Biodiversity and ecosystem functioning in semi-natural montane grasslands – Effects on productivity, nitrogen partitioning and stability

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von Ansgar Kahmen

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Erlärung

Die geltende Promotionsordnung der Biologisch-Pharmazeutischen Fakultät der Friedrich-Schiller-Universität ist mir bekannt. Die vorliegende Dissertation habe ich selbständig verfasst und keine anderen als die von mir angegebenen Quellen, persönliche Mitteilungen und Hilfsmittel benutzt.

Bei der Auswahl und Auswertung des Materials haben mich die in der Danksagung genannten Co-Autoren unterstützt. In den Kapiteln die wissenschaftlichen Experimente und deren Interpretation betreffend, spreche daher im Namen aller Autoren im Plural.

Ich habe nicht die Hilfe eines Promotionsberaters in Anspruch genommen, und Dritte haben weder unmittelbar noch mittelbar geltwerte Leistungen von mir für Arbeiten erhalten, die im Zusammenhang mit dem Inhalt der vorliegenden Dissertation stehen.

Ich habe die Dissertation noch nicht als Prüfungsarbeit für eine staatliche oder andere wissenschaftliche Prüfung eingereicht. Ferner habe ich nicht mit Erfolg versucht, diese Dissertation anderweitig einzureichen.

Ansgar Kahmen Jena, 7.10.2004

Content

1 Zusammenfassung

Bedingt durch den dramatischen Rückgang der globalen Biodiversität hat sich in den letzten Jahren das Interesse von Ökologen verstärkt auf den Zusammenhang zwischen Biodiversität und Ökosystemfunktionen konzentriert. Erste Untersuchungen in experimentell angelegten Grasländern haben gezeigt, dass Biodiversität einen positiven Effekt auf Ökosystemfunktionen, wie zum Beispiel auf die Produktivität hat. Diese Zusammenhänge wurden durch eine erhöhte Ressourcennutzung mit zunehmender Artenzahl erklärt. Die gefundenen Ergebnisse sowie die daraus abgeleiteten Interpretationen haben jedoch zu einem breiten wissenschaftlichen Diskurs geführt. Insbesondere wurde das experimentelle Design vieler Arbeiten kritisiert und die gefundenen Resultate, sowie die vorgeschlagenen zugrunde liegenden Mechanismen, als statistische Artefakte abgetan. Ebenso wurde kritisch hinterfragt, ob diese experimentellen Ergebnisse für natürliche Ökosysteme relevant seien. Diese Kritik an vorangegangenen Studien macht deutlich, dass es nur dann zu einem generellen Verständnis von Biodiversität und Ökosystemfunktionen kommen kann, wenn Untersuchungen von experimentellen Ökosystemen auf bestehende Ökosysteme ausgeweitet werden und die funktionalen Mechanismen der beobachteten Zusammenhänge experimentell getestet werden.

Die für die vorliegende Arbeit vorgenommenen Untersuchungen wurden daher auf bestehenden, natürlichen Grasländern durchgeführt um zu erklären, ob:

(1) Biodiversität einen Einfluss auf Produktivität in bestehenden, natürlichen Grasländern hat,

(2) komplementäre Stickstoffnutzung sich für einen positiven Zusammenhang zwischen Biodiversität und Produktivität verantwortlich zeigt und

(3) Biodiversität bei bevorstehenden Klimaveränderungen positive Auswirkungen auf die Stabilität von Ökosystemfunktionen hat.

(1) In meinen Untersuchungen in natürlichen Grasländern war kein Effekt zwischen Biodiversität und Produktivität erkennbar. Die Artenvielfalt in den untersuchten Ökosystemen, war im Vergleich zu experimentellen Grasländern jedoch relativ hoch. Ich vermute daher, dass Biodiversitätseffekte nur bis zu einem bestimmten Artenniveau

beobachtet werden können und dass Arten über dieses Niveau hinaus redundant im Bezug auf Ökosystemfunktionen sind.

(2) Die Ergebnisse aus (1) bestätigten sich, als die komplementäre Stickstoffnutzung von verschiedenen Arten untersucht wurde. Meine Ergebnisse haben gezeigt, dass sich die verschiedenen Arten in einem System zwar in der Ressourcennutzung unterscheiden, die Arten jedoch in wenige funktionelle Gruppen eingeteilt werden können innerhalb welcher die Arten funktional redundant sind. Das bedeutet, dass ein positiver Effekt zwischen Biodiversität und Ökosystemfunktionen nur solange zu erwarten ist, bis alle funktionellen Gruppen im System vertreten sind. Jede weitere Artenzunahme führt zu keiner Veränderung in den Ökosystemfunktionen.

(3) Da für die nächsten Jahrzehnte Klimaveränderungen für Mitteleuropa vorhergesagt wurden, habe ich abschließend getestet, ob auch unter sich ändernden Klimabedingungen nur wenige Arten für stabile Ökosystemfunktionen notwendig sind. Dazu habe ich auf den untersuchten Flächen eine Frühjahrsdürre simuliert und untersucht, ob Biodiversität zur Stabilität von Produktivität unter Niederschlagsdefiziten (Trockenstress) beiträgt. Die Ergebnisse haben ergeben, dass Biodiversität an sich zwar keinen stabilisierenden Effekt auf die Produktion von oberirdischer Biomasse hat, dass das Wurzelwachstum der untersuchten Wiesen bei Trockenstress jedoch in positivem Zusammenhang mit Biodiversität steht. Es lässt sich daher vermuten, dass in einem Ökosystem mit zunehmender Biodiversität auch die Wahrscheinlichkeit steigt, Arten zu enthalten, die resistent gegenüber Umweltveränderungen sind und dass diese Arten Ökosystemfunktionen für das gesamte System stabilisieren.

Zusammenfassend zeigen meine Ergebnisse, dass Erkenntnisse aus experimentellen Studien nicht ohne weiteres auf natürliche Systeme übertragen werden können. Dennoch legt meine Arbeit nahe, dass die zugrunde liegenden Mechanismen in experimentellen und natürlichen Systemen vergleichbar sind. Meine Arbeit hat weiterhin gezeigt, dass zur Beurteilung eines Biodiversitätseffektes auf Ökosystemfunktionen viele unterschiedliche Parameter herangezogen werden müssen. Arten, die für den einen Parameter funktional redundant sind, wie z.B. für Stickstoffnutzung, können in Bezug auf einen anderen Parameter, zum Beispiel Trockenresistenz, komplementär sein und einen positiven Effekt auf das System ausüben. Generell zeigt meine Untersuchung daher, dass unter Berücksichtigung vieler Parameter ein Großteil der in einem System vorhandenen Arten einen positiven Effekt auf das Funktionieren von Ökosystemen hat.

2 Introduction

2.1 General Introduction

The biosphere is a unique property of the earth, distinguishing our planet from all other known objects in the universe. In combination with physical and chemical processes, the biosphere dramatically influences the shape and condition of the earth. Through metabolic pathways, organisms move hundreds of thousands of tons of material, and therefore drive biogeochemical cycles in terrestrial, aquatic and marine systems and determine the composition of the atmosphere (Schlesinger 1997). Several of these biosphere driven processes supply mankind with an array of services that human society depends on. Among others, these services include the generation and conservation of fertile soils, providing clean freshwater, production of biomass as timber or food, control of agricultural pests and providing pollination for many crops (Daily 1997). Consequently, earth's living beings do not only shape the face of the planet but are also the basis of human existence.

The biosphere of the earth is, however, altered by human beings at an unprecedented rate (Turner *et al.* 1990; Vitousek *et al.* 1997). The breakdown of biogeographic barriers by international travel and trade, for example, has caused species to extend their range far beyond their natural range, invading and changing the properties of entire ecosystems (Brooks *et al.* 2004). Also, conversion of forests and grasslands to agricultural land and urban developments has altered one third to one half of the earth's ice free terrestrial surface, impacting ecosystem services on a continental scale (Turner *et al.* 1990). Probably the most dramatic of all man caused changes of the biosphere is, however, the rapid decline of biological diversity (Chapin *et al.* 2000). In contrast to agricultural land that can be reconverted to forests, or invading species that can – though with large effort only – be eradicated from an invaded area, the genetic code of extinct species is irreversibly lost.

In the earth history, extinction of species is not an unusual phenomenon. In fact, Raup (1991a) has estimated that for biological reasons, the average evolutionary lifespan of a species is roughly 4 million years, so that about 25% of all species disappear every one million years. Consequently, this so called "background extinction" has caused 95% of all organisms, that have ever lived on earth, to go extinct since the diversification of life has begun roughly 600 million years ago (Raup 1991b). Superimposed on this background extinction, however, five catastrophic extinction events occurred in the geologic past (Fig. 2.1). These catastrophic extinctions have caused up to 80% of all taxa living at a time to go

extinct in a single event (Sepkoski 1989). The causes of mass extinction events are still unclear and subject of vivid scientific debate (Alvarez *et al.* 1980; Kent 1981; Raup 1989). The consequences of catastrophic mass extinctions, however, are well understood. For example, paleontological data show that recovery of diversity levels took several million years and that the genetic composition of the biosphere was dramatically altered, even shifting to entirely new phyla that reshaped the face of the earth.

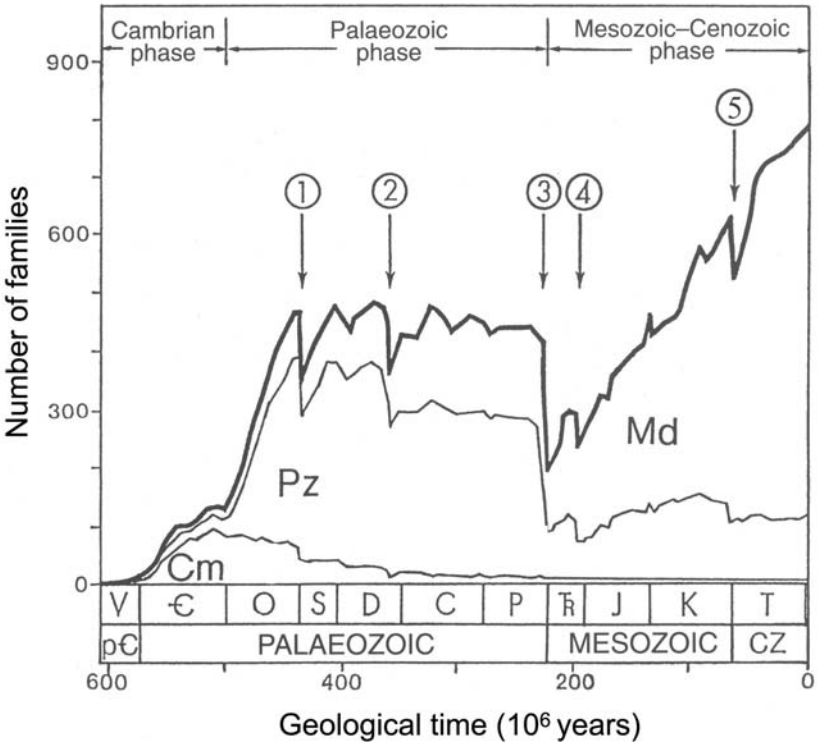

Fig. 1.1: Diversity of marine animal families during the last 600 million years based on fossil records. Arrows indicate mass extinction events. The upper line shows the total number of families. The fields below show the contributions of the three great evolutionary faunas to total family diversity: modern fauna (Md), Palaeozoic fauna (Pz) and Cambian fauna (Cm). Modified after Sepkoski (1995).

Similar to the five mass extinction events in the geologic past, extinction rates of plants, fungi and animals that are observed today, also exceed background extinction by several orders of magnitude (Pimm *et al.* 1995). Consequently, experts refer to this current decline in biodiversity as the 6th catastrophic mass extinction in the history of the earth (Hanski *et al.* 1995). In fact, estimates predict that of the estimated ~ 10 million species presently living on earth (May 1990), a large proportion will go extinct in the next 100 years (Pimm *et al.* 1995). Other than for the five mass extinctions in the geologic past, the causes of the

current extinction events are very well understood and have been described extensively in the scientific and non-scientific literature (Ehrlich & Ehrlich 1981). What remains largely unclear, however, are the consequences this dramatic decline in biological diversity will have for the shape and condition of the earth and consequently for the wellbeing of human beings.

Earth system models that predict biogeochemical cycles have traditionally a very simplistic view of the earth's biota. Only recently, ecosystem-averaged processes such as stomatal conductivity or canopy roughness were incorporated in the models. This has lead to a successful linking of processes from the earth surface with atmospheric phenomena, making valuable contributions in the understanding of biosphere atmosphere feedbacks (Mooney *et al.* 1987). The link between biodiversity and biogeochemical cycles has, however, hardly been included in earth system models, despite a fast growing body of literature, reporting experimental evidence for the effect of biodiversity on ecosystem functioning. Biodiversity effects have not been included in earth system models, partly because a disagreement in the scientific community on the generality of the available experimental results. To overcome this disagreement, a careful evaluation of the achieved experimental results, a detection of the underlying mechanisms and a verification of the experiments in natural ecosystems is therefore essential. Only a general agreement on the effects of biodiversity on ecosystem functions will provide reliable predictions that can be incorporated in earth system models, so that the global consequences of the 6th extinction crisis can be evaluated.

2.2 Biodiversity and ecosystem functioning research

The worldwide loss of biodiversity and the unknown consequences for the earth system has created huge research interest in the ecological community during the last 15 years. In fact, the relationship between biodiversity and what is termed 'ecosystem functioning' is currently one of the largest and most widely discussed topics in the scientific ecological community (Naeem *et al.* 1999).

The interest in the effect of species diversity on ecosystem functioning is, however, not new but one of the oldest questions in ecology. Nobody else but Charles Darwin postulated 1859 in "The origin of Species" that "*It has been experimentally proven that if a plot of ground be sown with one species of grasses, a greater number of plants and a greater weight of dry herbage can thus be raised*" (Darwin 1859). In 2002 Hector and Hooper (Hector & Hooper 2002) were able to determine the original early 19th century

reference ‘Hortus Gramineus Woburnensis’ Darwin was referring to. In fact they discovered a description of an experiment, where the performance of different species in mixture with different diversities was tested, a study very similar to the large biodiversity and ecosystem functioning experiments conducted today. To their knowledge this reference is the oldest reported ecological experiment, putting the question of biodiversity and ecosystem functioning at the beginning of experimental ecology.

Modern Biodiversity and Ecosystem functioning research was largely triggered by a state of the art conference near Bayreuth, Germany in 1991, with the proceedings published in 1993 (Schulze & Mooney 1993). Since then a large number of experimental studies has been conducted, mainly in Ecotrons (Naeem *et al.* 1994), microcosms (McGrady-Steed *et al.* 1997) and experimental grasslands (Tilman *et al.* 1997; Hector *et al.* 1999, for a complete review of experimental biodiversity ecosystem functioning studies see Loreau *et al.* 2002). All of these experiments created a diversity gradient while controlling extrinsic factors and investigated numerous ecosystem functions as response variables. Following these experiments and other theoretical considerations, more that 50 theories on the relationship between biodiversity and ecosystem functioning have been suggested (Schlapfer & Schmid 1999).

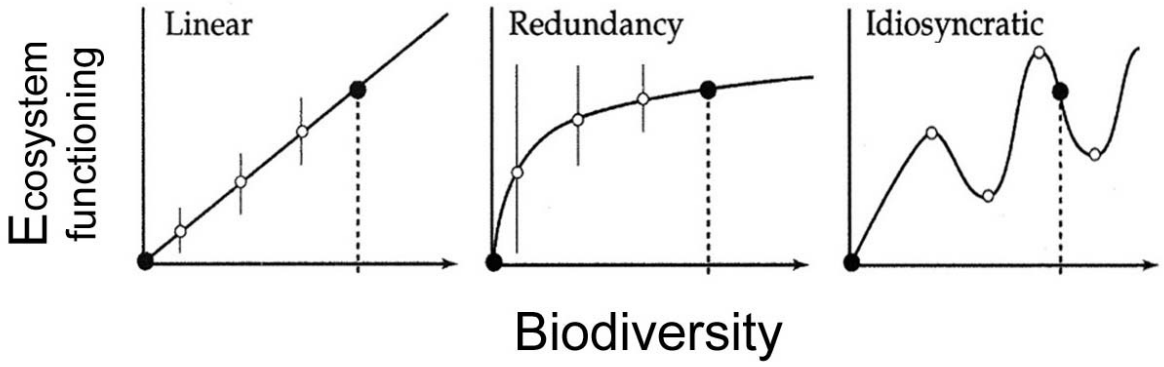

Fig. 1.2: Suggested relationships between biodiversity and ecosystem function. From left to right the figures describe relationships where (a) each species adds to ecosystem functioning, (b) species are functionally redundant, and (c) effects are species specific. Modified after Naeem (2002).

In general the different hypothesis can be summarized in three groups (Fig. 2.2) (Naeem *et al.* 2002): a) Species have specific functional traits so that loss or addition of species to an ecosystem causes a change in ecosystem functioning. The relationship between biodiversity and ecosystem functioning is therefore roughly linear. b) Species have different but largely

redundant traits. Above a critical diversity level, where all functional traits are present, addition or deletion of species does not change ecosystem functioning. The relationship between biodiversity and ecosystem functioning therefore has an asymptotic shape. c) Species traits are context dependent and thus unpredictable or idiosyncratic. The effect of species additions or species deletions from a system depends on intrinsic and extrinsic factors, so that a variety of different slopes are possible and no simple relationship between biodiversity and ecosystem functioning can be determined.

Positive effects of biodiversity on ecosystem function, independently of the actual shape of the relationship, have largely been explained by niche complementarity (Tilman *et al.* 1996; Hector 1998; Loreau 1998; Loreau & Hector 2001) or resource facilitation (Cardinale *et al.* 2002; Spehn *et al.* 2002). The niche complementarity hypothesis implies that plant species in an ecosystem occupy distinct ecological niches and use complementary resources, so that increasing numbers of species result in more effective resource exploitation, leading to enhanced ecosystem functions. Resource facilitation suggests that species alter the environment such that it benefits another species, leading to a greater resource use and thus positive effects of biodiversity and ecosystem functioning.

