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Explaining grassland biomass production – the importance of biodiversity and climate changes with fertilization and mowing frequency

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Abstract

Climate and biodiversity are known to influence grassland biomass production, but to date no study quantified their relative importance in relation to different management treatments. This is, though, of principal importance to deduce implications for land-users in the context of global climate change. In the current study, we ask if we can detect differences between management treatments (i) in biomass production, and (ii) in the effects of climate and biodiversity on biomass production. We analyzed changes in biomass production over the last 37 years on a grassland site in North-West Germany, with mowing at five frequencies (once per year to eight times per year), each with and without fertilization. Biomass production and vegetation composition were recorded annually. Biodiversity was included using the presence-absence based indices species and functional richness, and the abundance weighted indices species evenness, functional evenness and functional divergence.

The results showed clearly that nutrient status and management frequency had a strong impact on grassland biomass production. Biomass production was generally enhanced on fertilized plots, and within each fertilization treatment, highest at intermediate mowing frequencies. With an increasing intensity of disturbance we detected for species and functional richness increasing effects on biomass production. Both indices refer to the probability to which optimally functionally adapted species occur in the local species pool. In contrast, species evenness alludes to dominance structures which describe patterns of niche partitioning or interspecific facilitation. These are of principal importance at low management intensities when strong competitors occur. Furthermore, high growth rates of strong competitors are related to temperature, which had an enhanced effect on biomass at low mowing frequencies. However, on the fertilized plots functional divergence increased in importance with increasing mowing frequency, indicating that next to the filters for highly specialized plant species, dominance structures are important. As functional divergence measures the agglomeration of the functional identity of most abundant species, it refers to mechanisms of co-existence.

With reference to the effects of climate and biodiversity on biomass production, we can highlight the importance of the interaction between nutrient status and management frequency when analyzing grassland biomass production.

Keywords: Plant functional trait; Life-history trait; Long term permanent plots; Grassland management; Temperate grassland; Species richness; Species Evenness; Functional diversity; Functional richness; Functional divergence; Ecosystem service

1 Introduction

An old, but still current question of vegetation ecology is how different environmental factors influence primary ecosystem services such as biomass production. In terrestrial ecosystems, biomass production is often constrained by water availability (Rosenzweig 1968, Churkina and Running 1998), which is driven by edaphic and climatic factors. On a continental or biome scale, ecosystem productivity is well predictable from temperature and precipitation (Knapp and Smith 2001), but at local scales such models are not able to explain the variability in biomass production very well (Lauenroth and Sala 1992, Knapp and Smith 2001). On small scale unmanaged semi-arid grasslands, Heisler-White et al. (2008) explained variability in biomass production by frequency and size of rainfall events. In the temperate zones, with a mostly sufficient water supply and often more intensive land-use however, it is very likely that fertilization and frequency of disturbance play a major role in influencing biomass production.

In general, fertilization increases biomass production (Tilman 1982, 1988), but also the interactions between nutrient status (productivity of the ecosystem), frequency of disturbance, and biodiversity pattern influence grassland biomass production. Several authors have shown that disturbance-productivity interactions result in productivity-diversity and disturbance-diversity relationships (Huston 1979, Huston 1994, Kondoh 2001, Cardinale et al. 2006). Maximal species richness as well as, maximal biomass production could be expected under balanced disturbance and productivity conditions (Connell 1978): if productivity is high, strong competitors are favored, and if disturbance is high, good colonizers (resprouters) increase in importance. If disturbance is high and productivity is low, species richness decreases since strong competitors cannot survive. If disturbance decreases and productivity increases, strong competitors out-compete good colonizers, again resulting in decreased species richness (Kondoh 2001). These interactions stress the importance to directly analyze the combined effects of fertilization, disturbance frequency, biodiversity pattern and climatic factors on biomass production of temperate grasslands. However, to our knowledge, no study has yet quantified the relative importance of the abovementioned factors on biomass production in relation to different management treatments. This is, though, of principal importance for assessing implications for land-users in the context of global climate change.

