The Rengen Grassland Experiment: determinants of vegetation structure, species richness and the yield paradox hypothesis
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Abstract
The Rengen Grassland Experiment (RGE), begun on grassland dominated by Nardus stricta in 1941, is one of the oldest properly designed still running fertiliser experiment worldwide. RGE consisted of following treatments arranged in five randomised blocks: an unfertilized control, Ca, CaN, CaNP, CaNP-KCl, and CaNP-K2SO4. In 2005, soil chemical properties data were collected aiming to analyze effect of soil parameters on biomass production, plant species composition, and species richness of vascular plants counted in five spatial scales.

Soil properties (concentration of K, P, C/N ratio, and pH) and biomass production were strictly dependant on fertilizers applied. In treatments without P application, biomass production was negatively correlated with soil P concentration despite of extremely low P concentration.

The explanatory power of all measured soil parameters on plant species composition was almost the same like the power of the treatment effect (61.7% versus 62% of explained variability in RDA). The most powerful predictor of sward structure was the soil P concentration explaining 36.3 % of plant species data variability followed by pH value explaining 20 %.

The soil P concentration and biomass production were the only parameters significantly affecting species richness.

Relatively parallel increase in species richness with increasing sampling area was detected in all treatments and constant differences among treatments were independent of the sampling area.

From a discontinuous relationship between soil P content and above ground biomass, the authors formulated the “yield paradox hypothesis” which indicates that an increase in plant available P does not inevitably indicate an increase in biomass. In fact, this relation is strongly dependant on the occurrence and adaptation of species either exhibiting high P use efficiency or, in contrary, low P use efficiency but high competitiveness on well P supplied soils. Further, the extraction of plant fertilizer P increased with the addition of nitrogen (N). As a practical implication, the long-term application of N on mesotrophic grassland might be an adequate measurement to deplete P rich soils aiming to restore species richness grasslands.

Introduction
Determining which environmental gradients control species richness and plant species composition of agro-ecosystems still remains a central goal in ecology. Moisture, for example, was identified as the main gradient controlling species composition of mesotrophic grasslands in Central Europe. Nutrients and soil base status, surprisingly, were considered as secondary, affecting the sward structure to a lower extent than moisture (Havlíková et al. 2004). If grasslands of a given moisture status are considered, N and/or P are generally the most growth limiting nutrients responsible for changes in floristic composition of the sward or biomass production after fertilizer application (Gusewell 2005). According to the “resource balance hypothesis” (Braakhekke and Hoofman 1999), species richness in these grasslands is greatest when the availability of N and P is balanced and the N/P ratio in the plant biomass is close to 15. Several studies were performed to test this hypothesis in N or P limited plant communities showing that threshold N/P ratios vary from 8 to 30 among vegetation types (Gusewell et al. 2005, Soudzikovskaia et al. 2005, Mamolos et al. 2005).

Wassen et al. (2005) showed that many of the endangered plant species persist in a P rather than N limited environment. According to this study, enhanced P supply is more likely to cause a loss of species than enhanced N supply. It has been shown previously, that applied P can affect the ecosystem functioning for a very long time. For example, even 37 years after the cessation of P fertilisation in a set aside experiment, the sward structure was found to differ between treated and untreated plots (Hejcman et al. 2006). Consequently, in view of landscape management and conservation, attention must be paid to the reduction of plant available P as well as to the
competitive ability of highly productive species under optimal soil P content. This is important mainly because the depletion of soil P is a long-term process (Bullock & Pywell 2005).

Potassium is another frequently growth limiting nutrient especially on regularly cut and unfertilized grasslands on sandy soils. The removal of potassium with the harvested biomass as well as the K fertilizer application plays a decisive role in potassium cycling on grasslands. As reviewed by Kayser and Isselstein (2005), high K inputs negatively affect Mg and Ca uptake by plants and potentially accelerate the leaching of these cations. Furthermore, a negative effect of K fertilization on species richness has been documented in the Park Grass Experiment (PGE) by Crawley et al. (2005), although not as strong as with long-term P or P+N application. In the case of P, highest species richness was frequently recorded far below an optimal concentration of P in the soil for nutrition of most plants, whereas with K the threshold lies within that optimum for the nutrition of most plants. This is why the soil P content affects plant species richness more than that of K. Janssens et al. (1998) recorded always low species numbers when the content of available P in the soil was above 50 mg · kg⁻¹.

