Direct and indirect associations between plant species richness and productivity in grasslands: regional differences preclude simple generalization of productivity-biodiversity relationships

Přímé a nepřímé vztahy mezi druhovou bohatostí a produktivitou travních společenstev: regionální rozdíly znemožňují jednoduché zobecnění

Valentin H. K l a u s[1], Norbert H ö l z e l[1], Steffen B o c h[2], Jörg M ü l l e r[3], Stephanie A. S o c h e r[2], Daniel P r a t i[2], Markus F i s c h e r[2,3] & Till K l e i n e b e c k e r[1]

[1]*Universität Münster, Institute of Landscape Ecology, Robert-Koch-Str. 28, 48149 Münster, Germany, e-mail: v.klaus@uni-muenster.de;* [2]*Universität Bern, Institute of Plant Sciences, Botanical Garden and Oeschger Center, Altenbergrain 21, 3013 Bern, Switzerland;* [3]*Universität Potsdam, Institute of Biochemistry and Biology, Maulbeerallee 1, 14469 Potsdam, Germany*

Plant species richness of permanent grasslands has often been found to be significantly associated with productivity. Concentrations of nutrients in biomass can give further insight into these productivity-plant species richness relationships, e.g. by reflecting land use or soil characteristics. However, the consistency of such relationships across different regions has rarely been taken into account, which might significantly compromise our potential for generalization. We recorded plant species richness and measured above-ground biomass and concentrations of nutrients in biomass in 295 grasslands in three regions in Germany that differ in soil and climatic conditions. Structural equation modelling revealed that nutrient concentrations were mostly indirectly associated with plant species richness via biomass production. However, negative associations between the concentrations of different nutrients and biomass and plant species richness differed considerably among regions. While in two regions, more than 40% of the variation in plant species richness could be attributed to variation in biomass, K, P, and to some degree also N concentrations, in the third region only 15% of the variation could be explained in this way. Generally, highest plant species richness was recorded in grasslands where N and P were co-limiting plant growth, in contrast to N or K (co-) limitation. But again, this pattern was not recorded in the third region. While for two regions land-use intensity and especially the application of fertilizers are suggested to be the main drivers causing the observed negative associations with productivity, in the third region the little variance accounted for, low species richness and weak relationships implied that former intensive grassland management, ongoing mineralization of peat and fluctuating water levels in fen grasslands have overruled effects of current land-use intensity and productivity. Finally, we conclude that regional replication is of major importance for studies seeking general insights into productivity-diversity relationships.

Keywords: anthropogenic effect, Biodiversity Exploratories project, fen grasslands, generalizability, land-use history, nitrogen, phosphorus, potassium, plant species richness, structural equation modeling

Introduction

The relationship between grassland productivity and biodiversity is a hotly debated topic in ecological research (Adler et al. 2011, Fridley et al. 2012, Grace et al. 2012). Besides

interest in mechanistic interactions between productivity and biodiversity, effects on fundamental ecosystem functions and services are of economical and societal importance (Tilman & Downing 1994, Myers 1996, Tscharntke et al. 2005). Modern agriculture, targeting the maximization of yield, has drastically increased land-use intensity at the landscape scale and often resulted in a radical drop in agrobiodiversity (Reidsma et al. 2006).

Although the relationship between productivity and plant species richness in grasslands was found to be (theoretically) hump-shaped along the entire gradient of productivity (Grime 1979), studies dealing with agricultural grasslands mostly assessed only the right, decreasing slope of the curve where high productivity restricts diversity, because vegetation on extremely nutrient-poor soils was widely excluded from the sampling. Thus, plot selection in several studies dealing with European grasslands resulted in the mostly significant negative relationships between productivity and plant species richness recorded (e.g. Vermeer & Berendse 1983, Olde Venterink et al. 2003, Gross et al. 2009, Socher et al. 2012).

Usually, grassland productivity is assessed as yield (above-ground biomass), but the concentrations of nutrients in plant biomass are also regarded as a reliable proxy for productivity integrating relevant factors for plant growth over time and space (Güsewell & Koerselman 2002, Marschner 2005). Biomass nutrient concentrations can integrate several aspects affecting grassland diversity, for instance, functional composition, land-use practice such as intensity of fertilizer application, and other environmental factors such as soil type or ground water level, thereby incorporating information independent of productivity. Thus, biomass nutrient concentrations can provide a deeper insight into productivity-biodiversity relationships as well as other important drivers of plant species richness (e.g. Olde Venterink et al. 2003, Hejcman et al. 2010, Klaus et al. 2011a, b, Blüthgen et al. 2012). Additionally, nutrient ratios in biomass can be used to estimate the relative importance of a specific nutrient for productivity, growth limitation and subsequently biodiversity (Koerselman & Meuleman 1996, Aerts & Chapin 2000, Güsewell 2004). However, nutrient concentrations may be closely correlated with biomass production, which complicates the analysis of how different types of nutrient limitation and productivity affect plant communities and their diversity (Willby et al. 2001, Olde Venterink et al. 2009). Disentangling the effects of nutrient limitation and productivity is thus of wide ecological relevance, as limitation may directly affect species composition and richness (Olde Venterink et al. 2003).

Additionally, the biodiversity-productivity relationship can vary strongly due to regional or local peculiarities, including climatic, topographical or pedological factors and their modification by anthropogenic influences (Grace 1999, Crawley et al. 2005). However, in ecological studies using biomass nutrient concentrations such confounding factors are rarely considered, thus the topic of regional differences in the described relationships need further examination (Gross et al. 2000, Cornwell & Grubb 2003). Particularly for the generalization of driving mechanisms, a high number of observations and the detection of regional patterns are of crucial importance (Belovsky et al. 2004).

We assessed relationships between plant species richness, productivity and nutrient concentrations in agricultural grasslands in three regions in Germany and selected a total of 295 plots covering a wide gradient of land-use intensity and productivity. In a previous study, we showed how components of land use affected plant diversity, based on a smaller number of plots (Socher et al. 2012). The present paper focuses on how nutrient concen-

trations can be used to predict diversity of vascular plants. For each plot, we recorded plant species richness and measured above-ground biomass, nutrient concentrations in biomass and calculated nutrient ratios to assess the type of nutritional growth limitation. To overcome inter-correlations among productivity and nutrient concentrations in biomass, we used structural equation modelling (SEM) to test the following hypotheses: (i) biomass nutrient concentrations are mostly indirectly related to plant species richness via biomass production and (ii) plant species richness is similarly related to different types of nutrient limitation. For both hypotheses, we tested for differences among study regions to assess to what degree observed productivity-biodiversity relationships vary with regional factors.