For the current study we used a long-term permanent plot experiment. Ten different management regimes, including different disturbance and fertilization treatments, were applied on grasslands which have developed on former arable-fields since they were abandoned 37 years ago. On these sites we analyzed the development and variability of biomass production with respect to mowing frequency, fertilization, precipitation, temperature and biodiversity. However, biodiversity has different aspects. Grime (1998) stressed the importance of vegetation composition for assessing the contribution of species with different abundances on ecosystem processes formulating the ‘mass ratio’ hypothesis: The extent to which a plant species affects ecosystem functioning is closely predictable from its contribution to total biomass, which is well described by abundance data. Recently Cardinale et al. (2007) showed that both the number of species and the dominance of single species in an ecosystem have significant impacts on biomass productivity. One step forward in the discussion of the biodiversity-productivity relationship was made by incorporating diversity of life-history-traits: There is growing evidence that functional diversity is another important component of biodiversity influencing ecosystem services (see summaries in Díaz and Cabido 2001, Villéger et al. 2008). As shown for species diversity, also functional diversity has two facets, ‘functional richness’ and ‘functional composition’ (Díaz and Cabido 2001, Villéger et al. 2008). Nevertheless, many studies have used functional groups (such as grasses, legumes, small or tall herbs, Marquard et al. 2009) as surrogates for functional diversity; but by merging species to groups according to their functional attributes a lot of information is lost because of the normally continuous structure of functional differences between species (Gitay and Noble 1997, Villéger et al. 2008). Furthermore, many studies ignored species abundances, thus describing patterns of functional richness only, not of dominance structures (Díaz and Cabido 2001). In the past, a complete estimation of these competing components of functional diversity was restricted by the limits of the available indices (see review by Petchey and Gaston 2006), but recently Villéger et al. (2008) provided a general statistical framework for quantifying functional diversity. Accordingly, we will also include indices describing functional and species diversity (based on presence/ absence and abundance weighted vegetation data) in our model. Specifically our study has two main objectives:

1. Is there a change in biomass production at all? Given the fact that management treatments including mowing frequency and fertilization influence biomass production, we can hypothesize that it is maximized under balanced disturbance and productivity conditions, and that biomass production is generally enhanced on fertilized plots.
2. What are the driving forces behind biomass changes? When relating biomass production to precipitation, temperature, functional and species diversity, we assume differences in their importance for explaining the development and variability of biomass production under different management treatments.

2 Materials and Methods

2.1 Study site and field data

The permanent plots used in the current study are located in the Experimental Botanical Garden of the University of Göttingen, Germany (180 m a.s.l., 51°34’0’’N, 9°56’60’’E; mean annual temperature: 8.5°C; average annual rainfall: 635 mm; Schmidt 2006). The plots were established in 1969 on a former arable field cultivated until 1968. The soil is deep, calcareous and fertile, on alluvial loamy brown earth. All experimental sites were situated close to each other, and had therefore identical environmental conditions at the time of experimental set-up. The surrounding landscape is characterized by a mixture of arable fields, grasslands, ruderal communities, and forests (dominated by *Fagus sylvatica)*. Each management treatment was set up on a 125m² plot once with and once without fertilization. The fertilization annually replaced the entire amount of nutrients (N, P, K) which were removed the previous year by adding mineral fertilizer, starting in 1970 (Schmidt 1993, 2006). The following management treatments, which were related to a disturbance gradient, were analyzed in the current study:

1. Mowing once per year in autumn (at the end of the growing season).
2. Mowing once per year in spring (at the beginning of the growing season).
3. Mowing twice per year (end of May and end of July).
4. Mowing four times per year (May, June, July, and September).
5. Mowing eight times per year (2× May, 2× June, July, August, September, and October).

In comparison to mowing once in the spring, mowing in the autumn was assumed to be less intensive, as here the yearly growing circle can be completed.

2.2 Vegetation sampling, biomass production and climatic data

From 1972 to 2006 (with a three year gap between 1999 and 2003), percentage coverage of all vascular plant species was visually estimated on each 125 m² plot. These estimations were made twice per year at corresponding phenologic dates to cover plants whose development peaks in the spring as well as, in the summer. For each plot the mean coverage of each species was calculated. Additionally, the mown aboveground biomass per plot was determined at every harvest and the sum per year was calculated (for details on the method see Schmidt 2006).

Monthly recorded data of temperature and precipitation were available from the meteorological station Göttingen, provided by the German Meteorological Service (station number 1564). To describe the climatic conditions during the vegetation period, we included data from April to October (mean vegetation growth period for grasslands in central Europe) and used mean temperature and the sum of precipitation for further analyses.