In a vivid and occasionally highly emotional debate in the scientific literature experimental biodiversity and ecosystem functioning studies have been highly criticized for quality of the experimental design and the applicability of their results (Kaiser 2000). In summary, critics have argued that the positive relationship between biodiversity and ecosystem functioning detected in experimental studies, was based on statistical artifacts such as sampling effects: The higher the diversity in a plot, the greater the chance of highly productive species to be present in the plot, leading to a greater overall productivity in the system, independently of niche complementarity or facilitation (Aarssen 1997; Huston 1997). Furthermore, several authors have questioned the applicability of the experimental studies for natural ecosystems, where biodiversity will be insignificant compared to the overwhelming influences of environmental and anthropogenic factors on ecosystem functioning (Grime 1997; Wardle *et al.* 1997; Huston & McBride 2002). While this discussion has certainly fuelled biodiversity and ecosystem functioning research, it also indicated that general and reliable predictions on the effect of biodiversity and ecosystem functioning cannot yet be made.

2.3 Objectives of the study

Despite the impressive development of research and a growing body of literature during the last decade, the relationship between biodiversity and ecosystem functioning if far from being fully understood. In particular, it is difficult to predict if the results achieved in experimental studies can be extrapolated to natural ecosystems. Also, very few studies have specifically addressed the actual mechanisms behind the biodiversity and ecosystem functioning relationships observed in experimental studies. For example, little is known if plant species in an ecosystem in fact exploit different resources so that an enhanced resource use is the cause of increased productivity with increasing diversity. Expanding the field of biodiversity and ecosystem functioning research to natural ecosystems and addressing the ecophysiological mechanisms behind the observed biodiversity effects is therefore essential for a more general understanding of the relationship between biodiversity and ecosystem functioning. A general understanding of these effects is urgently needed to include the effect of biodiversity in earth system models, so that the consequences of the 6th extinction crisis can be predicted for the earth system and the ecosystem services provided to the human society.

The aim of my research therefore was to address the relationship between biodiversity and ecosystem functioning in natural ecosystems and determine some of the functional mechanisms behind the observed patterns. Specifically, my objectives in this study were:

(1) to test the relationship between plant diversity and productivity in semi-natural montane grasslands and to distinguish the effect of biodiversity from other confounding factors such as species composition, management or soil properties.

(2) to test the niche complementarity hypothesis with respect to soil nitrogen uptake as an explanation for the relationship between biodiversity and ecosystem functioning.

(3) to evaluate the effect of plant diversity on stabilizing productivity, above and below ground in the face of a changing climate.

3 Effects of plant diversity, community composition and environmental parameters on productivity in montane European grasslands

3.1 Introduction

The consequences of the observed worldwide loss in biodiversity for ecosystem functions are a hotly debated topic in ecological research (Aarssen 1997; Huston 1997; Grime 1998; Hector et al. 2000; Troumbis 2001; Wardle 2001; Loreau et al. 2002). In most of the recent laboratory and field experiments, the effect of biodiversity on productivity was tested in artificial plant communities where different diversity levels were established by drawing plant species from a random species pool. Generally, these experiments have shown an asymptotic increase of productivity with increasing number of species (Naeem *et al.* 1994; Naeem *et al.* 1996; Tilman *et al.* 1996; Hooper & Vitousek 1997; Tilman *et al.* 1997; Hector *et al.* 1999). The observed patterns have largely been attributed to niche complementarity (Tilman *et al.* 1996; Hector 1998; Loreau 1998; Loreau & Hector 2001). Niche complementarity predicts that an increase in species richness will lead to a more efficient use of available resources and thus increased productivity. Several authors have questioned the applicability of those studies for natural ecosystems, where biodiversity will be insignificant compared to the overwhelming influences of environmental and anthropogenic factors on ecosystem functioning (Grime 1997; Wardle *et al.* 1997; Huston & McBride 2002). It has also been argued that the results achieved in experimental studies may have little predictive value for species loss in natural ecosystems where species extinction is not random but directed (Grime 2002; Diaz et al. 2003). In recent reviews, (Chapin *et al.* 2000; Loreau *et al.* 2001) have therefore suggested to expand the study of biodiversity and ecosystem functioning to natural ecosystems.

In studies of natural ecosystems, biodiversity has traditionally been viewed as a response rather than a predictive variable. Diversity has been hypothesized to peak at intermediate levels of productivity and decrease at high or low productivity and a number of data sets support this theory (Al-Mufti *et al.* 1977; Rosenzweig & Abramsky 1993; Grace 1999; Waide *et al.* 1999; Mittelbach *et al.* 2001). Although productivity *per se* has historically been considered as the main variable driving the productivity-diversity relationship, recent studies have demonstrated that this pattern can arise from covariation of productivity with other abiotic or management factors, illustrating the complexity of

environmental regulation of species diversity in natural communities (Gough *et al.* 1994; Chase & Leibold 2002; Schaffers 2002; Fukami & Morin 2003; Rajaniemi 2003).

The traditional view of biodiversity, where high productivity results in low diversity, seems inconsistent with the experimental results, where high diversity results in increased productivity. Both approaches are, however, complementary rather than contradictory (Loreau 2000; Huston & McBride 2002; Schmid 2002). While the traditional approach attempts to identify the spatial variation of diversity across environmental gradients, the experimental approach tries to determine the consequences of species loss in a given system where all environmental factors remain constant. Testing the effect of biodiversity on productivity in complex natural communities would therefore require the control of environmental gradients, which is difficult because of the large number of variables that influence diversity (Wardle 2001). An alternative is to apply multivariate models that permit to control environmental variables statistically and detect direct and indirect effects of diversity and environmental variables on ecosystem functions.

While most experimental studies and the traditional analyses of the productivity-diversity relationship have focused on species richness as a measure of plant biodiversity, different aspects of diversity should be considered when the effects on productivity are investigated. Several studies have, for example, shown that the number of plant functional groups or evenness influenced productivity more strongly than species richness (Tilman *et al.* 1997; Wilsey & Potvin 2000; Diaz & Cabido 2001; Spehn *et al.* 2002). Also, it has been shown that the presence of one or a few dominant species with strong ecosystem effects is likely to mask simple relationships of species richness and productivity (Chapin *et al.* 1997; Huston 1997; Hooper & Vitousek 1998; Aarssen 2001; Huston & McBride 2002). Consequently, the effect of specific species and community composition need to be considered if diversity effects on ecosystem functions are tested in a semi-natural ecosystem.

In this study, we aimed to determine the effect of different aspects of plant diversity on productivity in semi-natural managed grasslands. Specifically, we tested (1) the direct effects of plant diversity (using different indices) and community composition on productivity as well as (2) the direct and indirect effects of environmental parameters such as soil properties, management and site characteristics on both diversity and productivity. In a final step, we applied a path analysis to distinguish between direct and indirect effects of environmental variables on plant diversity and productivity.

3.2 Material and Methods

Study area and study sites

The study was conducted in the Thüringer Schiefergebirge/Frankenwald, a plateau-like mountain range at the Thuringian/Bavarian border in central Germany, which reaches a maximum height of 870 m. The bedrock material in the investigated area produces a carbonate-free, nutrient-poor soil. Average annual precipitation is above 1000 mm with a slight summer maximum. Annual average temperature is 5°C. Before human settlement in the middle ages, montane spruce-fir-beech forests formed the natural vegetation in the area. Thereafter, much of the forest was converted into an agricultural landscape, with a high proportion of different montane hay meadow and pasture grasslands (*Geranio- Trisetetum*, Knapp ex Oberd. 1957) (Hundt 1964).

In 2001, 78 managed grasslands were studied. All sites were located between 500 and 840 m altitude on high elevation plateaus of the mountain range, so that orographic and edaphic factors were relatively comparable among sites. To qualify for the study, grasslands had to be free of woody plants as a sign for recent management, and had to be uncut or ungrazed by the time of the study. The minimum size of a site had to be one hectare. In each site, a two by two meter plot was established at a distance of about 50 m from other habitats or roads. In each plot, plant species richness, percent cover, above ground biomass (following used as surrogate for productivity), soil pH, soil moisture, soil C:N and plant available soil nutrients were determined.

Sampling of environmental, productivity and vegetation data

During a field campaign (May 28th to June 9th 2001), two soil cores (4.5 x 10 cm) were taken within each plot. Soil of each core was sieved to 2 mm. One part of the soil was extracted with 1M KCl on the same day of sampling. KCl extracts were frozen at -20°C and later analyzed using a Continuous Flow Analyzer (SAN Plus, Skalar, Erkelenz, Germany) for NH_4^+ and NO_3^- and an ICP-AES (Optima 3300 DV, Perkin-Elmer, Norwalk, USA) for Ca^{2+}. The remaining soil was dried at 35°C and extracted using a 1M Calcium-Acetate-Lactate (CAL) solution. CAL extracts were analysed with ICP-AES (Optima 3300 DV, Perkin-Elmer, Norwalk, USA) for P, K^+, $Mg^{2+}$and SO_4^{2-}. Soil pH was measured in a water extract. For C:N, N_{tot} and C_{tot} determinations, dry soil was ground and analyzed with an Element Analyser (Vario EL II, Elementar, Hanau, Germany). Soil moisture (Vol %) was

measured in the field using time domain reflectometry (ThetaProbe, Delta-T Devices Ltd., Cambridge, UK) at four different locations within each plot.

All plant species within the 2 x 2 m plot were identified to the species level and the percent cover of each species was estimated visually. We used above ground standing biomass as a surrogate for productivity in this study. Biomass was harvested at peak standing biomass in two 25 x 50 cm rectangles 2 cm above ground in each plot. The plant material was dried at 60°C for 48 h and the dry weight determined thereafter.

For an orographic characterization of the sites, geographic position (GPS coordinates), altitude, exposition, inclination as well as the distance to the next woodland habitat was recorded. Based on the mean exposition and inclination, the mean potential direct solar insolation (PDSI), was calculated for each site (Homann, Schumacher and Perner, unpublished software program based on an algorithm by Volz (1959)).

Information about the management regimes of the investigated sites was collected using a standardized questionnaire. Each farmer was interviewed in December 2001 or January 2002 about the following topics: (1) approximate age of grassland, (2) mowing intensity (number and timing of cuts, separately for 2001 and the past 10 years), (3) grazing intensity (animal species, grazing density, timing, duration, separately for 2001 and the past 10 years), (4) fertilization (type of fertilizer, amount of fertilizer applied, timing of fertilization, separately for 2001 and for the past 10 years). For statistical analysis, management data were converted into numeric values. For the cutting regime, dates of cutting were weighted to reflect that early cuts have a stronger effect on plant diversity than later cuts (Klapp 1971): a value of "3" was assigned to cuts in early summer (prior to June 15th), a value of "2" for cuts between June 15th and September 1st, and a value of "1" for cuts after September 1st. In case grasslands were cut more than once during the season, the numbers assigned to the date of each cut were summed to yield a single value for the statistical analysis. For grazing, values between "1" and "4" were assigned. For each value, grazing time, intensity and frequency as well as type of grazing animal (cattle, cow, horse and sheep) were considered. High "grazing-values" reflect a high grazing impact on the grassland (Klapp 1971). For fertilization, values between "1" and "8" were assigned, with low values for "light-impact-fertilization" and high values for "high-impact-fertilization". Values between "1" and "4" were assigned to sites that received dung from grazing animals, with higher stocking densities resulting in larger values. Values of "5"," 6" and "7"were assigned to sites with applications of less than 50 kg ha^{-1}a^{-1}, 50 to 100 kg ha^{-1}a^{-1} and more

that 100 kg $ha^{-1}a^{-1}$ of industrial NPK fertilizer, respectively. Sites treated with solid manure received the value "8", while liquid manure application was weighed with "9".

Statistical analyses

To improve normality of variances and avoid distortions plant species cover data were square-root transformed before analyses. In a first step, the number of edaphic site characteristics and management variables was reduced using Principal Component Analysis (PCA, CANOCO, ter Braak & Smilauer 2002). This procedure summarizes the information of the variables as four major axes of a standardized PCA. Since PCA axes are by definition orthogonal and independent of each other, this procedure creates composite independent variables and avoids the danger of spurious correlations (i.e., multicollinearity). PCAs were performed separately for edaphic, management and orographic parameters. From each PCA, the axes explaining most of the variance (but no more than the first four) were extracted resulting in new PCA-derived variables. These PCA-derived variables were used in all consecutive analyses as independent parameters. Very little information was lost by this procedure since the extracted axes explained most of the total variance contained in the original parameter groups.

From the plant cover data, we calculated plant species richness, effective diversity (heterogeneity or exponential Shannon-Wiener), and Camargo's evenness (calculation algorithms see Krebs 1999). To analyze the compositional differences among the plant communities of the 78 studied grassland sites, Non-Metric Multidimensional Scaling (NMDS) ordination techniques were applied using the program PC-ORD (McCune & Mefford 1997). NMDS is an iterative search for a ranking and placement of n entities (samples) in k dimensions (ordination axes) that minimizes the stress of the k-dimensional configuration. The 'stress'-value is a measure of departure from monotonicity in the relationship between the dissimilarity (distance) in the original p-dimensional space and in the reduced k-dimensional ordination space (Clarke 1993). As a distance measure, the Bray-Curtis coefficient was used (also known as Sørensen or Czekanowski coefficient), which is one of the most robust measures for this purpose (Faith et al. 1987). NMDS ordination was based on square-root-transformed cover data. To analyze which of the species are mainly responsible for the compositional changes within the investigated plant communities (along the extracted NMDS axes), we performed linear regressions of species cover vs. the scores of the NMDS axes.

We used least square linear regressions to analyze the effects of plant diversity and community composition (species richness, effective diversity, Camargo's evenness, NMDS axes) on productivity. Thereafter, we performed multiple regression analysis to test the effect of the same diversity measures on productivity in combination with different sets of environmental parameters. The multiple regression analyses were performed separately for each diversity measure and one of the PCA constructed parameter groups edaphic variables, site characteristics and management variables.

In a next step, we used multiple stepwise regressions to test whether the PCA-derived variables were significant predictors for plant diversity measures that were significantly correlated with productivity. In addition, we tested the predictive value of the PCA-derived variables for productivity itself. For each dependent variable (diversity measures and productivity), separate regression models were calculated for each parameter group edaphic variables, site characteristics and management variables, respectively. Regression analyses were performed using SPSS Version 11 (SPSS Inc. 2001).

In a final path analysis, we used structural equation modeling (AMOS version 4.0, Arbuckle & Wothke 1995-1999) to test the hypothesis that environmental and management parameters influence productivity both directly or indirectly by affecting plant species composition in the sites. Starting from the most complex model that included all significant variables from the multiple regression analyses, model simplification was based on the significance of the regression weights. The competing models were compared by bootstrapping each model 1000 times and using the Akaike Information Criterion (AIC), the Browne-Cudeck-Criterion (BCC), and the Consistent Akaike Information Criterion (CAIC) (Arbuckle & Wothke 1995-1999). Based on (Schmid 2002), the model assumed that productivity is a response variable only, having no effect on environmental variables or species composition.

3.3 Results

Plant diversity and environmental parameters

Plant species richness in the 78 sites varied between 8 and 33 species per 4 m^2, effective diversity between 4.3 and 19.4, and Camargo's evenness between 0.28 and 0.54. Mean aboveground plant biomass was 359 g_{dw} m^{-2} (range: 125 g_{dw} m^{-2} to 610 g_{dw} m^{-2}) (Table 3.1). For range and descriptive statistics of plant available soil nutrients and site characteristics see Table 3.1.

Table 3.1: Descriptive statistics (mean, standard deviation, min and max values and coefficient of variation) of productivity, biodiversity parameters, soil variables and site characteristics of the 78 investigated sites.

	Unit	Mean	SD	Min	Max	CV
Biomass	g_{dw}/m^2	359.43	106.97	124.64	609.60	29.76
Species richness		20.5	5.8	8	33	28.5
Effective diversity		11.43	3.56	4.27	19.44	31.17
Carmago's evenness		0.43	0.06	0.28	0.54	13.58
Soil Carbon	mg/g	49.79	11.17	28.58	80.27	22.43
Soil Nitrogen	mg/g	4.10	0.67	3.04	6.12	16.22
C:N		14.10	1.81	9.85	21.31	12.81
K^+	mg/g	0.06	0.06	0.00	0.30	99.84
Mg^{2+}	mg/g	0.23	0.15	0.05	0.95	64.56
P_{tot}	mg/g	0.04	0.06	0.01	0.58	173.76
SO_4^{2+}	mg/g	0.03	0.01	0.00	0.08	49.89
Ca^{2+}	mg/g	1.15	0.68	0.08	2.91	59.41
N_{min}	µg/g	2.91	2.84	0.00	16.35	97.33
pH		5.47	0.59	4.35	7.17	10.80
Soil moisture	%vol	28.28	7.34	13.48	45.08	25.96
Altitude	m asl	672	68.37	499	841	10.17
Inclination	°	4.30	3.76	0.00	20.00	87.37
Potential insolation	kJ $cm^{-2}d^{-1}$	3.043	86.72	2.713	3.194	2.85
Distance to nearest grassland border	m	63	35.42	14	188	55.78

The majority of the investigated grasslands were cut for haymaking (58%). Fewer sites were grazed (12%) or cut and grazed (27%). One site was not managed in the year of the investigation. In most cases, cutting occurred once a year (N=54), although some sites were cut twice (N=18) or even three times (N=3) per season. Grazing occurred mainly with cows or cattle (N=17), with only some sites grazed by horses (N=8) or sheep (N=4). Only 22% of all sites were fertilized. Applied fertilizer included industrial NPK, dung or liquid manure. Recent management (2001) was closely correlated to the management in the last 10 years ($p<0.001$).

