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Impact of long-term nutrient supply on plant species diversity in grassland: an experimental approach on conventionally used pastures

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Summary

The research was initiated to determine the impact of long-term (16 years) differentiated N, P, K supply on the floristic diversity of conventionally used pastures classified as *Lolio-Cynosuretum*. At four different sites the factors N supply (0, 160 and 320 kg N ha^{-1} a^{-1}), P supply (0.26 and 52 kg P ha^{-1} a^{-1}) and K supply (0.66 and 133 kg K ha^{-1} a^{-1}) were tested in 27 different supply combinations in a factorial design with three replicates. Dry matter (DM) yields of the 1st cut, soil chemical values (pH, P and K concentrations) and the number of species were determined.

Site-independent N fertilisation had the largest influence on the diversity, reducing the number of species as a consequence of light competition due to an increase in biomass productivity as well as a decrease in soil pH-levels. Mostly, also the factor K had a significant effect. Recorded species numbers ranged from 7 up to 35 species 25 m^{-2}. On most sites a ‘humpback relationship’ (unimodal relationship) could be observed between productivity and the species number, with maximum species numbers reached with first cut yield levels between 2.5 and 3.5 t DM ha^{-1}. The humpback relationship between productivity and species richness however was not a curve, but an envelope filled with points, indicating that besides productivity also other factors influence the attained species number. In this view the highest number of species were recorded in case of a co-limitation of N and K, indicated by a N:K ratio in the above ground biomass between 1 and 1.5, as well as soil pH-levels between 4.5 and 5.5.

Introduction

The increased use of mineral fertilisers and frequency of utilisation clearly benefited the agricultural productivity of grasslands however at the same time seriously degraded the botanical diversity of these grassland communities (Chapman, 2001). Recent results suggest however that preserving and restoring grassland diversity may be beneficial to maintaining desirable levels of several ecosystem processes such as biological control of potential pest organisms, ecological resilience, recycling or retention of nutrients, control of local microclimate and regulation of local hydrological processes and may therefore have applications in land management and agriculture. Other important motivations to enhance floristic diversity include species conservation and aesthetic value of the landscape (Altieri 1999; Duelli and Obrist, 2003; Minns et al., 2001; Sanderson et al., 2004). As a consequence grassland management is now confronted with the task of developing systems which regenerate or conserve a stable floristic composition of meadows and pastures so that biodiversity is encouraged or maintained. For such systems to result in improved biodiversity, detailed knowledge of the effects of soil nutrient supply on floristic succession is required. In various studies the relationship between ecosystem functioning and plant diversity has been approached differently, leading to diverging views on the role of nutrient supply/availability in controlling plant diversity. In large-scale, observational studies Al-Mufti et al. (1977) and Grime (1979) find a hump-shaped relationship between biomass and plant diversity. Connecting productivity with soil nutrient availability Janssens et al. (1998) and McCrea et al. (2001) indicate that there also appears to be an unimodal relationship between soil extractable phosphorus (P) and potassium (K) and plant diversity. More recently, small-scale experimental approaches examining the effect of simulated random species extinctions on productivity, reveal a positive asymptotic relationship between species richness and productivity (Bullock et al., 2001; Hector et al., 1999; Tilman et al., 1996; Tilman et al., 2001). Other studies focus on the hypothesis that plant species diversity is related to the number of limiting resources, in which plant species may co-exist that are differentially limited by resources (Braakhekke and Hooftman, 1999). In this view several studies have related the species diversity with ratios of N:P and N:K in the aboveground biomass (Aerts et al., 2003; Koerselman and Meuleman, 1996; Roem and Berendse, 2000; Verhoeven et al., 1996). Considering how these different experimental and observational studies and approaches can be reconciled in setting targets applicable in practice a multiple-site N-, P-, K-fertiliser experiment was conducted on conventionally used pastures located in central Germany. The effect of application of N-, P- and K-fertilisers on floristic change in grassland is only obvious in most communities after many years. Therefore the experiment started in 1986 after which vegetation surveys took place first in 2002. Moreover, in order to reveal more direct causal relationships between influencing factors and floristic diversity the experiment was established as a factorial design.

Material and methods

At four different sites in Central Germany the factors N supply (0, 160 and 320 kg N ha^{-1} a^{-1}), P supply (0.26 and 52 kg P ha^{-1} a^{-1}) and K supply (0.66 and 133 kg K ha^{-1} a^{-1}) were tested in 27 different supply combinations during 16 consecutive years (1989 - 2002). The experiment was arranged on each site in a Latin rectangle design with three replicates. The plot size amounted 25 m^2. The pastures at all four sites were conventionally used, situated on mineral soils and classified as *Lolio-Cynosuretum*. The altitude as well as soil chemical values in unfertilised condition are for the different sites presented in Tab. 1.