2.3 Data analysis

Changes of biomass production over time

Biomass data were available for the years 1972 to 2006. To reveal trends in biomass development with time, generalized linear models (GLM) were applied to search for differences in biomass production between the management treatments. As we deal with time series data, we considered temporal autocorrelation and possibly heteroskedasticity by correcting the covariance structure of the regression model using heteroskedasticity and autocorrelation consistent (HAC) covariance estimators. First we fitted a model containing time as a continuous variable and management as a factor. This model was simplified according to Occam's razor to the minimal adequate model by merging management treatments showing no significant differences in the estimators for intercepts and slopes (Crawley 2007).

Functional traits related to management intensity

To find which functional traits are related to management intensity we used a multivariate ordination technique called RLQ. The overall goal of this technique is the investigation of the relationship between the trait data (Q-table) and the environmental characteristics (R-table) by the use of a third, connecting table (L-table; species-relevés matrix). As a result the RLQ-axes display maximum covariance between the traits and environment. Bernhardt-Römermann et al.

(2008) extended that method by applying an optimization process to select those traits which are optimal for describing the investigated environmental gradient (here mowing intensity). For further details on this method see Doledec et al. (1996), Bernhardt-Römermann et al. (2008) and Appendix 1.

To characterize the development of the selected functional traits with management frequency, we used the covariance structure of the final RLQ-ordination between traits and management frequency. This relationship was tested for significance using randomization tests (compare also approach in Römermann et al. 2009).

Diversity indices

Species diversity was described by species richness (SR) which is the number of species; and species evenness (SE) which is a measure for the equal distribution of species abundances. SE was calculated following $SE= H/\log(SR)$, with $H = -\sum(A_i(\ln(A_i)))$, where A_i is the proportional abundance (A) of species i (Magurran 2004).

As our aim is to estimate functional diversity not based on a priori defined functional groups, we used the traits detected by the abovementioned RLQ-analysis as optimal for describing the management intensity gradient, and calculated functional diversity indices in the framework presented by Villéger et al. (2008):

Functional richness (FR) in a single trait system can be seen as the difference between the minimal and maximal attribute of the respective trait. For the actual multi-trait system, functional richness was estimated by calculating the volume of a convex hull (with as many dimensions as functional traits; T-dimensional trait space) as a measure of the functional space occupied by a community (Cornwell et al. 2006). This value reflects the range of the trait attributes, thus it is affected by the number of the species in the actual community but does not consider species abundances. Functional evenness (FE) describes the evenness of abundance distributions in a functional trait space (Mason et al. 2005). The trait distribution in the T-dimensional trait space was calculated as the length of a minimal spanning tree, which is the minimum sum of branch length that connects all points contained in the T-dimensional trait space, weighted by the relative abundance of the species. FE is independent of the convex hull volume and is not biased by species richness (Villéger et al. 2008). It quantifies the regularity with which functional space is filled by species weighted by their abundances. The index of functional divergence (FD) represents how abundance is distributed within the volume of functional trait space occupied by species. If the most abundant species have traits close to the center of the convex hull (here the center of gravity) FD is low; if the most abundant species are located further from the center it will be high (Villéger et al. 2008).

Relating biomass production to climate, biodiversity, and management

To explain changes in biomass production over time, we calculated separate GLMs (with a HAC correction to account for temporal autocorrelation) for each management treatment (treatments not showing significant differences in biomass development were merged). Climate (temperature and precipitation), and biodiversity indices (species and functional richness, species and functional evenness, functional divergence) were used as explanatory variables. We simplified the maximal model via backward selection of least significant variables until the final minimal adequate model contained significant terms only and a minimal AIC was obtained. From this final model we extracted the explained variance for each term still included: As all variables were normalized, they had the same scales with values ranging between zero and one. Thus, the proportion of each estimate of the final GLM on the total sum of all estimates corresponds to the variance explained.

All calculations were done in R 2.9.2 (R Development Core Team 2008), with the additional packages sandwich (Zeileis 2004), ape (Paradis et al. 2004), and vegan (Oksanen et al. 2007). Only the convex hull calculations were done with the Quickhull algorithm using the TraitHull program (http://www.pricklysoft.org/software/traithull.html) implemented in Python 2.5.2.