Aggregation of environmental data

Four axes were extracted as independent variables from the Principal Component Analysis (PCA) of the edaphic parameters and labeled soil1 – soil4 (Table 3.2). These four axes explained 77.2% of the total variance of all edaphic parameters. Table 3.2 also

Table 3.2: Eigenvalues and eigenvector coefficients (loadings) of a standardized Principal Component Analysis (PCA). PCA was performed separately for edaphic factors, site characteristics and management parameters of 78 sites. Loadings >0.5 are shown in bold to highlight the meaning of the representative axis.

PCA	axis1	axis2	axis3	axis4
Edaphic factors				
	soil1	soil2	soil3	soil4
Eigenvalue	0.357	0.219	0.105	0.091
Soil Carbon	0.483	0.849	-0.042	-0.013
Soil Nitrogen	0.297	0.708	-0.368	-0.073
C:N	0.461	0.596	0.416	0.078
K^+	-0.211	-0.002	0.765	0.349
Mg^{2+}	-0.657	0.405	0.201	-0.102
P_{tot}	-0.363	0.262	-0.212	0.706
SO_4^{2+}	0.799	0.058	-0.066	0.439
Ca^{2+}	-0.768	0.404	-0.053	-0.189
N_{min}	-0.654	0.291	-0.328	0.241
pH	-0.817	0.432	0.189	-0.106
Soil moisture	0.678	0.401	0.157	-0.250
Site characteristics				
	site1	site2	site3	site4
Eigenvalue	0.392	0.254	0.223	0.132
Altitude	-0.439	-0.679	-0.550	0.211
Inclination	0.834	-0.126	0.099	0.528
Potential insolation	-0.680	0.585	-0.041	0.441
Distance	-0.464	-0.443	0.760	0.108
Management				
	manage1	manage2	manage3	manage4
Eigenvalue	0.506	0.363	0.070	0.040
Cutting 2001	-0.430	0.849	0.211	0.048
Cutting prior 2001	-0.377	0.872	0.208	-0.095
Grazing 2001	0.934	-0.094	0.272	-0.184
Grazing prior 2001	0.927	-0.039	0.325	0.150
Fertilization 2001	0.708	0.566	-0.310	-0.277
Fertilization prior 2001	0.689	0.605	-0.242	0.310

illustrates the species loadings of the individual axes. Soil1 was mainly related to pH, SO_4^{2+}, Ca^{2+}, Mg^{2+}, N_{min} and soil moisture. Except for the last two variables, all of these parameters are somehow related to soil acidity. Soil2 was correlated with total soil carbon and nitrogen as well as C:N. Soil3 was correlated mainly with K^+, while soil4 was strongest correlated with extractable P (Table 3.2).

The PCA on the site characteristics extracted four axes (site1 - site4), explaining 100% of the total variation. Site1 was mainly correlated with inclination and potential insolation, site2 with altitude and potential insolation, site3 with altitude and distance to next habitat and site4 with inclination (Table 3.2).

For the management variables, the PCA extracted only two axes explaining 86.9% of the total variation (manage1 and manage2), reflecting the close correlations between current and past management. Manage1 was mainly correlated with present and past grazing and fertilization regimes while manage2 was mainly correlated with present and past cutting as well as fertilization regimes.

Plant community composition

Based on their plant species composition, the 78 investigated grasslands can be separated into two overlapping groups, a more productive *Geranio-Trisetetum alopecuretosum* and a less productive *Geranio-Trisetetum nardetosum* (Fig. 3.1).

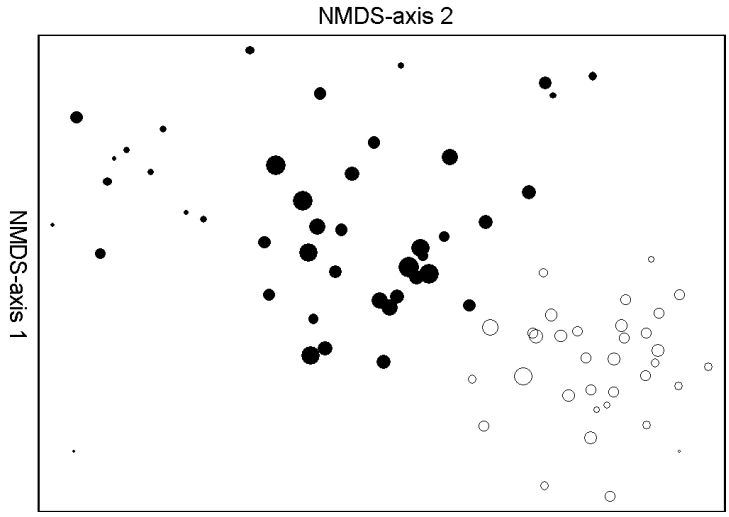

Fig. 3.1: Non-metric multidimensional scaling (NMDS) ordination of the 78 montane grassland sites. Increasing symbol size indicates increasing plant species richness (range: 8-33). Empty circles: more productive *Geranio-Trisetetum alopecuretosum* sites; filled circles: *Geranio-Trisetetum nardetosum* sites.

Table 3.3: Relative presence and average cover of plant species in all 78 sites that explain more than 25% of the variance of NMDS axis and more than 10% of variance in productivity based on simple linear regressions. Plus or minus signs in parenthesis behind the regression coefficients represent the direction of the relationship.

	Presence	Average cover	NMDS1	NMDS2	Productivity
	[%]	[%]	R^2	R^2	R^2
Alopecurus pratensis	40	5.0	-	-	0.138*** (+)
Anthriscus sylvestris	44	10.4	-	0.263*** (+)	0.146*** (+)
Crepis biennis	3	1.5	-	-	0.102** (+)
Dactylis glomerata	71	12.5	-	0.301*** (+)	0.110** (+)
Festuca rubra	62	17.5	-	0.398*** (-)	0.162*** (-)
Holcus mollis	15	2.1	0.271*** (+)	-	-
Meum athamanticum	53	21.6	0.282*** (+)	0.482*** (-)	0.118** (-)
Nardus stricta	14	4.4	-	-	0.111*** (-)
Poa trivialis	59	12.0	0.320*** (-)	0.298*** (+)	-
Rumex acetosa	87	15.0	-	0.331*** (+)	0.114** (+)
Taraxacum officinale	74	15.3	-	0.340*** (+)	-
Trifolium repens	59	10.9	-	0.280*** (+)	-
Trisetum flavescens	42	7.4	-	-	0.164*** (+)

Table 3.4: Multiple stepwise regression models for NMDS2 and productivity. Separate models were calculated for the parameter groups soil, site characteristics and management.

Dependent variable	Independent parameter group	Details of multiple regression model				Model summary	
		Variable	b	*p*	r^2	r^2	*p*
NMDS2							
	soil					0.750	<0.001
		soil1	-0.817	<0.001	0.668		
		soil4	-0.236	<0.001	0.723		
		soil2	0.163	0.006	0.750		
	site characteristics					0.065	0.024
		site3	0.255	0.024	0.065		
	management					0.388	<0.001
		manage2	0.552	<0.001	0.304		
		manage1	0.290	0.002	0.388		
Productivity							
	soil					0.121	0.002
		soil1	-0.348	<0.002	0.121		
	site characteristics	no variable significant					
	management					0.189	<0.001
		manage2	0.435	<0.001	0.189		

Both grassland types are closely related and belong to the same phytosociological association (*Geranio (Sylvatici)- Trisetetum*, Knapp ex Oberd. 1957) (Hundt 1964). Plant species richness was not correlated with species composition. Non-Metric Multidimensional Scaling (NMDS) showed that a two dimensional solution was sufficient to achieve low stress values (1st axis/dimension = 23.3, 2nd axis/dimension = 16.1, $r^2 = 0.73$) to explain plant composition (Fig. 3.1). For further analyses, we therefore used the scores of the first two axes as parameters for plant community composition (NMDS1 and NMDS2). Several dominant plant species showed a strong positive or negative relation with the NMDS axes (Table 3.3).

The relationship between diversity and productivity

The diversity measures, plant species richness, effective diversity and Camargo's evenness had, no significant effect on productivity (aboveground standing biomass) when tested in linear regressions (Fig. 3.2). However, community composition represented as NMDS1 and NMDS2 was significantly related to productivity. While NMDS1 was negatively but only weakly related to productivity (R^2=0.05, p=0.050), NMDS2 showed a positive and highly significant effect on productivity (R^2=0.31, p<0.001) (Fig. 3.2). The explanatory value of the five diversity measures increased only marginally when environmental variables were included in the analysis using multiple regressions (data not shown).

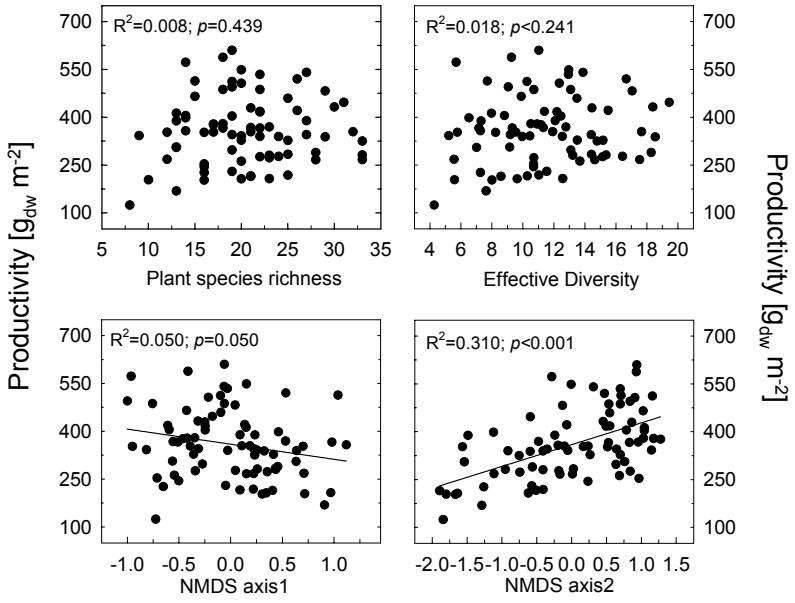

Fig. 3.2: Relationships of different plant diversity measures and community measures to productivity in semi-natural grasslands.

Environmental parameters, plant community composition and productivity

When tested in multiple stepwise regression models, 75.0% of the total variability in NMDS2 was explained by the edaphic parameters soil1, soil4 and soil2 (Table 3.4). In the regressions with either site characteristics or management parameters as independent variables, the PCA-derived parameters site3, and manage1 and manage2 explained only 6.5% and 38.8 % of the variation in NMDS2 scores, respectively (Table 3.4). When productivity was used as dependent variable in multiple regression analyses, the PCA-derived variables had little explanatory power. Only 12% of variation in productivity was explained by soil1 and only 18% by manage2 (Table 3.4). None of the site characteristics emerged as a significant predictor variable (Table 3.4).

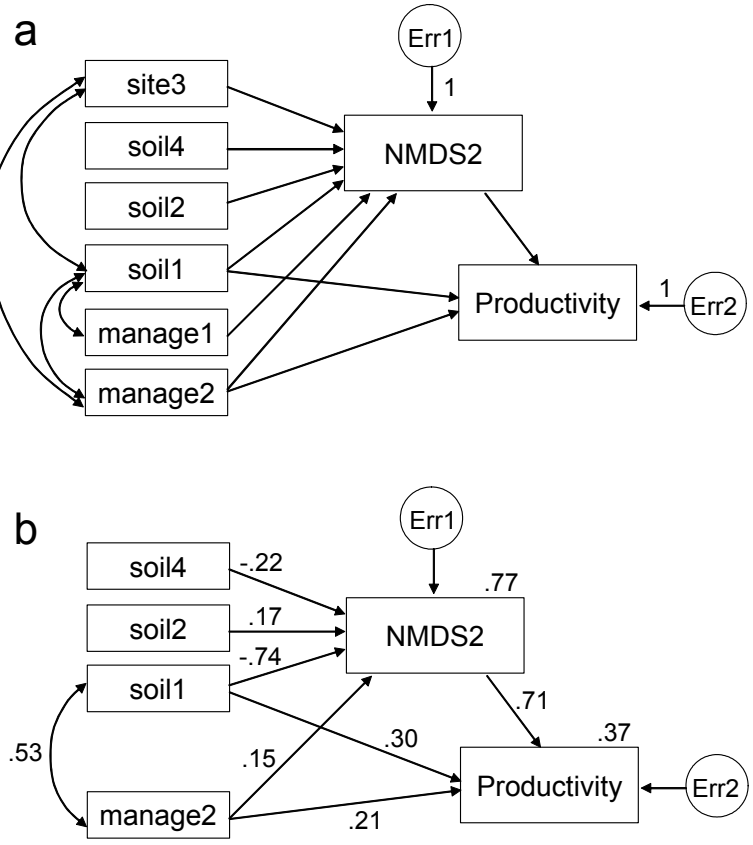

Fig. 3.3: Structural equation modeling (cf. Table 3.5). 3.3a: Initial model. Single-headed arrows indicate paths. Double-headed arrows show covariances that were included in the model based on modifications proposed by AMOS (procedure modification indices). The exogenous unobserved variables err1 and err2 account for the unexplained error in the estimation of NMDS2 and productivity, respectively. Their regression weights were a priori set to unity. 3.3b: Standardized regression weights (along paths), correlations (along double-headed arrows) and squared multiple correlations (along the productivity and NMDS2 boxes) for the best-fitting model C (Table 3.5).

Table 3.5: Fit measures for the competing structural equation models tested using the bootstrapping procedure implemented in AMOS (Arbuckle & Wothke 95-99). The most complex starting model (Model A) is shown in Fig. 3.3a. The table shows the number of times (out of 1000) that the likelihood function could not be maximized, mean discrepancy (standard error in brackets), the Browne-Cudeck-Criterion (BCC), the Akaike Information Criterion (AIC), the Consistent AIC (CAIC), the squared multiple correlation (SMC) of the variable Productivity, the SMC of the variable NMDS2 and the standardized regression weight of the regression of NMDS2 on productivity. Model C is the best-fitting model based on AIC and BCC (Fig. 3.3b).

Model	Model details	Failures	Mean discrepancy	BCC	AIC	CAIC	SMC Productivity	SMC NMDS2	Regression weight
Model A	Full model (Fig. 3a)	0	56.68 (0.62)	60.7	54.9	124.6	0.37	0.77	0.71 (p<0.001)
Model B	Variable site3 excluded	0	45.39 (0.58)	48.1	42.0	98.4	0.37	0.77	0.70 (p<0.001)
Model C	Variables site3 and manage1 excluded	0	35.80 (0.52)	35.4	32.5	78.9	0.37	0.77	0.71 (p<0.001)
Model D	Variables site3 and manage1 excluded. Regression soil1 on productivity excluded	0	38.0 (0.52)	36.6	33.9	77.0	0.35	0.77	0.46 (p<0.001)
Model E	Variables site3 and manage1 excluded. Regressions of soil1 and manage2 on productivity excluded	0	39.3 (0.50)	36.7	34.2	74.0	0.33	0.77	0.57 (p<0.001)

Structural equation modeling (Path analysis)

For structural equation modeling, we only considered the variable NMDS2 as diversity or composition measure because this was the only variable correlated with productivity. The initial model tested in AMOS consisted of all PCA-derived edaphic, management and site parameters that were significantly correlated with either productivity or NMDS2 in the multiple regression analyses (Table 3.4). Thus, the initial model included the environmental variables soil1, soil2, soil4, site3, manage1 and manage2 (Fig. 3.3a). Productivity was assumed to be dependent on NMDS2 so the model included only a path from NMDS2 to productivity and not vice versa (testing a model in which paths were drawn in both directions resulted in non-significant regression weights for both paths). This initial model was simplified by removing variables and paths according to the measures of fit (Table 3.5). All of the tested models were significant. The model excluding the variables site3 and manage1 but including the regressions of the variables soil1 and manage2 on productivity resulted in the best AIC value and the highest explained proportions of variance for the variables productivity and NMDS2 (Table 3.5, Fig. 3.3b). Thus, environmental variables influenced productivity, both directly as well as indirectly via affecting plant species composition.

3.4 Discussion

The data presented in this study illustrate that simple measures of biodiversity such as species richness are weak predictors for productivity in semi-natural grasslands. Community composition, however, explained productivity very well and was a better predictor for productivity than environmental variables and management parameters together. Nevertheless, some of the edaphic, management and site parameters showed a direct effect on productivity, although their influence was not as strong as maybe expected. More importantly, these variables influenced productivity indirectly via their influence on community composition. Our results show that complex measures such as community composition are important predictors of ecosystem functions in semi-natural ecosystems.

The grasslands selected for this study cover a wide range of species diversity, productivity and environmental parameters, representing a good sub-sample of montane semi-natural grasslands found in central Europe (Hundt 1964). Aboveground biomass was comparable to those given in other studies where the effect of plant diversity on productivity was studied in grasslands of Europe or North America (Hector et al. 1999; Tilman et al. 2002). Although the investigated sites cover a wide range in plant species richness (8 to 33

species, Table 3.1), average plant species richness of 20 species was low when compared to other semi-natural European grasslands (Baur et al. 1996). Montane grasslands such as investigated in this study are, however, generally lower in species diversity than comparable calcareous grasslands (Hundt 1964). In addition, we tested the quality of our sampling method by nested subset sampling using Modified Whittaker Plots in adjacent grasslands and found that the error of underestimating species richness was small and proportional to species richness in the sites (Kahmen, unpubl. data). Consequently, the number of plant species in a 2 m by 2 m plots presents a good relative estimate of plant diversity of the investigated sites.