According to this study, diverse grasslands can only persists below this critical value. From many fertilizer experiments, different short-term and long-term responses of the grassland sward to fertilisation were reported (see Gusewell et al. 2002 and citations therein). The most prominent example is the Park Gras Experiment (PGE) in Rothamsted, UK. The initial plant species composition changed rapidly after the establishment of the PGE in 1856, and it has been observed, that the communities continued to change over the following 40 years and never reached “equilibrium” until the early 20th century (Silvertown et al. 2006). Results from the PGE emphasize the high importance of long-term studies in plant ecology, which enables to examine the stability of plant communities by separating trends induced by fertilizer application from year to year fluctuations.

The Rengen Grassland Experiment (RGE), set up in the Eifel Mts. (Germany) in 1941, is one of the longest still running grassland fertilizer experiments worldwide. The original objective of the experiment was to investigate if and how the applied nutrients N, P, and K in combination with lime application improve yield and quality of the forage produced on low productive grassland. Today, the RGE has acquired new relevance for the study of basic ecological processes and questions concerning the protection and restoration of species rich plant communities. From previous studies it has been concluded that nearly all species indicative of extensive grassland management disappeared when Ca, N, P, and K fertilizers were applied at the same time (Schellberg et al. 1999). Hejcman et al. (2006) performed a detailed analysis of sward structure 64 years after the onset of the experiment. Calculated by redundancy analysis (RDA), the effect of treatments was found to be a significant predictor of sward structure explaining 62 % of cover data variability.

In previous analyses, sward structure, plant species richness, and soil parameters have been analyzed separately in the RGE. The objective of the present study was to analyse soil nutrient status, sward structure and species richness simultaneously and to answer the following questions, (i) is the explanatory power of the treatment effects differing from the explanatory power of measured soil parameters and (ii) which soil nutrients do affect sward structure, plant species richness and biomass yield mostly? Further, species richness is a scale dependant parameter and scale dependency could therefore be affected by the nutrients applied (Crawley et al. 2005). So, another question was, whether or not the scale dependency of species richness differs in relation to fertilizer application.

Materials and methods

Study site and treatments

In 1941, a fertilization experiment was set up on Rengen Grassland Experimental Station of the University of Bonn in the Eifel mountains (Germany, 50°13’N, 6°51’E) at 475 m a.s.l. The experiment was arranged in a completely randomised block design with five treatments and the same number of replicates (Table 1). Control plots without any fertilizer input were added in 1999 on an area that has to our knowledge never been fertilized. Further details of the location and the experimental design are given in Schellberg et al. 1999 and Hejcman et al. 2007.

Soil genesis

The soils of the study site were developed from Lower Devonian sand stones and clay slates. During the Mesozoic and Tertiary, the parent rock was deeply weathered and partially eroded. During the Pleistocene, a thin loess cover accumulated. Subsequent erosion and mixing due to solifluction led to layered soils with silty topsoils and dense, stone-rich, often clayey subsoils. The reference soil profile at the edge of the experiment revealed 23 % of sand, 54 % of silt, and 23 % of clay in the topsoil. The saturated hydraulic conductivity decreases from 256 cm · d⁻¹ in the topsoil to 4.6 cm · d⁻¹ in the subsoil. In consequence, stagnic properties occur, i.e. very wet conditions after rainfall, and frequent drought during summer. According to the World Reference Base for Soil Resources, the soil is classified as a Stagnic Cambisol.
Aboveground biomass production
In 2005, above ground fresh biomass was measured by cutting the sward in each plot at a height of about 2 cm in swaths of 1 m by 5 m. Sub-samples of about 0.5 kg were then taken from the cut material and oven-dried at 60 °C for 48 h to determine the dry-matter content of the harvest and its total yield. Cutting was performed twice in mid-June and in mid-October.

Plant species composition
The percentage soil cover of all vascular plant species was visually estimated in each plot. To eliminate edge effects, relevés were taken in the centre of each 3 m \( \times \) 5 m plot only on an area of 1.5 m \( \times \) 3.2 m in mid-June 2005.

Total number of vascular plant species was counted directly in the field in June 2005 on plots of five scales: 0.0225 m\(^2\), 0.045 m\(^2\), 0.09 m\(^2\), 1 m\(^2\), and 5.76 m\(^2\).