3 Results

3.1 Changes of biomass production over time

As shown in Figure 1 and Table 1, biomass production increased over time for all management treatments, except for the unfertilized plots mown four and eight times per year where a slightly decreasing trend was found. For the unfertilized plots no difference in biomass production was found between mowing once in the spring and mowing twice a year, and between mowing four and eight times per year. Furthermore, that last pair also did not differ for the fertilized plots. Regarding differences between management treatments on the fertilized plots (Table 1, Fig. 1), biomass production was highest at an intermediate disturbance frequency, mowing twice per year (F-2). Mowing once in the spring (F-1S) had a comparable slope but smaller intercept; followed by mowing once in the autumn (F-1A) and plots mown four and eight times per year (F-4, F-8) showed lower biomass productivity. For the unfertilized plots, biomass production was highest for the treatments mown once in the spring and twice a year (U-1S, U-2), but on a lower level in comparison to the fertilized plots. Mowing in the autumn (U-1A) again showed an increasing trend but on a lower level, whereas for the unfertilized treatments, mowing four and eight times per year (U-4, U-8) biomass production decreased over time. Figures with absolute values of biomass production development over time are presented in Appendix 2.

3.2 Functional traits related to management intensity

The trait-management covariances presented in Table 2 increased with the intensity of the relationship between management frequency and traits. As described in Appendix 1, for the fertilized and unfertilized treatments different trait sets were found to be optimal for describing the gradient in management intensity (Table 2), e.g. specific leaf area, leaf persistence, or lateral spread for the unfertilized; plant life span, or clonal growth organ for the fertilized. However, for both fertilized and unfertilized plots we detected for several traits comparable relations to management intensity (e.g. decreasing canopy height or regular leaf distribution), but additionally both treatments showed their own trait reactions. For a detailed overview on trait responses with increasing management frequency see Table 2.

3.3 Relating biomass production to climate, biodiversity, and management

All models gave highly significant results. In none of the final GLMs did functional evenness remain. All other factors were included in the final models, though their effects differed considerably between management treatments (for further details on the GLMs see Table 3 and Appendix 3). Fig. 2 gives a comparative overview on the relevance of the different factors to explain biomass production over the last 37 years: with increasing management frequency for both fertilized and unfertilized plots we detected a decreasing importance of temperature and species evenness, while for species and functional richness an increasing trend was found. For species and functional richness on unfertilized plots, however, that increase began at lower mowing frequencies. On all fertilized plots mown more than once per year, functional divergence was reasonably relevant for explaining biomass production. The explanatory power of precipitation does not differ remarkably between treatments, but showed higher values for the unfertilized plots mown four and eight times per year.

4 Discussion

4.1 Biomass production and functional adaptations

The results of the current study showed clearly that grassland biomass production depends on disturbance intensity and fertilization. For all plots mown once or twice per year we found within each fertilization treatment comparable increasing slopes in biomass development over time. Such an increasing trend may occur due to ongoing adaptations of species to the available resources when annual nutrient removal by mowing does not lead to a decrease in nutrient availability (Tilman 1982, 1988). On the fertilized plots nutrient removal is compensated by fertilization, while we can assume at least a partial replacement of the nutrients removed by hay-making due to deposition from the air for the unfertilized plots at these low mowing frequencies (Bernhardt-Römermann et al. 2007). In contrast, for the fertilized and unfertilized plots mown four and eight times per year, the lower slopes indicated that nutrient replacement and removal by hay-making are no longer in equilibrium. This may explain the decreasing productivity of unfertilized frequently mown agricultural lands and old-field communities (Tilman 1988, Huberty et al. 1998). Additionally, on frequently mown sites the influence of intensive disturbance results in functional adaptations: with increasing mowing frequency, we found an increase in annual and rosette species as well as, species able to spread laterally; while taller species, species with a regular leaf distribution and higher specific leaf area (SLA, and hence higher growth rates, Cornelissen et al. 2003) decreased, indicating a shift towards lower competition (Römermann et al. 2008, Römermann et al. 2009). Such species are however, less productive in comparison to those typical for less frequently disturbed sites (Collins et al. 2001, Thompson et al. 2001, Schmidt 2006), again resulting in less steep (or even decreasing) slopes in biomass development over time.