Methods

Study areas and sampling

The grasslands studied are part of the Biodiversity Exploratories project for long-term ecological research (Fischer et al. 2010) and located in three regions in Germany: the UNESCO Biosphere Reserve Schorfheide-Chorin in the northeast, the National Park Hainich with surroundings (Dün) in the centre and the UNESCO Biosphere Reserve Schwäbische Alb in the southwest. There is a climatic gradient of increasing precipitation and altitude, and slightly lower mean annual temperatures from north to south (Table 1). Restricted to the most common soil types, in each study area 500 grassland plots were randomly selected to roughly assess the land use of these plots. From these 500 plots we selected about 100 plots per study region using mean Ellenberg nutrient values derived from vegetation relevés to achieve an evenly distributed data set across a wide gradient of grassland productivities (Table 1). In the more hilly regions Schwäbische Alb and in Hainich-Dün, grasslands were restricted to mineral soils, whereas in Schorfheide-Chorin about half of the plots were situated on drained fen soils (histosols). This selection resulted in a data set that well reflected the gradient of land-use intensities representative of large parts of the central-European grasslands (Fischer et al. 2010). The data set finally consisted of 295 grasslands of which 93 were situated in the Schwäbische Alb, 102 in Hainich-Dün and 100 in Schorfheide-Chorin. Most of the vegetation studied belongs to *Arrhenatherion elatioris* W. Koch 1926 and *Cynosurion cristati* Tx. 1947 communities, with transitions to *Polygono-Trisetion* Br.-Bl. et Tx. ex Marschall 1947 nom. invers. propos., *Calthion* Tx. 1937 and *Magnocaricion elatae* W. Koch 1926 communities depending on altitude and soil moisture. Additionally, *Bromion erecti* Koch 1926-communities occurred on shallow calcareous soils. For each plot, we assessed species richness of vascular plants in subplots of 4×4 m, during May and June, in one half of the plots in 2007 and the other in 2010. This difference in assessment time was not thought to pose a problem as plant species richness in grasslands remains relatively stable over this period of time and recordings repeated in 2007 and 2010 revealed a strong correlation between species numbers (n = 148, $r_S = 0.83$, P < 0.001). In May and early June 2010, above-ground biomass was harvested as mixed samples, each from four randomly placed quadrates of 0.25 m^2 in all three study areas, simultaneously to ensure comparability of data. At most plots, temporary fences ensured that the biomass was sampled before it was utilized for agricultural purposes. However, on nine plots there was a small amount of grazing prior to sampling.

Table 1. – Environmental characteristics and mean values ± SE of parameters of the vegetation in the grasslands in the three regions studied (Fischer et al. 2010). Small letters indicate significant differences between regions (Mann-Whitney U-test with Bonferroni correction, P < 0.05).

	Schwäbische Alb	Hainich-Dün	Schorfheide-Chorin
Number of plots	93	102	100
Landscape type	low mountain range	hilly land	lowland (glacial)
Soils substrate	limestone with clay layer	limestone with loess layer	fen peat and glacial sand
Altitude a.s.l.	720–840 m	300–400 m	10–140 m
Annual mean temperature	6.0–7.0 °C	6.5–7.5 °C	8.0–8.5 °C
Annual mean precipitation	700–1000 mm	750–800 mm	500–600 mm
Biomass N (g·kg^{-1})	23.5±0.4[ab]	23.0±0.4[b]	25.0±0.5[a]
Min/max	16.1/40.5	13.4/35.5	14.2/36.6
Biomass P (g·kg^{-1})	3.0±0.1[ab]	3.1±0.1[a]	2.9±0.1[b]
Min/max	1.3/4.1	1.9/4.0	1.8/4.6
Biomass K (g·kg^{-1})	22.2±0.8[b]	26.7±0.6[a]	19.5±0.9[b]
Min/max	8.4/38.6	9.7/39.6	3.2/47.6
Yield (g·m^{-2})	217±15[a]	223±12[a]	179±10[b]
Min/max	25/783	38/587	42/634
Number plant species	30.6±1.3[a]	27.3±1.2[a]	19.2±0.7[b]
Min/max	9/67	5/73	4/42
Ellenberg N value	5.2±0.2[b]	6.3±1.0 [a]	6.2±0.1[a]
Min/max	2.3/7.2	3.0/7.7	1.7/8.2
K (co-)limitation	n = 1	0	9
N limitation	n = 73	97	63
NP co-limitation	n = 19	5	24
No limitation	n = 0	0	4

Chemical analyses

Biomass samples were dried immediately after harvest for 48 h at 80 °C and ground fine enough to pass through the mesh of 0.5-mm sieve. Samples were analysed for N, P and K by means of near infrared reflectance (NIR) spectroscopy (Foley et al. 1998). We recorded the reflectance spectrum of each sample between 1250 to 2350 nm at 1 nm intervals. Each sample scan consisted of 24 single measurements, which were averaged to one spectrum. Calibration models that were used to predict N, P and K concentrations were derived from the laboratory data for half of the plots previously sampled in 2009 (Kleinebecker et al. 2011a). Accuracy of model predictions was checked by applying an external validation process. When concentrations of elements exceeded the range of values included in the original calibration models, we analysed the samples in the laboratory and added the results to the calibration data in order to improve the models. Multiple correlation coefficients (r) and root mean square errors of cross-validation (RMSECV) of the calibration models used were r = 0.99, 0.90 and 0.97, and RMSECV = 0.85, 0.45 and 2.60 g·kg^{-1} for N, P, and K, respectively. For methodological details of the laboratory reference measurements and NIR spectral analyses see Kleinebecker et al. (2011a).

Statistics

To determine the inter-correlations between yield and nutrient concentrations and separate direct and indirect effects on plant species richness, structural equation modelling (SEM)

of the total data set and that for each study area separately, was used (Shipley 2002). SEM makes it possible to distinguish between the direct effects of nutrient concentrations and indirect effects via biomass, which is necessary because nutrient concentrations and biomass were correlated to varying degrees. Compared with multiple regressions, SEMs are a more informative method of dealing with correlated explanatory variables. This method is limited to the same degree as regression analysis based on observational data in that one cannot infer causal relationships for any of the direct effects quantified. For all statistical tests, plant species richness and biomass were square root transformed to ensure normal distribution of the data. To analyse the results for the different major soil types in Schorfheide-Chorin separately, two additional SEMs were calculated. As detailed information on land use was not available for all grassland plots, intensities of mowing, fertilizer application and cutting could not be included in the SEM models. Models were first run with all paths and re-run after removing non significant inter-correlations between nutrient concentrations and biomass to save the degrees of freedom necessary for model testing. Standardized estimates for paths were gained by replicating the final model with data standardized by mean and SD of the respective data set (z-transformation) according to Shipley (2002). Additionally, we calculated linear models to explore relationships between plant species richness and biomass for plots with different types of nutrient limitation. All statistical tests were performed using R version 2.14.1 (R Development Core Team 2011) and the sem-package (Fox 2006).