The relationship between productivity and plant species richness has been described to peak at intermediate levels of productivity in numerous different grassland ecosystems (Al-Mufti *et al.* 1977; Rosenzweig & Abramsky 1993; Grace 1999; Waide *et al.* 1999; Mittelbach *et al.* 2001). The data of our study are consistent with this finding (Fig. 3.2, reversed axes). However, the hump-shaped relationship found in our study results from a line enveloping the outer-most data points rather than from a line of fitted average values as suggested by Al Mufti (1977). Our results are better explained by the theoretical model introduced by Schmid (2002) that combines the hump-shaped relationship from observational biodiversity studies with results from experimental studies where high diversity results in increased productivity. In his model, Schmid introduces site fertility as a third parameter in addition to productivity and biodiversity. The model assumes that productivity as well as biodiversity is ultimately driven by site fertility and that, given an intact species pool, species richness shows a hump-shaped relationship with productivity as suggested by Al Mufti (1977). If the species pool at a given fertility level is, however, reduced as a result of extinction or experimental manipulation, diversity and eventually productivity will drop below the ideal hump-shaped line.

We tested if reduced diversity in the observed grasslands had an effect on productivity but found that simple diversity measures such as species richness, effective diversity or Camargo's evenness showed no significant relationship with productivity (Fig. 3.2). The explanatory value of the simple diversity measures also did not increase, when potentially confounding environmental parameters such as soil variables or management parameters were included in the model using multiple regression analyses. Interestingly, our results are not consistent with experimental studies, where an asymptotic increase of biomass with increasing plant diversity or evenness was found (Naeem *et al.* 1996; Hooper & Vitousek 1997; Tilman *et al.* 1997; Hector *et al.* 1999; Wilsey & Potvin 2000; Polley *et*

al. 2003; Symstad *et al.* 2003). For these experimental studies, it was argued that the observed positive effects of biodiversity on productivity in experimental studies are largely due to niche complementary (Tilman *et al.* 1996; Hector 1998; Loreau 1998; Loreau & Hector 2001; Tilman *et al.* 2002). The niche complementary effect suggests that an increasing number of species results in a more efficient resource exploitation and thus enhanced ecosystem functions. The observed diversity effects on productivity in the experimental studies are, however, driven by very low species levels, which are not representative for natural grasslands. Tilman (2002) for example states that in his study about five species might account for the observed biodiversity effects. In contrast, the lowest diversity level in our study contained eight plant species. We therefore suggest that biodiversity effects based on niche complementary are strongest in ecosystems where diversity has dropped below a critical level such as in experimental grasslands.

In contrast to plant diversity, effective diversity or evenness, which are non-significant, it was community composition (NMDS1 and NMDS2) that had a significant effect on the productivity of the investigated grasslands (Fig. 3.2). Community composition (NMDS2) is correlated with several highly productive plant species (Table 3.3), suggesting that species with specific traits such as high competitive ability or high nutrient use efficiency may be the important drivers in the relationship of community composition and productivity. This would be analogous to results found in several experimental biodiversity studies where species composition or functional traits of specific species were a better predictor for ecosystem functioning than species richness (Hooper & Vitousek 1998; Symstad *et al.* 1998; Diaz & Cabido 2001). The influence of species specific traits does, however, not dismiss the so called “diversity-effects” from the relationship of community composition and productivity. Tilman (2002) for example suggested that communities with complementary functional composition should be more productive than communities with equal species numbers but redundant functional composition. Also, several studies have shown that legumes facilitated increased productivity by transferring fixed nitrogen to other plant species in the community (Mulder et al. 2002; Spehn et al. 2002; Scherer-Lorenzen et al. 2003). Testing the effects of functional diversity or the transfer of symbiotically fixed nitrogen was, however, not in the scope of this study. We therefore cannot exclude such effects from our interpretation of species composition.

It has long been acknowledged that ecosystem functions are influenced by biotic factors such as species specific traits and species interactions as well as abiotic parameters such as climate, soil and disturbance. The role of biodiversity in the creation, maintenance

and functioning of ecosystems has, however, only recently been addressed (Schulze & Mooney 1993; Lawton 1994; Chapin *et al.* 1997; Naeem 2002) and much of the recent debate about biodiversity and ecosystem functions has focused on the relative contributions of any of these factors to the observed ecosystem processes. While in experimental studies, environmental variables have been controlled, several authors have questioned their applicability for semi-natural ecosystems in the face of overwhelming influences of extrinsic factors (Grime 1997; Wardle *et al.* 1997; Huston & McBride 2002). In our study, we therefore tested the individual influences of species composition (NMDS2) and environmental variables on productivity in a single structural equation model (Fig. 3.3a). The model reveals that community composition is the most important parameter that is directly driving productivity in the investigated grasslands. While environmental parameters and management are highly important basic factors for ecosystem functions, their influence on productivity is indirect via driving community composition (Fig. 3.3b). Our model stresses that the community composition of an ecosystem with its species specific functional traits as well as its species interactions needs to be taken into account when ecosystem functions are to be understood.

4 Niche complementarity for nitrogen use – an explanation for the biodiversity and ecosystem functioning relationship

4.1 Introduction

The consequences of globally declining biodiversity for ecosystem functioning have been among the most actively debated questions in ecological research in the last decade (Schulze & Mooney 1993; Loreau *et al.* 2002). Several studies have tested the relationship between biodiversity and ecosystem functioning using diversity gradients in experimentally designed grassland communities (Tilman *et al.* 1996; Hector *et al.* 1999; Roscher *et al.* 2004). Generally, these experiments have detected a positive relationship between biodiversity and ecosystem functions, but the interpretation of these results and the potential underlying mechanisms have created considerable debate (Grime 1997; Huston 1997; Hector *et al.* 2000; Wardle 2001; Schmid 2002). As drivers for those patterns, hidden treatments and insufficient experimental design (i.e., sampling effects) have been suggested by critical voices, while 'true' diversity effects such as resource facilitation and, even more important, niche complementarity have been suggested by others (Naeem *et al.* 1994; Aarssen 1997; Tilman 1997; Loreau *et al.* 2001; Grime 2002).

The niche complementarity hypothesis implies that plant species or functional groups occupy functionally distinct niches in an ecosystem and use resources in a complementary way. Consequently, when species or functional groups go extinct, their niches remain unoccupied, leading to reduced resource exploitation and declining ecosystem functions. Experimental evidence for niche complementarity has so far only been given indirectly. For example, statistical analyses of the experimental studies mentioned above have revealed that productivity of diverse communities was higher than productivity expected from the weighted averages of the component plant species grown in monocultures (Hector 1998; Loreau 1998; Loreau & Hector 2001; Hector *et al.* 2002; Lambers *et al.* 2004). However, functional and ecophysiological evidence for niche complementarity is to our knowledge still very rare in the scientific literature.

In temperate grasslands, nitrogen (N) is known to be among the most critical resources limiting productivity (Klapp 1971; Tilman & Wedin 1991). Based on the niche complementarity hypothesis, the observed positive relationship between biodiversity and productivity in experimental grasslands may therefore be the result of different plant species or functional groups utilizing different N sources, leading to more efficient N exploitation

with increasing diversity. In fact, different forms of N acquisition such as symbiotic N fixation, internal N recycling or soil N uptake have been shown for different plant species in grasslands, suggesting complementary N strategies (Chapin *et al.* 1990; Spehn *et al.* 2002; Scherer-Lorenzen *et al.* 2003). Also, it has more recently been shown that different plant species in grasslands occupy different ecological niches with respect to their spatial, temporal and chemical N uptake patterns (McKane *et al.* 1990; Bol *et al.* 2002; Jumpponen *et al.* 2002; McKane *et al.* 2002; Miller & Bowman 2002; Weigelt *et al.* 2005). It remains, however, unclear if the observed traits with respect to N uptake patterns or N strategies are species or functional group specific and could thus serve as an explanation for the positive biodiversity effect on resource exploitation and ecosystem functioning. Alternatively, plants could be similar and thus exchangeable in their potential traits and the observed differences are merely the result of competitive interactions. In this case, no diversity effect on resource exploitation and ecosystem functioning is to be expected. For the understanding and functional interpretation of the biodiversity and ecosystem functioning relationship it is therefore not only essential to characterize functional traits such as N uptake patterns or N strategies of different plant species or plant functional groups, but also to address the consistency of these traits across different plant communities and thus to determine the species specific character of the observed traits.

In the study presented here, we experimentally tested complementarity N uptake patterns and N strategies of different plant species and plant functional groups across different grasslands, using ^{15}N labeled nitrogen compounds. Specifically, we tested (1) if different plant species or plant functional groups differ with respect to their spatial, chemical and temporal N uptake patterns, (2) if plant species or plant functional groups differ in their N strategies and, (3) if the observed traits with respect to N uptake patterns and N strategies are consistent across different plant communities and are thus species- or functional group specific, providing an explanation for the relationship between biodiversity and ecosystem functioning.

4.3 Methods

Study sites and environmental variables

We tested our objectives in three semi-natural grasslands in the Thüringer Schiefergebirge/ Frankenwald, a plateau-like mountain range, in Central Germany. The sites are moderately managed (two cuts per year, no grazing, and no fertilizer application during the last ten years). Edaphic variables, species composition and plant species diversity differed in the three grasslands. However, some plant species were consistently present in all three grasslands, yet at different abundances (Table 4.1).

To account for environmental variability among the three grasslands, soil samples were collected in each site, six times throughout the year 2002 and two times in 2003. Each soil sample collected in a grassland consisted of four pooled subsamples. The soil was air-dried at 35°C, and extracted for total P and K concentrations using a 1M Calcium-Acetate-Lactate (CAL) solution. CAL extracts were analyzed with ICP-AES (Optima 3300 DV, Perkin-Elmer, Norwalk, USA). Soil pH was measured in a water extract. For the determination of soil C:N ratios and total soil nitrogen (N_{tot}), dry soil was ground and analyzed with an elemental analyzer (Vario EL II, Elementar, Hanau, Germany). No seasonal trends were observed for the different soil variables so that samples for 2002 and 2003 were averaged before they entered the statistical analysis. At each site, the fraction of mineral soil in the upper 10 cm was determined by collecting 10 cores with a defined volume (4.3 cm diameter, 10 cm length). After separating samples into rocks, coarse organic material and mineral soil, the weights of the dried components were averaged and the fraction of mineral soil in the upper 10 cm calculated per m^2.

Plant available soil nitrate and ammonium concentrations were determined in each of the three sites as the sum of nitrate and ammonium pools at the beginning of the labeling experiment plus the respective daily net mineralization rates during the spring or summer labeling campaigns. Four soil samples were taken per site, pooled and sieved to 2 mm. To determine the nitrate and ammonium pools at the beginning of the experiment, 10 g of the sample was extracted for 60 min with 50 ml 1M KCl at the day of sampling. KCl extracts were frozen at -20°C and analyzed later for NO_3^- and NH_4^+ concentration, using a Continuous Flow Analyzer (SAN Plus, Skalar, Erkelenz, Germany). To determine the net mineralization rates, i.e., the daily production rates of plant available NO_3^- and NH_4^+, the remaining soil samples were split into four equal parts, sealed in polyethylene bags and incubated in situ for 24 or 16 days during spring and summer labeling campaigns,

respectively (Hart *et al.* 1994). After incubation, bags were collected, and soil extracted with 1M KCl and analyzed as described above. To determine daily mineralization rates, nitrate and ammonium concentrations at the beginning of the incubation were subtracted from the concentrations determined at the end of the incubation, and the difference divided by the number of incubation days.

^{15}N labeling

We determined spatial, chemical and temporal N uptake patterns of the present plant species in the three grasslands using ^{15}N labeled N compounds. In each site, we injected in separate treatments two different ^{15}N labeled N compounds (nitrate and ammonium) at two different soil depths (3 cm and 8 cm) at two times a year (spring: May 22nd to May 24th 2003 and summer: August 4th to August 6th 2003), resulting in eight treatments per grassland with 1 m^2 each (factorial design 2 x 2 x 2). During each campaign in spring and summer, one grassland was labeled per day. The ^{15}N labeled nitrate and ammonium compounds were injected (using spine syringes) as separate solutions of 9.66 mM $K^{15}NO_3$ and 9.66 mM $^{15}NH_4Cl$ (>98.9 at% ^{15}N). In order to offer both N compounds in each treatment, we added equal amounts (9.66 mM) ^{14}N of the non-treatment N compound to the ^{15}N solution. ^{15}N tracer concentrations were estimated to result in plant δ^{15}N target values of approximately 100‰. Injection points in each treatment were distributed evenly across the 1 m^2 plots using a 6.5 X 7.0 cm grid, resulting in 210 injections per plot. Assuming a 2 cm diffusion radius, we injected 2 ml of ^{15}N labeled solution at each injection point, leading to a total of 55.35 mg added $^{15}N\ m^{-2}$.

Three days after injecting the ^{15}N labeled N compounds into the soil, the vegetation in each treatment was clipped 2 cm above the ground, sorted to species, dried at 70ºC for 48 h and weighed. In order to calculate nitrate and ammonium uptake based on δ^{15}N values of the labeled plant species, background natural abundance δ^{15}N of the investigated plant species was determined in the three grasslands in close proximity to the labeled plots in July 2003. For δ^{15}N, plant material was ground and analyzed with an isotope ratio mass spectrometer (IRMS, Delta C Finnigan MAT, Bremen, Germany). N concentrations in above-ground biomass of the investigated plant species were determined using an elemental analyzer (Vario EL II, Elementar, Hanau, Germany).

Calculation of nitrogen uptake

Our calculations to determine the different plant species' daily nitrate or ammonium uptake were based on values of $\delta^{15}N$, which express the $^{15}N/^{14}N$ ratio of a sample (R_{sample}) over the $^{15}N/^{14}N$ ratio of a standard (R_{std}) in per mill (1).

(1) $$\delta^{15}N = \left(\frac{R_{(sample)}}{R_{(std)}} - 1 \right) * 1000$$

Based on equation one, we calculated (2) ^{14}N and (3) ^{15}N pools of plant available soil nitrate and ammonium before injection of the tracer and then determined (4) the ratio (Z) of ^{15}N- to ^{14}N- nitrate and ammonium pools present in the soil after ^{15}N labels were injected.

(2) $$^{14}N_{(soil)} = \frac{N_{(soil)}}{1 + \left(\frac{\delta^{15}N_{(soil)}}{1000} + 1 \right) R_{(std)}}$$

(3) $$^{15}N_{(soil)} = 1 - {}^{14}N_{(soil)}$$

(4) $$Z = \frac{^{15}N_{(soil)} + {}^{15}N_{(injected)}}{^{14}N_{(soil)} + {}^{14}N_{(injected)}}$$

$^{15}N_{(soil)}$ and $^{14}N_{(soil)}$ refer to the natural concentrations of ^{15}N- and ^{14}N- ammonium or nitrate (mol m^{-2} 4 cm^{-1}) in the soil during the experiment. $^{15}N_{(injected)}$ and $^{14}N_{(injected)}$ are the concentrations of ^{15}N- and ^{14}N- ammonium or nitrate injected into the soil (mol m^{-2} 4 cm^{-1}). $N_{(soil)}$ refers to the plant available nitrate or ammonium pool in the soil, $\delta^{15}N_{(soil)}$ to the natural abundance isotopic signature of either ammonium or nitrate. We used a value of 5‰ for the $\delta^{15}N$ of NH_4^+ and NO_3^- (W. Wanek, pers. comm.). Furthermore, we assumed that the injected ^{15}N solutions had a diffusion radius in the soil of 2 cm, resulting in 4 cm of vertically labeled soil. Molar concentrations in equations 2 and 3 therefore represent a soil volume of 4 cm depth and 1 m^2 area.

Similarely, we calculated the ^{14}N and ^{15}N pools (5 and 6, respectively) in the plants before and after labeling,

$$^{14}N_{(plant)} = \frac{N_{(plant)}}{1 + \left(\frac{\delta^{15}N_{(plant)}}{1000} + 1 \right) R_{(std)}} \quad (5)$$

$$^{15}N_{(plant)} = 1 - {}^{14}N_{(plant)} \quad (6)$$

with $N_{(plant)}$ as the total N concentration in the plant, and $\delta^{15}N_{(plant)}$ as the isotopic signature of plant N before or after labeling.

To determine the amount of ^{15}N taken up by a plant (^{15}N uptake (mol g_{dw}^{-1} m^{-2})) during the experiment (7), the natural abundance ^{15}N pool of a plant ($^{15}N_{(nat.\ abundance)}$) had to be subtracted from the total ^{15}N pool after labeling ($^{15}N_{(label)}$).

$$^{15}N_{(uptake)} = {}^{15}N_{(label)} - {}^{15}N_{(nat.abundance)} \quad (7)$$

In a final step, we calculated the amount of NO_3^- and NH_4^+ taken up by a plant (g N g_{dw}^{-1} day^{-1} (8),

$$N_{(uptake)} = \frac{\left({}^{15}N_{(uptake)} + \frac{{}^{15}N_{(uptake)}}{Z} \right) * 14.00674}{3} \quad (8)$$

where $N_{(uptake)}$ is the total amount of NO_3^- or NH_4^+ taken up by plants in µg per g dry biomass, $^{15}N_{(uptake)}$ the calculated ^{15}N uptake of plants from equation 7, 14.00674 molar weight of N and 3 the number of days during which uptake was determined.

Data analysis and statistics

The investigated plant species were assigned to functional groups to determine more general traits with respect to N uptake patterns and N strategies. Assignment to functional groups was based on N uptake data resulting from this study in agreement with taxonomical, morphological and physiological data reported in the literature.

Spatial, temporal and chemical N uptake patterns of plant species in the three grasslands were analyzed in two different ways, using (a) relative N uptake data to compare spatial, chemical and temporal N uptake patterns among plant species or functional groups, irrespective of a plant's total soil N uptake. Relative N uptake (in %) was calculated as the relative contribution of each treatment to a plant's total soil N uptake. In addition, (b) absolute N uptake was compared among different plant species or functional groups for each individual treatment to determine complementary N uptake patterns. We used Principal Component Analyses (PCA) for general analyses of relative and absolute N uptake rates of species or functional groups (CANOCO; ter Braak & Smilauer 2002). PCA summarizes the multidimensional information on chemical, temporal and spatial N uptake patterns of individual plant species and allows the comparison of these patterns among plant species in reduced dimensionality. In the analysis of absolute N uptake, data were log-transformed prior to the analyses to account for outliers. In addition, relative and absolute N uptake in the different treatments were compared within and among functional groups, respectively, in one-way ANOVAs using LSD post-hoc tests.