Comparing all fertilized plots, highest biomass production was found when the plots were mown twice per year. This finding is in accordance with Huston (1979), Kondoh (2001), and Haddad et al. (2008), who predicted highest biomass production at intermediate disturbance regimes. At an intermediate disturbance intensity, an equilibrium between nutrient removal from the system, which favours species with lower competitive strength, and nutrient replacement by deposition and from the soil, which favours strong competitors, can develop (Kondoh 2001, Haddad et al. 2008). A co-existence of several species, using the available nutrients most efficiently, is possible and biomass production is maximized. A comparable pattern was found for the unfertilized plots, though we could not find any difference between treatments mown once a year in the spring and those mown twice a year, indicating that both treatments represent comparable disturbance levels.

4.2 Relating biomass production to climate and biodiversity patterns

The results of this study showed clearly that the importance of biodiversity and climate on biomass production changed with disturbance frequency and fertilization. All facets of diversity, either focusing on species or functional identity, both calculated on presence/ absence or abundance weighted data, were needed to get the complete picture.

It is striking that the effect of biodiversity parameters and temperature differed for different mowing frequencies, whereas the effect of precipitation was constant for the fertilized plots and only increased slightly for the unfertilized plots. For the frequently mown unfertilized plots, biomass production is limited by nutrient availability. Plant nutrient uptake and water availability, however, are closely related: an additional water supply may allow an advanced nutrient uptake (e.g. Ellenberg 1996), an effect which is even more pronounced when less nutrients are available (Bernhardt-Römermann et al. accepted). Thus, the biomass production on sites where hay-making is frequent, but without nutrient replacement, is greater when precipitation is not limiting. Regarding temperature, we detected for both the unfertilized and fertilized plots a strong decrease in biomass production with increasing mowing frequency. Plants typical for less disturbed plots are mostly strong competitors (see above), with high growth rates related to greater photosynthetic capacity which is influenced by temperature.

Next to climatic factors, species and functional richness, species evenness and functional divergence were important in explaining variations in biomass production. The influence of biodiversity on biomass production can be described by two competing processes: (i) if the ecosystems are mainly influenced by high disturbance frequency (e.g. mowing), functional adaptations are important, and (ii) under less intensive management, without strong filters for highly specialized plant species, biomass production is maximized by the co-existence of species enabling a more efficient resource uptake (Hector et al. 1999, Hooper et al. 2005, Cardinale et al. 2007). We detected for species and functional richness an increasing importance of the level of disturbance to explain biomass productivity: only species optimally adapted to high disturbance may survive (Kondoh 2001, Dölle et al. 2008). Species and functional richness both refer to the probability to which a species, that contains trait attributes fitting to the requirements of the actual management treatment, occurs in the local species pool. This is independent from dominance structures.

In contrast, the importance of species evenness on biomass production decreased for both fertilization treatments with increasing disturbance. Under less intensive management, species with a high efficiency in resource-use (strong competitors) can dominate grassland communities (Wilson and Keddy 1986, Kahmen and Poschlod 2004) whereas filters for highly specialized plant species are less important (Kondoh 2001, Haddad et al. 2008). This is described by the concept of species complementarity, which refers to the theory that biomass production might be enhanced due to niche partitioning (either in space or time, Tilman 1999) or through interspecific facilitation (Cardinale et al. 2002, Brooker et al. 2008). Niche partitioning or interspecific facilitation both related to dominance structures (see 'mass ratio' hypothesis, Grime 1998) which may be described by species evenness. However, we detected for the fertilized plots an increase in the importance of functional divergence with increasing mowing frequency. Functional divergence is a diversity index which also alludes to (functional) dominance structures, indicating that next to the filters for highly specialized plant species (see above) additionally dominance structures are important. However, functional divergence refers to dominance structures of functional adaptations. It is a measure for the agglomeration of the functional identity of most abundant species (Mason et al. 2005, Villéger et al. 2008) and thus it describes patterns of co-existence.

Conclusion

The effects of climatic variables and biodiversity parameters on biomass production clearly differed with the frequency of disturbance and fertilization. Hence, our results stressed the importance of the interaction of nutrient status and management frequency when analyzing ecosystem services such as biomass production of grassland ecosystems and should be considered when making, e.g. management recommendations in the context of climate change.

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Table 1: Differences in biomass production between management treatments. Presented are the results of the GLM. Treatments that do not show a significant difference in intercept and slope were merged. The GLM was corrected for heteroskedasticity and autocorrelation (time series). Final model with null deviance 93.47 on 350 degrees of freedom, and residual deviance 5.55 on 336 degrees of freedom (r^2= 0.941***). Abbreviations for management treatments are according to Figure 1.