In November 2001 the soil of each plot was sampled (15 core samples) between 0 and 10 cm depth and analysed for: pH (0.01 M $CaCl^2$) and exchangeable P and K (calcium acetate lactate extraction). Before the first cut in May 2002 a complete list of the plant species present

Tab. 1: Altitude and soil chemical properties (unfertilised condition) of experimental sites.

	Altitude m above sea-level	Phosphorus mg P 100 g^{-1} soil	Potassium mg K 100 g^{-1} soil	pH
Site 1	210	3.1	10.5	5.3
Site 2	260	1.3	13.0	5.5
Site 3	360	3.0	9.4	5.6
Site 4	620	2.2	11.8	4.8

in the treatment plots was recorded. Subsequently the plots were mown and dry matter (DM) yields of this first cut determined by drying subsamples at 103 ºC. For selected supply combinations another subsample of the herbage from the first cut was analysed for N (Kjeldahl) and K content (absorption spectrometry).
The data were analysed by means of a factorial analysis of variance. To ensure normal distribution the species numbers were subjected to a square-root transformation before statistical analysis.

Results

The soil pH is most influenced by N fertilisation which lowers the soil pH (Tab. 2). On site 2 the highest soil pH values are found, here N supply lowers the soil pH least, with pH values ranging from 5.9 to 5.3. The lowest soil pH occurs on site 4 with values between 4.9 and 4.0. Largest sources of variance for the soil P and K concentrations are, except for the K concentration on site 1, respectively the factors P and K. Also N supply exerts an influence on the soil P and K content. On site 1, 2 and 3 the P concentration is reduced with N supply in combination with P fertilisation, here the interaction N x P is significant. The same applies for the soil K content with a combination of N and K fertilisation, the interaction N x K is significant on all sites. The highest soil-exchangeable P level is reached on site 1 with 14.4 mg P 100 g^{-1} soil, the lowest on site 2 with 1.2 mg P 100 g^{-1} soil. The soil K concentration ranges between 5.5 mg K 100 g^{-1} soil (site 1) and 53.4 mg K 100 g^{-1} soil (site 4).
The productivity is on all sites significantly increased with N and K fertilisation, whereas on most sites a combination of both N and K increases the production more compared to solely applicating N or K; the interaction N x K shows a significance (Tab. 3). On site 2 and 4 also P fertilisation raises the first cut yield. Both the highest and the lowest production is registered on site 2 with first cut yields ranging between 1.8 and 6.1 ton DM ha^{-1}. On the transformed species numbers the factor N exhibits the largest source of variance at all sites, with a reduction of the species number with increasing N supply (Fig. 1). Next to N-, K supply also lowers the number of species on site 1.3 and 4. On site 2 and 4 also P fertilisation results in occasional significant species number reductions.

Tab. 2: ANOVA of soil pH, soil extractable P and K.

Source of variation	d.f.	Mean squares: Soil pH Site 1	Site 2	Site 3	Site 4	Soil extractable P Site 1	Site 2	Site 3	Site 4	Soil extractable K Site 1	Site 2	Site 3	Site 4
Row	2	0.068 *	0.031	0.054	0.240 **	5.76 *	9.13 **	9.21 **	6.89 *	23.51	169.14 **	4.50	106.72
Column	2	0.144 **	0.221 **	0.259 **	1.153 **	0.31	8.38 **	13.31 **	38.14 **	40.53	24.24	72.10	47.92
N	2	4.570 **	0.729 **	2.592 **	2.003 **	37.24 **	18.08 **	19.84 **	7.64 *	1271.95 **	434.08 **	600.59 **	778.39 **
P	2	0.253 **	0.225 **	0.023	0.223 **	334.32 **	285.29 **	414.74 **	179.70 **	13.43	60.82	43.16	127.96 *
K	2	0.012	0.053	0.097 *	0.024	0.64	0.85	2.80	1.20	1058.67 **	1283.88 **	3916.51 **	6221.03 **
N x P	4	0.041	0.019	0.076 *	0.107 **	4.00 *	4.80 **	3.45 *	3.03	16.42	33.02	35.87	33.68
N x K	4	0.081 **	0.011	0.110 **	0.051	3.81 *	0.24	2.36	0.15	256.18 **	61.57 *	307.88 **	147.47 **
P x K	4	0.010	0.018	0.020	0.024	4.38 *	1.06	0.65	0.92	13.59	9.65	36.97	26.10
N x P x K	8	0.007	0.007	0.018	0.013	0.92	0.40	1.82	1.02	17.81	8.85	36.90	23.75
Error	50	0.016	0.039	0.029	0.020	1.40	0.86	1.34	1.75	14.55	19.51	29.00	36.06
Total	80												

**Significance at P < 0.01, *Significance at P < 0.05

Tab. 3: ANOVA of DM yield 1st cut and number of species.