To assess the extent to which the growth of the grasslands studied was limited by nutrients we calculated the nutrient ratios of N, P and K in plant biomass according to Koerselman & Meuleman (1996), Olde Venterink et al. (2003) and Güsewell (2004). N limitation was defined as N:P ≤ 10 and N:K < 2.1, NP co-limitation as N:P between 10 and 16 and K:P > 3.4, K (co-)limitation as N:K > 2.1 and K:P < 3.4 and P limitation as N:P > 16.

Results

Productivity estimates and plant species richness

Mean biomass nutrient concentrations were relatively similar among regions, but plant species richness and biomass were considerably lower in the region Schorfheide-Chorin (Table 1, Fig. 1A). For the Schwäbische Alb and Hainich-Dün, analyses revealed that more than 40% of the variation in plant species richness can be accounted for in terms of N, P and K concentrations and biomass, while at Schorfheide-Chorin productivity measures accounted for only 15% (Fig. 2). Thus, percentage of variance of the total dataset accounted for was only 24%.

Productivity and nutrient concentrations were largely negatively associated with plant species richness, although regional SEMs differed in the factors selected. Biomass was the most important explanatory variable in the regional and overall data sets, with the exception that P was slightly more strongly associated with plant species richness in the Schwäbische Alb (Fig. 2). In all regions, nutrient concentrations (especially P and K) were strongly positively inter-correlated with each other and with biomass. Thus, nutrient concentrations were mostly indirectly associated with plant species richness via biomass. The predictions of the SEM of the total dataset differed from these patterns in terms of K concentrations, as it was indirectly negatively but also directly positively associated with plant
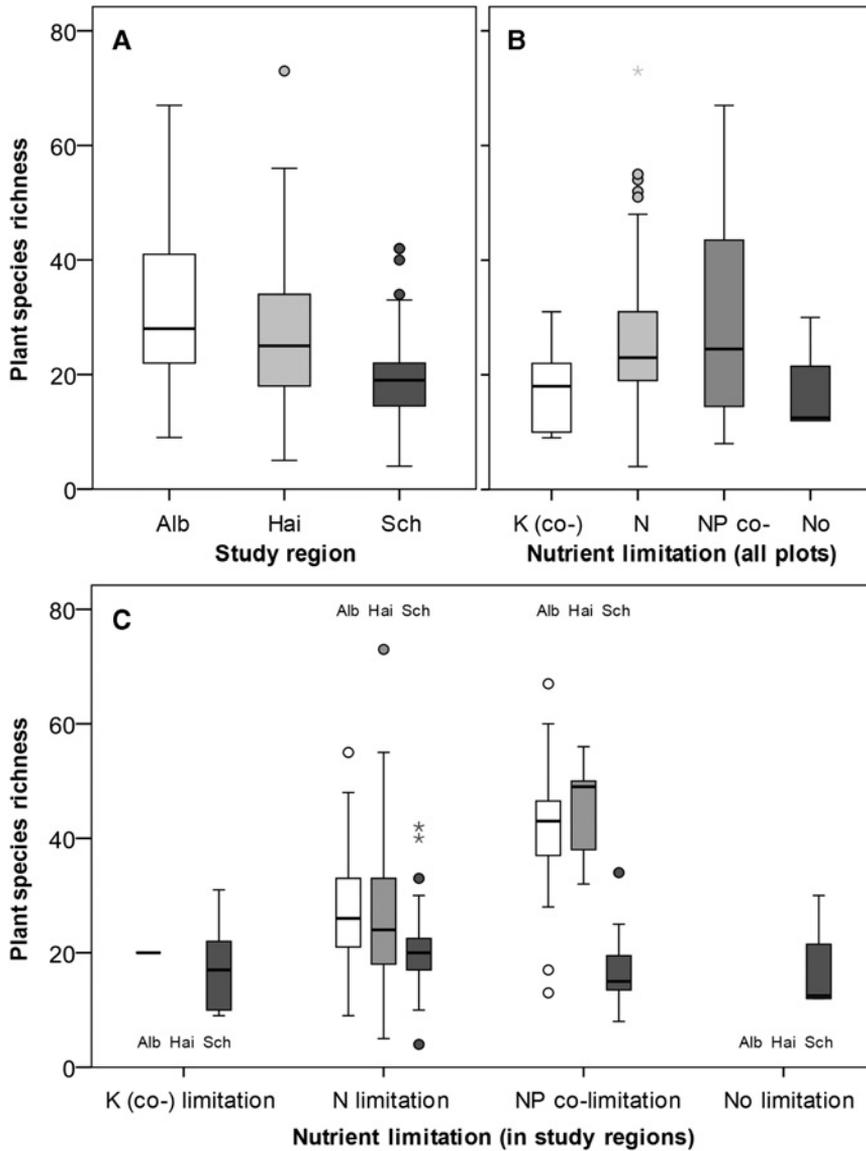
Fig. 1. – Mean plant species richness (A) in the regions studied, (B) in relation to types of nutrient limitation based on the total dataset and (C) that for each of the regions studied: Alb = Schwäbische Alb, Hai = Hainich-Dün, Sch = Schorfheide-Chorin. Limitation categories refer to Koerselman & Meuleman (1996), Olde Venterink et al. (2003) and Güsewell (2004). No limitation implies that grasslands could not be attributed to any nutrient limitation type. Absence of bars indicates no plot in this category. For respective n see Table 1. The box represents values within the 25th to 75th percentiles with the median as thick line. The whiskers range from the highest to the lowest values with outliers and extreme values as dots (1.5 to 3 times box length outside box) and stars (more than 3 times box length outside box).
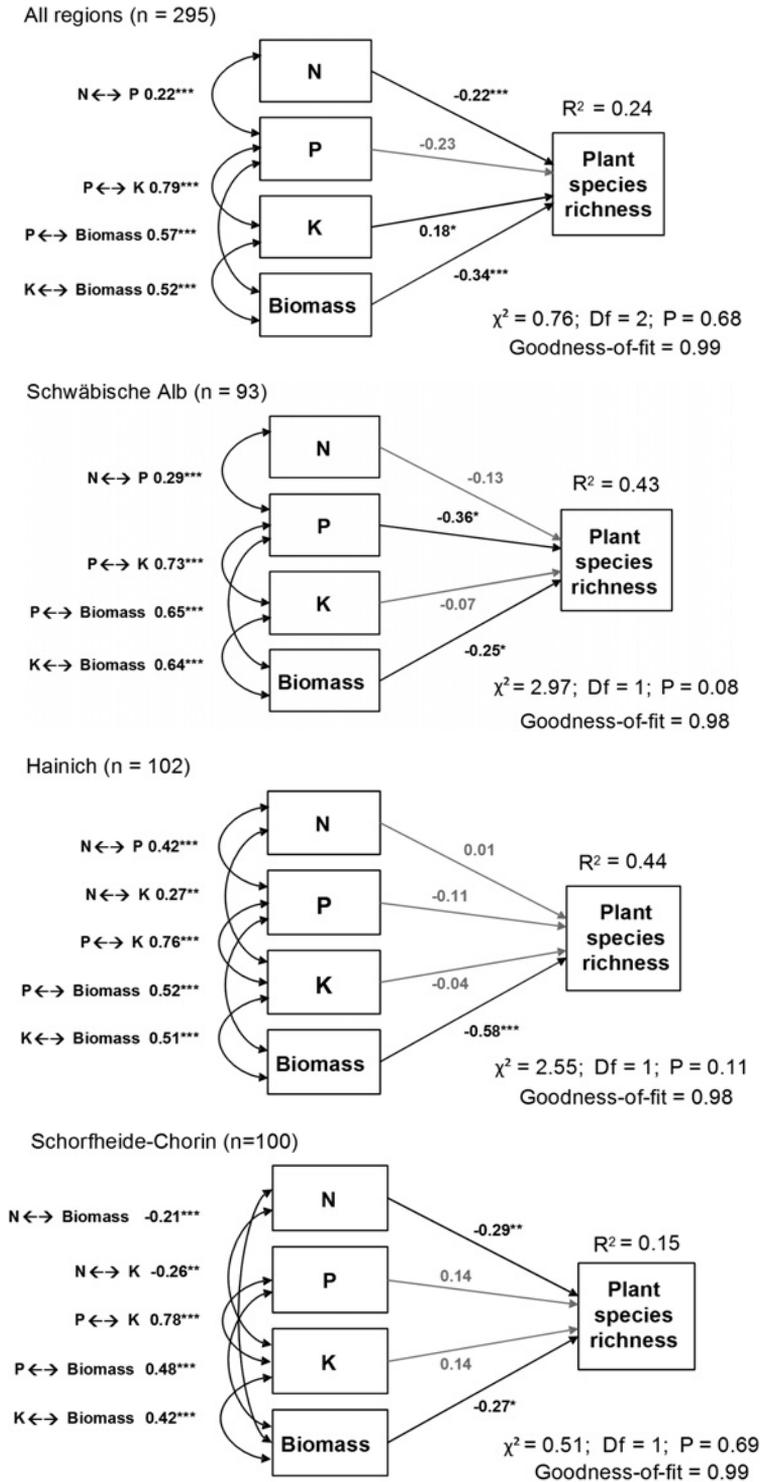
Fig. 2. – Statistical models resulting from the structural equation modeling, which relates above-ground biomass, nutrient concentrations in biomass and plant species richness, plotted together and separately for the three areas studied. Black arrows mark significant path between variables.