To determine different N strategies among different plant species or functional groups, we investigated if a plant's short-term N uptake from the soil was mirrored in its above-ground N content. We hypothesized that if a plant's N content in above-ground biomass was not consistent with its present N uptake from the soil, N sources other than soil N must be used to meet the plant's N demand. Thus, we determined separately for the spring and summer campaign the relationship of each plant's total daily N uptake from the soil per gram above-ground biomass to its N concentration per gram above-ground biomass. In addition, the total soil N uptake of a plant since beginning of the growing season (spring treatments) or since the last harvest (summer treatments) was estimated by multiplying a plant's total daily soil N uptake with its above-ground biomass and the respective growing time (28 and 35 days for spring and summer treatments, respectively). This estimated total N uptake from the soil was then related to the total N content in its above ground-biomass using simple linear regressions, forced through the origin. Finally, we estimated the relative contribution of additional N sources other than soil N to a plant's total N content and tested for significant differences among functional groups with one-way ANOVAs using LSD post-hoc tests.

We used ANOVAs (type I sum of squares) to test if N uptake within a treatment was consistent for plant species or functional groups across sites and was thus a species or functional group specific trait. To control for site effects, the factor 'site' was entered first

into each model, and the effects of functional group identity, the interaction between site and functional group identity, species identity, the interaction between site and species identity and finally abundance of a species as a covariate were then determined against the residual variation in a fixed hierarchical sequence. We used species abundances, estimated as % of total biomass in a site, as surrogate for competitive interaction, assuming that competitive ability increases with increasing abundance (Weigelt *et al.* 2002). All ANOVA models were calculated using SPSS 11 (SPSS Inc. 2001).

4.3 Results

		Site1	Site2	Site3
Species richness		17	33	33
Above-ground biomass	(g_{dw} m^{-2})	483.3	443.7	595.8
Taraxacum officinale agg.	(abundance %)	28.7	31.3	1.7
Dactylis glomerata	(abundance %)	22.3	2.1	10.9
Trifolium repens	(abundance %)	12.5	2.3	3.4
Lolium perenne	(abundance %)	11.6	2.3	23.3
Trifolium pratense	(abundance %)	4.9	0.7	11.6
Geranium sylvaticum	(abundance %)	n.d.	8.7	n.d.
Heracleum sphondylium	(abundance %)	n.d.	8.6	0.8
Trisetum flavescens	(abundance %)	0.4	8.5	0.5
Ranunculus acris	(abundance %)	0.1	8.0	13.9
Veronica chamaedrys	(abundance %)	n.d.	n.d.	7.4
$NO_{3\ (pool)}$	(mgN m^{-2})	63.7	43.1	102.1
$NO_{3\ (spring\text{-}flux)}$	(mgN m^{-2} day^{-1})	39.2	72.1	102.6
$NO_{3\ (summer\text{-}flux)}$	(mgN m^{-2} day^{-1})	92.2	85.7	125.7
$NH_{4\ (pool)}$	(mgN m^{-2})	270.2	304.9	485.0
$NH_{4\ (spring\text{-}flux)}$	(mgN m^{-2} day^{-1})	n.d.	n.d	2.5
$NH_{4\ (summer\text{-}flux)}$	(mgN m^{-2} day^{-1})	n.d.	n.d.	n.d.
Total soil nitrogen	(g m^{-2})	242.1	335.5	347.7
P	(g m^{-2})	4.05	1.10	2.16
K	(g m^{-2})	7.44	3.44	4.48
pH		6.26	5.68	5.78
Mineral soil	(kg m^{-2})	57.5	74.9	93.4

Table 4.1: Species richness, total above-ground total biomass and abundance of plants as well as N pools and fluxes and soil nutrients for each of the three investigated grasslands. For each site, abundance is shown at least for the five most common species. Abundance was estimated as % of total biomass in a site. $N_{(pool)}$ refers to extractable mineral soil N, $N_{(flux)}$ refers to mean daily net mineralization rates. N.d. = not detected.

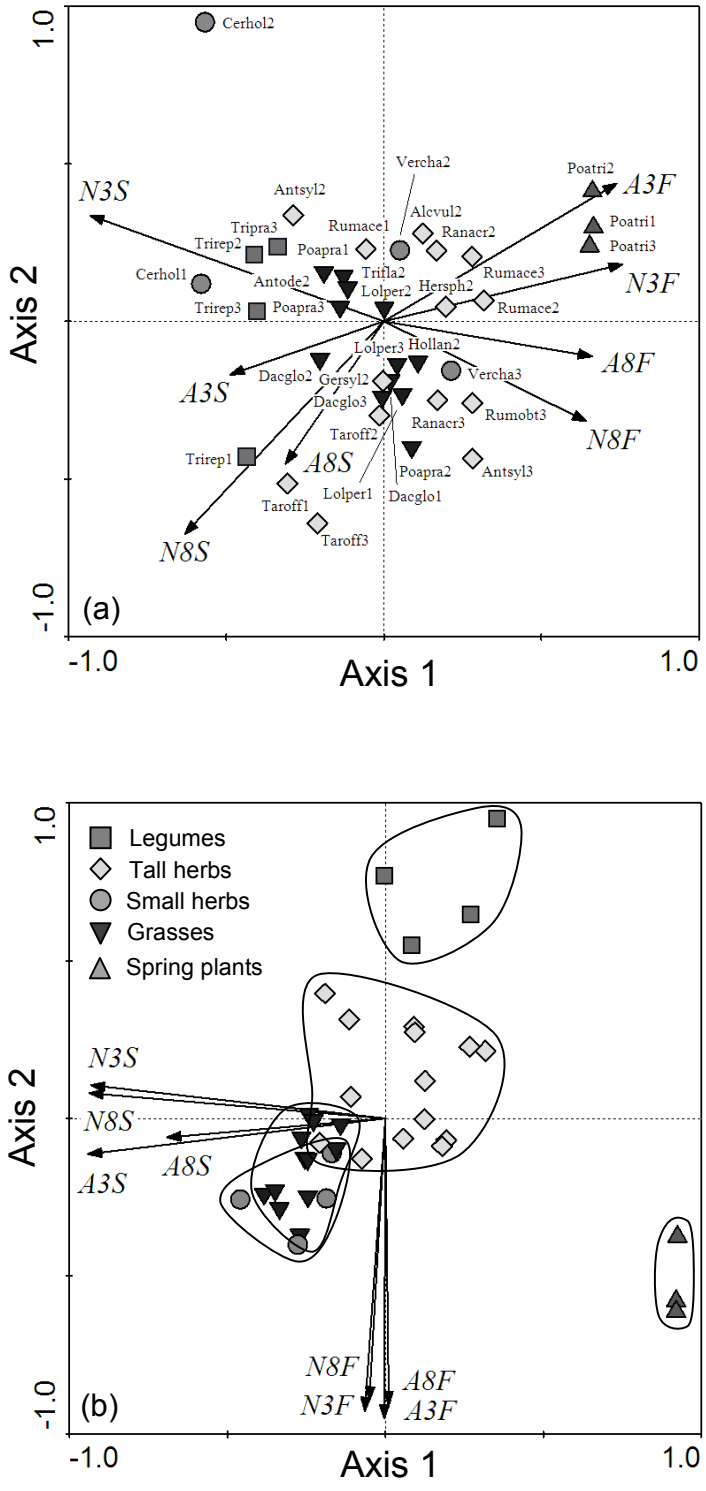

Fig. 4.1: Ordination diagram of the principal component analysis (PCA) with species (symbols) and treatments (arrows; N = nitrate, A = ammonium, 3 = 3 cm treatment, 8 = 8 cm treatment, F = spring, S = summer). Fig. 4.1a is calculated with relative N uptake data, Fig. 4.1b with absolute N uptake data (for details, see methods). The first two PCA axes explain 74.7% and 81.4% of the total variability in the data, in Fig. 4.1a and Fig. 4.1b, respectively. Functional group labels given in Fig. 4.1b refer to both diagrams.

Considerable differences in edaphic parameters were observed among the three investigated grasslands and all sites differed in species composition and diversity (Table 4.1). Injection of ^{15}N labeled N components into the soil lead to profound increases in $\delta^{15}N$ values over natural abundance background labels for all plant species in all treatments of the three sites. Across all treatments, enrichment in ^{15}N varied between 4,45 and 3616,02‰ with a mean of 247,78‰. Enrichment in ^{15}N was higher in the 3 cm treatments than in the 8 cm treatments, higher in spring than in summer, and higher for nitrate than for ammonium. Since the delta values themselves give no accurate information on N uptake, we used the equations presented above to determine nitrate and ammonium uptake of the different plants in the different grasslands.

PCA of relative N uptake data of the 19 investigated species revealed no patterns that allowed functional group assignment in agreement with taxonomical, morphological and physiological data known from the literature (Fig. 4.1a). In contrast, PCA of absolute N uptake data revealed similarities among species that agreed with taxonomical, morphological and physiological data from the literature resulting in the assignment of five functional groups: Legumes (*Trifolium pratense*, *Trifolium repens*), tall herbs (*Alchemilla vulgaris* agg., *Anthriscus sylvestris*, *Geranium sylvaticum*, *Heracleum sphondylium*, *Ranunculus acris*, *Rumex acetosa*, *Rumex obtusifolius*, *Taraxacum officinale* agg.), grasses (*Anthoxanthum odoratum*, *Dactylis glomerata*, *Holcus lanatus*, *Lolium perenne*, *Poa pratensis*, *Trisetum flavescens*), small herbs (*Veronica chamaedrys*, *Cerastium holosteoides*) and spring plants (*Poa trivialis*) (Fig. 4.1b).

When the relative contribution of different N treatments to a plant's total N uptake in the three sites was compared among plant species, the first two PCA axes explained 74.7% of the total variability in the dataset (axis1 = 60.3%; axis2 = 14.4%) (Fig. 4.1a). Separation of the species in the PCA can be explained to some extent by temporal and spatial differences in relative N uptake, where axis 1 was correlated with temporal treatments (arrows with label 'F' or 'S') and axis 2 with spatial treatments (arrows with label '3' or '8'). When relative N uptake of the individual treatments was analyzed separately within each functional group using one-way ANOVAs, several significant differences in the relative contribution of spatially, temporally and chemically different N pools with respect to a plant's total N uptake were detected (Fig. 4.2). Despite these differences, however, 74.4% of all tested species in spring, and 85.3% of all plant species in summer used nitrate in 3 cm as their preferred. N source.

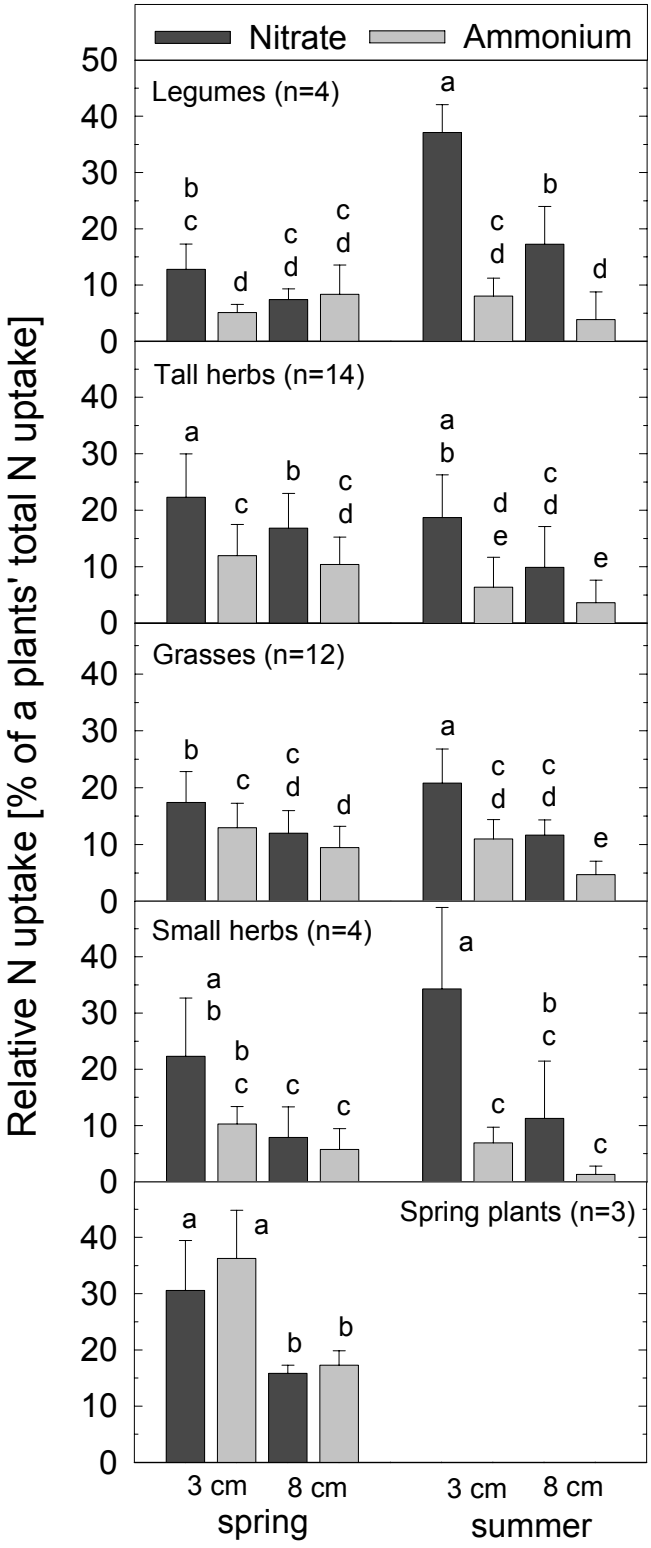

Fig. 4.2: Relative N uptake in functional groups for each treatment. Relative N uptake in a treatment was estimated for each species as the percent of a species total N uptake across treatments. Means for species within functional groups were compared in one way ANOVAs using LSD post hoc tests. Bars indicate one standard deviation.

For absolute N uptake the first two axis of the PCA explained 81.4% of the total variability in the dataset (axis1 = 56.1%; axis2 = 25.3%) (Fig. 4.1b). Other that expected, the explained variability in the data was not based on spatial, chemical and temporal differences in N uptake among species or functional groups. Rather, the explained variability in the data was mainly based on large differences in the plants' and functional groups' quantitative N uptake, irrespective of treatment (Fig. 4.3). In general, quantitative N uptake strongly increased from legumes to tall herbs, grasses, small herbs and spring herbs (Fig. 4.3). Due to the relatively low numbers of replicates for legumes (n=4), small herbs (n=4) and spring plants (n=3), some of these differences remain, however, statistically insignificant.
The plants' above-ground N concentrations showed a negative relationship with the total daily N uptake per gram above-ground biomass in spring and summer (Fig. 4.4a). Total N uptake per plant since beginning of the growing season (spring-treatment) or since last harvest (summer-treatment) correlated positively with total N content in the plants' above-ground biomass for all functional groups (Fig. 4.4b). However, the regression slopes were consistently different for individual functional groups in the spring and summer treatments.

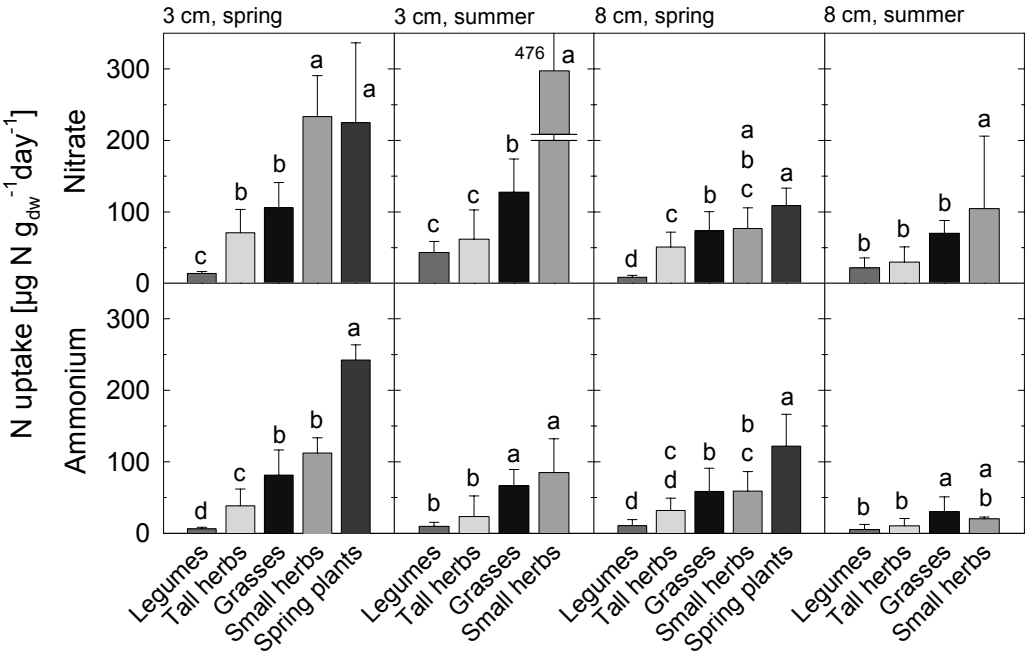

Fig. 4.3: Absolute N uptake of functional groups in different treatments. Values were determined as means across species in a functional group. Means were compared among different functional groups within treatments in one way ANOVAs using LSD post hoc tests. Bars indicate one standard deviation.