Chemical soil properties
Soil samples were taken in May 2004. In each plot, five separate samples were taken from 0 to 10 cm depth after removing plant residues, and joined to one representative sample. The soil samples were air-dried, ground in a mortar, and sieved to 2 mm after removing living roots.

All analyses were conducted in accordance to standardized methods of the Association of German Agricultural Analytical and Research Institutes (VDLUFA, 1991). Soil pH was potentiometrically measured in a suspension with 0.01 M CaCl\(_2\). Plant available P and K were extracted by a calcium-acetate-lactate solution and measured colorimetrically and photometrically, respectively. Magnesium (Mg) was extracted with 0.01 M CaCl\(_2\) and measured with flame atomic absorbance spectrometry (AAS). Total carbon (C) and N were quantified by elemental analyses (Carbo-Erba, Italy). With respect to the lack of inorganic carbon in the soil forming substrate and the low pH values, total C was regarded as organic C.

Data analysis
All uni-variate analyses were performed using the STATISTICA 5.0 software (StatSoft, 1995). One-way ANOVA followed by post-hoc comparison using Tukey’s test has been applied to identify significant differences between treatments for (i) soil parameters and (ii) aboveground biomass yield. Regression analysis was used to evaluate relationship between the following parameters: vascular plant species richness, chemical soil properties, and aboveground biomass yield.

A redundancy analysis (RDA) in the CANOCO 4.5 program (ter Braak and Šmilauer, 2002) was used to evaluate multivariate plant species data. RDA has been conducted because data sets were sufficiently homogeneous and co-variables, e.g. treatments and blocks, were in the form of categorical predictors. Further, a Monte Carlo permutation test with 999 permutations was used to reveal if the tested explanatory variables (environmental variables in the CANOCO terminology) had a significant effect on the plant species composition (for further details see Lepš and Šmilauer 2003). Results of the multivariate analyses were visualized in the form of a bi-plot ordination diagram by the CanoDraw software. The percentage of the plant species data variability explained by treatments was used as a measure of explanatory power.

Results
Soil properties in 0 to 10 cm depth
In all limed treatments (B, C, D, E, F), soil pH ranged from 6.5 to 6.6 and significantly differed from the control (A) where pH 4.9 was recorded (Tab. 2 and 3). No significant effect of fertilizer application on organic C and N content in the soil was detected. However, differences were recorded among C/N ratios which were the widest in the control (13.1) and significantly differed from the D treatment (11.8).

As expected, the content of P in 0 to 10 cm depth was strictly dependent on P fertilization. P contents up to 1.8 mg 100g-1 were measured in the A, B, and C treatment in contrast to the D, E, and F treatments (13 – 44 mg 100g-1). We tested the variability of P content in the unfertilized A, B, and C treatments separately; By doing so, the treatment A exhibited significantly higher P content in the soil than B and C treatments.

In the uppermost 10 cm of the soil, the K content was significantly affected by K fertilizer application. In the treatments E and F, the average K content amounted for 9.4 and 10.5 g kg-1, respectively, in contrast to an average K content of 2.3 – 4.3 g kg\(^{-1}\) in plots where K was not applied (A, B, C, D).

For the Mg content, no significant treatment effect was found, but an obvious trend indicating the importance of liming on the soil Mg status was recorded. On average, 13.2 g kg\(^{-1}\) of Mg was found in the control without lime, whereas 19.5 – 20.7 g kg\(^{-1}\) was determined in the limed treatments.

Aboveground biomass production
Biomass production was strongly affected by treatments (Table 2; Fig. 1). In 2005, the control plots (A) and the treatments limed only (B) did not differ significantly with respect to the mean biomass production which was 2.5 and 2.9 t ha\(^{-1}\), respectively. The mean biomass production increased with the addition of N and P up to 4.9 and
6.5 t ha\(^{-1}\) in the C and D treatments. These treatments differed significantly from A, B, E and F. Highest biomass production revealed under N, P, and K fertilization, i.e. 8.9 and 9.6 t ha\(^{-1}\) in E and F treatments, respectively. In treatments without P application, the soil P content was negatively correlated with biomass yield (R=0.63; F=8.6; P=0.012; Fig. 1).

