**
	1.3	monocots reduced	**–Mon**
Utilization	2.1	one cut (July)	**1**
	2.2	three cuts (May, July, September)	**3**
Nutrients	3.1	no fertilization	**x**
	3.2	180/30/100 kg NPK ha^{-1} yr^{-1} *	**NPK**

* N fertilizer: *calcium ammonium nitrate N27,* P&K fertilizer: *Thomaskali® (8%* P_2O_5*, 15%* K_2O*, 20% CaO)*

The combination of all factors and levels resulted in twelve treatments, which were replicated six times. To account for potential spatial gradients, the 72 experimental plots were arranged to form a Latin Rectangle with the upper part bordering a forest sloping gently (< 5% slope) towards the lower rows. Two columns form one block. A detailed description of the experiment can be found in Petersen *et al.* (2012).

Biomass and canopy measurements

The vertical distribution of biomass was analyzed by stratified clipping (Monsi & Saeki, 1953; Sheehy *et al.*, 1973). Prior to each of the scheduled harvests, we clipped three randomly selected 15 × 15 cm quadrats per plot at ground level. The cut bunch of grass was placed on a board and separated into 10-cm layers. The lowest layer was 7 cm thick, corresponding to the cutting hight of the forage harvester to ensure comparability of total biomass and harvested yield. The material of each layer was placed in a plastic bag and frozen before further processing. The three subsamples of each plot corresponding to the same layer were combined and sorted to the three functional groups grasses, forbs and legumes and dead plant material. The sorted material was dried at 105°C for 48 hours and weighed. Leaf area index (LAI) of the samples cut in July was determined via regression between leaf area (LA) and dry mass. Additionally to the stratified samples, a mixed sample of fresh plant material from each block separated according to cutting regime was taken, put into a cool box and transfered to the laboratory immediately. Legumes were collected separately from plots belonging to the same utilization × nutrient treatment, since preceeding tests had shown that in contrast to forbs and grasses, the specific leaf area (SLA) of the legumes (consisting of more than 90% *Trifolium repens*) was influenced not only by cutting regime but also by nutrient supply. Closely following the protocol by Garnier *et al.* (2001) for determining SLA, the material was kept damp and cool before scanning 20–30 subsamples of stems (including petioles) and leave blades, or laminae, of each functional group using the software WinRhizo (Version 2007 d, Regent Instruments Inc., Quebec, Canada). For SLA of flat stems and leave blades, the projected area (for flat stems we used twice the projected area) was used, for round stems and leaves (mainly leaves of *Festuca rubra*) the surface area was calculated. The SLA of each fraction was then used to calculate LAI of the stratified biomass samples taken in July, which had been separated into stems and leaves of grasses, forbs and legumes. Petioles and leave sheaths were counted as stems. To avoid sorting mistakes all fruits (except for the green, easy recognisable ones of *Veronica chamaedrys*) and flowers were classified as non-green biomass. Their SLA was not determined. Due to the large heterogeneity of stem diameters in legumes and forbs, some of the area–mass regressions had determination coefficients below 0.8. Consequently, we decided to exclude all LA calculated from stem biomass from further analyses and only used LA from laminae. Thus, the leaf area ratio (leaf area per sample dry weight, mm^2 mg^{-1}, LAR) was not based on total leaf area (Ryser & Lambers, 1995) but on leaf area from leave blades, likewise the LAI.

The species richness and the functional diversity, i.e. the proportions of grasses, forbs and legumes, of the experimental swards had been determined by vegetation relevés (9 m^2) in May and August 2009. Since the three sward types control, dicot reduced and monocot reduced differed significantly in their proportions of functional groups with grass contents of 70, 92 and 45% respectively and with no legumes present in the –Dic-swards (Petersen *et al.*, 2012), the sward types were taken as surrogates for functional diversity in this study.

Data processing

Univariate statstics were calculated in R version 2.12.2 (R Development Core Team, 2011). Into all (general) linear models (GLM) we applied on our data, row and block were included first of all factors to extract all environmental variablity before assessing treatment effects. The effects of species richness and the experimental factors sward, utilization and nutrients on LAI, LAR and biomass were tested using a three-way ANOVA including all treatment factors and their interactions. Model simplification by dropping insignificant interactions and factors (apart from row and block) followed the instructions given in Zuur *et al.* (2009) using the Aikaike Information criterion (AIC) to detect the best fitting models. For comparison of means of several factor levels, we used Tukey's ‘Honest Significant Difference’ method (Miller, 1981) with a confidence level of 0.95. To ensure better comparability of the layer-wise distribution of LA and biomass, these data were expressed as proportion of the total LA/biomass. We applied general linear models with binomial error distribution on all proportional data (percentage of harvested biomass above a sward height of 7 cm versus percentage of stubble biomass, percentage of biomass or LA in a given canopy layer versus total LA/biomass). All layers were compared up to the ones where 80 % of total biomass or LA was reached. This was at the layer 37–47 cm for biomass and 27–37 cm for LA. The models included the experimental factors or, to compare the means of single treatments, the 12 treatments themselves. Overdispersion larger than 1.5 was corrected by multiplication of standard errors with the overdispersion paramter Φ, using a quasi-GLM model or a model with negative binomial distribution of errors (Zuur *et al.*, 2009). Normal distribution and homogeneity of the residuals was inspected using QQ-plots and conditional boxplots of the residuals against all factor levels as suggested by Anscombe (1973) and Zuur *et al.* (2010). Inhomogeneity of variances was corrected using general least square (GLS) models including the “varIdent” variance structure (different variance per stratum, nlme package (Pinheiro *et al.*, 2009). Necessary data transformations are indicated in the results.

Results

At the first cut in May 2009, we found no influence of sward type on ratio of harvested to stubble biomass. It was only influenced by nutrient regime (Tab. 2). In the unfertilized plots, 21.9 ± 5.4% of the total biomass was harvested. The fertilized swards had grown taller and a slightly larger percentage (26.4 ± 6.4%) of biomass was located higher than 7 cm above the ground, forming the yield in these swards. The date of the stratified clipping (the samples had been cut blockwise at different days starting in block 1) had a larger influence on the biomass ratio than fertilization (data not shown). In July, these time series effects were also significant, being roughly as important as utilization and fertilization. The higher utilization frequency significantly decreased the yield–stubble ratio. In the fertilized plots cut three times, the ratio shift was significantly higher than in the plots cut only once (utilization × nutrients interaction). In the different sward types, fertilization had contrasting influences on the vertical biomass distribution.

Tab. 2 Influence of sward type and management on ratio of harvested biomass (biomass above 7 cm sward height) to stubble biomass (0-7 cm) at the three harvest dates 2009, evaluated by GLM with bionomial error distribution (link: logit). Overdispersion in data of July and September corrected. The coefficient c indicates a positive or negative influence of factors on ratio of harvested to stubble biomass.

	May 2009			**July 2009**			**September 2009**	
factors	Deviance/ $Dev._{total}$	P(>|Chi|)	c	Deviance/ $Dev._{total}$	P(>|Chi|)	c	Deviance/ $Dev._{total}$	P(>|Chi|)
sward	0.02	0.469		0.01	0.421		0.008	0.9
utilization				0.146	<0.001***	–		
nutrients	0.128	0.002**	+	0.291	<0.001***	+	0.019	0.462
sw × util				0.021	0.148			
sw × nut				0.034	0.05*	–/+		
util × nut				0.018	0.074.	+		
sw × util × nut				0.028	0.083.	–		

In the –Mon swards, the proportion of harvested biomass increased, whereas in the –Dic swards the proportion of stubble mass increased, albeit not significantly. This trend was not consistend across cutting regimes, indicated by the significant sward × utilization × nutrients interaction. A linear contrast with the single treatments as explaining factors and –Dic3NPK as reference level showed a significant sward effect in the fertilized swards cut three times. Both control and monocot reduced swards had a significantly larger yield–stubble ratio ($P = 0.025$ –Mon-sward, $P = 0.023$ Co-sward) than the –Dic-swards (see also Fig. 2, graphs j–l). For the other utilization × nutrient combinations we found no significant sward effects. At the third cut in September 2009, the ratio between stubble mass and harvested biomass did not differ among any of the treatments.

The amount of dead plant material within the swards mainly depended on age and nutrient status of the swards. A higher cutting frequency and fertilization significantly decreased the ratio of dead to green plant material (Fig. 1). However, also the amount of grasses present in the sward had a significant influence. The –Mon-swards, containing the least grasses also had the lowest amounts of dead biomass.

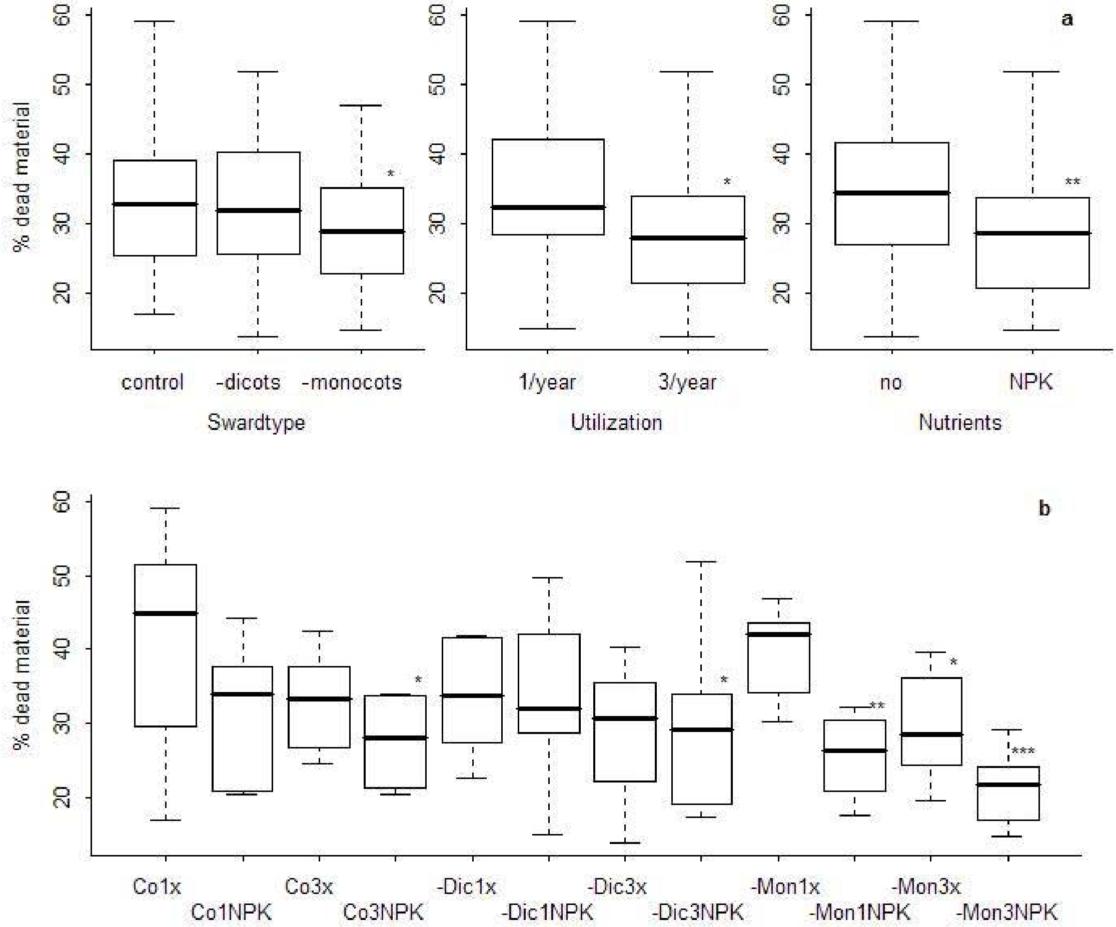

Fig. 1 Proportion of dead plant material found in the sward profiles shortly before the second harvest in July 2009 depending on experimental factors (graph a) and treatments (graph b). The boxes show the median and first and third quartiles. For abbreviations of treatments please refer to Table 1. Asterisks denote significant differences of factor or treatment levels compared to the reference level (sward control, utilization 1/year, fertilization no, treatment Co1x) in a GLM with negative binomial error distribution (link: logit). *** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$.