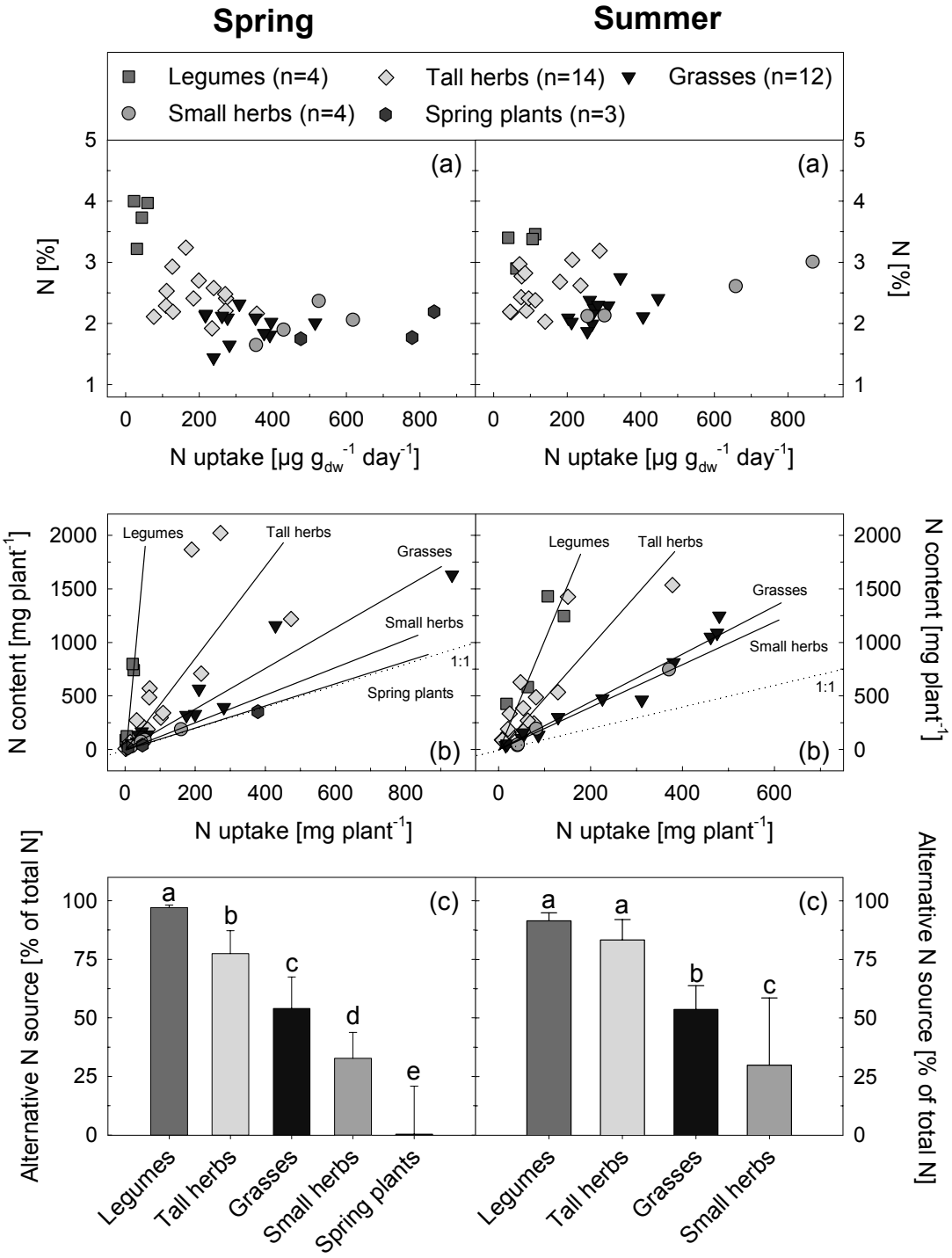

Fig. 4.4: The relationship between N uptake and N concentration in above-ground biomass for the 19 different plant species in five functional groups. Average daily N uptake per gram above-ground biomass of plants in relation to above-ground N concentration (Fig. 4.4a). Total N uptake per plant correlates positively with total above-ground N contents, but slopes are different for functional groups (Fig. 4.4b). For regression results see text. Estimated additional N sources other than soil N taken up during the growing season for the five functional groups (Fig. 4.4c). Means were compared among different functional groups in one way ANOVAs using LSD post hoc tests. Bars indicate one standard deviation.

In spring, legumes had a slope of 33.3 (R^2=0.96; p=0.0008), tall herbs a slope of 4.3 (R^2=0.51; p<0.0001), grasses a slope of 1.9 (R^2=0.93; p<0.0001), small herbs a slope of 1.3 (R^2=0.95; p=0.0008) and spring plants a slope of 1.1 (R^2=0.99; p=0.0002) (Fig. 4b). In summer, legumes had a slope of 10.4 (R^2=0.70; p=0.0054), tall herbs a slope of 4.9 (R^2=0.69; p<0.0001), grasses a slope of 2.2 (R^2=0.96; p<0.0001) and small herbs a slope of 2.0 (R^2=0.99; p=0.0002) (Fig. 4b). The relative contribution of N sources other than soil N uptake to a plant's above-ground N content varied significantly among different functional groups, with legumes having the largest alternative N source, followed by tall herbs, grasses, small herbs and spring plants (Fig. 4c).

Table 4.2: ANOVA (type I sum of squares) for nitrate and ammonium uptake and thus N strategy at different soil depths in spring and summer with factor site fitted first and effects of functional groups, functional group * site, species identity, species identity * site and abundance tested against the residual variation in a fixed hierarchical sequence.

Spring		**Nitrate 3 cm**		**Ammonium 3 cm**		**Nitrate 8 cm**		**Ammonium 8 cm**	
	df	ss	F	ss	F	ss	F	ss	F
Site	2	16640	16.22*	8346	2.67	8405	52.60**	5672	8.00*
Funct. group	4	151083	73.65***	121338	19.39**	18179	56.88**	23636	16.66**
Funct. group x Site	7	26675	7.43	464	0.04	5264	9.41*	5663	2.28
Species	13	19391	2.91	12389	0.61	5243	5.05	11491	2.49
Species x Site	5	5014	1.96	1296	0.17	2084	5.22	1149	0.65
Abundance	1	8	0.02	253	0.16	40	0.50	183	0.52
Residuals	4	2051		6257		320		1419	
Total	36	220863		150344		39535		49213	

Summer		**Nitrate 3 cm**		**Ammonium 3 cm**		**Nitrate 8 cm**		**Ammonium 8 cm**	
	df	ss	F	ss	F	ss	F	ss	F
Site	2	19340	2.94	1448	1.21	8505	12.65*	439	0.17
Funct. group	3	569046	57.63**	180054	10.07*	73498	72.88**	3273	0.86
Funct. group x Site	5	181236	9.18*	2313	0.77	51002	25.29*	473	0.08
Species	12	370740	8.67	13025	1.68	130835	29.94**	981	0.06
Species x Site	5	11587	0.70	3216	1.08	2810	1.67	435	0.07
Abundance	1	770	0.23	2567	0.04	50	0.15	85	0.07
Residuals	3	9874		1793		1008		3801	
Total	31	1162593		39875		267705		9487	

* $0.05 \geq p \geq 0.01$ ** $0.01 \geq p \geq 0.001$ *** $p \leq 0.001$

Functional group assignment had always the highest explanatory power for N uptake in all treatments when tested against the residual variation of the factor 'site' in ANOVAs (type I sum of squares). Species identity was not a strong predictor of N uptake in any treatment when the effect of functional group identity was controlled for except for the 8 cm nitrate treatment in summer (Table 4.2). Also, the factor 'site' showed some effect on N uptake but always accounted for less variability than the functional group assignment. Competitive interaction (indicated by abundance data) was not significant in any of the treatments, when functional group assignment and species identity were accounted for (Table 4.2).

4.4 Discussion

Several previous studies have described plant species occupying distinct niches with respect to spatial, temporal and chemical N uptake patterns (McKane *et al.* 1990; Jumpponen *et al.* 2002; McKane *et al.* 2002). Similar although weak trends were observed in our study, when the contribution of different labeled N compounds to a species' or functional group's total N uptake was determined (Figs. 4.1a and 4.2). Assessing niche occupancy of different plant species based on the relative contribution of different soil N pools to a plant's total N uptake gives important information on mechanisms avoiding competition among species (McKane *et al.* 2002). However, for the analyses of complementary resource use among different species or functional groups and thus for the relationship between biodiversity and ecosystem functioning, relative N uptake patterns give little information. To determine complementary resource use, quantitative differences in N uptake patterns need to be considered. In our study, we found strong differences with respect to quantitative soil N uptake among species or functional groups (Fig. 4.1b). However, these differences were not based on variability in spatial, chemical or temporal N uptake, but on differences in total N uptake, irrespective of treatment (Fig. 4.3). Consequently, we conclude that our study gives no evidence for complementary among the investigated plant species or functional groups with respect to spatial, temporal or chemical N uptake patterns and thus no evidence for a diversity effect on the exploitation of temporally, spatially or chemically different soil N pools in the investigated grasslands.

We tested if plants in different functional groups differed in their N strategies i.e. symbiotic N fixation, internal N recycling or soil N uptake and found that different functional groups relied to a varying degree on N sources other than soil N (Fig. 4.4). N sources other than soil N can easily be explained for legumes with their potential to host

symbiotic N fixing bacteria (Vitousek *et al.* 2002) for tall herbs, grasses, small herbs and sping plants, however, N fixation is not an option. For these functional groups, internal nutrient recycling could serve as a valid explanation for the alternative N source observed in our study (Schulze 1982; Heilmeier *et al.* 1986; Chapin *et al.* 1990). In particular in grasslands, where plants depend on rapid N mobilization to resprout in spring or after defoliation, N accumulation in storage organs and subsequent recycling has been shown in several studies (Richards 1993; Volenec *et al.* 1996; Louahlia *et al.* 1999). The size of the alternative N source of the non-legumes decreases in our study from tall herbs to grasses, small herbs and spring plants (Fig. 4.4c) These patterns agree with the average size of storage organs such as tubers or tap-roots that are typically larger for tall herbs than for grasses, small herbs or spring plants (Kutschera & Lichtenegger 1982, 1992). Consequently, our data give evidence that the different functional groups follow different N strategies by relying on different N pools such as atmospheric N, internally stored N and soil N to meet their N demands.

N uptake patterns and N strategies of plant species have been shown to depend on environmental conditions or community composition (Louahlia *et al.* 1999; Jumpponen *et al.* 2002; McKane *et al.* 2002). We therefore tested if competition or site specific effects influenced the observed N uptake or whether N uptake was consistent for species in the individual functional groups across different sites (Table 4.2). We found that functional group assignment of a species was the single most important factor explaining variability in N uptake in all treatments across the three different sites. This suggests that N uptake of plants in the individual functional groups and thus the observed differences in N strategies are functional group specific traits.

Testing in situ plant ecophysiological traits across a wide range of species and sites is difficult and several limitations occur in experiments, in particular for testing N uptake from the soil. Ammonium in the soil is readily oxidized to nitrate, so that ^{15}N uptake in the ammonium treatment can easily be obscured. In our study, however, we found significant differences for ammonium and nitrate uptake among different functional groups with nitrate being the preferred N compound for N uptake from the soil (Figs. 4.2 and 4.3). Had all ^{15}N labeled ammonium in the soil been converted to nitrate after its application, no differences in the plants' N uptake rates for nitrate or ammonium would have been anticipated. Consequently, intact ammonium labels must have been present in the respective treatments during plant uptake. Our study thus represents rather conservative estimates of complementarity among functional groups.

In addition, plant species in grasslands have been shown to extend their roots far beyond the soil depths labeled in this study (Kutschera & Lichtenegger 1982, 1992). Consequently, more effective spatial resource partitioning might occur on a larger scale and could have been overlooked in this study. However, in similar grasslands, N mineralization and thus availability of soil N to plants has been shown to be located to a large extent in the upper soil layers with little leaching to lower soil depths (Runge 1978; Scherer-Lorenzen *et al.* 2003). Therefore and for the technical difficulty involved with labeling lower soil depths, we selected 3 and 8 cm as our target soil depths as has been done in similar previous studies (McKane *et al.* 2002). Finally, we determined total seasonal N uptake from the soil by extrapolating N uptake during the course of the experiment to the entire growth period of the respective plants. Based on these calculations, we determined the size of alternative N sources. We selected young but fully developed leaves to determine N uptake. However, it is likely that N uptake was underestimated since incorporation of N is largest in the early developmental stages of a leaf. As a result, the total N uptake we determined for the entire growing period is therefore likely to be underestimated (Fig. 4.4b) and as a consequence the size of alternative N sources overestimated (Fig. 4.4c). For our study, however, the relative differences among species or functional groups were of interest and the potential errors discussed above apply to all investigated species so that these drawbacks do not flaw the presented results.

In summary, our data show that the investigated plant species or functional groups are not complementary with respect to their spatial, chemical and temporal N uptake patterns but that different functional groups in the investigated grasslands rely on different and specific N strategies to meet their N demands: Legumes mainly use N that derives from N fixing bacteria and are therefore independent of the soil N pool. Tall herbs are to a high degree able to remobilize accumulated N from an internal N pool. Grasses are also able to remobilize accumulated soil N, but at a lower level than tall herbs. However, grasses are highly effective competitors for soil N (Fig. 4.3). Small herbs, which also have high N uptake from soil N rely only to a small degree on internally recycled N and finally, spring plants seem to lack the ability to store N over the course of the season and depend entirely on soil N uptake during their growing season (Figs. 4.3 and 4.4). According to the theory of niche complementarity, co-occurring species with different ecological traits will lead to increased resource exploitation and thus to a positive relationship between biodiversity and ecosystem functioning. Based on the the observed functional group specific differences with respect to N strategies we therefore conclude that the different functional groups are

complementary and that a positive effect of functional group diversity on ecosystem functioning is to be expected.

The consistency of traits with respect to N strategies within functional groups suggests that species within functional groups are largely redundant (Table 4.2). For the investigated grasslands this means that functional diversity is lower than the observed species diversity in these semi-natural grasslands and that the loss of species should be compensated until at least one species of each functional group remains present in the system. This supports findings from previous studies in semi-natural grasslands, where at natural diversity levels no diversity effect on ecosystem functioning was observed (Kahmen *et al.* 2005a). It is, however, important to note that plant species in the study presented here were investigated in relation to a single functional trait only, ignoring traits that relate to other resources such as light or water. In addition, the present study as most other biodiversity – ecosystem functioning studies was conducted under stable environmental conditions. Yet, species that are functionally redundant in an ecosystem during stable environmental conditions might in fact be complementary in a more variable environment, supporting stable ecosystem functions (Kahmen *et al.* 2005b). Consequently, more than a single trait and responses of species in a variable environment need to be considered if predictions on the full functional diversity of an ecosystem and the resulting effects on ecosystem functioning are to be made (Eviner 2004, Petchey *et al.* 2004).

5 Diversity-dependent productivity in semi-natural grasslands following climate perturbations

5.1 Introduction

There is a long standing debate in ecological research about the relationship between biodiversity and stability (Leps, Osbornovakosinova & Rejmanek 1982; MacArthur 1955; McNaughton 1977; Pimm 1984). The focus of the debate has, however, shifted in recent years from population and food-web levels to the ecosystem level, where the influence of biodiversity on the stability of ecosystem functions is of interest. This is a consequence, partly, of the dramatic worldwide loss in species diversity (Chapin *et al.* 1997), and the predicted increase in extreme climatic events such as flood, frost, fire, storm and drought as a result of global climate change (IPCC 2001). Climate change scenarios as well as the causes and consequences of decreasing diversity are beginning to be well understood (Loreau *et al*. 2001). However, it remains somewhat unknown if ecosystems with high diversity can buffer the effects of climate change and if consequently ecosystems reduced in diversity are more sensitive to climate change. If so, climate change effects on ecosystem functions will become more severe if diversity is continuously lost.

According to the so-called 'insurance hypothesis', species diversity influences the stability or resistance of ecosystem functions against environmental perturbations (Doak *et al.* 1998; McNaughton 1977; Yachi & Loreau 1999). The hypothesis is based on the assumption that different species react differently to environmental change. With increasing species diversity the range of species with different responses to environmental change will therefore also increase in an ecosystem. Consequently, a more diverse ecosystem has a higher likelihood to contain species that are adapted to a changed environment and can compensate the decline of less adapted species, and thus maintaining stable ecosystem functions.

Evidence that stability of ecosystem functions increases with species diversity has been given in theoretical studies (Doak *et al.* 1998; Ives, Klug & Gross 2000; Loreau & Behera 1999; Yachi & Loreau 1999), and laboratory experiments (McGrady-Steed, Harris & Morin 1997; Mulder *et al*. 1999; Naeem & Li 1997). In field studies it was observed that interannual variability of productivity was reduced by increasing species diversity, suggesting a positive relationship between diversity and stability of ecosystem functions (Dodd *et al*. 1994; Frank & McNaughton 1991; Tilman & Downing 1994). The only field

study, however, that has experimentally addressed the relationship between diversity and stability, found no effect of plant diversity on the stability of above-ground productivity during disturbance in grasslands (Pfisterer & Schmid 2002). Potential effects on below-ground productivity, however, were ignored in this study (Schmid & Pfisterer 2003).

In the work reported here, we investigated the role of plant diversity for ecosystem functions during extreme weather events which are predicted as a consequence of global climate change for central Europe (Schär *et al*. 2004). Specifically, we investigated 1) if plant diversity influences productivity above- and below-ground in semi-natural grasslands during experimentally induced early summer drought, and 2) if in a grassland community, the range of species with different drought responses increased with increasing diversity, giving physiological evidence for the insurance hypothesis.

5.2 Methods

Study sites and experimental design

The study was conducted in semi-natural grasslands in the Thüringer Schiefergebirge/ Frankenwald, a plateau-like mountain range, in central Germany. In early spring 2002, 19 grassland sites were selected that differed in plant diversity and were similar in edaphic conditions. Only sites that were ungrazed, cut twice a year in late June and late August with no fertilizer application in the past 10 years were selected.