Source of variation	d.f.	Mean squares: DM yield 1st cut Site 1	Site 2	Site 3	Site 4	Number of species[1] Site 1	Site 2	Site 3	Site 4
Row	2	0.691	1.080	0.558	0.401	0.157	0.411 *	0.559	0.009
Column	2	0.035	0.505	1.044	0.631	0.936 **	0.071	0.594	0.162
N	2	23.890 **	23.333 **	4.820 **	1.817 **	16.855 **	2.735 **	21.330 **	11.054 **
P	2	0.922	15.452 **	0.146	3.958 **	0.227	0.448 *	0.073	0.915 **
K	2	3.102 **	12.667 **	2.488 **	2.845 **	1.289 **	0.019	4.701 **	1.427 **
N x P	4	0.877	0.670	0.244	0.688	0.239	0.133	0.116	0.027
N x K	4	1.549 *	1.454 *	0.455	1.038 *	0.076	0.040	0.248	0.176
P x K	4	0.967	1.034	0.025	0.164	0.118	0.058	0.209	0.054
N x P x K	8	0.438	0.488	0.131	0.223	0.069	0.078	0.170	0.039
Error	50	0.471	0.565	0.328	0.358	0.105	0.121	0.190	0.106
Total	80								

**Significance at P < 0.01, *Significance at P < 0.05
[1]Square root transformed

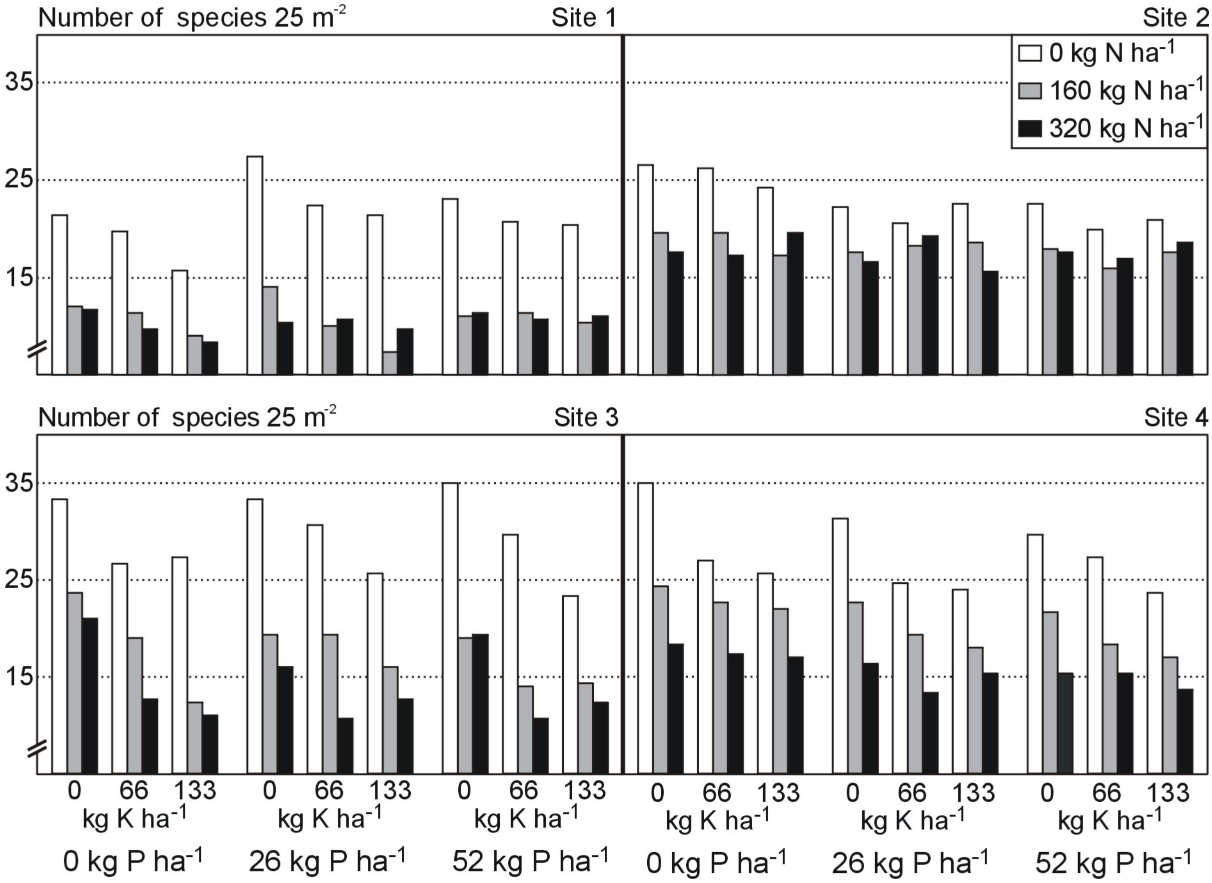

Fig. 1: Number of species 25 m^{-2} depending on long-term N, P and K supply and site.