Total biomass and LAI of the July sward profiles belonging to the same management regime did not differ among the sward types (means and standard deviations displayed in Fig. 2+3). Likewise, species richness had no effect on either biomass or LAI (when included first of all experimental factors in a GLS with different variances per fertilization level). Just the ability to transform nutrients into leaf area was significantly higher in the –Dic-swards (interaction sward × nutrients, $P = 0.015$, GLS allowing for different variances per fertilization level). Likewise, both the manipulated swards gained significantly more biomass from fertilization than the control swards (interaction sward × nutrients, $P = 0.045$ for –Dic and $P = 0.023$ for –Mon swards respectively, GLS allowing for different variance in each cut × nutrient combination).

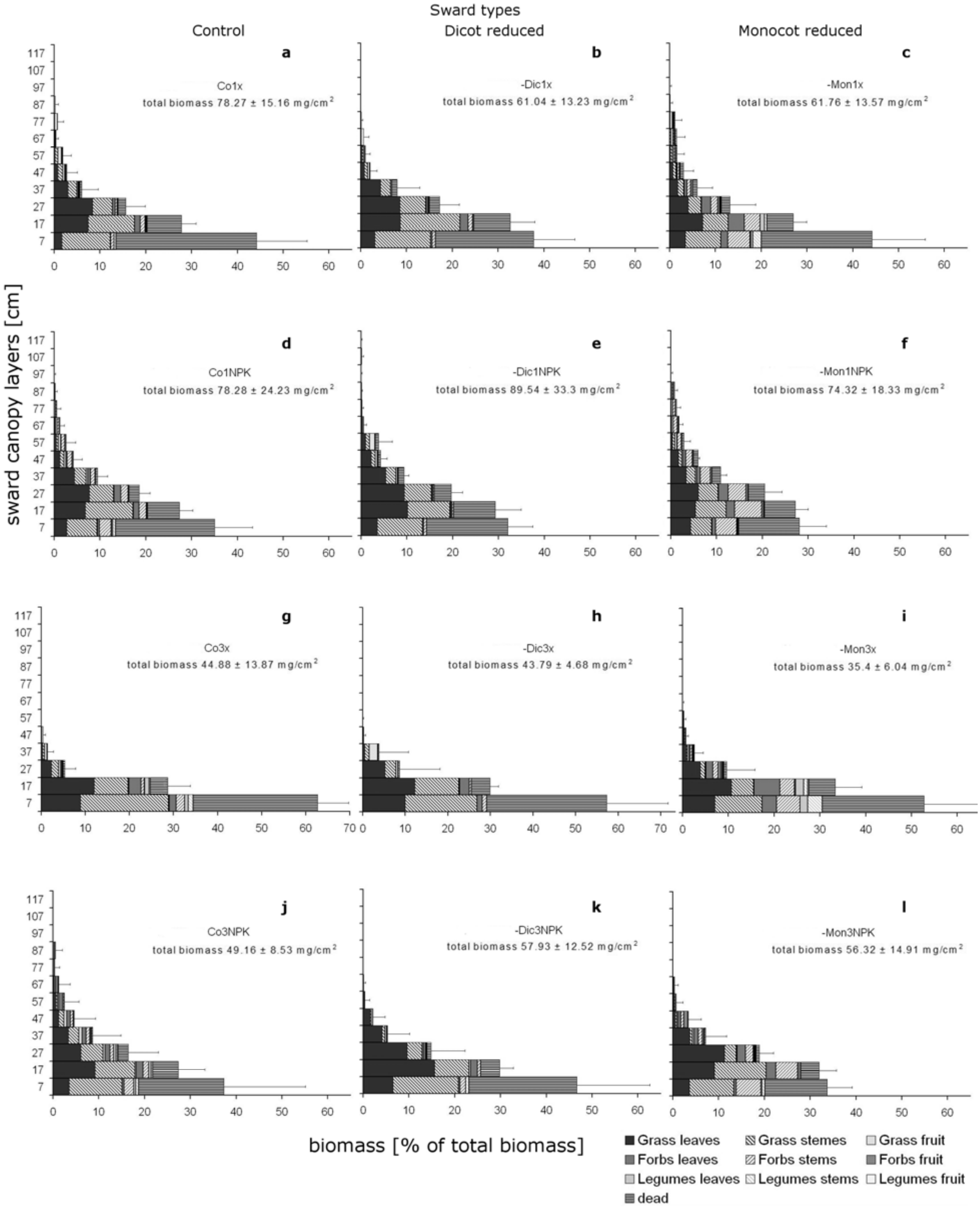

Fig. 2 Vertical distribution of the different functional fractions of biomass for all 12 experimental treatments (July 2009). Means of each fraction per layer and standard deviations of each layer.

Averaged over all management treatments, the –Mon swards had produced the least biomass (P = 0.012). However, the spatial arrangement showed significant sward effects in single management regimes, albeit not for all of them. The diagrams (Fig. 2+3) show that a large proportion of the total biomass (30–60%) was concentrated in the lowest layer and remained as stubble after the harvest. Most of the structural differences were observed between –Mon (graphs c, f, i, l) and –Dic-swards (graphs b, e, h, k).

At 7–17 cm, the ratio of layer biomass versus biomass outside this layer (or the proportion of biomass of the total biomass), was not influenced by the sward type within one management treatment. However, compared to the swards cut once, the proportion of biomass belonging to layer 7–17 in the 3-cut treatments increased significantly more in the –Mon-swards than in the –Dic-swards (significant sward × cut interaction, $P = 0.020$). The –Mon-swards cut once had allocated a lower proportion of biomass to layer 7-17 than the –Dic-swards ($P = 0.034$, graphs b, c, e, f), where around 30% of total biomass belonged to this layer. Biomass proportions in layer 17–27 were only influenced by management, but not by sward type. 10 cm higher up in the profile, the control swards had concentrated significantly more biomass than the –Dic-swards ($P = 0.027$), at least in the 3NPK treatment (graphs j, k). In the fertilized plots cut once, the highest proportion of biomass was found in the –Mon-swards (graphs d–f). They had allocated significantly more biomass to this canopy layer than the –Dic-swards ($P = 0.023$). Under fertilization, both control and monocot reduced swards had increased their biomass proportions in layer 27–37 significantly more than the –Dic-swards (sward × nutrient interaction in Co-swards cut thrice, $P = 0.003$ and –Mon-swards cut once $P = 0.006$). In the canopy layer 37–47, again we found no sward effects on proportion of layer biomass.

The vertical distribution of LA within the swards showed a more pronounced correlation with sward type. The profiles had more distinct shapes than the biomass profiles (Fig. 3). In contrast to the biomass, the main part of LA was allocated to the second and third layer of the profile (17–37 cm above the ground). In the layer closest to the ground, the control swards of the 1x-treatment had the lowest proportion of LA, significantly less than the –Mon-swards ($P = 0.048$, graphs a, c). Consequently, the –Mon-swards showed the least differences between 1-cut and 3-cut treatments (Interaction sward × cut, $P = 0.004$). In the layer 7–17 cm, around 30 % of the LA was concentrated. In the most intensive management treatment 3NPK, the –Mon-swards had significantly higher proportions of LA than the –Dic-swards ($P = 0.050$, graphs k, l). Compared to the other swards, the –Mon-swards allocated significantly less LA to that layer after fertilization (sward × nutrients interaction, $P = 0.017$). In the next layer from 17-27 cm, the sward types reacted differently to the cutting treatment (sward × cut interaction, $P < 0.001$).

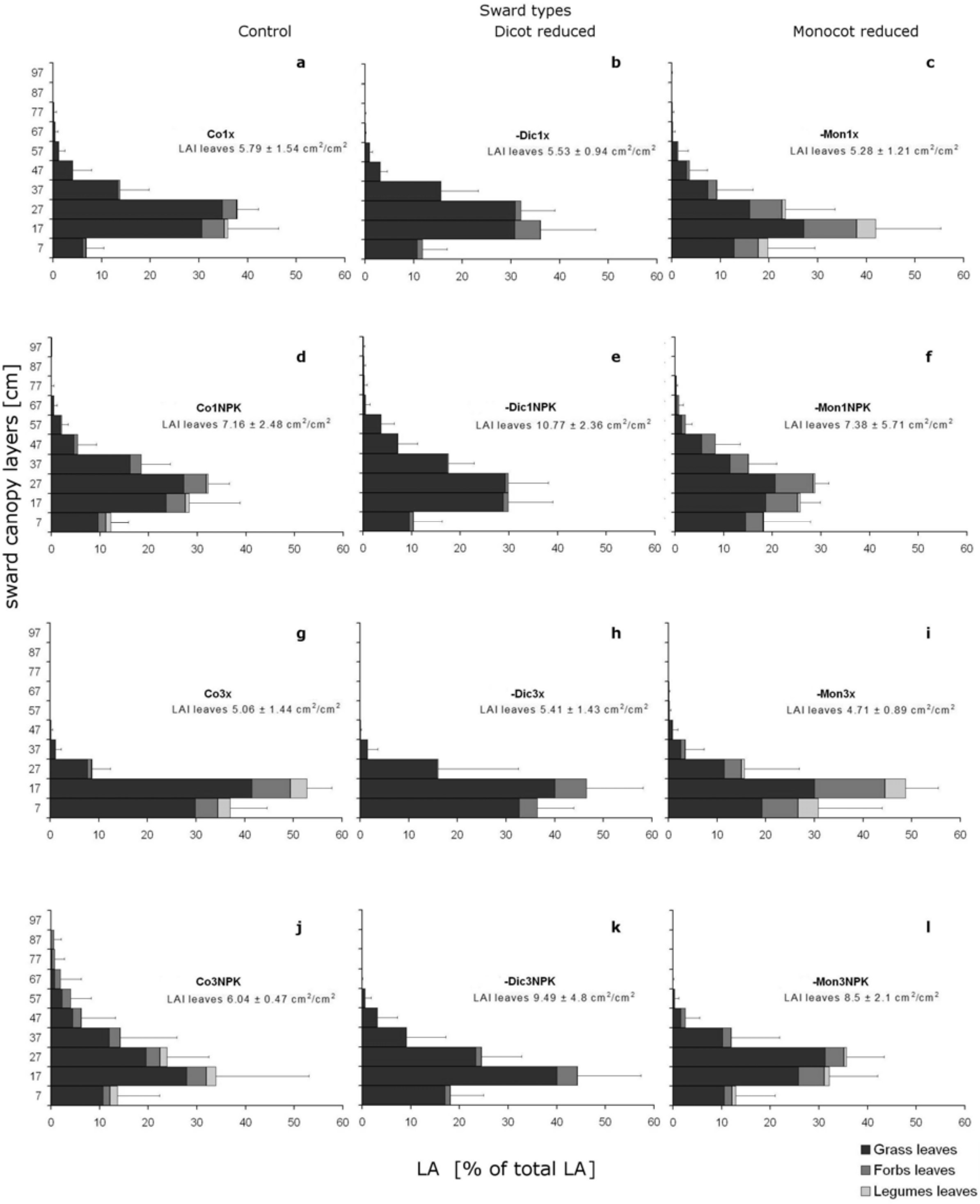

Fig. 3 Vertical distribution of LA per layer and functional group in all 12 treatments (July 2009). Proportional data showing means of each fraction in every layer and standard deviations of each layer.