**Plant species composition in relation to soil parameters**

All measured soil parameters together explained 61.7 % of the variability of plant species composition (Table 4). Most of this variability was caused directly by the treatment as a steep decrease in the explanatory power of soil parameters was recorded after removing the treatment effect from the analysis. This is well visible when comparing results of analyses a1 and a2 in the Tab. 4. Results of the a1 analysis were visualised in the form of the ordination diagram in Fig. 2. The majority of species characteristic for oligotrophic semi-natural grasslands was negatively correlated with soil P and K content, but relatively independent from soil pH.

The most decisive soil parameter affecting sward structure was the soil P content explaining 36.3 % of plant species data variability. Only a slight decrease in explained variability by P content to 27.9 % was detected after removing the effect of other soil parameters. On the contrary, a steep decrease in the explanatory power of P content was revealed when the effect of treatment was removed from the analysis (compare results of analyses a3 – a5 in Tab. 4). This result indicated a high correlation of P content in the soil with the treatment effect on plant species composition.

Further, the pH was the second soil parameter explaining more than 20 % of the variability in plant species data. However, the effect of pH correlated with other measured soil parameters as well as with the treatment effect. This is indicated by a steep decrease in the explanatory power of pH when the variability caused by other variables was removed from the analyses (compare analyses a9 – a11). The K contents in the soil solely explained 17.7 % variability of plant species composition data. Similarly as in the case of P, the effect of K on sward structure was correlated with the treatment effect, but relatively independent from other measured soil parameters (analyses a6 – a8). The Mg content itself explained a significant part of plant species data variability, but its explanatory power was more than four times lower than that of P.

The effect of N and organic C content on sward structure was not significant in all cases (analyses a12 – a18), but the C/N ratio explained a significant part of plant species composition. The explanatory power of the C/N ratio decreased after removing any effect of the remaining measured soil parameters, but increased when the variability caused by treatment was removed from the model (compare analyses a18 – a20). This result indicated that part of the variability explained by C/N ratio was independent from the treatment.

**Species richness in relation to soil parameters and biomass production**

The P content in the soil was the only soil parameter significantly affecting species richness in the RGE (Tab. 5). A decrease of species richness with increasing biomass production is visible from Fig. 3, however, this relationship was relatively weak due to considerable data variability.

**Species richness as a function of sampling area**

Species richness was significantly affected by both the factors sampling area and treatment, but their interaction was not significant (Table 2). This indicated (i) a relatively parallel increase in species number with increasing sampling area in all treatments and (ii) constant differences among treatments to be independent of the sampling area. When the data were transformed to percentages of species of the control, a significant effect of sampling area, treatment and their interaction was revealed. Differences among treatments decreased with an increase of area where species were counted.

**Discussion**

The RGE is a unique demonstration of how the application of various fertilizers affects grassland ecosystem diversification and functioning on a long-term perspective. Data derived from this experiment can be, in many aspects, directly compared to results from other long-term fertilizer experiments like with the PGE (Silvertown et al. 2006).

**Soil parameters**

The measured chemical soil properties were clearly affected by the different treatments. Especially soil pH as well as the P, K, and Mg contents in the uppermost 10 cm were strongly influenced by fertilizer application. These results are consistent with previous data collected in the same experiment in 1973 and 1993 (Schellberg et al. 1999). In plots with lime and nitrogen application (treatment B and C), the low soil P content is likely the result of an increased removal of P due to an enhanced biomass production stimulated by lime and / or N application.

The results of the regression analysis in figure 1 as well as data in table 3 confirm that soil P contents are generally lower with higher biomass production. This mechanism seems paradox following the Liebig-Sprengel’s law of the minimum (van der Ploeg et al., 1999), because with higher soil P content generally higher...
Biomass yields would be expected. We conclude that the total content of a yield limiting nutrient at a certain threshold limit for the occurrence of a particular plant community is not necessarily decisive for aboveground biomass production. With low P availability, the nutrient efficiency of the species present in the grassland sward determines the relationship between biomass and soil nutrients rather than the plant available P content itself. The observed higher biomass production in extremely P poor plots illustrates an excellent example of long-term effects of fertilizer application on the adaptation of plant species composition. The N/P ratio in the biomass, a frequently used parameter describing nutrient efficiency and growth limitation (Tessier and Raynal 2003), was calculated from the data of the B, C, D, E, and F treatments as previously published by Schellberg et al. (1999). The N/P ratio in the biomass harvested with the first cut in 1993 was 9.77, 14.2, 6.19, 6.34, and 5.90 in B, C, D, E, and F treatments, respectively, indicating highest P efficiency of the plant community in the C treatment, where the content of P in plant biomass was lowest of all. In long-term fertilizer experiments, the adaptation of sward structure to the fertilizers applied is obviously and predominately driven by their N/P ratio in the biomass. Further, each type of grassland grown and cultivated under a certain fertilization regime is characterized by a particular N/P ratio which is highest in Carex dominated and lowest in tall grass dominated plant communities (Gusewell 2005).