Discussion

Nutrient supply might influence the floristic diversity directly through soil nutrient availability (JANSSENS et al., 1998) or indirectly through productivity, i.e. light competition (AL-MUFTI et al., 1977; GRIME, 1979) and soil pH (MARRS, 1993). Tab. 4 shows the results of linear correlation analysis between the species number, soil pH and 1st cut yield.

Although not highly correlated, the species number and soil pH are, except for site 2, related positively. This agrees with observations from EJRNAES and BRUUN (1995), MARRS (1993), MCCREA et al. (2004) and ROEM and BERENDSE (2000) who find higher floristic diversity on neutral or basic soils compared with diversity on acidic soils. N fertilisation reduces the soil pH on site 1, 3 and 4 probably because long-term N supply results in an accumulation of soil organic matter (BAKKER and BERENDSE, 1999) which induces increased nitrification rates with a decrease of soil pH (MENGEL, 1991; OPITZ V. BOBERFELD, 1994). Contrary on site 2 the reduction of the soil pH by N supply is less pronounced. Possibly on this site the soil extractable P in unfertilised condition is that low that nitrification activity of soil organisms is depressed (ALEXANDER, 1965; JANSSENS et al., 1998). BOHNER (2005) finds a relatively strong relationship between soil P content and the N mineralisation potential of grassland. The low soil P level-induced moderate reduction of the soil pH by N supply could explain the small decrease of the species number by N fertilisation as well as the deviating correlation coefficient between soil pH and the number of species for site 2, see Fig. 1 and Tab. 3. The exclusion of species caused by light competition with increasing productivity (GRIME, 1979) is reflected in negative correlation coefficients between 1st cut yields and the species number on all sites, see Tab. 3. The large number of factors influencing floristic diversity prohibit however that coefficients of determination $r^2 > 0.5$ are reached for the relation between the number of species and productivity as well as soil pH. The 1st cut yield and soil pH are not correlated; the differentiated N-, P- and K application affect both diversity-influencing factors in a different way. The soil pH level is obviously reduced with long-term N fertilisation, P supply has however a buffering effect (MENGEL, 1991) and brings about a small rise in soil pH levels. Productivity on the other hand is influenced by N and K supply; the N induced yield increase is further strengthened with K supply (see factor N and K as well as N x K interaction for 1st cut yield in Tab. 2). The same N x K interaction on productivity is also described by VOIGTLÄNDER (1987).

Tab. 4: Linear correlation coefficients between species number, soil pH and DM yield.

		Soil pH	DM yield 1st cut
Number of species	Site 1	0.59**	- 0.56**
	Site 2	- 0.21	- 0.46**
	Site 3	0.40**	- 0.58**
	Site 4	0.46**	- 0.35**
Soil pH	Site 1		- 0.29*
	Site 2		- 0.04
	Site 3		- 0.10
	Site 4		0.22*