While the control and –Dic swards clearly reduced LA in this third layer when cut trice, this reduction was much less pronounced in the –Mon swards. In the 3NPK treatment, their third layer even showed an increased LA compared to the 1NPK treatment. In a canopy height of 27–37 cm, we only found management induced LA differences and no significant interactions between management and sward, indicating a homogeneous LA allocation to this layer.

The LAR was influenced mainly by management, but also by the amount of grasses present in a sward. Overall, the –Dic-swards had a higher LAR than the control swards (Fig. 4a). The comparison of the single treatments however, did not show any sward effects (Fig. 4b). The highest LAR was found in the fertilized –Dic-swards cut three times.

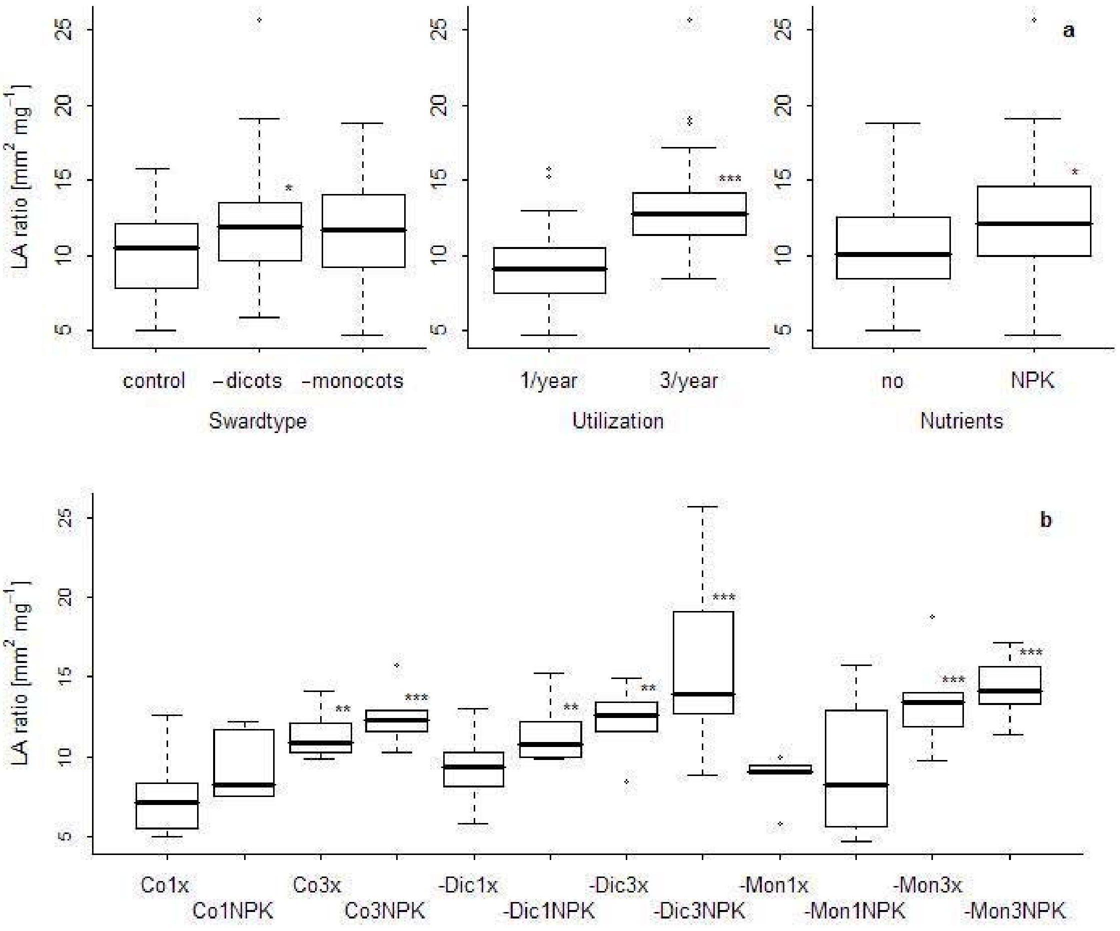

Fig. 4 Leaf area ratio (median, first and third quartiles) per experimental factor (a) and treatment (b) in July 2009. For abbreviations of treatments please refer to Table 1. Asterisks denote significant differences of factor or treatment levels compared to the reference level (sward control, utilization 1/year, nutrients no, treatment Co1x) in a linear model (with log transformation of the response variable for comparison of treatments). *** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$.

Discussion

In this study we compared aspects of sward structure and texture, vertical biomass distribution and LAI of functionally contrasting sward types under different management regimes. The allocation of biomass to harvestable sward layers (> 7cm) in the different sward types depended mainly on the nutrient regime. In comparison with the yield harvested with the Haldrup® forage combine harvester the harvested biomass measured by stratified clipping was generally lower, especially in fertilized plots. However, the order of the treatments according to biomass was similar to the ranking according to yields, allowing for a relative comparison of biomasses. Just the magnitude of the fertilizer effect was somewhat obscured in the clipped plots due to the small plot size. The small plots could not capture the slightly larger scaled mosaic of small (e.g. *Veronica chamaedrys*) and tall (e.g. *Rumex acetosa, Dactylis glomerata*) species. This lead to a large variability in biomass (and consequently LA and LAR) within the plots of one treatment. This again was especially obvious in the fertilized plots, where the height and mass differences between these types of species were pronounced (see Fig. 4).

In young swards (first spring regrowth) and in the third regrowth in September, the swards did not show structural differences, probably due to the generally lower sward height (20-25 cm average hight of the topmost leaves and buds). Liira *et al.* (2000) also reported an indistinct sward architecture in young swards which had been cut regularly compared to mature, tall swards. This was different in the more mature swards cut in July. Since grasses are known to respond to sudden defoliation with increased tillering, the grass contents in the swards increased after the first cut, especially in the fertilized plots (3NPK), leading to a denser sward close to ground level. The amount of dead plant material was mainly influenced by the nutrient regime. If enough nutrients were present, the plants did not have to transfer nutrients from older to younger tissues, programmed cell dead was less pronounced (Lambers *et al.*, 1998; Cheng *et al.*, 2009). The lower amounts of dead biomass in the –Mon-swards might be due to lower grass content. Since graminoids invest more of their photosynthates in aboveground biomass (Körner, 1994), there is more accumulated biomass which dies when nutrient (1x treatment) or light deficiencies (1NPK) occur. This being the only reason, the control swards should also have differed slightly from the –Dic-swards, which they did not. In the 1x treatment, the percentage of dead material even seemed to be higher than in the –Dic-swards. Possibly, the diffenrences in functional group composition between control and –Dic-swards were not large enough to overcome the variation within one sward type. Differences within one plant community increase towards small plot sizes (Økland *et al.*, 1990). Likewise, the small differences in the absolute amounts of biomass might be due to the small sample size. The yields harvested from an area of 6 × 15 m^2 (Petersen *et al.*, 2012, cf. chapter 3), did not show this trend. However, having the least amount of biomass in the lowest canopy layer, the –Mon-swards could have yielded as much as the other sward types despite a lower total biomass.

The reason for a higher LAI in grass-rich vegetation, especially after fertilization lies in the growing architecture of grasses compared to dicots as discussed above. If fertilized, grasses allocate a lot more biomass to increase leaf area than dicots. This was visible throughout all the profiles; the fertilized swards had higher proportions of grass LA than the unfertilized. The LA ratio undermined these findings. The more grasses a sward contained, the higher was its LAR. The typical concave and convex forms of the biomass and LA profiles in nutrient rich and nutrient deficient areas as described by Werger *et al.* (1986) were partly visible. They are usually more pronounced for LA. However, since we did not include the stem LA in our calculations with stems contributing most of the biomass to the lowest layer; our LA profiles had a convex-concave shape. Including the assimilating surfaces of the stems into the diagrams presenting the total LA transferred at least 10% of the LA from higher canopy layers into the lowest layer, but it did not change the profile shape. Using the total LA instead of leaf LA lead to significant changes in statistical calculations involving the LAR. Since the swards rich in forbs gained more "additional" LA from the stems than the swards rich in grasses, contrary to the results shown above, the –Mon-swards had the highest LAR (differing from the control swards, $P < 0.05$). This shows that the high LAR of the –Dic swards was mainly due to a high amount of assimilating tissue in the leaves (see Fig. 4). Further, unlike the leave LA, the total LA was influenced by cutting regime. This is not surprising since the swards cut three times contained much lower amounts of stem tissue than the swards cut only once, leading to significantly different LAs. However, as suspected considering the mass-area regression coefficients for the forb and legume stems, the assimilating area derieved from these regressions was not as exact as that for grass stems. Otherwise we are not able to explain the high total LA and LAR in swards rich in forbs and legumes. A certain amount of biomass from grass stems (= a high number of mainly thin stems) should have resulted in a larger assimilating area than a similar amount of biomass composed of forb or legume stems, which are thicker and heavier and consequently have a lower SLA, leading to a lower LA in the end. Further, the stem biomass of grasses weighed at least as much as that of forbs and legumes combined (even in the –Mon-swards, see Fig. 2), which should have resulted in more pronounced total LA differences.

The first hypothesis was proven, as we found structural differences (both in layering of biomass and LA) among the functionally different sward types. Swards rich in forbs contained less dead biomass, supporting the second hypothesis. Admittedly, all the effects were not consistent across all management regimes, indicating that the functional groups reacted individually to the applied treatments. Contrary to the results of Spehn *et al.* (2000), we found, as predicted in the third hypothesis, no correlation between species richness and LAI. However, the likewise nonexistent relation between biomass and species richness was also mirrored in Spehn's results. The biodiversity–biomass relationship described in their study levels out after a number of 8 species is reached. Since our species numbers were clearly higher, potential biomass increases due to species richness were hardly detectable. Above all, we can conclude, that the functional different swards used distinct forms of sward architecture to reach the same goals; the same amounts of harvestable biomass in the end.

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General discussion

I conducted this study to complement the results of the ongoing biodiversity–ecosystem functioning research by using a new method for creating the necessary biodiversity gradient. Further, the management of the experiment was adapted to agricultural principles. I investigated how the new manipulation method affected sward composition, looked at forage yield and quality derived from the manipulated swards and analyzed the sward structure in terms of vertical distribution of biomass and LAI. The results of this study should give answers to the following questions: Is the method of removing species and functional groups from established swards by herbicide application a useful tool to create a platform for biodiversity experiments? Does the positive biodiversity-productivity relationship often found in experiments hold for the manipulated swards or is their reaction rather comparable to that of semi-natural swards in observational studies? Do the manipulated swards have different means of using the above ground space or are forbs and graminoids in some parts redundant?

The herbicide application cleary changed the sward composition in terms of species composition, consequently also biodiversity indices and distribution of functional groups (grasses, forbs, legumes) among the swards. However, compared to seeded experiments, our species richness gradient was rather narrow and species richness levels intermediate (Schläpfer & Schmid, 1999). We did not use the usual logarithmic scale starting with monocultures and ending at species richness levels of 32 or 64 species (Esser *et al.*, 2006). Our diversity gradient was rather comparable to natural biodiversity gradients which could be found in managed grasslands as postulated by Wrage *et al*. (2011). The differentiation according to functional groups could have been more defined (some plots could be assigned to two different sward types if considering the composition of functional groups therein). This could have been achieved by manual application of herbicides or weeding (McLaren & Turkington, 2010), which would have meant a substantial amount of extra work – or a reduction of plot size. The latter would have meant that management according to agricultural principles would not have been possible anymore due to the large size of the machinery. The impact of herbicides with regard to the insensitivity of some species should be tested in advance to find the optimal mix with the best vigor. Since the swards tend to become more similar after a few years, also observed by Pfisterer *et al.* (2004) after the cessation of weeding of their experimental plots, a reapplication of herbicides after around three years has to be considered. Nevertheless, removal experiments like GrassMan can provide useful knowledge on the complex relationship of biodiversity and ecosystem functioning.