	Value	Std. Error	z-value	p-value
Intercepts				
U-1A	-11.76	4.279	-2.75	0.006**
U-1S & U-2	-13.08	3.026	-4.32	0.000***
U-4 & U-8	6.16	3.026	2.04	0.042*
F-1A	-38.22	4.279	-8.93	0.000***
F-1S	-45.56	4.279	-10.65	0.000***
F-2	-44.74	4.279	-10.45	0.000***
F-4 & F-8	-20.20	3.026	-6.68	0.000***
Slopes				
U-1A	0.006	0.002	2.80	0.005**
U-1S & U-2	0.001	0.003	0.28	0.779
U-4 & U-8	-0.009	0.003	-3.41	0.001***
F-1A	0.013	0.003	4.40	0.000***
F-1S	0.017	0.003	5.65	0.000***
F-2	0.017	0.003	5.53	0.000***
F-4 & F-8	0.004	0.003	1.68	0.094

Table 2: Covariance between the gradient in management intensity and functional traits for the fertilized and unfertilized plots. Covariance increases with the intensity of the relationship between the time gradient and the species traits through the species abundance table. Different symbols indicate significant differences from random distribution with ***P <0.001, **P <0.01, *P <0.05. For details on the selection procedure of the relevant traits see Appendix 1.

	Unfertilized	Fertilized
Max. canopy height	-0.38***	-0.46***
Specific leaf area (SLA)	-0.13**	-
Leaf distribution: Rosette plant	0.20	0.42***
Leaf distribution: Hemirosette plant	0.06	0.12*
Leaf distribution: Regular	-0.30**	-0.60**
Mesomorphic leaf anatomy	0.24***	-
Scleromorphic leaf anatomy	0.11*	-
Leaf persistence: Persistent green	0.47***	-
Leaf persistence: Summer green	-0.41***	-
Leaf persistence: Over-wintering green	0.09	-
Lateral spread: No	-0.09	-
Lateral spread: < 0.01 m	-0.08	-
Lateral spread: 0.01- 0.25 m	-0.06	-
Lateral spread: > 0.25 m	0.33*	-
Duration of flowering: Short (1-2 months)	-0.04	-
Duration of flowering: Medium (3-4 months)	-0.43***	-
Duration of flowering: Long (≤ 4 months)	0.39***	-
Type of pollination: Animals	0.12**	-
Type of pollination: Selfing	-0.29**	-
Type of pollination: Abiotic	0.21*	-
Plant life span: Annuals	-	0.45***
Plant life span: Bi-annuals	-	-0.17
Plant life span: Perennials	-	-0.03
Clonal growth organ: No	-	0.15
Clonal growth organ: Above ground runners	-	0.92***
Clonal growth organ: Above ground plant parts	-	-0.25
Clonal growth organ: Below ground runners	-	-0.12
Clonal growth organ: Below ground storage organs	-	-0.62
Seed mass	-	-0.02
Dispersal type: Zoochory	-	0.34***

Table 3: Estimates and standard errors of the GLMs fitted to biomass production with different mowing and fertilization treatments. The covariance estimates in the regression model were corrected for heteroskedasticity and autocorrelation; all estimates were significant. Full summary statistics are presented in Appendix 3; abbreviations for climatic and biodiversity parameters are according to Figure 2, abbreviations for management treatments follows Fig. 1.

	U-1A	U-1S & U-2	U-4 & U-8	F-1A	F-1S	F-2	F-4 & F-8
T	0.91 ± 0.15	0.53 ± 0.15		0.94 ± 0.11	2.20 ± 0.35	1.91 ± 0.25	
P	0.33 ± 0.16	0.15 ± 0.06	0.22 ± 0.04	0.27 ± 0.08	0.24 ± 0.22	0.49 ± 0.18	0.27 ± 0.08
SR		0.40 ± 0.10	-0.28 ± 0.09				0.89 ± 0.20
FR		-0.47 ± 0.17	0.39 ± 0.11			-0.45 ± 0.24	-0.98 ± 0.21
SE	-0.77 ± 0.21	-.035 ± 0.17		-0.92 ± 0.11	-1.44 ± 0.30	-0.51 ± 0.08	
FD						-0.98 ± 0.32	-0.81 ± 0.29
r^2	0.91	0.93	0.93	0.94	0.92	0.95	0.92