The significance of correlation is indicated as **P < 0.01 and *P < 0.05

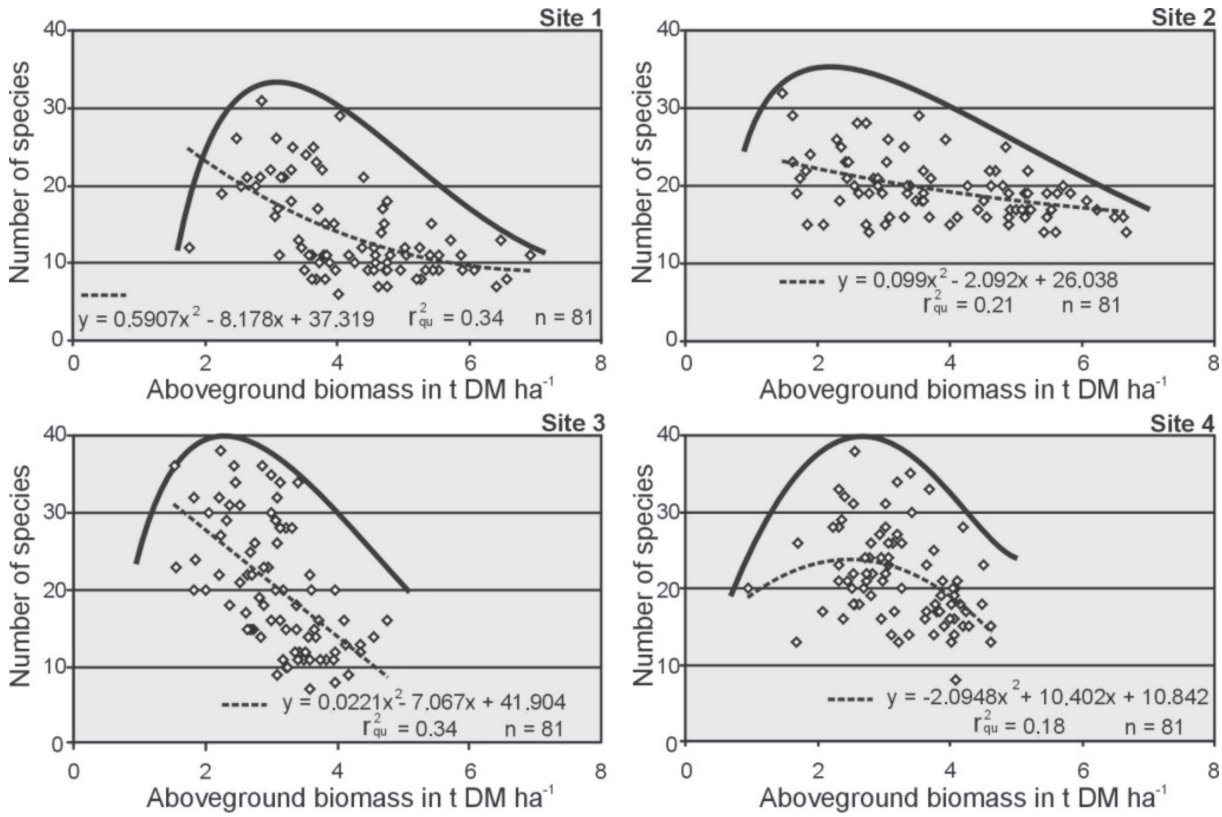

Fig. 2: Relation between DM yield and the number of species 25 m^{-2}

The graphic presentation of the relationship between productivity and the species number in Fig. 2 reveals, except for site 2, an unimodal relation (humpback) according to AL-MUFTI et al. (1977) and GRIME (1979). The hump-shaped relationships between diversity and productivity are not curves, but clouds filled with points. This variance can be related to the point of criticism from MARRS (1993) that the humpback-model has been produced empirically from comparisons across a range of communities, and it is not clear if the relationship holds when the fertility, i.e. productivity, of a given site is manipulated. Also MOORE and KEDDY (1989) warned that, although the model held for comparisons between vegetation types in their study of wetlands, the relationship was less useful for comparisons within vegetation types. Moreover it indicates the problems of extrapolating from a model derived from a few points (14 in AL-MUFTI and GRIME's study) to a large area with many sample points (MARRS, 1993). Another approach towards explaining this variance comes from the 'Resource Balance Hypothesis' from BRAAKHEKKE and HOOFTMAN (1999). From the idea that species richness is related to the number of limiting resources, BRAAKHEKKE and HOOFTMAN (1999) hypothesize that plant species diversity is favoured when actual resource supply ratios are balanced according to the optimum resource supply ratios for the vegetation as a whole. In this view the envelope filled with points occurs because high species diversity is not consequently reached when the productivity level is between 2.5 and 3.5 ton DM ha^{-1}, however when also other diversity influencing factors, such as soil chemical values, are in an optimal range. Further Fig. 2 reveals that for the none of the sites an asymptotic relation between the species number and productivity (see also negative correlation between species number and 1st cut yield, Tab. 3) can be observed. This in contradiction to the results of experimental research by BULLOCK et al. (2001), HECTOR et al. (1999), TILMAN et al. (1996) and TILMAN et al. (2001) that reveal a positive asymptotic relation between the number of species and productivity. LOREAU et al. (2001) and SCHMID (2002) state that the large-scale, observational approach as performed by AL-MUFTI et al. (1977) and GRIME (1979) and the small-scale experimental approach conducted by BULLOCK et al. (2001), HECTOR et al. (1999), TILMAN et al. (1996) and TILMAN et al. (2001) examine different causal relationships under different sets of conditions. Although this study is experimentally designed on similar plant communities – contrary to the observational research from AL-MUFTI et al. (1977) and GRIME (1979) referring to different plant communities – the productivity is nevertheless not only influenced by plant diversity however also by the here differentiated soil nutrient availability. This differs from above-mentioned experimental researches where the effects of diversity on productivity are detected after the effects of other environmental factors have been removed. Another difference between this fertiliser experiment and above-mentioned experimental studies is the duration of the experiment. The obtained positive relationships between diversity and productivity refer to rather short-term experimental manipulations of diversity. One of the proposed mechanisms behind the positive relation between diversity and productivity, the 'selection probability effect' (HUSTON, 1997) in which more diverse plant communities have a higher probability of containing, and becoming dominated by, a highly productive species, reflects only an initial condition (LOREAU, 2000). Through a selective process towards dominance of highly productive species the number of species should be reduced again.