These findings are in accordance with the “ration resource model” of Tilman (1997) showing that the abundance of species in low productive soils is regulated by the competition driven nutrient depletion. In the RGE, the plots indicating lowest P contents (C treatment) were dominated by Carex species especially by C. panicea which is well known for its high P use efficiency and its ability to grow in extremely poor environments (van der Hock et al. 2004, Gusewell et al. 2005). In plots where soil P content was higher, sedges were probably unable to out-compete species with lower nutrient efficiency and higher P demand. But, these species were probably not able to produce the same amount of biomass as sedges in an extremely P limited environment.

Based on the finding that the biomass production was negatively correlated with soil P contents despite an extremely low soil P status, we formulated the “yield paradox hypothesis” (Fig. 6). According to this hypothesis, the aboveground biomass production can be surprisingly high in an environment with an extremely low P availability (point II in Fig. 6). Further along the gradient of P availability, biomass production can decrease (range from point II to III). It is part of our theory, that the classical nutrient-yield relationship achieved on eutrophic grassland is only valid above a certain level, which is indicated by point III.

The paradox of a non-continuous relationship between soil P content and biomass can be explained by interspecies competition enabling species with higher nutrient efficiency to exhibit their growth potential and accordingly to provide lower nutrient extraction with the biomass. This is the case in grassland fields where these species are not suppressed by competing high productive species indicative of lower P efficiency. On the other hand, species with lower P efficiency suffer from low soil P content already at a higher threshold (compare point II to III). They can therefore produce only a limited amount of biomass, which might be even lower than that of a plant community well adapted to nutrient poor environments.

Apart from the formulation of such a theoretical hypothesis, the RGE also allows practical implications in view of nature conservation on grassland. The long-term fertilizer N application resulted in the lowest soil P content of all observed fertilizer treatments. In plots where the residual P or K contents are generally found too high, the long-term application of N in the form of ammonium nitrate without P or K can therefore serve as a valuable measure to deplete surplus soil nutrients. This is in accordance with conclusions by Edwards et al. (2002) and Crawley et al. (2005) who stated that N application can be used to restore semi-natural plant communities on localities previously fertilized with P and where a decrease in soil P content is required.

The pH value in the 0-10 cm soil layer of the RGE was strictly dependant on the addition of fertilizer lime. In the localities previously fertilized with P and where a decrease in soil P content is required.

**Plant species composition and species richness**

Surprisingly, the explanatory power of measured soil parameters was almost the same like the power of the treatment effect. The results indicate that 61.7% of the variability of plant species composition was explained by soil parameters and 62% were explained by the treatment effect. This points out that the soil properties were absolutely decisive for the creation of diverse plant communities. Originally, we hypothesized a higher explanatory power of the treatment effect compared to the effect of measured soil parameters. Obviously, the treatment effect was predominately a function of not one but several measured soil parameters. If other undetected gradients would have affected plant species composition, they probably might have been highly correlated with those soil parameters employed in the RDA analyses.

The results of the RDA analyses illustrate, that the soil P content was the most important experimental parameter affecting sward structure (Table 4, Fig. 2). In recent studies, the negative effect of increased P content in the soil on species richness has been presented (Peeters et al. 1994, Crawley et al. 2005, Bohner et al. 2005, Wassen et al. 2005). However, sward structure has not been evaluated in these studies. The potential of multivariate
analyses becomes obvious with the introduction of additional parameters like presence and absence of species as well as the cover of each species. They also have been affected by the P content in the top soil layer. Results from the RGE are in accordance with conclusions performed by Janssens et al. (1998) that 5 mg P 100 g-1 can be seen as a threshold for the existence of species rich grassland. In the RGE, no species that are indicative of extensive grasslands have been identified in plots where P content in the top soil layer exceeded 5 mg P 100 g-1 (treatment D, E, and F). The relation of species characteristic for oligotrophic grasslands to P content is well visible from the ordination diagram in figure 2; the arrows for all these species are directed towards the opposite of arrows for P content.