The manipulated swards in the GrassMan experiment reacted comparably to semi-natural swards described in observational studies as we found no relationship between biodiversity and productivity at all. This might be due to the shorter biodiversity gradient and the larger variability within treatments as discussed in chapter 3. Further, due to the non random species allocation to our plots (the most common species were common in all plots), the traits of the dominate species excerted a larger influence on yield than species number or functional diversity. This trait dependance was also demonstrated for natural grasslands (Mokany *et al.*, 2008). Even in an experimental community, the influence of tall species (like in our study) on yield was detected (Frankow-Lindberg *et al.*, 2009; Marquard *et al.*, 2009). Considering the fact, that species “used” in agriculture are often bred to meet the demands of the farmers, it is not surprising, that they should have high yields. Consequently, even at low species numbers, high yields can be reached, as also found by Sanderson (2010) who reanalyzed experiments with agriculturally bred forage grasses. Hence, in agriculturally managed grassland, the biodiversity–productivity relationship is of minor importance, since the species numbers are either high enough anyway or since the yield is influenced by the trait of the best adapted (to intensive management) or best bred species. However, the role of forbs in influencing forage quality is not to be underestimated as already discussed in chapter 3.

Since the structural differences between graminoids and dicots have been widely studied, it was not surprising that swards composed of different proportions of these groups should differ in their architecture. However, a large shift in the grass:dicot ratio is needed to result in visible structural differences. The –Mon- and –Dic-swards had ratios of 90:10 and 45:55 respectively, and still their architecture did not differ in all treatments. It would have been interesting to integrate light distinction curves into this study to learn more about the efficiency in light absorption in the different swards. Since the dominating species in both sward types were the same (though their proportions were different depending on the functional group), the sward architecture was already defined by them as found for semi-natural wet grasslands (Werger *et al.*, 1986). Like the yield and quality, the structure in our experiment rather depended on special traits or functional groups than on species richness. A generally elevated species number in grasslands might still be of advantage. Due to the short duration of our experiment, climatic fluctuations have not been taken into accout. But especially in times of changing climate including unpredictable weather phenomena, a higher species richness might act as some kind of insurance (Isbell *et al.,* 2011).

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Summary

The relationship between biodiversity and ecosystem functions of grasslands has received increasing attention in recent years. Scientists have sought to disentangle this complex relationship by sown biodiversity experiments and observational studies. However, both methods have their advantages and shortcomings. Hence, by using a complementary approach, namely a removal experiment involving manipulation of established vegetation, we might gain new and interesting insight into the effects of biodiversity on productivity and other ecosystem functions.

In this study, a removal experiment was set up in the Solling Uplands in 2008 where a permanent grass sward was manipulated by herbicides to obtain either pure grass swards (dicot reduced) or swards with relatively high amounts of forbs and legumes (moncot reduced), on top of untreated control swards. Species numbers were larger than 10/m^2 and thus covered the upper part of the usually examined logarithmic scale. They were comparable to average spechies richness on European grassland. The manipulated swards were then examined under different environmental conditions, i.e. we created a gradient in management intensity, regulated by both the cutting regime and the nutrient supply.

Three main aspects were investigated. At first, we were interested to see how the herbicide application changed the grass swards and if we could create an appropriate biodiversity gradient on our experimental area. The regrowth of swards after herbicide application was also monitored, focusing on plant functional traits (growth height, reproductive strategy) of colonizer plants. The second aspect was the productivity and quality of the manipulated swards under different management treatments. We hypothesized that a more diverse sward would yield more and higher quality forage than one with a lower diversity in terms of species richness, functional diversity (proportions of grasses, forbs and legumes) or biodiversity indices. Finally, we analyzed whether the functional diversity, the amounts of graminoid and dicot species influenced the sward structure in terms of leaf area index and vertical biomass distribution.

Compared to the baseline data before treatment implementation, the combination of treatments, especially the herbicide application, led to a broad variety of swards with the sward type alone accounting for more than 25% of all variance in composition. The functional composition of the sward changed slightly, since mainly vegetatively

reproducing species were able to expand after herbicide application. In grass rich swards these were mainly the smaller grasses, leading to a slightly lower canopy. We conclude that this kind of sward manipulation was successful because the swards differed significantly in species number, evenness and composition of functional groups. Neither the biodiversity nor the distribution of functional groups influenced the yield in this experiment. However, in fertilized plots, larger amounts of tall grasses and tall species altogether increased yields significantly. The swards rich in legumes and forbs tended to have a better quality than the control and grass-rich swards. Consequently, part of the forage quality parameters showed correlations with biodiversity indices since these increased with increasing forb content. Although the yields did not differ among the swards, the sward architecture showed different vertical patterns between moncot reduced and dicot reduced swards. The latter also had converted more of the fertilized nutrients into leaf area. Species richness did not influence sward structure, the main source of variation lay – apart from the management – in the grass:dicot ratio.

Compared with artificial biodiversity experiments, in our experiment, biodiversity only had moderate effects on examined ecosystem functions probably due to the shorter and more natural range of biodiversity levels realized in our experiment.

Zusammenfassung

In den letzten Jahren wurde der Zusammenhang von Biodiversität und Ökosystemfunktionen im Grünland intensiv erforscht. Wissenschaftler versuchten diesen komplexen Zusammenhang mit Hilfe von angesäten Biodiversitätsexperimenten und beobachtenden Studien zu erklären. Allerdings haben beide Methoden ihr Vor- und Nachteile. Mit einem ergänzenden Ansatz, einer Manipulation der Grasnarbe durch „Entnahme“ von Arten und funktionellen Gruppen durch Herbizidanwendung, hofften wir, neue interessante Einblicke in die Beziehung zwischen Biodiversität und Produktivität sowie anderen Ökosystemfunktionen zu bekommen.

Für diese Studie wurde 2008 ein Biodiversitätsexperiment in den Mittelgebirgslagen des Solling angelegt, bei dem wir die bestehende Grasnarbe so manipulierten, dass wir neben den unbehandelten Kontrollgrasnarben fast reine Grasbestände (dikotyl reduziert) und Grasnarben mit relativ hohen Anteilen von Leguminosen und Kräutern (monokotyl rediziert) erhielten. Die Artenzahl lag über 10/m^2, so dass wir uns am oberen Ende der sonst bei Biodiversitätexperimenten verwendeten logarithmischen Skala befanden. Die Artenzahl war vergleichbar mit der durchschnittlichen Artenzahl auf Europas agrarisch genutzten Grünländern. Die manipulierten Grasnarben wurden dann in verschieden Umwelten untersucht. Das heißt, wir schufen mittels Schnitthäufigkeit und Düngung einen Nutzungsintensitätsgradienten.

Die Arbeit umfasst drei Hauptthemen. Erstens waren wir daran interessiert zu sehen, wie sich die Herbizide auf die Grasnarben auswirkten und ob damit ein ausreichender Biodiversitätsgradient auf unserer Fläche erzeugt werden konnte. Der Aufwuchs nach Herbizidanwendung wurde erfasst, wobei das Augenmerk auf funktionelle Eigenschaften der kolonisierenden Pflanzen (Wuchshöhe, Ausbreitungsstrategie) gelegt wurde. Der zweite untersuchte Aspekt war die Produktivität und Qualität der Grasnarbe unter den verschiedenen Bewirtschaftungsintensitäten. Es wurde die Hypothese aufgestellt, dass artenreichere Grasnarben qualitativ höherwertige und mehr Erträge erbringen als artenarme. Es wurden dabei verschiedene Aspekte der Biodiversität, nämlich Artenvielfalt, Biodiversitätindizes, funktionelle Diversität (Gras-, Kraut- und Leguminosenanteile) in Betracht gezogen. Als letztes wurde untersucht, wie sich die funktionelle Diversität, speziell das Verhältnis von grasartigen

zu dikotylen Arten auf die Grasnarbenstruktur, genauer die vertikale Biomassenverteilung und den Blattflächenindex auswirkte.

Verglichen mit den Grunddatenaufnahmen führten die einzelnen Behandlungen, vor allem die Herbizidanwendung, zu einer großen Grasnarbenvielfalt, wobei der Faktor Grasnarbentyp allen 25 % der gesamten in den Daten vorhandenen Varianz erklärte. Die funktionelle Zusammensetzung der Grasnarbe änderte sich leicht, da sich vor allem Arten mit vegetativer Ausbreitungsstrategie in den frei gewordenen Raum ausbreiten konnten. In den grasreichen Narben waren das vor allem Untergräser, was die mittlere Grasnarbenhöhe leicht reduzierte. Wir schlossen daraus, dass die Manipulation erfolgreich war, da die neuen Grasnarben sich signifikant in Artenzahl, Evenness und Anteilen der funktionellen Gruppen unterschieden.

Weder die Artenvielfalt noch die Verteilung der funktionellen Gruppen hatte Auswirkungen auf den Ertrag in diesem Experiment. Allerdings sorgten in den gedüngten Parzellen eine größere Menge Obergräser sowie die Summe aller hochwüchsigen Arten für signifikante Ertragsgewinne. Die Grasnarben mit hohem Kraut- und Leguminosenanteil waren tendenziell eine besserer Futterqualität als die Kontroll- und dicotyl reduzierte Grasnarbe. Folglich zeigte auch ein Teil der Futterqualitätsparameter eine Korrelation mit Biodiversitätindizes, da diese vom Krautanteil abhingen. Obwohl sich die Erträge der einzelnen Grasnarben nicht unterschieden, zeigte sich im vertikalen Aufbau der Grasnarben in monokotyl reduzierten und dikotyl reduzierten Grasnarben unterschiedliche strukturelle Muster. Letztere hatten zudem einen größeren Teil des zugeführten Düngers in Blattfläche umgewandelt als die anderen Grasnarbentypen. Artenzahl beeinflusste die Grasnarbenstruktur nicht, die größte Variation lag – abgesehen vom Management – im Gras:Kraut Verhältnis begründet.

Verglichen mit künstlich angelegten Biodiversitätsexperimenten hatte die Biodiversität in unserem Experiment nur einen moderaten Einfluss auf die untersuchten Ökosystemfunktionen, was wahrscheinlich in der kürzeren und eher natürlichen Länge des untersuchten Biodiversitätsgradienten begründet lag.

Curriculum Vitae

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Education:

2000	Abitur at the Detlefsengymnasium, Glückstadt/ Schleswig-Holstein
2001-2004	study of biology at the University of Hamburg
2004-2005	studies in ecology and soil sciences at the University of Canterbury, Christchurch, New Zealand
2005-2008	study of biology at the University of Göttingen
2008	Diploma in Biology, thesis title: “Floristisch-strukturelle und standörtliche Differenzierung der Vegetation der Marabout-Friedhöfe im Vergleich zur Weidelandschaft im Westlichen Anti-Atlas (Marokko)”
2008-dato	PhD student at the Institute of Grassland Science, University of Göttingen, research in the “Grassland management experiment” Cluster of Excellence “FBR”

Since June 2011 research assistant (teaching) at the Department of Crop Sciences, division of Grassland Science

Work experience:

2000-2001	Voluntary Ecological Year (Freiwilliges Ökologisches Jahr, FÖJ) on an organic farm in Ahrensburg/Schleswig-Holstein
2006-2007	undergraduate assistant at the Department Vegetation & Phytodiversity Analysis, University of Göttingen

Scientific interests:

Biodiversity of grassland ecosystems
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Landscape Ecology
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List of Publications

2009

- Petersen, U., Isselstein, J., 2009: Einfluss von P- und N-Düngung auf Struktur und Lichtverteilung in naturnahem Grasland mit unterschiedlicher Artenvielfalt. Mitteilungen der Arbeitsgemeinschaft Grünland und Futterbau 10, 69-72.
- Poster on the same topic „Einfluss von P- und N-Düngung auf Struktur und Lichtverteilung in naturnahem Grasland mit unterschiedlicher Artenvielfalt“, presented at the „53. Jahrestagung der AGGF“, 27.-29.8.2009 in Kleve

2010

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  Along with these articles three posters with the same titles presented at the EGF conference 29.8.-2.9.2010 in Kiel.