Table 2. – Environmental characteristics and mean values ± SE of parameters of the vegetation in the grasslands in the region Schorfheide-Chorin, separated based on soil type (mineral versus organic). Letters indicate significant differences between soil types (t-test, P <0.05).

	Schorfheide-Chorin	
Number of plots	54	46
Substrate	organic	mineral
Soil types	histosol	luvisol, albeluvisol, cambisol, regosol and gleyosol
Biomass N (g·kg^{-1})	27.4±0.6[A]	22.1±0.8[B]
Min/max	19.6/36.6	14.2/35.5
Biomass P (g·kg^{-1})	2.6±0.1[B]	3.2±0.1 [A]
Min/max	1.9/4.1	1.8/4.6
Biomass K (g·kg^{-1})	13.6±0.9[B]	26.5±1.1[A]
Min/max	3.2/33.7	12.3/47.6
Yield (g·m^{-2})	150±9[B]	214±18[A]
Min/max	61/369	42/634
Number plant species	17.0±0.8[B]	21.9±1.0[A]
Min/max	4/34	10/42
Ellenberg N value	6.4±0.1[A]	6.0±0.2[B]
Min/max	4.3/7.4	1.7/8.2
Plant species richness in different types of nutrient limitation		
K (co-)limitation (n)	17.2 (9)	– (0)
N limitation (n)	17.6 (19)	22.1 (44)
NP co-limitation (n)	16.4 (22)	17.5 (2)
No limitation (n)	16.8 (4)	– (0)

species richness. Furthermore and in contrast to all other analyses, N concentrations at Schorfheide-Chorin were significantly negatively associated with biomass and K concentrations (Fig. 2). Separate analyses of organic and mineral soils from plots at Schorfheide-Chorin revealed a negative association between biomass and plant species richness for mineral soils, and no significant association between species richness and any of the productivity measures for organic fen soils (Table 2, Fig. 3).

In summary, the analyses revealed that the negative associations between plant species richness and nutrient concentrations differed in the three regions and that biomass had indirect mediating effects on nutrient concentrations, although direct effects of N, P or K concentrations on plant species richness were also recorded.

Type of nutrient limitation

Types of nutrient limitation differed between grasslands and were closely associated with species richness. About 79% of all the grasslands studied were limited by N, 16% by N and P together, 3.5% by K and 1.5% did not appear to be limited by these three nutrients (Table 1, Fig. 1B). Based on the applied threshold of N:P > 16, P limitation did not occur. Mean biomass per square meter was 230 g in N limited, 115 g in NP co-limited and 121 g in K (co-)limited grasslands. Limitations of the different nutrients accounted for 29% of the variance in total plant species richness (P < 0.001). At the Schwäbische Alb and Hainich-Dün, by far the highest species richness was recorded in NP co-limited grasslands
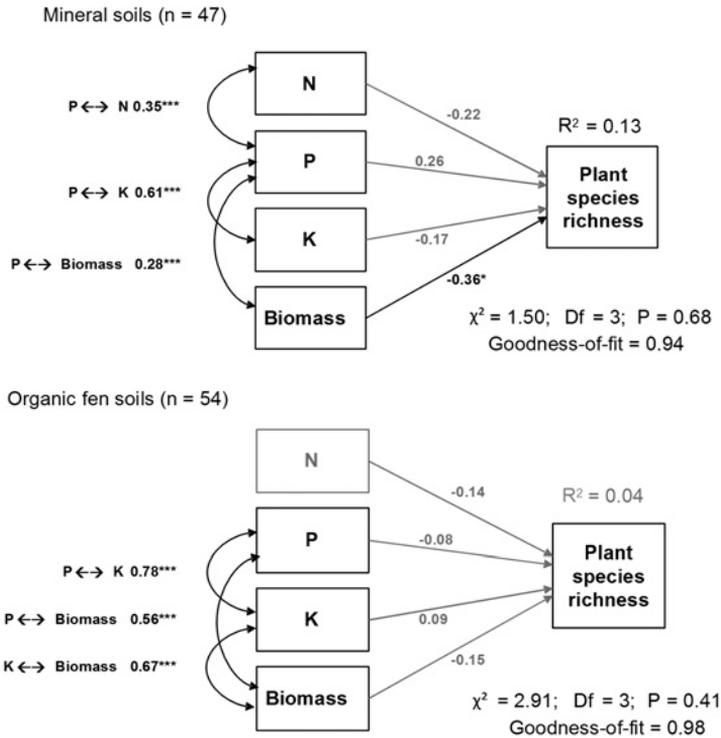
Fig. 3. – Statistical models resulting from the structural equation modeling of the results for Schorfheide-Chorin grasslands, which relate above-ground biomass, nutrient concentrations in biomass and plant species richness for mineral and organic fen soils (drained histosols) separately. Black arrows mark significant path between variables. Further details are given in Table 2.