In each site, two 5 by 5 m plots were established. In the center of each plot a 1 by 2 m area was established for vegetation, biomass and soil sampling. While one plot in each site served as control, the other plot was roofed from April 23rd to June 12th 2003 to simulate drought. Roofs were located in the center of the plot, covering an area of 3 by 3.5 m. Roofs were constructed with a steel frame and covered with transparent foil that permitted 90% penetration of PAR (Cello Flex 4TT, Prosyn Polyane, St. Chamond, France). To ensure air circulation, roofs were 2.3 m in height and tunnel-shaped with the two ends open. For a true control of drought effects, roofs should have ideally been established for both control plots and drought treatments, with the collected water added back to the control plot. However, given the large amont of labor involved for such true controls, we roofed only the treatments and tested for roof effects other than drought using meteorological measurements in six of the 19 sites. Specifically, air temperature in 60 cm height, soil temperature (5-10 cm below-ground) and soil moisture (5-10 cm below-ground) were measured continuously during the entire year in roofed and control plots.

Sampling of vegetation, productivity, $\delta^{13}C$ and environmental data

In a central 3 by 3 m area of each 25 m^2 plot, we recorded number of plant species and per cent cover of each species at peak standing biomass. We harvested above-ground biomass twice a year, in mid June 2003 and early September 2003 following the local management regime. In the central sampling area of each plot, we collected eight 25 by 50 cm subsamples. Biomass was clipped 2 cm above ground, dried for 48 h at 60ºC and weighed thereafter. We sampled below-ground biomass using ingrowth cores (4.3 cm diameter, 10 cm length). In early spring, prior to the beginning of the vegetation period, four ingrowth cores were installed in the central sampling area of each plot. For each plot, we sieved soil from the respective grassland to 10 mm and filled the cores with this root-free soil. At the end of the vegetation period in mid September, ingrowth cores were collected and ingrown roots separated from soil in the lab. Thereafter the roots were dried for 48 h at 60ºC and weighed.

To gain physiological evidence for the insurance hypothesis, we investigated if in a community bulk leaf $\delta^{13}C$ values of individual species were affected by experimental drought and biodiversity and if the range of species with different drought responses increased with increasing diversity in a community. The isotopic composition of carbon in plant tissue gives evidence for leaf stomatal conductance during the time when the carbon was assimilated and can therefore be utilized as an integrated measure of photosynthetic water use efficiency and drought stress of plants (Farquhar & Richards 1984). The number of plant species sampled for $\delta^{13}C$ in control and roofed plots was proportional to the species richness in each plot and covered two thirds of the most dominant species in a site. Plant material was dried, ball milled and analyzed for $\delta^{13}C$ with an isotope ratio mass spectrometer (IRMS, Delta C Finnigan MAT, Bremen, Germany). For analysis of community $\delta^{13}C$ in a site, the values of all investigated species in a site were averaged for each plot and the differences between treatment and control compared (see statistical analyses). To test if in a community the range of species with different drought responses increased with increasing diversity, the difference between $\delta^{13}C$ values of treatment and control was individually calculated for each sampled species, the difference averaged for each site and the standard deviation of the averaged $\delta^{13}C$ differences determined as a measure for within site variability.

We collected soil samples in each plot to separate diversity effects from confounding background effects of edaphic variables. Soil was collected six times throughout the year

2002 and two times in 2003. In each plot, four soil subsamples were collected and pooled. One part of each soil sample (~ 10 g) was extracted with 50 ml 1M KCl for 60 minutes on the same day of sampling. KCl extracts were filtered and then frozen at -20°C and later analyzed using a Continuous Flow Analyzer (SAN Plus, Skalar, Erkelenz, Germany) for NH_4^+ and NO_3^-, and an ICP-AES (Optima 3300 DV, Perkin-Elmer, Norwalk, USA) for Ca^{2+}. The remaining soil was dried at 35°C and extracted for one hour using a 1M Calcium-Acetate-Lactate (CAL) solution. CAL extracts were analysed with ICP-AES (Optima 3300 DV, Perkin-Elmer, Norwalk, USA) for P, K^+, $Mg^{2+}$and SO_4^{2-}. Soil pH was measured in a water extract. For the determination of the soil C:N ratio and the total soil nitrogen (N_{tot}) and carbon (C_{tot}), dry soil was ground and analyzed with an Element Analyzer (Vario EL II, Elementar, Hanau, Germany). No seasonal trend was observed within soil variables. Therefore, subsamples of variables sampled in 2002 and 2003 were averaged for each plot before they entered the statistical analyses.

Quantifying diversity, species composition and soil properties

To test for the effect of plant diversity on productivity following drought, we calculated for each plot the effective diversity (heterogeneity or exponential Shannon-Wiener; $N_1 = e^{H'}$, $H' = -\sum (p_i) (\ln p_i)$, p_i = species cover / sum of cover for all species) that corrects species richness for differences in evenness (for more details see Krebs, 1999). In order to account for effects of community composition (plant composition and abundance), we performed Non-Metric Multidimensional Scaling (NMDS) ordination for control and treatment plots in the 19 studied grassland sites and used the scores of the resulting NMDS axes as numeric values for community composition in consecutive analyses. The NMDS ordination was based on plant cover data to calculate a distance matrix. The plant cover data were square root transformed to linearize the data set and to reduce the importance of extreme values as suggested by Krebs (1999). As a distance measure, we used the Bray-Curtis coefficient (also known as Sørensen or Czekanowski coefficient), written in shorthand as 1–2W/(A+B), where W is the sum of shared species cover in control and roof plots and A and B are the sums for cover for all species in the control and roof plots. The Bray-Curtis coefficient is one of the most robust measures for this purpose. NMDS is an iterative search procedure that places objects of a distance matrix (e.g. different sampling sites) in a space of minimized dimensionality while preserving their rank order of distances as well as possible. The coordinates (scores) that position an object along the axes of the minimized dimensional space can then be used as numeric values in consecutive analysis, representing

solution with highly reduced dimensionality of the previously multivariate dataset. For more details see Legendre & Legendre (1998). NMDS analysis were performed using the program PC-ORD (McCune & Mefford 1997).

Soil variables were aggregated using Principal Component Analysis (PCA; using the program CANOCO, ter Braak & Smilauer, 2002). PCA summarizes the multivariate information of the soil variables as four major axes. Since PCA axes are by definition orthogonal and independent of each other, this procedure creates composite independent variables and avoids the danger of spurious correlations (i.e., multicollinearity). Consequently, these axes were used in all consecutive analyses as independent soil variables for the plots.

Statistical analysis

To differentiate the diversity-dependent effects of experimental drought on the parameters productivity above- and below-ground as well as on community $\delta^{13}C$ from edaphic background variation, we performed in a first step multiple regression analyses for each parameter with the PCA constructed variables soil1, soil2 and soil3 as independent variables. For each parameter, the residuals of the multiple regression analysis were then added to the parameters' arithmetic mean to get an estimate of productivity above- and below-ground as well as for community $\delta^{13}C$ that was corrected for edaphic background variation. In a second step, we used these corrected values of each of the three parameters to calculate the difference between treatment and control for each site. In a final step, we determined for each parameter the effect of species composition (NMDS1 and NMDS2) as well as effective diversity on the difference between treatment and control using general linear models (type I sum of squares). In the analysis, the means between treatment and control plots of NMDS1, NMDS2 and effective diversity were entered as covariates in a fixed hierarchical sequence. We decided for a conservative approach and entered the composition variables NMDS1 and NMDS2 first, so that composition effects were removed from the model before the actual diversity effect was tested. To account for general differences in productivity among sites, above and below-ground biomass data were log-transformed before the analysis, which corresponds to an analysis of relative changes in productivity and meets the assumptions of general linear models.

5.3 Results

Plant species richness in the investigated plots varied between 13 and 38 species and effective diversity between 6.5 and 23.3. Non-Metric Multidimensional Scaling (NMDS) showed that a two dimensional solution was sufficient (minimum stress values: 1st axis/dimension = 20.1, 2nd axis/dimension = 12.4, $R^2 = 0.90$) to explain plant community composition. The scores of both NMDS axes described a gradual compositional change from Geranio-Trisetetum nardetosum grasslands (low NMDS scores) to Geranio-Trisetetum alopecuretosum grasslands (high NMDS scores) (Hundt, 1964). For further analyses, we used the scores of the first two NMDS axes as numeric variables for plant community composition (NMDS1 and NMDS2). In the PCA analysis, the first three axes explained 72% of the variance of all tested soil variables (Table 5.1). Therefore PCA axes 1-3 were used for consecutive analysis as variables "soil1-3". While soil1 was mainly correlated with pH related variables (pH, SO_4^{2+}, Ca^{2+}), soil C, NO_3^- as well as N_{min}, soil2 was correlated with NH_4^+, N_{min}, K^+ and soil N. Soil3 was strongest correlated with P_{tot} (Table 5.1).

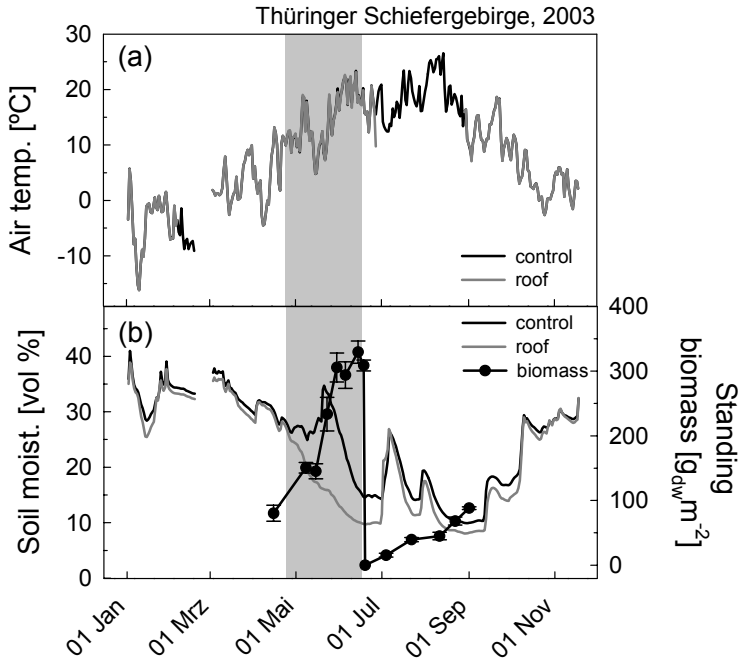

Fig. 5.1: Effects of experimentally induced drought (shaded area) on mean daily air temperature and mean daily soil moisture in one representative control site of the study. No differences between treatment (gray line) and control plots (black line) were observed for air temperature (Fig. 5.1a, control behind treatment), while soil moisture was affected substantially by the drought treatment (Fig. 5.1b). The drought experiment was timed during the time of highest above-ground biomass production in the control plots (Fig. 5.1b). For air temperature, data are missing for treatment and control between February 15th and 28th as well as for treatment between June 23rd and August 15th.

Roof establishment in mid April did not affect mean daily air temperature (Fig. 5.1a) but resulted in a significant reduction of mean daily soil moisture compared to control plots (Fig. 5.1b). Differences in soil moisture between treatment and control were highest in the phase of highest biomass productivity on control plots (Fig. 5.1b).

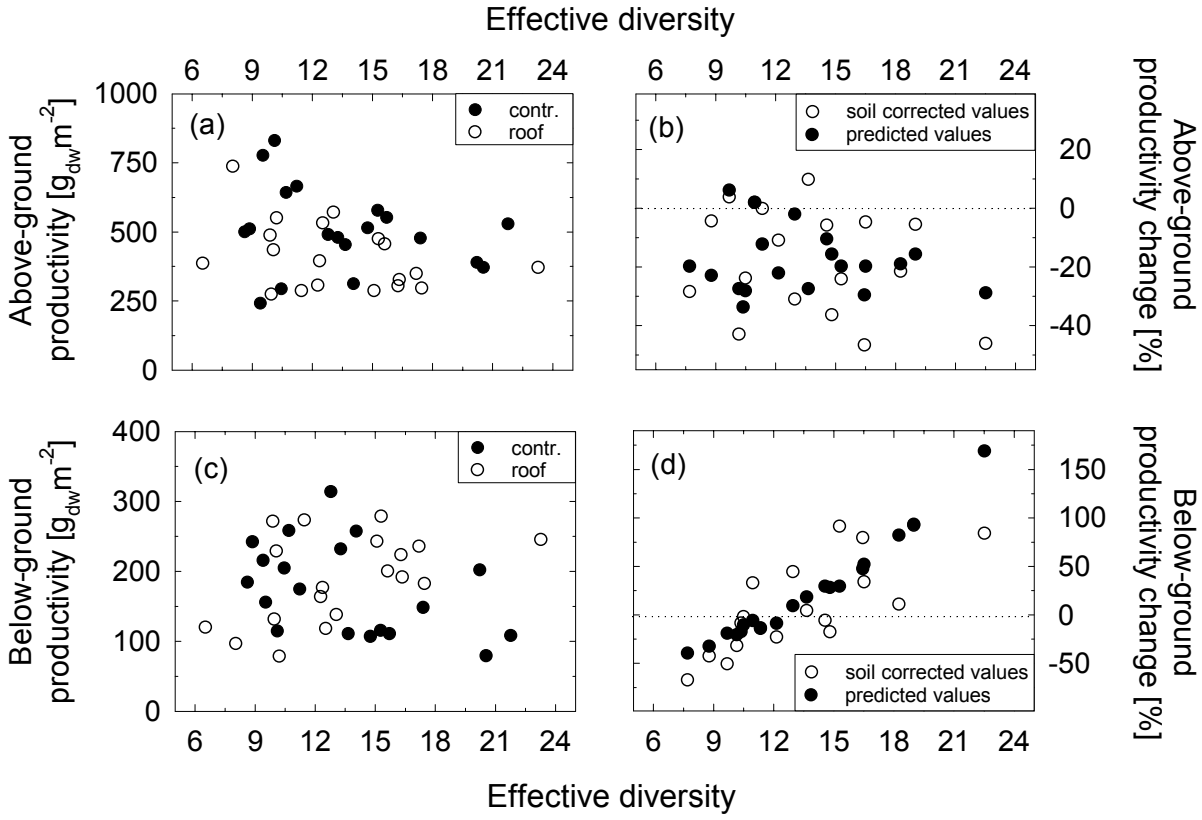

Fig. 5.2: Relationship between effective plant diversity and above- and below-ground productivity in control and treatment plots (Fig. 5.2a,c) as well as the relative change of above-and below-ground productivity caused by drought (Fig. 5.2b,d). For a and c, full symbols indicate control plots while open symbols indicate treatment (roof) plots. For b and d, full symbols indicate change in productivity when corrected for edaphic background variation and open symbols indicate values predicted by the general linear models (Table 5.3).

Mean annual above-ground productivity in the control plots was 506.0 $g_{dw}m^{-2}$ ± 152.6 SE and 412.5 $g_{dw}m^{-2}$ ± 124.0 SE in the roofed plots (Fig. 5.2a). Mean annual below-ground productivity in the control plots was 175.7 $g_{dw}m^{-2}$ + 66.2 SE and 189.6 $g_{dw}m^{-2}$ ± 62.6 SE in the roofed plots (Fig. 5.2c). When background variation in productivity above- and below ground was analyzed in multiple regression analyses, above-ground productivity showed a significant relationship with soil variables, specifically soil1 (Table 5.2). In contrast, below-ground productivity was not significantly influenced by soil variables (Table 5.2). The effects of species composition and diversity following experimental drought on the changes in

Table 5.1: Eigenvalues and eigenvector coefficients (loadings) of the standardized Principal Component Analysis of soil variables.

PCA	soil1	soil2	soil3	soil4
Eigenvalue	0.4336	0.1706	0.1262	0.0957
NO^{3-}	-0.7528	-0.0894	-0.4272	-0.0366
NH^{4+}	-0.4182	-0.7174	0.0401	0.2269
N_{min}	-0.7226	-0.5849	-0.2032	0.1508
K^{+}	-0.1975	0.6178	-0.4851	-0.0893
Mg^{+}	-0.8665	-0.2935	0.0039	-0.0326
Na^{+}	0.4642	-0.3608	0.3979	0.0323
P_{tot}	-0.4465	0.1967	-0.7175	-0.0873
SO_4^{2+}	0.7965	-0.2070	-0.4131	0.2365
Ca^{2+}	-0.8087	-0.2100	0.1300	-0.4460
Soil C	0.6903	-0.5007	-0.3030	-0.4060
Soil N	0.5911	-0.6143	-0.4045	-0.1591
C:N	0.5161	0.0388	0.0842	-0.7694
pH	-0.8873	-0.0188	0.2368	-0.3366

Table 5.2: Multiple regression models for the parameters productivity above- and below-ground as well as community $\delta^{13}C$. Separate models were calculated for each parameter with the variables soil1, soil2 and soil3 entered into each model.

	Details of multiple regression model			Model summary	
Independent parameter	**variable**	**b**	***p***	**r^2**	***p***
Above-ground biomass				0.498	<0.001
	soil1	-0.695	<0.001		
	soil2	-0.010	0.937		
	soil3	-0.123	0.317		
Below-ground biomass				0.055	0.582
	soil1	0.168	0.321		
	soil2	-0.116	0.491		
	soil3	0.116	0.491		
$\delta^{13}C$				0.389	0.001
	soil1	-0.535	<0.001		
	soil2	-0.157	0.249		
	soil3	-0.280	0.044		

above and below-ground productivity (that was corrected for edaphic background variation) were tested using general linear models. NMDS1 and NMDS2 as well as effective diversity had no significant effect on changes in above-ground productivity (Table 5.3, Fig. 5.2b). In contrast, differences in below-ground productivity were significantly influenced by NMDS1 and highly significantly influenced by effective diversity (Table 5.3, Fig. 5.2d).