Sampling a large number of old permanent grasslands in West and Central Europe and in the UK JANSSENS et al. (1998) and MCCREA et al. (2001) resp. find also an unimodal relation between soil extractable P and K and the diversity of species. Relating the soil K content with the number of species following the ceteris-paribus principle, i.e. regarding only the N- and P-unfertilised variants, here the species richest communities are found for soil K concentrations between 10 and 30 mg K 100 g^{-1} soil (Fig. 3). This is in accordance with the findings of JANSSENS et al. (1998) and MCCREA et al. (2001).

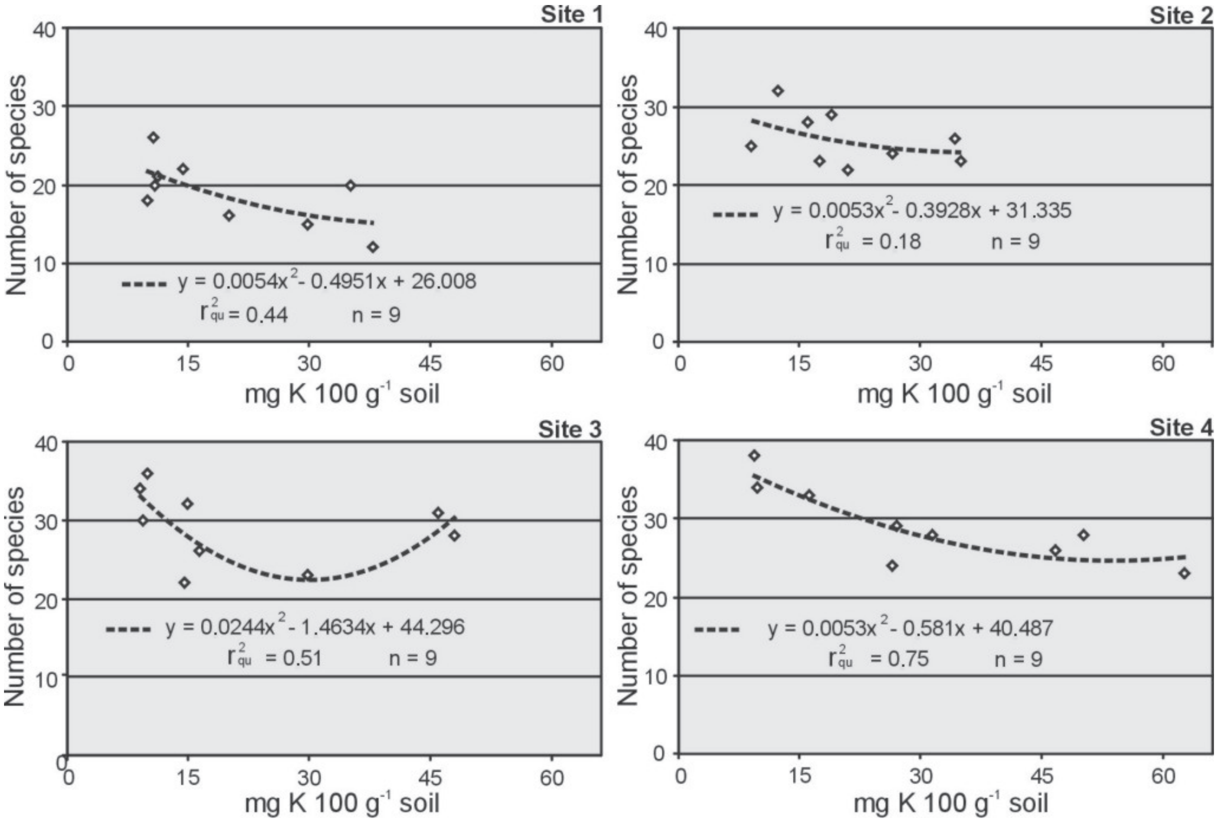

Fig. 3: Relation between soil extractable K and the number of species 25 m-2

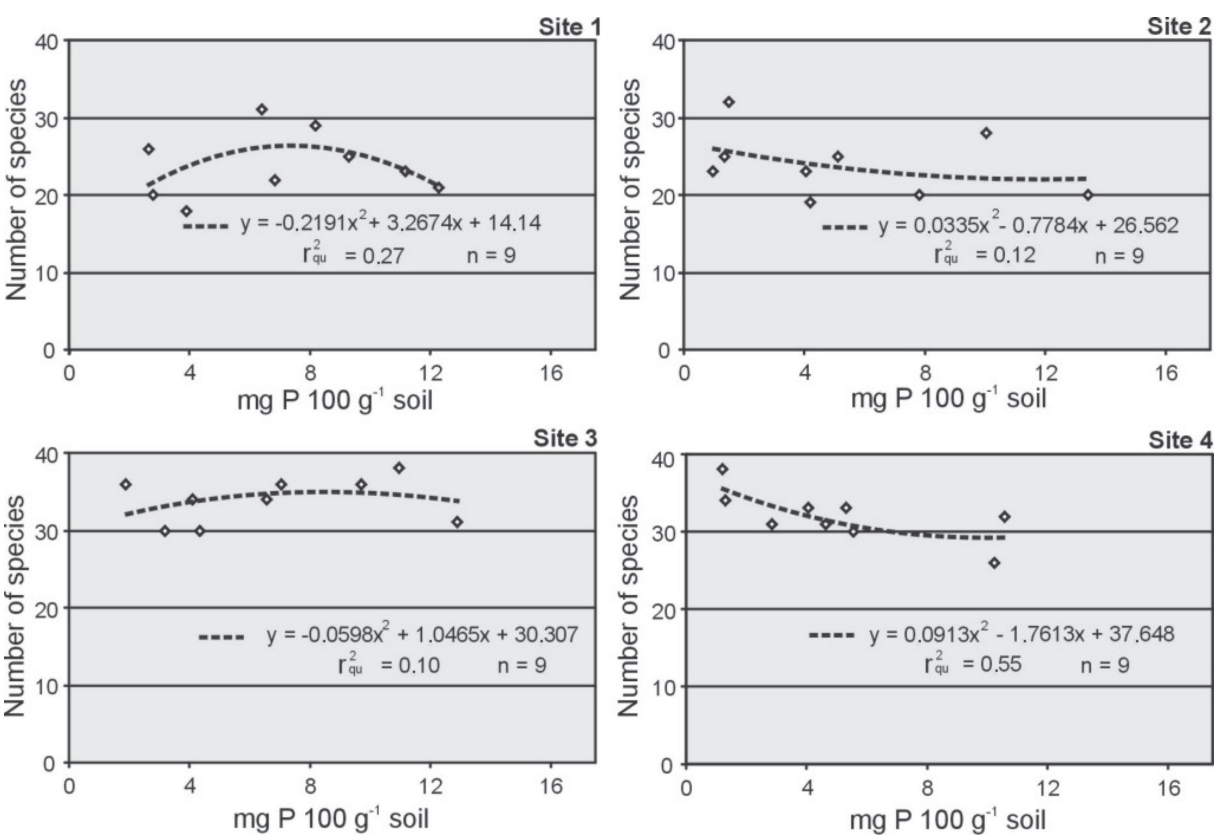

Fig. 4: Relation between soil extractable P and the number of species 25 m-2

However, the relation between the soil P content and the species number for the N- and K-unfertilised variants, contrary to the results of JANSSENS et al. (1998) and MCCREA et al. (2001), does not reveal an upper boundary of 20 species 100 m^{-2} when the soil P content exceeds 5 mg 100 g^{-1} soil (Fig. 4). On site 2 and 4 the species diversity is reduced with P supply, which is probably an indirect P effect on the N availability through an increased legume proportion (data published in OERLEMANS, 2006) or an increased mineralisation regarding the yield increase on these sites with P supply, see Tab. 2 and Fig 1. Nevertheless for soil P concentrations higher than 5 mg 100 g^{-1} soil on all sites still species numbers exceeding 20 species 25 m^{-2} are found. There is a probability that inter-correlations with other soil chemical characteristics occur for the relation between soil P content and diversity, and to a less extent also for