(Fig. 1C). At Schorfheide-Chorin species richness did not vary substantially in areas with different types of nutrient limitation (Fig. 1C), even if organic fen and mineral soils were analysed separately (Table 2). Above-ground biomass and plant species richness were significantly negatively associated with N and NP co-limited but not K limited grasslands. Compared to N limitation, NP co-limitation was only recorded in areas with a low to intermediate biomass production, which resulted in a significantly steeper slope of the species richness-biomass relationship (Fig. 4).

Discussion

Negative associations between plant species richness and estimates of grassland productivity differed to a certain degree not only among the regions but also among different types of nutrient limitation. However, compared to nutrient concentrations in biomass, above-ground biomass production is clearly the better measure for determining the association between species diversity and productivity of agricultural grasslands located in different regions. Nevertheless, the concentrations of nutrients in biomass and data on nutrient
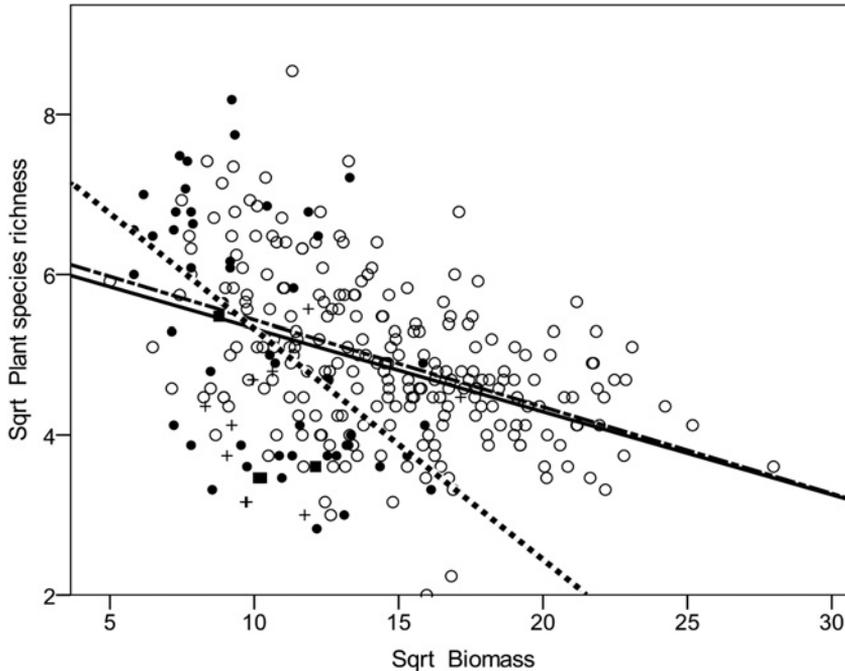
Fig. 4. – Association between plant species richness and biomass in the grasslands studied (n = 295). Different symbols indicate different types of nutrient limitation: open circles = N limitation (n = 233), filled circles = NP co-limitation (n = 48), crosses = K (co-)limitation (n = 10), filled quadrates = could not attribute a limitation (n = 4). Only significant regression lines are shown. Solid line = all plots, broken line = N limited plots, dotted line = NP co-limited plots. Regression axis of N limited and NP co-limited plots differ significantly (P < 0.001).

limitation provide additional information on the mechanistic aspects of these associations, which are supported by the significant direct effects of nutrient concentrations on species richness. Below, we firstly mention what can be concluded from regionally consistent findings and then discuss possible explanations for the differences observed.

Plant species richness associated with productivity and nutrient limitation

At the Schwäbische Alb and Hainich-Dün, biomass, P, K and to some degree concentrations of N make up a complex of highly inter-correlated factors, negatively associated with plant species richness. In this study, nutrient concentrations were mostly indirectly associated with plant species richness, via biomass. This pattern, plus the direct effects of P on species richness are thought to be mainly driven by the application of fertilizers and intensity of land use, which result in the uptake and storage of (added) nutrients in plants and additional growth causing an increase in competition for light and the exclusion of several species of plants (Grime 1979, Hautier et al. 2009). Concentrations of P and K, increase in grassland biomass when fertilizers containing these nutrients are applied, whereas N concentrations are much less affected due to the so called dilution effect, as the concentrations of N can decrease after application of fertilizer due to the stimulation of additional plant

growth (Hejcman et al. 2007, Kleinebecker et al. 2011b). Consequently, N concentrations are often less strongly associated with land use-intensity and productivity (Klaus et al. 2011a). This is also in accordance with the mostly indirect, productivity mediated effects of land-use intensity on plant species richness in grasslands (Socher et al. 2012).

Plant species richness differed considerably depending on the type of nutrient limitation and was highest at sites in Schwäbische Alb and Hainich-Dün with NP co-limitation, where it was more than 50% higher than at sites where there were other types of nutrient limitation. However, in Schorfheide-Chorin this was not the case. The strong importance of P compared to N enrichment for (endangered) plant species richness is in line with findings for herbaceous vegetation by Wassen et al. (2005) and Ceulemans et al. (2011). In contrast, Van de Riet et al. (2010) records K (co-)limited wet grasslands that are rich in species and do not respond to the addition of P. Nevertheless, Aerts & Chapin (2000) and Harpole & Tilman (2007) suggest that if two or more nutrients simultaneously limit plant growth (strong co-limitation by N and P) then it is more likely that productivity will be restricted and niche separation fostered resulting in the coexistence of more plant species. This is supported by the results of experiments in which the simultaneous application of NPK to grassland resulted in the strongest decrease in species richness (Crawley et al. 2005).