Figure legends

Fig. 1: Change in the biomass production from 1972 to 2006. Presented is the result of the GLM shown in Table 1. Management treatments are printed together, when the respective GLM does not show a significant difference in intercept and slope. Absolute values are presented in Appendix 2. Abbreviations: the first letter refers to the fertilization treatment (U: unfertilized, F: fertilized), the numbers behind the hyphen refer to the management frequency (1A: mowing once in the autumn, 1S: mowing once in the spring, 2: mowing twice per year, 4: mowing four times per year, 8: mowing eight times per year).

Fig. 2: Effect of different parameters (A-F) on the change in biomass production over the last 35 years separated by management frequency and fertilized (solid lines) vs. unfertilized (dotted lines) treatments. Presented are the estimates converted into percent for the variables temperature (T), precipitation (P), species and functional richness (SR/ FR), species evenness (SE), and functional divergence (FD) as deduced from separate GLMs shown in Table 3 and Appendix 3. For these GLMs management treatments were merged according to the results presented in Table 1. Non-significant estimates (not included in the final models) do not significantly differ from 0 and are shown here for comparative presentation.

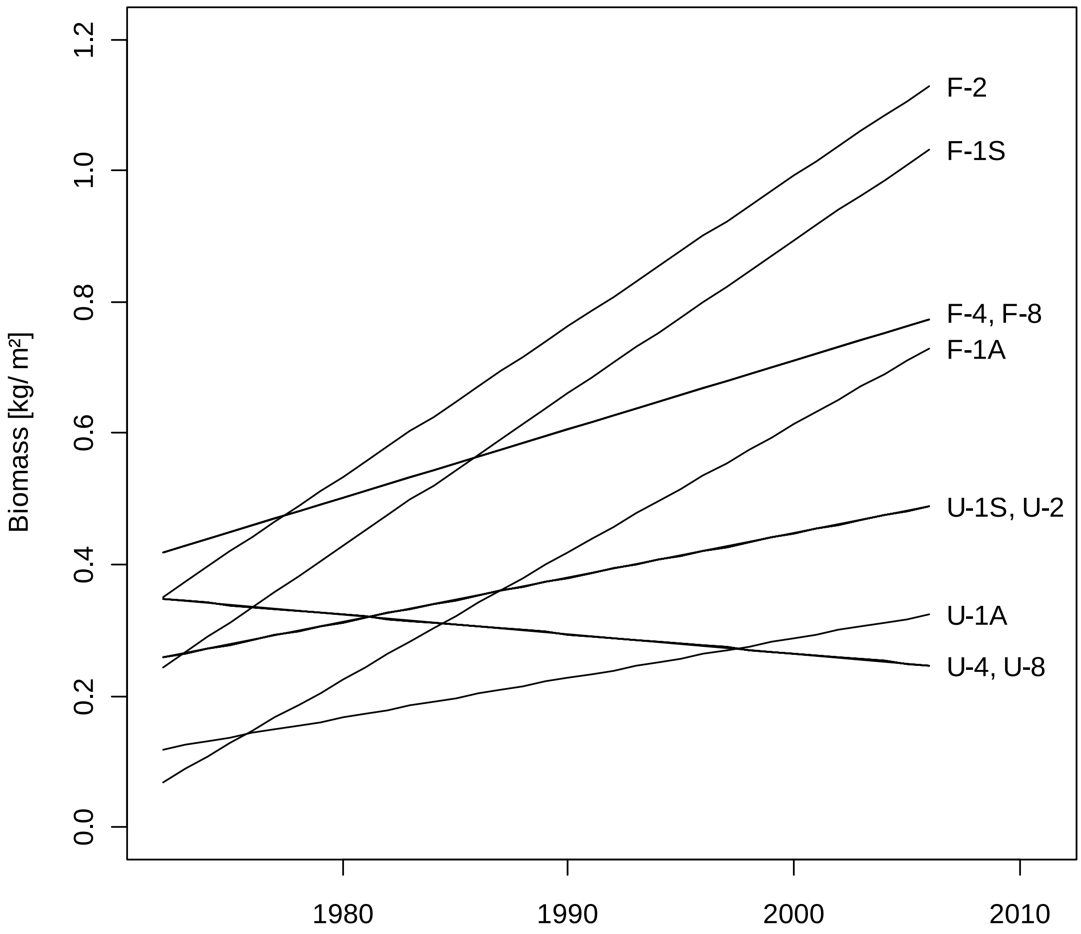

Fig. 1: Bernhardt-Römermann et al.