the relation between soil K content and diversity, as found in the not-experimental designed empirical sampling research from JANSSENS et al. (1998) and MCCREA et al. (2001). As all soils are inherently low in P, the effects of agricultural improvement through fertiliser addition with accompanying influence on the floristic diversity, are most easily recognised in terms of the soil P level (CRITCHLEY et al., 2002). Moreover after cessation of fertiliser application, N availability may be reduced in 5 to 10 yr by mowing, whereas reducing K availability may take 15 to 20 yr and reducing P availability more than 50 yrs (OLFF and PEGTEL, 1994). The fact that in this factorial designed fertiliser experiment no upper boundary of 20 species 100 m^{-2} with soil P content exceeding 5 mg 100 g^{-1} soil occurs could be explained by that the soil P content in the empirical studies from JANSSENS et al. (1998) and MCCREA et al. (2001) could be seen as a good indicator of the long-term level of fertiliser application and utilisation intensity in present and past with accompanying floristic diversity (BOHNER, 2005).

From the view that a co-limitation of nutrients through a differential resource limitation of species leads to increased diversity, the significant N x K interaction found for the 1st cut yield could be interpreted as a co-limitation of N and K on most sites. Fig. 5 shows for the P-unfertilised variants the relation between the N:K ratio in the aboveground biomass and the species number. In accordance with results from ROEM and BERENDSE (2000) an unimodal relationship with an optimum N:K ratio in aboveground biomass between 1 and 1.5 can be found. As for the 1st cut yield no interactions with P occur, a co-limitation of N and P can for this experiment not be derived.