In summary, our results show that plant species richness in agricultural grasslands was only to a certain degree associated with productivity, in this study up to 40%, as direct effects of land use, regional species pool size and other environmental factors also control local species richness (Pärtel et al. 1996, Grace 1999, Socher et al. 2012). Similarly, whether K, P or biomass are more closely associated with plant species richness at a single site might also be the result of a multiplicity of different factors at the plot scale and moreover vary from year to year.

Generalizability of productivity-biodiversity relationships

The patterns observed in the region Schorfheide-Chorin differed significantly from those in the Schwäbische Alb and Hainich-Dün, both in mean plant species richness but also mechanistically based on the relationships between plant species richness and productivity and nutrient limitation. Two associated factors are likely to have caused these deviations in Schorfheide-Chorin: (i) the inclusion of grasslands on drained fen soils and (ii) depleted regional species richness due to former intensive land use.

Unlike the clay-rich mineral soils, which dominate two of the regions included in this study, drained fen soils can strongly deplete of K even if moderate amounts of K containing fertilizer are added, triggering K (co-)limitation of vegetation growth (Olde Venterink et al. 2001, 2003, 2009). As the species richness of the grasslands on mineral soils in the Schorfheide-Chorin region was significantly higher than that of fen grasslands, the observed positive association between K and plant species richness is due to the soil K supply, which is closely connected to K in the biomass (Schaffers 2002). Contrary to K depletion in drained fen soils, the supply of N and P can be excessive, due to ongoing mineralization and continuous nutrient release from the peat (Lamers et al. 2002), which is in line with our findings. This underlines the additional information stored in biomass nutrient concentrations, which are particularly useful for determining site specific peculiarities (e.g. due to soil conditions) and general mechanisms.

Furthermore, in the fen grasslands studied neither biomass nor any of the nutrients in the biomass were significantly associated with plant species richness. Here, additional factors at the regional and local scale are likely to overrule expected relationships. Among these, the land-use history of this area is considered to be of outstanding importance, as similarly shown for e.g. dry grasslands (Chýlová & Münzbergová 2008, Karlík & Poschlod 2009), because until the 1960/70s intensification of land use in this area involved improving the drainage, ploughing and reseeding, which resulted in a severe decline in the species richness of many grasslands (Kaiser et al. 2005, Flade et al. 2006). Although the intensity with which local land was used was significantly reduced in the 1990s (Luthardt et al. 2005), intensive land use has long-lasting negative consequences for plant species richness, in particular that of fen grasslands, even after more than 30 years without fertilizer application (Käding & Schmidt 1995). Thus, species richness may still not reflect the current management intensity but that of former intensive land use (Haas et al. 2001, Isselstein et al. 2005), although current mean biomass yield was significantly lower here compared to the two other regions. The depleted regional species richness in the Schorfheide-Chorin region can also be seen as the reason for the steeper slope of the species richness-productivity relationship in NP co-limited grasslands, because NP co-limited grasslands with high biomass production from this region are all generally species-poor plots. Thus, to investigate and generalize the differences in slope between N and NP co-limited grasslands, further research is needed.

Furthermore, clear and significant relationships between plant species richness and productivity measures often strongly depend on including sites with high species richness (Grace 1999), which was not the case for Schorfheide-Chorin. However, in summary, the results for Schorfheide-Chorin indicate that historic land use can potentially significantly override the relationships recorded between current species richness, nutrient concentrations and biomass in the other two regions. This could also indicate a gap between realized and potential plant species richness, which might be bridged by the transfer of plant propagules in order to overcome seed and dispersal limitation (Käding & Petrich 1998, Donath et al. 2003, Poptcheva et al. 2009).

Conclusion

This study revealed that the plant species richness of grasslands is closely associated with biomass production and also either directly or indirectly with biomass nutrient concentrations, especially P and to some degree N. However, this study also indicates that this pattern only applies if there are no additional factors such as land-use history, which can obscure the expected patterns. While plant species richness was usually highest in NP co-limited grasslands, this was not the case in one of the study regions in which they were located in a highly anthropogenically modified landscape, which diminished the degree to which the findings could be generalized. The results indicate that ecological studies that aim to generalize their findings should carefully consider regional differences, as previous studies found strong effects of e.g. species assembly and disturbance history (Pärtel et al. 1996, Chýlová & Münzbergová 2008). In particular, investigations on productivity-biodiversity relationships should consider as many factors as possible, including land-use history and regional species pools, although this might be challenging. Moreover, our

findings highlight the need for many replicates at different spatial scales if one is to distinguish general patterns from regional characteristics and avoid making premature generalizations.

Acknowledgements

Souhrn

V literatuře bylo opakovaně doloženo, že druhová bohatost trvalých travních společenstev souvisí s produktivitou. Studium koncentrace živin v biomase může poskytnout detailnější poznatky o tomto vztahu, neboť odráží vlastnosti půdy a vliv obhospodařování krajiny. Jen zřídka je však zohledněna regionální variabilita, která může značně omezit možnosti zobecnění poznatků o vztahu druhové bohatosti a produktivity. Na 295 plochách v travních společenstvech ve třech oblastech v Německu jsme zaznamenali druhovou bohatost a nadzemní biomasu a změřili koncentraci živin v biomase. Modelování strukturálními rovnicemi ukázalo, že koncentrace živin nepřímo ovlivňuje druhovou bohatost prostřednictvím produkce biomasy. Negativní vztah mezi různými druhy živin a biomasou a druhovou bohatostí se však v jednotlivých regionech značně lišil. Zatímco ve dvou regionech vysvětloval více než 40 % variability v druhové bohatosti obsah draslíku, fosforu, a do určité míry i dusíku v biomase, ve třetím bylo pomocí těchto proměnných možno vysvětlit pouze 15 %. Obecně platí, že druhově nejbohatší jsou porosty, kde růst rostlin společným působením omezuje koncentrace dusíku a fosforu, nikoli dusíku a draslíku; ani v tomto případě však toto zjištění neplatí pro třetí oblast. V prvních dvou regionech lze za hlavní příčinu pozorovaného negativního vztahu s produktivitou označit intenzitu využívání krajiny a aplikaci hnojiv; ve třetím je vliv současného obhospodařování překryt intenzivním obhospodařováním travních porostů v minulosti a probíhající mineralizací rašeliny a kolísající hladinou vody na prameništních loukách. Práce poukazuje na to, že obecně platné zákonitosti vztahu mezi produktivitou a diverzitou lze odhalit pouze při srovnání výsledků z více oblastí.