2011

- Petersen U., Isselstein J., (2011): From biodiversity down to species identity – where do we find effects on yield in grassland of different species composition? Poster presented at the international conference “Functions and Services of Biodiversity”, Göttingen (20.-22.06.).
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  Including a poster presented at the 55. Jahrestagung der Arbeitsgemeinschaft Grünland und Futterbau, Oldenburg (25-27.08.).

2012

- Petersen, U., Wrage, N., Köhler, L., Leuschner, C., Isselstein, J. (2012): Manipulating the species composition of permanent grasslands—A new approach to biodiversity experiments. Basic and Applied Ecology 13, 1-9.

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I only managed the large amounts of field and lab work (especially the sorting of endless numbers of grass samples) with the support of numerous student helpers and the technical staff of the department.

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I thank all my collegues (the present ones as well as the ones which finished their PhD before me) at the insitut for lively discussions (mainly on statistical problems), the diverting mensa breaks and their friendship.

Without my parents’ support I would not have been able to study, least of all complete a PhD thesis. They always believed in me and gave me the necessary support and safety.
My sister introduced me into the depth of Adobe photoshop, essential knowledge to avoid to much programming in R for sophisticated graphs.
I thank Hinni for all his patience and thoughtfulness during the creation of this thesis.

Appendix

Appendix 1 Phytosociological table of the baseline vegetation at the experimental area sorted according to diagnostic species.

Appendix 2 Functional classification of the species of the experimental area.

		Plot	1.1	1.2	2.1	2.2	3.1	3.2	4.1	4.2	5.1	5.2	6.1	6.2	7.1	7.2	8.1	8.2
Characteristic species		**species no**	**17**	**16**	**16**	**15**	**17**	**16**	**16**	**18**	**20**	**14**	**17**	**17**	**17**	**19**	**15**	**16**
Trifolium repens	Association		0.2	0.2	0.2	0.2	1	0.2	0.2	1	0.2	0.2	1	2	1	2	5	3
Lolium perenne	Lolio-Cynosuretum Br.-Bl. et Deleeuw 1936		3	2	4	4	3	12	5	5	2	2	0.2	5	5	5	7	12
Cirsium arvense	Alliance		.	.	.	.	.	.	5	0.2	15	0.2	.	.	2	.	.	.
Poa annua	Cynosurion-cristati R.Tx. 1947		.	0.2	.	.	.	.	.	0.2	0.2	.	0.2	.	0.2	0.2	0.2	0.2
Plantago major			.	.	.	.	.	.	.	.	.	.	.	.	.	0.2	.	.
Veronica serpyllifolia			.	.	0.2	.	.	.	.	.	.	.	.	0.2	.	0.2	.	.
Phleum pratense			.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Leontodon autumnalis			.	.	.	.	.	.	.	.	.	.	.	0.2	.	0.2	.	.
Cirsium vulgare			1	.	.	.	.	.	.	.	.	.	.	.	.	0.2	.	.
Elymus repens			.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Bellis perennis			.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Capsella bursa-pastoris			.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Cynosurus cristatus			.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Veronica chamaedrys	Order		0.2	0.2	1	1	0.2	1	1	1	1	2	1	1	0.2	1	1	1
Taraxacum Sec. Ruderalia	Arrhenateretalia R. Tx. 1931		1	1	1	0.2	0.2	0.2	1	1	.	0.2	.	2	0.2	2	.	0.2
Dactylis glomerata			12	5	1	24	4	13	5	.	3	.	1	.	8	10	3	3
Achillea millefolium			.	0.2	.	1	0.2	0.2	.	.	0.2	.	.	.	0.2	.	.	.
Festuca rubra	Class		23	35	46	20	22	28	12	34	12	63	37	35	32	15	17	10
Poa trivialis	Molinio-Arrhenateretea R. Tx. 1937		29	18	20	17	26	22	31	27	23	10	15	13	25	27	33	25
Ranunculus repens			3	3	3	7	5	5	4	3	8	3	10	7	5	5	7	5
Cerastium holosteoides			1	0.2	0.2	0.2	1	0.2	0.2	0.2	0.2	.	0.2	0.2	0.2	1	2	1
Poa pratensis ag.			5	10	8	.	5	2	1	1	0.2	1	7	3	1	0.2	1	7
Rumex acetosa			12	12	8	10	8	8	7	7	5	10	8	15	7	13	8	12
Cardamine pratensis			.	.	0.2	.	.	.	0.2	0.2	1	0.2	0.2	0.2	0.2	.	0.2	0.2
Holcus lanatus			.	.	.	.	.	.	.	.	18	.	.	.	.	.	.	.
Alopecurus pratensis			0.2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Trifolium pratense			.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Lotus pedunculatus	moisture indicator-species		.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Deschampsia cespitosa			.	.	.	1	7	.	.	2	.	.	1	.	.	.	.	.
Juncus effusus			.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Agrostis capillaris	Alchemillo-Cynosuretum Müll. ex Görs 1968		8	13	7	12	17	7	27	17	10	8	18	15	13	18	15	20
Stellaria graminea	indicating nutrient shortage		0.2	0.2	0.2	0.2	.	.	.	0.2	0.2	0.2	0.2	1	.	0.2	0.2	0.2
Anthoxanthum odoratum			1	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.
Hypericum maculatum			.	.	.	.	.	0.2	.	.	0.2	.	.	.	.	.	.	.
Luzula campestris			.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Lotus corniculatus			.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Alchemilla vulgaris ag.	montane distribution		.	.	.	.	0.2	.	.	.	.	.	.	.	.	.	.	.
Holcus mollis			.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Rumex obtusifolius	indicating excess nutrients		.	.	.	.	.	1	0.2	.	1	.	.	0.2	.	.	.	.
Urtica dioica			.	.	.	.	0.2	.	.	.	.	.	.	.	.	.	.	.
Anthriscus sylvestris	associated species		.	.	.	.	.	.	.	0.2	.	.	0.2	.	.	.	.	.
Poa angustifolia			.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Carex ovalis			.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Veronica arvensis			.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Hypericum perforatum			.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Cardamine hirsuta			.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.

	Plot	9.1	9.2	10.1	10.2	11.1	11.2	12.1	12.2	13.1	13.2	14.1	14.2	15.1	15.2	16.1	16.2
Characteristic species	**species no**	**17**	**17**	**18**	**18**	**18**	**14**	**21**	**14**	**16**	**14**	**18**	**19**	**16**	**19**	**16**	**18**
Trifolium repens	Association	5	2	2	0.2	2	3	2	0.2	5	1	0.2	1	4	2	6	6
Lolium perenne	Lolio-Cynosuretum Br.-Bl. et Deleeuw 1936	13	7	5	8	7	5	1	.	11	8	4	1	9	8	12	18
Cirsium arvense	Alliance	.	.	6	5	.	.	1	.	0.2	0.2	2	.	.	4	0.2	1
Poa annua	Cynosurion-cristati R.Tx. 1947	0.2	0.2	0.2	1	0.2	0.2	0.2	0.2	.	.	.	.	.	.	.	.
Plantago major		.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Veronica serpyllifolia		.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	0.2
Phleum pratense		.	0.2	.	0.2	.	.	.	.	.	.	.	.	.	0.2	.	0.2
Leontodon autumnalis		0.2	.	.	.	.	.	.	.	.	.	0.2	.	.	.	.	.
Cirsium vulgare		.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Elymus repens		.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Bellis perennis		.	.	.	.	0.2	.	.	.	.	.	.	.	.	.	.	.
Capsella bursa-pastoris		.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Cynosurus cristatus		.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Veronica chamaedrys	Order	1	2	1	1	1	1	1	0.2	0.2	0.2	0.2	1	0.2	1	0.2	0.2
Taraxacum Sec. Ruderalia	Arrhenateretalia R. Tx. 1931	.	1	.	0.2	0.2	.	2	.	.	.	0.2	0.2	0.2	.	0.2	0.2
Dactylis glomerata		.	.	5	5	5	.	0.2	.	8	15	23	3	17	2	6	.
Achillea millefolium		0.2	0.2	1	.	0.2	.	0.2	.	0.2	0.2	0.2	.	0.2	0.2	1	.
Festuca rubra	Class	20	40	37	28	40	27	43	26	15	30	8	4	0.2	0.2	9	29
Poa trivialis	Molinio-Arrhenatheretea R. Tx. 1937	23	13	13	17	12	7	12	13	25	23	30	27	21	35	31	15
Ranunculus repens		5	8	8	9	7	7	7	5	3	2	4	2	7	8	4	3
Cerastium holosteoides		2	1	0.2	1	1	1	1	0.2	1	.	2	1	1	0.2	0.2	1
Poa pratensis ag.		2	0.2	0.2	0.2	1	1	0.2	3	1	2	3	3	12	5	2	12
Rumex acetosa		5	10	10	12	10	7	12	10	7	12	6	14	10	0.2	15	7
Cardamine pratensis		.	0.2	.	0.2	0.2	0.2	0.2	0.2	.	.	.	.	.	0.2	.	0.2
Holcus lanatus		.	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.
Alopecurus pratensis		.	.	.	.	.	.	.	.	.	.	.	14	.	.	.	.
Trifolium pratense		.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	0.2
Lotus pedunculatus	moisture indicator-species	.	.	.	.	.	.	.	.	.	.	.	.	.	0.2	.	.
Deschampsia cespitosa		3	.	0.2	.	.	.	.	25	.	.	.	3	.	.	.	.
Juncus effusus		.	.	.	.	.	.	.	5	.	.	.	5	.	.	.	.
Agrostis capillaris	Alchemillo-Cynosuretum Müll. ex Görs 1968	20	15	10	12	13	40	15	12	22	6	17	18	18	30	13	7
Stellaria graminea	indicating nutrient shortage	0.2	0.2	0.2	0.2	0.2	0.2	0.2	.	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2
Anthoxanthum odoratum		.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Hypericum maculatum		0.2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Luzula campestris		.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Lotus corniculatus		.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Alchemilla vulgaris ag.	montane distribution	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Holcus mollis		.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Rumex obtusifolius	indicating excess nutrients	.	.	.	.	.	.	1	.	1	.	0.2	1	0.2	3	.	.
Urtica dioica		.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.
Anthriscus sylvestris	associated species	.	.	.	.	.	.	0.2	.	.	.	.	.	.	.	.	.
Poa angustifolia		.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Carex ovalis		.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Veronica arvensis		.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Hypericum perforatum		.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.
Cardamine hirsuta		.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.