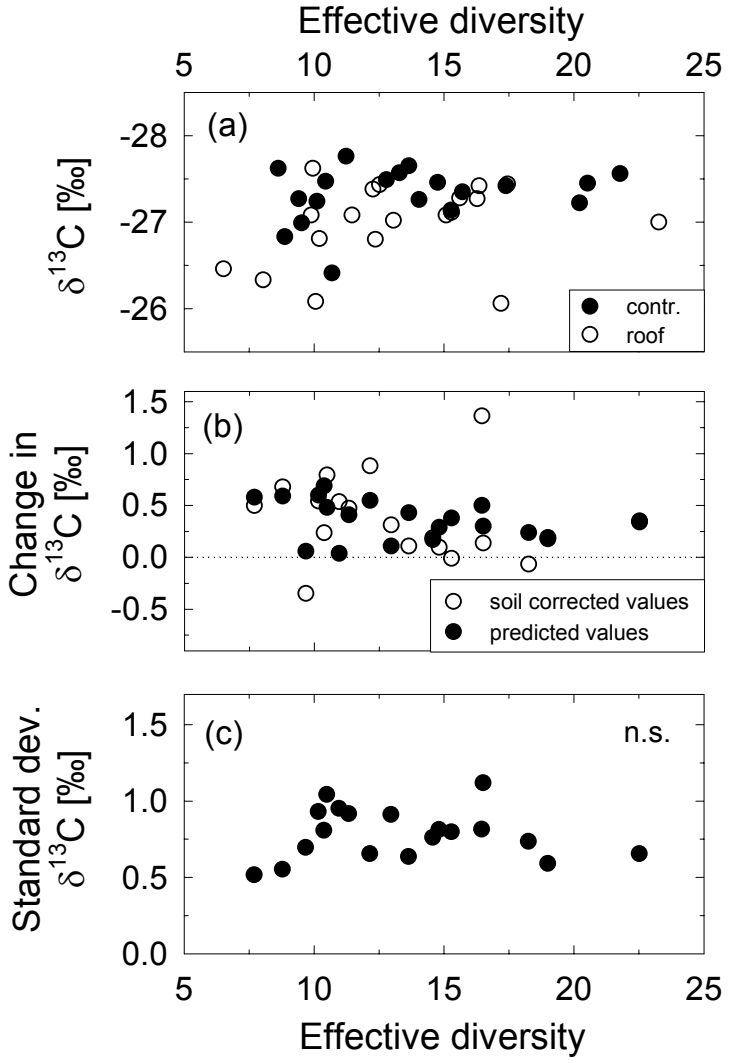

Fig. 5.3: Average differences of carbon isotopic composition of plant communities between control and treatment plots as related to effective diversity: a) community $\delta^{13}C$ values for control (full symbols) and treatment (open symbols) plots; b) change in $\delta^{13}C$ values when corrected for edaphic background variation (open symbols) and predicted $\delta^{13}C$ values (full symbols) in the general linear models (Table 5.3); c) correlation between standard deviation of mean differences in $\delta^{13}C$ values between control and treatment plots.

Table 5.3: Effects of species composition (NMDS1 and NMDS2) and plant diversity (effect. diversity) on drought induced changes in above- and below-ground productivity (corrected for edaphic background variation) as well as community $\delta^{13}C$, tested using general linear models (type I sum of squares).

Above-ground biomass

Source of variation	sum of squares	df	F	*p*
model	0.304	3	2.434	0.105
NMDS1	0.125	1	3.005	0.103
NMDS2	0.075	1	1.797	0.200
effect. diversity	0.104	1	2.492	0.135
residuals	0.625	15		

Below-ground biomass

Source of variation	sum of squares	df	F	*p*
model	2.663	3	7.964	0.002
NMDS1	0.623	1	5.589	0.032
NMDS2	0.050	1	0.452	0.512
effect. diversity	1.990	1	17.852	0.001
residuals	1.672	15		

$\delta^{13}C$

Source of variation	sum of squares	df	F	*p*
model	0.688	3	1.674	0.215
NMDS1	0.612	1	4.467	0.052
NMDS2	0.066	1	0.482	0.498
effect. diversity	0.010	1	0.073	0.790
residuals	2.054	15		

Mean community $\delta^{13}C$ values in the control plots was -27.32 $\pm$ 0.32 SE and -26.99 $\pm$ 0.46 SE in the treatment plots (Fig. 5.3a). Interestingly, soil variables had a significant effect on community $\delta^{13}C$ values when tested in a multiple regression analysis (Table 5.2). Changes in $\delta^{13}C$ following the experimental drought treatment showed however no significant relationship with species composition (however, marginal significances for NMDS1, $p = 0.052$) or effective diversity when tested using general linear models (Table 5.3, Fig. 5.3b). Also, the range of species with different drought responses, i.e. the standard deviation of the average differences between $\delta^{13}C$ in treatments and controls of individual species, did not correlate with effective diversity (Fig. 5.3c).

5.4 Discussion

A positive effect of diversity on productivity has been detected in several previous experimental studies (Hector *et al.* 1999; Loreau, Naeem & Inchausti 2002; Tilman, Wedin & Knops 1996). The relationship observed in these studies was, however, largely influenced by very low species numbers. At the diversity levels typically found in natural plant communities, no direct relationship between plant diversity and productivity has been observed (Kahmen *et al.* 2005). The results we obtained in the control plots of our semi-natural grasslands are in line with these observations (Fig. 5.2a). It has been argued, that at high diversity levels, plant species are functionally redundant and thus no direct effect of diversity on productivity can be observed (Vitousek & Hooper 1993; Walker 1992). Few studies, however, have tested if species diversity, which has little or no effect on ecosystem function in a stable environment, influences the stability of ecosystem functions following environmental perturbations (Loreau *et al*. 2001). The results from this study show that independently of plant diversity above-ground productivity was reduced by drought, while increasing plant diversity enhanced below-ground productivity during drought, thus maintaining more stable overall productivity of the respective community (Table 5.3, Fig. 5.2).

Drought can influence various aspects of plant productivity and carbon allocation depending on the severity of water deficiency in the soil (Kramer & Boyer 1995; Lambers, Chapin & Pons 1998). As a first reaction to drought, plant roots sensing dry soil produce abscisic acid (ABA), which is transported to the leaves. In the leaves, ABA reduces stomatal conductance, leaf expansion and eventually photosynthesis, leading to a reduction or cessation of productivity (Davies & Zhang 1991; Tardieu *et al*. 1992). At moderate water deficiency in the soil, however, below-ground plant parts are less sensitive to drought than leaves, since root growth is less affected by ABA than leaf expansion (Saab *et al.* 1990). Also, moderate water stress can reduce leaf growth prior to photosynthesis, resulting in a surplus of assimilates that are exported to the roots and enhance root productivity (Boyer 1970). As a consequence, enhanced root production through shifts in carbon allocation in moderately water stressed plants might exceed that of well watered plants and is presumably an adaptation to dry soils, allowing the exploitation of reduced soil moisture levels (Jupp & Newman 1987; Lambers, Chapin & Pons 1998; Sharp & Davies 1979).

Different plant species react, however, differently to drought disturbance, depending on their specific water use efficiency or drought tolerance (Molyneux & Davies 1983).

Several studies have shown that for some plant species productivity above- and below-ground was reduced as a consequence of drought, while for other species total productivity was less affected but a shift in carbon allocation caused reduced above-ground productivity but enhanced below-ground productivity (Carter, Theodorou & Morris 1997; Foulds 1978; Guenni, Marin & Baruch 2002; Stevenson & Laidlaw 1985). Similarly, we found in our study that the productivity of the investigated grasslands was affected differently by drought. While in some grasslands, productivity was reduced above- and below-ground, in other sites a decrease in above-ground productivity was partly balanced by an increase of below-ground productivity (Fig 5.2d). Interestingly, drought effects on below-ground productivity were significantly related to plant diversity, suggesting that a more diverse community has a higher likelihood to contain drought tolerant species that allow carbon allocation to below-ground parts.

We used $\delta^{13}C$ values of leaf tissue as drought stress indicators of individual plant species and as a potential functional explanation of the insurance hypothesis. Specifically, we tested if the range of species with different drought responses (i.e. $\delta^{13}C$ ratios of foliage) increased in communities with increasing plant diversity. Carbon isotope ratios ($\delta^{13}C$) of plant tissue are determined, in part, by the ratio of intercellular to ambient CO_2 concentrations (c_i/c_a) (Farquhar, O'Leary & Berry 1982). Increasing $\delta^{13}C$ values indicate low c_i/c_a ratios resulting from either high photosynthetic demand or low stomatal conductance (Ehleringer & Cooper 1988; Farquhar et al., 1989). Thus, carbon isotope composition of plant tissue can be used as an integrating measure of the photosynthetic water use efficiency during the time when the respective carbon was assimilated (Farquhar & Richards 1984). We collected leaf tissue of individual species at the end of the experimental drought period and analyzed the bulk leaf material for $\delta^{13}C$. The experimentally induced drought had, however, only small effects on mean $\delta^{13}C$ values of the analyzed leaf material in the sites, with slightly less negative $\delta^{13}C$ values for drought stressed plants (Fig. 5.3a and b). Consequently, the variability of drought responses did also not change with increasing diversity in a community (Fig. 5.3c). The experimentally induced reduction in soil moisture (Fig. 5.1b) and the reduced above-ground biomass production (Fig. 5.2a) were substantial in the experiment, suggesting drought effects on the investigated grassland communities. Since a reduction in stomatal conductance is among the first responses of plants to drought, changes in the $\delta^{13}C$ values of carbon assimilated during the drought experiment were to be expected. However, the small observed changes in $\delta^{13}C$

values of leaf tissue and the constant variability along the diversity gradient are probably due to the relatively short duration of our experiment. It is likely, that the time of the drought treatment was not sufficient to alter the overall isotopic signature of bulk leaves, due to large fractions of leaf-carbon assimilated before the drought experiment. Consequently, we view the lack of functional evidence for the insurance hypothesis based on $\delta^{13}C$ values of leaf tissue as a result of the short duration of the experiment rather than a result of non-existing diversity effects.

Experimental design, data interpretation and potentially confounding 'hidden treatments' in studies investigating the effect of biodiversity on ecosystem functions have been highly debated in the literature (Aarssen 1997; Hector *et al*. 2000; Huston 1997; Schmid & Pfisterer 2003; Wardle 2001; Wardle & Grime 2003). To account for such 'hidden treatments' in our study, we incorporated soil variables and community composition as covariables into our data analysis (Table 5.2 and 5.3). Our results are consistent with previous studies that have determined the importance of species composition for the stability of ecosystem functions (Grime *et al*. 2000; MacGillivray *et al.* 1995; Wardle *et al.* 2000). However, species composition was only significant in the model for below-ground productivity, when this covariable was entered in the analysis prior to effective diversity (Table 5.3). If the sequence was reversed and effective diversity was entered first, the significant effect of NMDS1 vanished, suggesting only a weak effect of composition (data not shown). In our analyses we used effective diversity as a measure of plant diversity. We also tested the effects of species richness on drought resistance of productivity. In general, the same statistical trends were observed, when either species richness or effective diversity was used in the general linear models. However, effective diversity proved to explain more of the variability in the data, suggesting that it is important to consider not only species diversity but also the evenness of species in the analyses of ecosystem functions.

Despite the lack of physiological evidence using $\delta^{13}C$ values the data of this study show strong diversity effects on productivity following drought. Following water limitation drought tolerant species enhance root productivity by shifting carbon allocation to below-ground parts and as a result maintain overall community productivity. Enhanced root production during drought will also positively influence many other ecosystem services and functions such as nutrient cycling and retention, water holding capacity during rainfalls following drought periods, and maintenance of overall community stability (Daily 1997). Our study, therefore gives strong evidence for the insurance hypothesis, suggesting that an increasing number of plant species leads to a higher likelihood of a community to contain

drought tolerant species that maintain stable ecosystem functions (Doak *et al.*, 1998). Consequently, high biodiversity levels might buffer some of the anticipated consequences of a globally changing climate on ecosystem services by maintaining ecosystem functions during environmental perturbations (IPCC 2001).

6 Concluding discussion

We expanded the investigations of the relationship between biodiversity and ecosystem functioning from experimental plant communities to semi-natural montane grasslands to address the following questions:

(1) What is the effect of plant diversity on productivity in combination with community composition, management and environmental parameters in semi-natural grasslands?
(2) Does niche- and resource partitioning for soil nitrogen explain the relationship between plant diversity and productivity in these systems?
(3) Does plant diversity effect productivity in the face of global climate change.

Most studies that have used experimentally established grassland communities to test the effect of plant diversity on ecosystem functions, in particular productivity, have found a positive, asymptotic relationship (Loreau *et al.* 2001). In this study, where we investigated a diversity gradient in semi-natural grasslands, we found no such effect of plant species richness on productivity (Chaper 3), so that our findings seem to contradict earlier findings from experimental studies (Hector *et al.* 1999; Tilman *et al.* 2002). The observed relationship between biodiversity and productivity in experimental studies are, however, driven by very low species numbers. Tilman for example suggests that in his study only about five species account for the observed relationship (Tilman *et al.* 2002). The lowest number of species observed in our study, however, was eight plant species, a diversity level where even in experimental plant communities no relationship between biodiversity and ecosystem functioning was observed. Our study therefore seems to support rather than contradict the findings of earlier experimental studies: Biodiversity effects are largely driven by low species numbers, but once diversity is above a critical level, no effects can be observed.

Diversity effects on productivity in experimental studies have largely been explained by niche complementarity. Niche complementarity suggests that different species in an ecosystem occupy different ecological niches with respect to resource use, so that an increasing number of species results in more efficient resource exploitation and consequently increased productivity. For grasslands it was suggested that, among others, spatial, temporal and chemical nitrogen (N) partitioning among plant species drives the

observed positive relationship between biodiversity and ecosystem functioning. We tested N partitioning among different plant species in three different grasslands but found very little differences in spatial, temporal and chemical N uptake among the different plant species (Chapter 4). Interestingly, however, we found that the investigated plants relied not only on soil N but also on other N pools to meet their N demand, suggesting different N use strategies among different plant species. In fact, we were able to distinguish distinct functional groups among the different investigated plant species based on different N use strategies. Legumes for example, relied largely on symbiotically N fixation from the air and were therefore independent from the soil N pool. Herbs on the other side, had below-ground storage organs, and were therefore able to exploit their internal N pool in times where availability of soil N was reduced and competition for soil N high. Grasses, that do not have large storage organs, and are very efficient competitors for soil N, largely supply their N demand with N uptake from the soil. The different N use strategies detected in this study suggest the complementary use of N among the different functional groups in the investigated grasslands and propose a positive relationship between functional group diversity and productivity.

With respect to N use strategy we found a large amount of functional redundancy in all investigated grasslands, suggesting that the loss of species can be compensated by the remaining species of the same functional group (Chapter 4). Only if the last species of a group goes extinct and thus functional group diversity declines effects on ecosystem functioning can be expected. Complementary N use strategies among different functional groups and especially functional redundancy within functional groups seems to be a valid explanation for the observed relationship between biodiversity and ecosystem functioning in experimental studies as well as in the natural diversity gradient analyzed in this study (Chapter 3). As mentioned above, these studies shown an effect of increasing biodiversity on ecosystem functioning only at very low species numbers, where based on our results functional group diversity will also increase, but that above a critical diversity limit, where species are functionally redundant no effect can be observed.

Relating functional group diversity to ecosystem functioning needs, however, to be treated with care (Petchey & Gaston 2002; Diaz *et al.* 2003; Petchey *et al.* 2004). In the present study, we grouped the species based on a single functional trait, N use strategy. Other criteria, for example water use efficiency, specific leaf area or photosynthetic capacity, that also drive ecosystem functioning might result in very different group assignments. Consequently, species that are functionally redundant for one trait can be

functionally complementary for another. For a full quantification of functional diversity that allows predictions of biodiversity effects on ecosystem functioning, several functional traits need to be combined in a single measure (Petchey *et al.* 2004). For wild plant species that are in the center of attention in biodiversity research data on functional traits that exceed morphological or taxonomical descriptions are, however, rare. Especially, studies that address functional complementarity among wild plant species with respect to resource use are virtually absent from the scientific literature, although urgently needed to predict biodiversity effects on ecosystem functioning. Consequently, our study on complementary N use strategies can be a valuable contribution to the functional understanding of biodiversity and might fuel further research in this direction.

The results from chapter 3 and chapter 4 suggest high functional redundancy among species in semi-natural grasslands. However, these experiments were each conducted in a single season and ignored environmental variability. In the face of global climate change, however, environmental variability will become a large driver of ecosystem functions. For Europe, for example, not only rising temperatures and declining precipitation have been predicted by recent climate models, but also increased temporal heterogeneity in weather patterns (Schär *et al.* 2004). Evidence that biodiversity has a positive effect on ecosystem functioning during environmental fluctuations has come from theoretical studies and laboratory experiments, while results from field studies are scarce (McGrady-Steed *et al.* 1997; Doak *et al.* 1998; Yachi & Loreau 1999). In general these studies refer to the so called 'insurance hypothesis' that predicts that with increasing diversity the range of species with different responses to environmental change will increase (McNaughton 1977). We tested the insurance hypothesis in the semi-natural grasslands also investigated in chapter 1 and 2, by simulating extended drought periods in early summer. While we did not find any effect of biodiversity on above ground productivity, below-ground productivity was significantly enhanced with increasing biodiversity, suggesting a positive biodiversity ecosystem functioning relationship.

Our findings in all three chapters illustrate, that the relationship between biodiversity and ecosystem functioning in semi-natural grasslands is highly complex and context dependent. While no diversity effects were observed in the absence of environmental fluctuations in 78 semi-natural grasslands, simulated climate change stressed the influence of diversity on ecosystem functioning in these ecosystems. Equally, plants that were functionally redundant with respect to different N use strategies might be functionally complementary with respect to other resources. Consequently, we suggest that a number of

different parameters need to be considered if the effect of biodiversity on ecosystem functioning is to be understood. Therefore, further research should focus more on the functional mechanisms behind the observed biodiversity and ecosystem function relationships. Especially with respect to resource partitioning, facilitation and competition, new analytical tools such as the use of stable isotopes or different molecular methods should increasingly be used to address general functional patterns. Only if these general functional patterns are understood, the effects of biodiversity and ecosystem functioning can be included in earth system models, which is essential to predict the consequences of the current 6^{th} mass extinction crisis to ecosystem functioning and consequently the human society.

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