References

Adler P. B., Seabloom E. W., Borer E. T., Hillebrand H., Hautier Y., Hectos A., Harpole W. S., O'Halloran L. R., Grace J. B., Anderson T. M., Bakker J. D., Biederman L. A., Brown C. S., Buckley Y. M., Calabrese L. B., Chu C.-J., Cleland E. E., Collins S. L., Cottingham K. L., Crawley M. J., Damschen E. I., Davies K. F., DeCrappeo N. M., Fay P. A., Firn J., Frater P., Gasarch E. I., Gruner D. S., Hagenah N., Lambers J. H. R., Humphries H., Jin V. L., Kay A. D., Kirkman K. P., Klein J. A., Knops J. M. H., La Pierre K. J., Lambrinos J. G., Li W., MacDougall A. S., McCulley R. L., Melbourne B. A., Mitchell C. E., Moore J. L., Morgan J. W., Mortensen B., Orrock J. L., Prober S. M., Pyke D. A., Risch A. C., Schütz M., Smith M. D., Stevens C. J., Sullivan L. L., Wang G., Wragg P. D., Wright J. P. & Yang L. H. (2011): Productivity is a poor predictor of plant species richness. – Science 333: 1750–1752.

Aerts R. & Chapin F. S. (2000): The mineral nutrition of wild plants revisited: a re-evaluation of processes and patterns. – Adv. Ecol. Res. 30: 1–67.

Belovsky G. E., Botkin D. B., Crowl T. A., Cummins K. W., Franklin J. F., Hunter M. L., Joern A., Lindenmayer D. B., MacMahon J. A., Margules C. R. & Scott J. M. (2004): Ten suggestions to strengthen the science of ecology. – Bioscience 54: 345–351.

Blüthgen N., Dormann C. F., Prati D., Klaus V. H., Kleinebecker T., Hölzel N., Alt F., Boch S., Gockel S., Hemp A., Müller J., Nieschulze J., Renner S. C., Schöning I., Schumacher U., Socher S. A., Wells K., Birkhofer K., Buscot F., Oelmann Y., Rothenwöhrer C., Scherber C., Tscharntke T., Weiner C. N., Fischer M., Kalko E. K.

V., Linsenmair K. E., Schulze E.-D. & Weisser W. W. (2012): A quantitative index of land-use intensity in grasslands: integrating mowing, grazing and fertilization. – Basic Appl. Ecol. 13: 207–220.

Ceulemans T., Merckx R., Hens M. & Honnay O. (2011): A trait-based analysis of the role of phosphorus vs nitrogen enrichment in plant species loss across North-west European grasslands. – J. Appl. Ecol. 48: 1155–1163.

Chýlová T. & Münzbergová Z. (2008): Past land use co-determines the present distribution of dry grassland plant species. – Preslia 80: 183–198.

Cornwell W. K. & Grubb J. P. (2003): Regional and local patterns in plant species richness with respect to recource availability. – Oikos 100: 417–428.

Crawley M. J., Johnston A. E., Silvertown J., Dodd M., de Mazancourt C., Heard M. S., Henman D. F. & Edwards G. R. (2005): Determinants of species richness in the Park Grass Experiment. – Am. Nat. 165: 179–192.

Donath T. W., Hölzel N. & Otte A. (2003): The impact of site conditions and seed dispersal on restoration success in alluvial meadows. – Appl. Veg. Sci. 6: 13–22.

Fischer M., Bossdorf O., Gockel S., Hänsel F., Hemp A., Hessenmöller D., Korte G., Nieschulze J., Pfeiffer S., Prati D., Renner S., Schöning I., Schumacher U., Wells K., Buscot F., Kalko E. K. V., Linsenmair K. E., Schulze E.-D. & Weisser W. W. (2010): Implementing large-scale and long-term functional biodiversity research: the Biodiversity Exploratories. – Basic Appl. Ecol. 11: 473–485.

Flade M., Plachter H., Schmidt R. & Werner A. (2006): Nature conservation in agricultural ecosystems: results of the Schorfheide-Chorin research project. – Quelle & Meyer, Wiebelsheim.

Foley W. J., McIlwee A., Lawler I., Aragones L., Woolnough A. P. & Berding N. (1998): Ecological applications of near infrared reflectance spectroscopy: a tool for rapid, cost-effective prediction of the composition of plant and animal tissues and aspects of animal performance. – Oecologia 116: 293–305.

Fox J. (2006): Structural equation modeling with the SEM package in R. – Struct. Eq. Model. 13: 465–486.

Fridley J. D., Grime J. P., Huston M. A., Pierce S., Smart S. M., Thompson K., Börger L., Brooker R. W., Cerabolini B. E. L., Gross N., Liancourt P., Michalet R. & Le Bagousse-Pinguet Y. (2012): Comment on "Productivity is a poor predictor of plant species richness". – Science 335: 1441.

Grace J. B. (1999): The factors controlling species density in herbaceous plant communities: an assessment. – Persp. Plant Ecol. Evol. Syst. 2: 1–28.

Grace J. B., Adler P. B., Seabloom E. W., Borer E. T., Hillebrand H., Hautier Y., Hector A., Harpole W. S., O'Halloran L. R., Anderson M. T., Bakker J. D., Brown C. S., Buckley Y. M., Collins S. L., Cottingham K. L., Crawley M. J., Damschen E. I., Davies K. F., DeCrappeo N. M., Fay P. A., Firn J., Gruner D. S., Hagenah N., Jin V. L., Kirkman K. P., Knops J. M. H., La Pierre K. J., Lambrinos J. G., Melbourne B. A., Mitchell C. E., Moore J. L., Morgan J. W., Orrock J. L., Prober S. M., Stevens C. J., Wragg P. D. & Yang L. H. (2012): Response to comments on "Productivity is a poor predictor of plant species richness". – Science 335: 1441.

Grime J. P. (1979): Plant strategies and vegetation processes. – Wiley, Chichester.

Gross K. L., Willig M. R., Gough L., Inouye R. & Cox S. B. (2000): Patterns of species density and productivity at different spatial scales in herbaceous plant communities. – Oikos 89: 417–427.

Gross N., Bloor J. M. G., Louault F., Maire V. & Soussana J. F. (2009): Effects of land-use change on productivity depend on small scale plant species diversity. – Basic Appl. Ecol. 10: 687–696.

Güsewell S. (2004): N:P ratios in terrestrial plants: variation and functional significance. – New Phytol. 164: 243–266.

Güsewell S. & Koerselman W. (2002): Variation in nitrogen and phosphorus concentrations of wetland plants. – Persp. Plant Ecol. Evol. Syst. 5: 37–61.

Haas G., Wetterich F. & Köpke U. (2001): Comparing intensive, extensified and organic grassland farming in southern Germany by process life cycle assessment. – Agr. Ecosyst. Environ. 88: 43–53.

Harpole W. S. & Tilman D. (2007): Grassland species loss resulting from reduced niche dimension. – Nature 446: 791–793.

Hautier Y., Niklaus P. A. & Hector A. (2009): Competition for light causes plant biodiversity loss after eutrophication. – Science 324: 636–638.