The soil pH is second to soil P with respect to sward structure. This is at least partly consistent with results from the PGE where soil acidification played a substantial role in the decrease of species number in plots receiving ammonium sulphate (Crawley et al. 2005). In the RGE, P content was the only measured soil parameter affecting species richness. It should be pointed out here, that the P effect in the RGE was identified based on a soil extraction method considering the decreasing P availability with decreasing pH. Hence, the P effect was not a hidden pH effect. In contrast to the PGE, no acidifying fertilizer has been used in the RGE. The effect of pH on plant species composition was positively correlated with the Mg content in the soil, but negatively with C/N ratio of soil organic matter. Obviously, these effects were associated with the long-term application of lime. After all, a major disadvantage of the RGE experimental design is the absence of separate N, P, and K fertilizer treatments. Therefore, it is impossible to strictly separate the effect of P and K since both nutrients were applied together with N.

Species richness as a function of sampling area
An increase in species richness as a function of the sampling area on which they have been recorded was revealed in all treatments. Surprisingly, the increase in species richness was similar in all treatments indicating that the effect of treatment on species richness was almost sampling area independent (see also Crawley et al. 2005). Only one exception was recorded: species richness on a 1 m² sampling area was highest in the A and lowest in the B treatment, but on a 5.76 m² sampling area the opposite was the case (Fig. 4). Obviously, the control without any lime and fertilizer application promoted highest species richness already on small sampling areas whereas the B treatment exhibited highest richness only on the largest (5.76 m²) sampling area. This indicates that the spatial distribution of species was more heterogeneous in B as compared to A.

Conclusions
The impact of fertilizer application on the interaction between plant species can statistically very well be evaluated by means of RDA; the ordination diagram clearly indicates the response of individual species to soil parameters. However, major results of this long-term experiment can be interpreted only in view of a two cut system maintained in the RGE. For instance, the response of Lolium perenne to soil N content was found low in these swards as the morphology does not allow strong competition in tall swards on hay meadows. Further, the soil pH was uncommonly high due to permanent lime application. However, the interaction between soil acidity and plant available nutrient content obviously had no significant effect on species composition. We conclude that any strategy to increase or maintain species richness in view of nature conservation on grassland must consider soil P as one of the strongest soil nutrient parameters. However, the interaction of fertilizer P with other soil parameters deserves further investigation, especially in relation to fertilizer N. Imbalanced nutrient content might impose similar growing conditions to the plants as does nutrient deficiency. Artificially induced nutrient depletion can therefore only be induced if plants are enabled to extract considerable amounts of nutrients with optimal growth.

The yield paradox hypothesis needs to be corroborated in different environments. This hypothesis is exclusively based on shifting contributions of species more or less favoured by P availability. The metabolic strategy of species dominating under low P availability has not yet been understood, in contrast to the role of N which is well documented especially with forage grasses.

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References


Figure 1 Aboveground biomass production in 2005 as affected by treatments A to F (a) and as a function of phosphorus concentration in the soil in treatments without P application (b).
Figure 3 Species richness of vascular plants as a function of biomass production (a) and phosphorus concentration in the soil (b).

Figure 4 Species richness of vascular plants (a) and species richness of vascular plants as a percentage from control (b) in relation to scale of investigation. Treatment abbreviations are given in Table 1: A, B, C, D, E, F.
Figure 5. Aboveground biomass yield as a function of soil P concentration in the fertiliser experiment of Dr. Štursova in the Giant Mts. (Czech Republic). Figure is based on data published by Hejcman et al. (2006). Plots with contrasting plant communities were presented. NS – plant community dominated by N. stricta, AF – plant community dominated by Avenella flexuosa. Similar distribution of the data were recorded in the case of soil K concentration as well (not shown here).
Figure 6. Scheme of the yield paradox hypothesis indicating the reaction of above ground biomass yield on plant available P content in the soil. NUE = nutrient use efficiency of the plant community. Capital letters indicate curve sections where (A) biomass yield increases with P content at nutrient poor locations, (B) competitive ability of plants with high NUE supports growth on oligotrophic soils, (C) change in floristic composition (towards E) and imbalanced N/P ratio decrease potential yield, (D) demanding forage species outcompete species indicative of oligotrophic grassland, (E) nutrient availability supports growth of forage grasses and herbs.