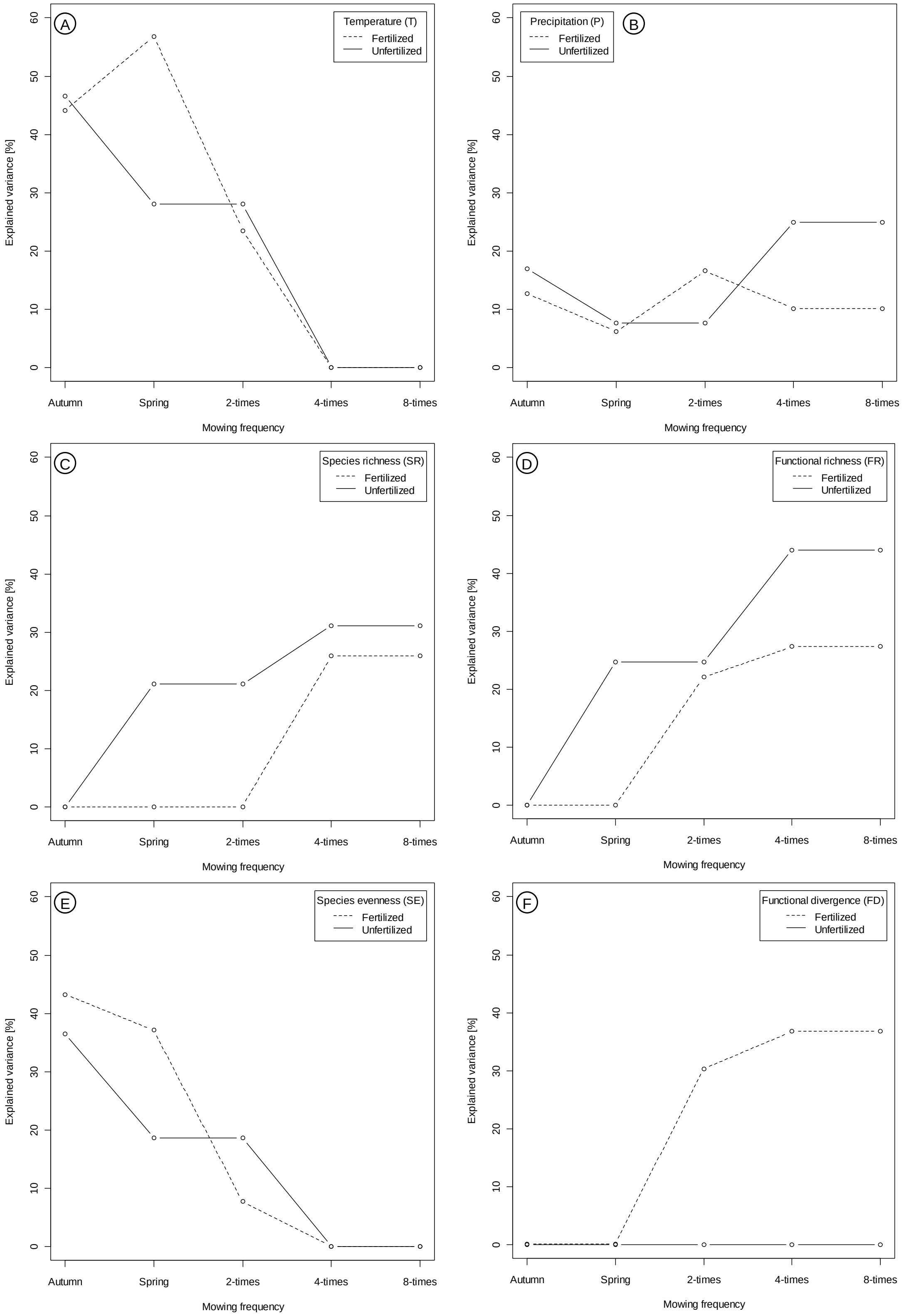

Fig. 2: Bernhardt-Römermann et al.