Hejcman M., Klaudisová M., Schellberg J. & Honsová D. (2007): The Rengen Grassland Experiment: plant species composition after 64 years of fertilizer application. – Agr. Ecosyst. Environ. 122: 259–266.

Hejcman M., Szaková J., Schellberg J. & Tlustoš P. (2010): The Rengen Grassland Experiment: relationship between soil and biomass chemical properties, amount of elements applied, and their uptake. – Plant Soil 333: 163–179.

Isselstein J., Jeangros B. & Pavlů V. (2005): Agronomic aspects of biodiversity targeted management of temperate grasslands in Europe: a review. – Agr. Res. 3: 139–151.

Käding H. & Petrich G. (1998): Kräutereinsaaten auf Niedermoorgrünland zur Erhöhung der Artenvielfalt. – Arch. Agr. Soil Sci. 42: 487–497.

Käding H. & Schmidt W. (1995): Extensivierung von Niedermoorgrünland nach 30 Jahren intensiver N-Düngung. – Arch. Agr. Soil Sci. 39: 69–74.

Kaiser T., Käding H., Kiesel H., Müller L., Hierold W. & Behrendt A. (2005): The derivation of grassland vegetation types on the basis of site and land use characteristics. – Arch. Agr. Soil Sci. 51: 405–416.

Karlík P. & Poschlod P. (2009): History or abiotic filter: which is more important in determining species composition of calcareous grasslands? – Preslia 81: 321–340.

Klaus V. H., Kleinebecker T., Hölzel N., Boch S., Müller J., Socher S., Prati D. & Fischer M. (2011a): Nutrient concentrations and fibre contents of plant community biomass reflect diversity patterns in a broad range of agricultural grasslands. – Persp. Plant Ecol. Evol. Syst. 13: 287–295.

Klaus V. H., Sintermann J., Kleinebecker T. & Hölzel N. (2011b): Sedimentation-induced eutrophication in large river floodplains: an obstacle to restoration? – Biol. Cons. 144: 451–458.

Kleinebecker T., Klaus V. H. & Hölzel N. (2011a): Reducing sample quantity and maintaining high prediction accuracy of quality parameters in grassland biomass with near-infrared reflectance spectroscopy (NIRS). – J. Near Infrared Spec. 19: 495–505.

Kleinebecker T., Weber H. & Hölzel N. (2011b) Effects of soil conditions, seasonality and grazing on aboveground biomass quality in calcareous grasslands. – Plant Ecol. 212: 1563–1576.

Koerselman W. & Meuleman A. F. M. (1996): The vegetation N:P ratio: a new tool to detect the nature of nutrient limitation. – J. Appl. Ecol. 33: 1441–1450.

Lamers L. P. M., Smolders A. J. P. & Roelofs J. G. M. (2002): The restoration of fens in the Netherlands. – Hydrobiologia 478: 107–130.

Luthardt V., Brauner O., Witt B., Friedrich S., Zeidler M., Hofmann G., Jenssen M., Meisel J., Kabus T., Täuscher L., Krüger G. & Schmidt D. (2005): Lebensräume im Wandel: Bericht zur ökosystemaren Umweltbeobachtung (ÖUB) in den Biosphärenreservaten Brandenburgs. – Fachbeiträge des Landesumweltamtes, Potsdam.

Marschner H. (2005): Mineral nutrition of higher plants. – Academic Press, Amsterdam.

Myers N. (1996): Environmental services of biodiversity. – Proc. Natl. Acad. Sci. USA 93: 2764–2769.

Olde Venterink H., Karde I., Kotowski W., Peeters W. & Wassen M. J. (2009): Long-term effects of drainage and hay-removal on nutrient dynamics and limitation in the Biebrza mires, Poland. – Biogeochemistry 93: 235–252.

Olde Venterink H., van der Vliet R. E. & Wassen M. J. (2001): Nutrient limitation along a productivity gradient in wet meadows. – Plant Soil 234: 171–179.

Olde Venterink H., Wassen M. J., Verkroost A. W. M. & de Ruiter P. C. (2003): Diversity-productivity patterns differ between N-, P-, and K-limited wetlands. – Ecology 84: 2191–2199.

Pärtel M., Zobel M., Zobel K. & van der Maarel E. (1996): The species pool and its relation to species richness: evidence from Estonian plant communities. – Oikos 75: 111–117.

Poptcheva K., Schwartze P., Vogel A., Kleinebecker T. & Hölzel N. (2009): Changes in wet meadow vegetation after 20 years of different management in a field experiment (North-West Germany). – Agr. Ecosyst. Environ. 134: 108–114.

R Development Core Team (2011): R: a language and environment for statistical computing. – R Foundation for Statistical Computing, Vienna.

Reidsma P., Tekelenburg T., van den Berg M. & Alkemade R. (2006): Impacts of land-use change on biodiversity: an assessment of agricultural biodiversity in the European Union. – Agr. Ecosyst. Environ. 114: 86–102.

Schaffers A. P. (2002): Soil, biomass and management of semi-natural vegetation Part I. Interrelationships. – Plant Ecol. 158: 229–246.

Shipley B. (2002): Cause and correlation in biology: a user's guide to path analysis, structural equations and causal inference. – Cambridge Univ. Press, Cambridge.

Socher S., Prati D., Müller J., Klaus V. H., Hölzel N. & Fischer M. (2012): Direct and productivity-mediated indirect effects of fertilization, mowing and grazing intensities on grassland plant species richness. – J. Ecol. 100: 1391–1399.

Tilman D. & Downing J. A. (1994): Biodiversity and stability in grasslands. – Nature 367: 363–365.

Tscharntke T., Klein A. M., Kruess A., Steffan-Dewenter I. & Thies C. (2005): Landscape perspectives on agricultural intensification and biodiversity: ecosystem service management. – Ecol. Lett. 8: 857–874.

Van de Riet B. P., Barendregt A., Brouns K., Hefting M. M. & Verhoeven J. T. A. (2010): Nutrient limitation in species-rich *Calthion* grasslands in relation to opportunities for restoration in a peat meadow landscape. – Appl. Veg. Sci. 13: 315–325.

Vermeer J. G. & Berendse F. (1983): The relationship between nutrient availability, shoot biomass and species richness in grassland and wetland communities. – Vegetatio 53: 121–126.

Wassen M. J., Olde Venterink H., Lapshina E. D. & Tanneberger F. (2005): Endangered plants persist under phosphorus limitation. – Nature 437: 547–550.

Willby N. J., Pulford I. D. & Flowers T. H. (2001): Tissue nutrient signatures predict herbaceous-wetland community responses to nutrient availability. – New Phytol. 152: 463–481.