		Plot	17.1	17.2	18.1	18.2	19.1	19.2	20.1	20.2	21.1	21.2	22.1	22.2	23.1	23.2	24.1	24.2
Characteristic species		**species no**	**18**	**17**	**16**	**17**	**17**	**17**	**21**	**20**	**19**	**19**	**19**	**15**	**18**	**18**	**17**	**15**
Trifolium repens	Association		5	1	2	1	5	11	10	6	11	7	4	16	4	4	5	4
Lolium perenne	Lolio-Cynosuretum Br.-Bl. et Deleeuw 1936		7	3	12	0.2	7	15	23	8	8	13	12	12	7	7	10	15
Cirsium arvense	Alliance		3	3	2	0.2	5	2	0.2	18	7	13	.	.	5	8	.	.
Poa annua	Cynosurion-cristati R.Tx. 1947		.	.	.	.	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2	1	0.2	0.2
Plantago major			.	.	.	.	.	.	.	0.2	.	.	0.2	.	.	0.2	1	0.2
Veronica serpyllifolia			.	.	.	.	.	.	0.2	.	.	.	.	.	.	.	.	.
Phleum pratense			.	.	.	.	.	.	.	.	.	2	.	.	.	.	.	.
Leontodon autumnalis			.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Cirsium vulgare			.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Elymus repens			.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Bellis perennis			.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Capsella bursa-pastoris			.	.	.	.	.	0.2	.	.	.	.	.	.	.	.	.	.
Cynosurus cristatus			.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Veronica chamaedrys	Order		0.2	0.2	0.2	0.2	1	1	0.2	1	0.2	0.2	0.2	0.2	0.2	3	0.2	0.2
Taraxacum Sec. Ruderalia	Arrhenateretalia R. Tx. 1931		1	1	1	1	.	.	.	2	1	0.2	1	0.2	.	.	0.2	.
Dactylis glomerata			4	1	0.2	.	10	8	5	13	0.2	.	7	.	0.2	2	.	.
Achillea millefolium			0.2	0.2	0.2	.	.	1	0.2	0.2	.	1	0.2	.	1	0.2	.	0.2
Festuca rubra	Class		34	32	42	44	5	2	8	5	2	3	15	17	22	28	23	17
Poa trivialis	Molinio-Arrhenateretea R. Tx. 1937		14	17	10	11	22	20	15	18	24	21	17	12	10	7	7	13
Ranunculus repens			8	3	3	4	7	5	5	5	10	8	13	12	12	11	10	7
Cerastium holosteoides			0.2	0.2	0.2	0.2	2	1	1	1	1	1	1	1	1	1	0.2	1
Poa pratensis ag.			6	10	7	5	0.2	8	1	5	2	5	0.2	5	3	4	1	0.2
Rumex acetosa			13	18	14	18	8	5	.	2	2	7	10	7	8	10	8	5
Cardamine pratensis			0.2	.	.	0.2	.	.	.	0.2	0.2	.	0.2	0.2	0.2	0.2	0.2	0.2
Holcus lanatus			1	.	.	.	3	.	1	.	6	.	.	.	0.2	.	.	.
Alopecurus pratensis			.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Trifolium pratense			.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Lotus pedunculatus	moisture indicator-species		.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.
Deschampsia cespitosa			.	.	.	.	.	.	10	.	.	.	1	.	.	.	.	.
Juncus effusus			.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Agrostis capillaris	Alchemillo-Cynosuretum Müll. ex Görs 1968		3	8	6	12	17	20	15	12	13	17	18	17	26	13	34	37
Stellaria graminea	indicating nutrient shortage		0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2	.
Anthoxanthum odoratum			.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Hypericum maculatum			.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Luzula campestris			.	.	.	.	.	.	0.2	.	.	.	.	.	.	.	.	.
Lotus corniculatus			.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Alchemilla vulgaris ag.	montane distribution		.	.	.	.	.	.	.	.	.	0.2	.	.	.	.	.	.
Holcus mollis			.	.	.	3	.	.	.	.	.	.	.	.	.	.	.	.
Rumex obtusifolius	indicating excess nutrients		.	.	.	.	7	.	4	3	12	1	.	.	.	.	.	.
Urtica dioica			.	.	.	.	.	.	.	.	.	.	.	.	.	.	0.2	.
Anthriscus sylvestris	associated species		.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Poa angustifolia			.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Carex ovalis			.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Veronica arvensis			.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Hypericum perforatum			.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Cardamine hirsuta			.	.	.	0.2	.	.	.	.	.	.	.	.	.	.	.	.

	Plot	25.1	25.2	26.1	26.2	27.1	27.2	28.1	28.2	29.1	29.3	30.1	30.2	31.1	31.2	32.1	32.2
Characteristic species	**species no**	**16**	**16**	**16**	**13**	**13**	**15**	**17**	**15**	**15**	**15**	**16**	**16**	**17**	**16**	**18**	**18**
Trifolium repens	Association	7	3	8	5	0.2	0.2	3	10	1	3	2	1	1	3	1	3
Lolium perenne	Lolio-Cynosuretum Br.-Bl. et Deleeuw 1936	16	6	5	21	.	8	9	18	4	3	8	4	10	19	3	9
Cirsium arvense	Alliance	2	3	8	6	4	6	.	.	.	.	1	3	.	1	0.2	5
Poa annua	Cynosurion-cristati R.Tx. 1947	.	.	.	.	.	.	0.2	.	.	.	0.2	.	0.2	.	0.2	.
Plantago major		.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Veronica serpyllifolia		.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Phleum pratense		.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1
Leontodon autumnalis		.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Cirsium vulgare		.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Elymus repens		.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Bellis perennis		.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Capsella bursa-pastoris		.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Cynosurus cristatus		.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Veronica chamaedrys	Order	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2	1	2	0.2	0.2	0.2	1
Taraxacum Sec. Ruderalia	Arrhenateretalia R. Tx. 1931	1	.	0.2	.	0.2	.	0.2	0.2	.	0.2	.	0.2	0.2	0.2	0.2	0.2
Dactylis glomerata		3	14	11	.	22	12	10	7	6	3	.	2	11	5	7	1
Achillea millefolium		0.2	.	.	.	.	.	2	0.2	0.2	0.2	0.2	.	0.2	0.2	1	.
Festuca rubra	Class	.	7	2	0.2	6	1	9	9	16	24	28	23	.	1	27	2
Poa trivialis	Molinio-Arrhenateretea R. Tx. 1937	28	18	16	27	30	15	18	13	12	13	10	10	25	20	13	25
Ranunculus repens		5	5	6	13	5	8	9	10	8	11	9	4	6	4	3	5
Cerastium holosteoides		0.2	0.2	0.2	1	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2	1	0.2
Poa pratensis ag.		18	4	1	2	9	7	6	17	8	8	6	11	8	19	11	13
Rumex acetosa		11	3	4	6	.	13	15	9	9	6	15	12	10	13	20	12
Cardamine pratensis		.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Holcus lanatus		.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Alopecurus pratensis		.	.	.	.	.	.	.	.	.	.	.	.	0.2	.	.	.
Trifolium pratense		.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Lotus pedunculatus	moisture indicator-species	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Deschampsia cespitosa		.	.	.	.	.	20	.	.	23	16	.	.	.	.	.	.
Juncus effusus		.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Agrostis capillaris	Alchemillo-Cynosuretum Müll. ex Görs 1968	8	20	19	18	23	9	18	6	12	12	18	1	24	14	12	19
Stellaria graminea	indicating nutrient shortage	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2
Anthoxanthum odoratum		.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Hypericum maculatum		.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Luzula campestris		.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Lotus corniculatus		.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Alchemilla vulgaris ag.	montane distribution	.	.	.	.	.	.	.	.	.	.	.	.	.	.	0.2	.
Holcus mollis		.	.	.	.	.	.	.	.	.	.	1	26	4	.	.	.
Rumex obtusifolius	indicating excess nutrients	0.2	12	19	.	.	.	0.2	.	.	.	.	.	.	.	.	3
Urtica dioica		.	4	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Anthriscus sylvestris	associated species	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Poa angustifolia		.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Carex ovalis		.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	0.2
Veronica arvensis		.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Hypericum perforatum		.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Cardamine hirsuta		.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.

		Plot	33.1	33.2	34.1	34.2	35.1	35.2	36.1	36.2	37.1	37.2	38.1	38.2	39.1	39.2	40.1	40.2
Characteristic species		**species no**	**17**	**17**	**13**	**21**	**17**	**17**	**15**	**16**	**18**	**16**	**17**	**22**	**17**	**16**	**20**	**15**
Trifolium repens	Association		5	2	4	5	1	4	3	1	3	4	2	5	5	4	12	4
Lolium perenne	Lolio-Cynosuretum Br.-Bl. et Deleeuw 1936		26	6	0.2	8	3	16	2	7	10	7	8	7	3	15	16	5
Cirsium arvense	Alliance		.	.	.	2	3	0.2	.	8	.	.	.	.	.	.	.	.
Poa annua	Cynosurion-cristati R.Tx. 1947		0.2	.	.	0.2	.	.	.	.	0.2	0.2	.	0.2	0.2	.	0.2	0.2
Plantago major			0.2	.	.	0.2	.	.	.	.	.	.	.	.	.	.	0.2	.
Veronica serpyllifolia			.	.	.	.	.	0.2	.	.	.	.	.	.	.	.	.	.
Phleum pratense			.	0.2	.	.	.	4	.	.	.	.	.	.	.	.	.	.
Leontodon autumnalis			.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Cirsium vulgare			.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.
Elymus repens			.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Bellis perennis			.	.	.	.	.	.	.	.	.	.	.	0.2	.	.	.	.
Capsella bursa-pastoris			0.2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Cynosurus cristatus			.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.
Veronica chamaedrys	Order		0.2	0.2	1	1	0.2	1	1	0.2	2	1	2	0.2	1	0.2	0.2	1
Taraxacum Sec. Ruderalia	Arrhenateretalia R. Tx. 1931		.	0.2	.	0.2	.	2	0.2	0.2	1	.	2	1	.	3	1	.
Dactylis glomerata			.	28	2	7	1	0.2	.	.	5	26	25	12	0.2	.	1	.
Achillea millefolium			0.2	.	.	.	0.2	.	0.2	.	1	1	2	0.2	1	0.2	0.2	0.2
Festuca rubra	Class		16	30	36	5	21	22	18	27	8	15	3	.	0.2	1	4	34
Poa trivialis	Molinio-Arrhenateretea R. Tx. 1937		19	8	15	21	11	18	16	16	20	13	22	23	27	20	20	15
Ranunculus repens			1	5	13	5	4	9	13	4	10	3	7	10	10	4	12	10
Cerastium holosteoides			1	1	1	0.2	0.2	1	0.2	2	0.2	1	0.2	1	1	1	0.2	0.2
Poa pratensis ag.			18	3	5	7	1	.	12	5	1	8	1	1	0.2	0.2	0.2	2
Rumex acetosa			2	6	8	12	9	12	16	8	12	7	8	8	12	8	7	7
Cardamine pratensis			.	.	.	.	.	0.2	.	0.2	0.2	.	0.2	0.2	0.2	.	.	.
Holcus lanatus			.	.	.	.	.	.	.	.	.	.	.	.	2	.	.	.
Alopecurus pratensis			.	.	.	5	.	.	.	.	.	.	.	.	.	.	.	.
Trifolium pratense			.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Lotus pedunculatus	moisture indicator-species		.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Deschampsia cespitosa			.	.	.	2	.	.	.	.	.	.	.	2	.	.	.	.
Juncus effusus			.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Agrostis capillaris	Alchemillo-Cynosuretum Müll. ex Görs 1968		9	10	15	15	6	10	15	3	23	13	16	26	36	20	19	18
Stellaria graminea	indicating nutrient shortage		0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2
Anthoxanthum odoratum			.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Hypericum maculatum			.	.	.	0.2	.	.	.	.	.	.	.	.	1	.	.	.
Luzula campestris			.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Lotus corniculatus			.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Alchemilla vulgaris ag.	montane distribution		.	0.2	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Holcus mollis			.	.	.	4	38	.	3	18	.	.	.	1	.	22	5	3
Rumex obtusifolius	indicating excess nutrients		2	.	.	.	1	.	.	.	3	1	1	1	.	1	1	.
Urtica dioica			.	.	.	.	.	.	.	.	.	.	.	.	.	.	0.2	.
Anthriscus sylvestris	associated species		.	0.2	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Poa angustifolia			.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Carex ovalis			.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Veronica arvensis			.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Hypericum perforatum			.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Cardamine hirsuta			.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.