Regarding the large number of factors influencing the floristic di-

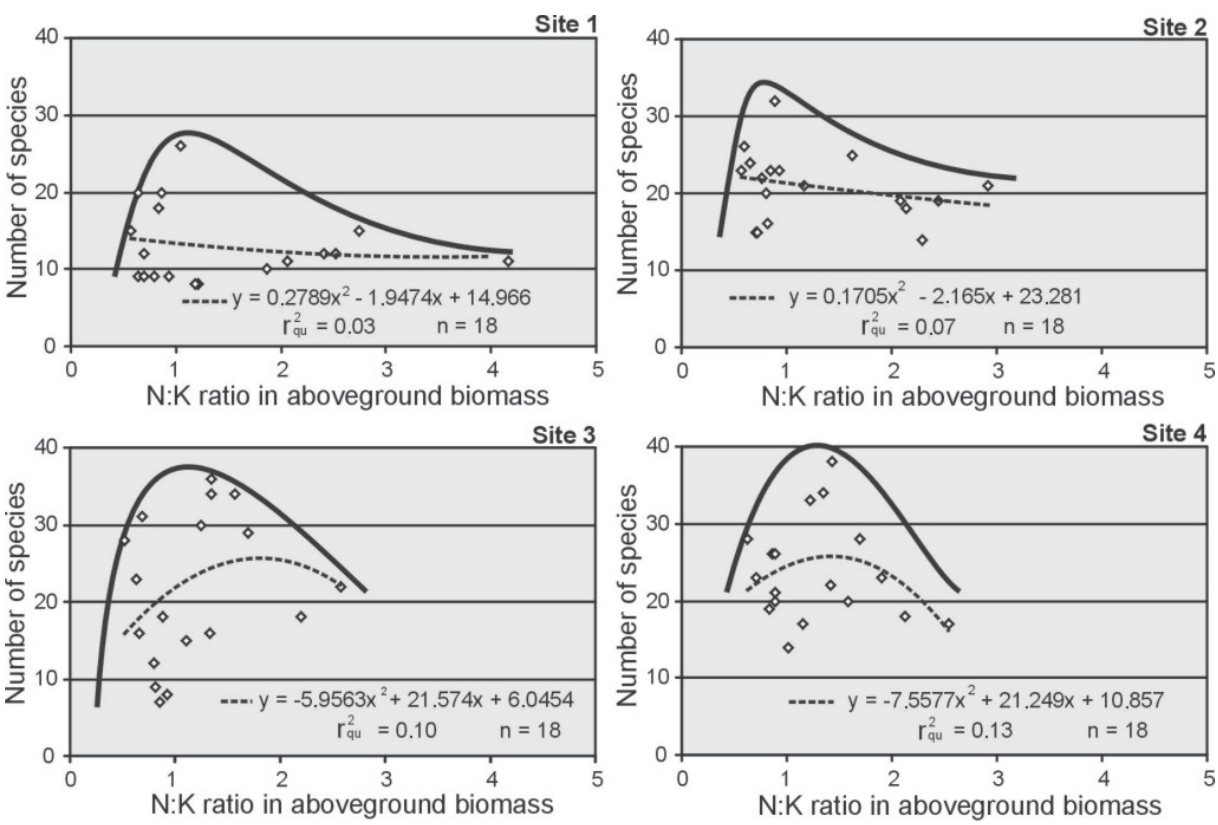

Fig. 5: Relation between N:K ratio in aboveground biomass and the number of species 25 m^{-2}

Tab. 5: 95%-confidence intervals for the means of soil pH, DM yield and N:K ratio in aboveground biomass for diversity level $\geq$ 25 species 25 m^{-2}.

	Site 1	Site 2	Site 3	Site 4
	n = 6	n = 11	n = 25	n = 22
soil pH	5.2 – 5.5	5.4 – 5.6	5.4 – 5.6	4.5 – 4.8
DM yield (ton ha^{-1}) 1st cut	2.7 – 3.8	2.2 – 3.6	2.5 – 2.9	2.7 – 3.2
	n = 3	n = 5	n = 11	n = 11
N:K ratio in aboveground biomass	0.3 – 1.4	0.5 – 1.4	0.8 – 1.4	0.9 – 1.4

versity on pastures as well as different approaches towards examining/explaining the relations found between these influencing factors and diversity Tab. 5 summarises some results: the 95%-confidence intervals for the means of soil pH, 1st cut yield and N:K ratio in above-ground biomass for the plots with a species number $\geq$ 25 species 25 m^{-2} are shown. These confidence intervals could be indicative for setting targets applicable in the conservation or restoration of floristic diversity on pastures (*Lolio-Cynosuretum*) in central Europe.

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