Characteristic species		Plot species no	41.1 **17**	41.2 **17**	42.1 **18**	42.2 **17**	43.1 **15**	43.2 **15**	44.1 **17**	44.2 **17**	45.1 **19**	45.2 **16**	46.1 **19**	46.2 **16**	47.1 **16**	47.2 **17**	48.1 **16**	48.2 **19**
Trifolium repens	Association		1	2	0.2	3	6	1	0.2	0.2	1	1	1	1	4	0.2	1	1
Lolium perenne	Lolio-Cynosuretum Br.-Bl. et Deleeuw 1936		7	4	9	5	11	4	5	6	7	15	6	2	14	2	2	2
Cirsium arvense	Alliance		.	.	2	.	.	.	4	1	1	.	.	.	.	.	.	.
Poa annua	Cynosurion-cristati R.Tx. 1947		.	0.2	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Plantago major			.	.	.	0.2	.	.	.	.	0.2	0.2	.	.	.	.	.	.
Veronica serpyllifolia			.	.	0.2	0.2	0.2	.	.	0.2	.	.	.	.	.	1	.	.
Phleum pratense			.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.
Leontodon autumnalis			.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Cirsium vulgare			.	.	.	.	.	.	.	.	5	.	.	.	.	.	.	.
Elymus repens			.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Bellis perennis			.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Capsella bursa-pastoris			.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Cynosurus cristatus			.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Veronica chamaedrys	Order		1	1	0.2	1	0.2	0.2	0.2	1	1	1	1	1	2	.	0.2	1
Taraxacum Sec. Ruderalia	Arrhenateretalia R. Tx. 1931		0.2	1	0.2	2	.	0.2	0.2	0.2	0.2	0.2	1	1	0.2	0.2	.	0.2
Dactylis glomerata			4	.	1	0.2	3	9	13	28	3	0.2	5	3	.	2	3	.
Achillea millefolium			0.2	0.2	0.2	0.2	1	.	2	.	0.2	0.2	1	0.2	0.2	0.2	0.2	.
Festuca rubra	Class		12	32	29	38	.	0.2	0.2	0.2	26	4	36	39	2	47	34	26
Poa trivialis	Molinio-Arrhenateretea R. Tx. 1937		26	21	11	4	28	13	23	21	11	12	9	7	13	17	13	15
Ranunculus repens			5	6	11	8	5	17	11	7	7	13	9	12	7	3	8	8
Cerastium holosteoides			0.2	1	1	0.2	1	0.2	1	0.2	1	1	0.2	1	0.2	0.2	0.2	0.2
Poa pratensis ag.			4	2	5	7	6	18	12	1	7	17	2	7	10	2	3	5
Rumex acetosa			13	12	8	12	8	13	7	9	17	11	11	9	15	9	9	11
Cardamine pratensis			0.2	.	.	.	.	.	.	0.2	.	.	0.2	.	0.2	0.2	0.2	0.2
Holcus lanatus			.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Alopecurus pratensis			.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Trifolium pratense			.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Lotus pedunculatus	moisture indicator-species		.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Deschampsia cespitosa			.	6	.	.	0.2	4	.	.	.	.	5	.	.	4	18	21
Juncus effusus			.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Agrostis capillaris	Alchemillo-Cynosuretum Müll. ex Görs 1968		25	9	21	19	30	20	19	24	12	23	11	12	28	12	8	7
Stellaria graminea	indicating nutrient shortage		0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2	1	0.2	0.2	0.2	0.2	0.2	0.2
Anthoxanthum odoratum			1	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Hypericum maculatum			.	.	.	.	.	.	.	.	0.2	.	.	.	.	.	.	1
Luzula campestris			.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Lotus corniculatus			.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	0.2
Alchemilla vulgaris ag.	montane distribution		.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	0.2
Holcus mollis			.	.	.	.	.	.	.	.	.	.	1	5	4	.	.	1
Rumex obtusifolius	indicating excess nutrients		.	.	.	.	.	.	2	.	.	.	.	.	.	.	.	.
Urtica dioica			.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Anthriscus sylvestris	associated species		.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Poa angustifolia			.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Carex ovalis			.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Veronica arvensis			.	.	.	.	.	.	.	.	.	.	0.2	.	.	.	.	.
Hypericum perforatum			.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Cardamine hirsuta			.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.

		Plot	49.1	49.2	50.1	50.2	51.1	51.2	52.1	52.2	53.1	53.2	54.1	54.2	55.1	55.2	56.1	56.2
Characteristic species		**species no**	**16**	**16**	**18**	**15**	**19**	**17**	**18**	**18**	**16**	**15**	**15**	**15**	**16**	**15**	**17**	**15**
Trifolium repens	Association		1	2	5	1	2	1	1	3	0.2	3	1	0.2	1	5	2	3
Lolium perenne	Lolio-Cynosuretum Br.-Bl. et Deleeuw 1936		8	14	14	11	12	4	0.2	9	5	12	3	5	16	16	4	7
Cirsium arvense	Alliance		.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Poa annua	Cynosurion-cristati R.Tx. 1947		.	.	.	.	.	0.2	.	.	.	.	.	.	.	.	.	.
Plantago major			.	.	0.2	.	.	.	.	.	.	.	.	.	.	.	.	.
Veronica serpyllifolia			.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Phleum pratense			.	.	.	.	0.2	.	.	.	.	.	.	.	.	.	.	.
Leontodon autumnalis			.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Cirsium vulgare			.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Elymus repens			.	.	0.2	.	.	.	.	.	.	.	.	.	.	.	1	0.2
Bellis perennis			.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Capsella bursa-pastoris			.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Cynosurus cristatus			.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Veronica chamaedrys	Order		0.2	0.2	0.2	1	0.2	1	1	0.2	0.2	0.2	2	0.2	1	0.2	0.2	0.2
Taraxacum Sec. Ruderalia	Arrhenateretalia R. Tx. 1931		0.2	.	.	0.2	3	.	1	0.2	0.2	1	.	1	2	1	1	.
Dactylis glomerata			2	4	.	.	14	6	8	1	.	.	.	7	1	4	5	.
Achillea millefolium			2	0.2	.	.	0.2	1	0.2	0.2	.	0.2	.	.	0.2	1	0.2	0.2
Festuca rubra	Class		17	19	21	18	14	28	7	22	65	28	33	37	14	.	8	.
Poa trivialis	Molinio-Arrhenateretea R. Tx. 1937		23	23	17	10	11	14	4	15	6	12	11	9	20	21	31	21
Ranunculus repens			4	3	8	11	7	3	13	5	6	10	7	12	7	15	13	11
Cerastium holosteoides			0.2	0.2	1	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2	1	0.2	0.2
Poa pratensis ag.			18	5	0.2	7	9	13	36	8	4	10	2	7	6	7	4	22
Rumex acetosa			12	12	9	13	13	9	8	9	5	14	10	9	12	14	14	13
Cardamine pratensis			0.2	.	0.2	.	0.2	0.2	0.2	0.2	0.2	0.2	0.2	.	.	.	0.2	0.2
Holcus lanatus			.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.
Alopecurus pratensis			.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Trifolium pratense			.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Lotus pedunculatus	moisture indicator-species		.	.	.	.	.	.	.	4	.	.	.	.	.	.	.	.
Deschampsia cespitosa			.	.	.	.	.	.	7	.	.	.	0.2	.	.	.	.	.
Juncus effusus			.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Agrostis capillaris	Alchemillo-Cynosuretum Müll. ex Görs 1968		12	16	22	25	13	19	13	22	8	9	26	12	16	14	16	17
Stellaria graminea	indicating nutrient shortage		0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2
Anthoxanthum odoratum			.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Hypericum maculatum			.	.	.	.	0.2	0.2	.	.	.	.	.	0.2	.	.	.	.
Luzula campestris			.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Lotus corniculatus			.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Alchemilla vulgaris ag.	montane distribution		.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Holcus mollis			.	.	.	1	.	.	.	.	.	.	4	.	3	1	.	5
Rumex obtusifolius	indicating excess nutrients		.	0.2	0.2	1	0.2	.	0.2	1	0.2	.	.	.	.	.	.	.
Urtica dioica			.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Anthriscus sylvestris	associated species		.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Poa angustifolia			.	.	.	.	.	.	.	.	0.2	.	.	.	.	.	.	.
Carex ovalis			.	.	0.2	.	.	.	.	.	.	.	.	.	.	.	.	.
Veronica arvensis			.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Hypericum perforatum			.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Cardamine hirsuta			.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.

		Plot	57.1	57.2	58.1	58.2	59.1	59.2	60.1	60.2	61.1	61.2	62.1	62.2	63.1	63.2	64.1	64.2
Characteristic species		**species no**	**22**	**15**	**16**	**17**	**14**	**15**	**18**	**17**	**17**	**17**	**16**	**14**	**15**	**16**	**19**	**17**
Trifolium repens	Association		2	0.2	2	4	2	3	3	2	0.2	1	2	1	1	2	0.2	2
Lolium perenne	Lolio-Cynosuretum Br.-Bl. et Deleeuw 1936		13	6	14	9	14	11	11	5	4	3	4	8	4	10	13	3
Cirsium arvense	Alliance		.	.	0.2	.	.	.	0.2	1	.	.	.	.	.	.	.	.
Poa annua	Cynosurion-cristati R.Tx. 1947		.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Plantago major			0.2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Veronica serpyllifolia			0.2	.	0.2	.	.	.	.	.	.	.	.	.	.	.	.	.
Phleum pratense			.	.	.	.	.	.	.	.	.	0.2	.	.	.	.	.	.
Leontodon autumnalis			.	.	.	0.2	.	.	.	.	.	.	.	.	.	.	.	.
Cirsium vulgare			0.2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Elymus repens			.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Bellis perennis			.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Capsella bursa-pastoris			.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Cynosurus cristatus			.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Veronica chamaedrys	Order		1	0.2	0.2	0.2	0.2	1	1	0.2	0.2	0.2	1	1	1	0.2	0.2	0.2
Taraxacum Sec. Ruderalia	Arrhenateretalia R. Tx. 1931		0.2	0.2	.	0.2	1	1	0.2	1	0.2	1	1	2	1	2	1	.
Dactylis glomerata			7	.	.	.	.	.	.	4	1	5	1	.	6	.	11	2
Achillea millefolium			0.2	0.2	.	.	.	0.2	0.2	.	0.2	0.2	2	0.2	.	.	0.2	0.2
Festuca rubra	Class		6	22	19	29	16	34	18	27	43	26	36	22	42	27	18	14
Poa trivialis	Molinio-Arrhenateretea R. Tx. 1937		16	23	25	21	27	16	16	21	27	17	7	16	14	19	12	14
Ranunculus repens			5	12	6	4	11	7	13	11	5	11	16	12	6	8	6	11
Cerastium holosteoides			1	0.2	0.2	0.2	1	1	1	0.2	0.2	1	2	1	0.2	0.2	0.2	0.2
Poa pratensis ag.			12	3	2	5	4	4	2	2	1	4	4	7	7	6	6	9
Rumex acetosa			9	9	12	9	15	7	11	13	9	7	12	9	9	10	13	10
Cardamine pratensis			.	0.2	0.2	0.2	0.2	0.2	0.2	0.2	.	.	.	0.2	0.2	0.2	0.2	0.2
Holcus lanatus			0.2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Alopecurus pratensis			.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Trifolium pratense			.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Lotus pedunculatus	moisture indicator-species		.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Deschampsia cespitosa			2	.	.	4	.	.	0.2	1	2	9	.	.	.	.	.	12
Juncus effusus			.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Agrostis capillaris	Alchemillo-Cynosuretum Müll. ex Görs 1968		24	23	19	14	8	14	23	11	7	14	11	21	8	13	13	12
Stellaria graminea	indicating nutrient shortage		0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2	.	0.2	0.2	0.2	0.2
Anthoxanthum odoratum			.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Hypericum maculatum			.	.	.	.	.	.	0.2	.	0.2	.	.	.	.	.	.	.
Luzula campestris			.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Lotus corniculatus			.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Alchemilla vulgaris ag.	montane distribution		.	.	.	.	.	.	.	.	.	.	.	.	.	.	0.2	.
Holcus mollis			0.2	.	0.2	0.2	.	.	.	.	.	.	0.2	.	.	2	5	10
Rumex obtusifolius	indicating excess nutrients		.	.	.	.	.	.	.	.	.	.	.	.	.	0.2	.	.
Urtica dioica			.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Anthriscus sylvestris	associated species		.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Poa angustifolia			1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Carex ovalis			.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Veronica arvensis			.	.	.	.	.	.	.	.	.	.	.	.	.	.	0.2	.
Hypericum perforatum			.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Cardamine hirsuta			.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.

		Plot	65.1	65.2	66.1	66.2	67.1	67.2	68.1	68.2	69.1	69.2	70.1	70.2	71.1	71.2	72.1	72.2
Characteristic species		**species no**	**18**	**19**	**17**	**17**	**18**	**17**	**15**	**16**	**20**	**19**	**19**	**19**	**16**	**16**	**15**	**17**
Trifolium repens	Association		4	0.2	0.2	2	0.2	3	0.2	1	1	1	3	1	2	10	4	2
Lolium perenne	Lolio-Cynosuretum Br.-Bl. et Deleeuw 1936		13	7	4	8	2	3	.	5	12	6	14	5	11	7	7	9
Cirsium arvense	Alliance		.	.	.	.	.	.	.	.	.	.	4	.	.	.	.	.
Poa annua	Cynosurion-cristati R.Tx. 1947		.	.	0.2	.	.	.	.	.	.	.	.	.	.	.	.	.
Plantago major			.	0.2	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Veronica serpyllifolia			.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Phleum pratense			.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Leontodon autumnalis			.	.	.	.	.	.	.	.	.	.	.	0.2	.	.	.	.
Cirsium vulgare			.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Elymus repens			.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Bellis perennis			.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Capsella bursa-pastoris			.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Cynosurus cristatus			.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Veronica chamaedrys	Order		0.2	1	1	1	2	1	1	1	0.2	0.2	0.2	1	1	0.2	0.2	1
Taraxacum Sec. Ruderalia	Arrhenateretalia R. Tx. 1931		1	2	3	0.2	.	1	.	0.2	0.2	0.2	1	1	1	0.2	1	0.2
Dactylis glomerata			.	3	.	1	9	7	1	4	5	15	.	4	.	.	.	4
Achillea millefolium			0.2	0.2	0.2	0.2	5	0.2	0.2	.	1	0.2	0.2	0.2	1	0.2	0.2	.
Festuca rubra	Class		15	27	44	19	4	13	16	27	23	23	16	26	40	20	23	23
Poa trivialis	Molinio-Arrhenateretea R. Tx. 1937		7	11	16	12	14	8	14	18	13	12	16	17	12	12	9	24
Ranunculus repens			4	5	9	9	6	5	13	11	7	6	16	9	13	14	6	5
Cerastium holosteoides			1	0.2	0.2	0.2	0.2	0.2	1	1	0.2	1	0.2	0.2	0.2	1	0.2	0.2
Poa pratensis ag.			8	9	5	4	2	1	2	6	2	6	2	3	3	6	3	4
Rumex acetosa			9	9	9	12	8	13	8	12	8	9	12	11	6	12	5	9
Cardamine pratensis			0.2	0.2	0.2	0.2	0.2	.	.	0.2	0.2	0.2	0.2	0.2	0.2	0.2	.	0.2
Holcus lanatus			.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Alopecurus pratensis			.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Trifolium pratense			.	.	.	.	.	.	.	.	.	.	0.2	.	.	.	.	.
Lotus pedunculatus	moisture indicator-species		.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Deschampsia cespitosa			3	.	.	.	29	30	33	.	7	9	3	15	.	.	37	5
Juncus effusus			.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Agrostis capillaris	Alchemillo-Cynosuretum Müll. ex Görs 1968		34	13	8	6	18	9	8	13	19	8	11	6	9	10	4	6
Stellaria graminea	indicating nutrient shortage		0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2	1	0.2	0.2
Anthoxanthum odoratum			.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.
Hypericum maculatum			.	0.2	.	.	0.2	.	.	.	.	2	.	.	0.2	.	.	.
Luzula campestris			.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Lotus corniculatus			.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Alchemilla vulgaris ag.	montane distribution		.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Holcus mollis			0.2	12	.	25	.	5	2	.	0.2	1	0.2	0.2	.	6	.	7
Rumex obtusifolius	indicating excess nutrients		0.2	.	.	.	.	.	.	0.2	0.2	.	.	.	.	.	.	.
Urtica dioica			.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Anthriscus sylvestris	associated species		.	.	0.2	.	.	.	.	.	.	.	.	.	.	.	.	.
Poa angustifolia			.	.	.	.	0.2	.	.	.	.	.	.	.	.	.	.	.
Carex ovalis			.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Veronica arvensis			.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Hypericum perforatum			.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Cardamine hirsuta			.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.

Data taken from:		Klapp/ Opitz v. Boberfeld (2006)	BiolFlor 1.1		Dierschke/Briemle 2002		
	functional	growth height	start	end	Symphenological group		
Species	group	tall-small	of flowering (month)		1-9	Name	
Anthoxanthum odoratum	G	S	5	6	4	Ajuga reptans-Alopecurus-stage	
Poa annua	G	S	1	12	2	Anemone-nemoroas-Primula-stage	
Alopecurus pratensis	G	T	5	6	4	Ajuga reptans-Alopecurus-stage	
Luzula campestris	G-like	S	3	4	3	Cardamine partensis-Taraxacum-stage	
Cerastium holosteoides	F	S	3	6	4	Ajuga reptans-Alopecurus-stage	
Viola tricolor	F	S	4	9	4	Ajuga reptans-Alopecurus-stage	
Veronica chamaedrys	F	S	5	7	4	Ajuga reptans-Alopecurus-stage	
Veronica serpyllifolia	F	S	5	9	4	Ajuga reptans-Alopecurus-stage	
Anemone nemorosa	F	S	3	5	2	Anemone-nemoroas-Primula-stage	
Cardamine hirsuta	F	S	3	6	2	Anemone-nemoroas-Primula-stage	
Taraxacum Sect. Ruderalia	F	S	3	10	3	Cardamine partensis-Taraxacum-stage	
Veronica arvensis	F	S	3	10	3	Cardamine partensis-Taraxacum-stage	
Cardamine pratensis	F	S	4	6	3	Cardamine partensis-Taraxacum-stage	
Bellis perennis	F	S	1	11	1	Pre-stage	
Capsella bursa-pastoris	F	S	1	12	1	Pre-stage	
Stellaria media	F	S	1	12	1	Pre-stage	
Plantago lanceolata	F	S	5	10	4	Ajuga reptans-Alopecurus-stage	**1. harvest**
Poa angustifolia	G	S	5	6	6	Leucanthemum-Lychnis flos-cuculi	
Poa humilis	G	S	5	6	6	Leucanthemum-Lychnis flos-cuculi	
Poa pratensis	G	S	5	6	6	Leucanthemum-Lychnis flos-cuculi	
Festuca rubra	G	S	6	7	6	Leucanthemum-Lychnis flos-cuculi	
Poa trivialis	G	S	6	7	6	Leucanthemum-Lychnis flos-cuculi	
Bromus hordeaceus	G	S	5	8	7	Cirsium palustre-Galium album	
Lolium perenne	G	S	5	10	7	Cirsium palustre-Galium album	
Cynosurus cristatus	G	S	6	7	7	Cirsium palustre-Galium album	
Agrostis capillaris	G	S	6	7	8	Centaurea jacea-Filipendula ulmaria	
Dactylis glomerata	G	T	5	7	6	Leucanthemum-Lychnis flos-cuculi	
Arrhenatherum elatius	G	T	6	10	6	Leucanthemum-Lychnis flos-cuculi	
Holcus lanatus	G	T	6	8	7	Cirsium palustre-Galium album	
Phleum pratense	G	T	6	8	7	Cirsium palustre-Galium album	
Deschampsia cespitosa	G	T	6	7	8	Centaurea jacea-Filipendula ulmaria	
Elymus repens	G	T	6	8	8	Centaurea jacea-Filipendula ulmaria	
Holcus mollis	G	T	6	8	8	Centaurea jacea-Filipendula ulmaria	
Carex ovalis	G-like	S	6	7	6	Leucanthemum-Lychnis flos-cuculi	
Juncus inflexus	G-like	S	6	8	8	Centaurea jacea-Filipendula ulmaria	
Juncus effusus	G-like	T	6	8	6	Leucanthemum-Lychnis flos-cuculi	

Species	functional group	growth height tall-small	start of flowering (month)	end	Symphenological group 1-9	Name	
Stellaria graminea	F	S	5	7	6	Leucanthemum-Lychnis flos-cuculi	
Ranunculus repens	F	S	5	8	5	Anthriscus sylvestris-Ranunculus acris	
Alchemilla vulgaris agg.	F	S	6	8	5	Anthriscus sylvestris-Ranunculus acris	
Matricaria recutita	F	S	5	8	6	Leucanthemum-Lychnis flos-cuculi	
Myosotis scorpioides	F	S	5	9	6	Leucanthemum-Lychnis flos-cuculi	
Hypochaeris radicata	F	S	6	9	6	Leucanthemum-Lychnis flos-cuculi	
Persicaria amphibia	F	S	6	9	6	Leucanthemum-Lychnis flos-cuculi	
Campanula rotundifolia	F	S	6	10	6	Leucanthemum-Lychnis flos-cuculi	
Leontodon autumnalis	F	S	7	9	6	Leucanthemum-Lychnis flos-cuculi	
Galium saxatile	F	S	6	8	7	Cirsium palustre-Galium album	
Plantago major	F	S	6	10	7	Cirsium palustre-Galium album	
Prunella vulgaris	F	S	6	9	8	Centaurea jacea-Filipendula ulmaria	
Rumex acetosa	F	T	5	7	5	Anthriscus sylvestris-Ranunculus acris	
Anthriscus sylvestris	F	T	5	8	5	Anthriscus sylvestris-Ranunculus acris	
Ranunculus acris	F	T	5	9	5	Anthriscus sylvestris-Ranunculus acris	
Galium album	F	T	6	9	7	Cirsium palustre-Galium album	
Achillea millefolium	F	T	6	10	7	Cirsium palustre-Galium album	
Hypericum perforatum	F	T	7	8	7	Cirsium palustre-Galium album	
Rumex obtusifolius	F	T	7	8	7	Cirsium palustre-Galium album	
Urtica dioica	F	T	7	10	7	Cirsium palustre-Galium album	
Cirsium vulgare	F	T	6	9	8	Centaurea jacea-Filipendula ulmaria	
Lotus pedunculatus	L	T	6	7	8	Centaurea jacea-Filipendula ulmaria	
Trifolium repens	L	S	5	9	6	Leucanthemum-Lychnis flos-cuculi	
Lotus corniculatus	L	T	6	8	6	Leucanthemum-Lychnis flos-cuculi	
Trifolium pratense	L	T	6	9	6	Leucanthemum-Lychnis flos-cuculi	
Lathyrus pratensis	L	T	6	8	7	Cirsium palustre-Galium album	**2. harverst**
Epilobium tetragonum	F	T	7	8	8	Centaurea jacea-Filipendula ulmaria	
Hypericum maculatum	F	T	7	8	8	Centaurea jacea-Filipendula ulmaria	
Cirsium arvense	F	T	7	9	8	Centaurea jacea-Filipendula ulmaria	

3. harvest