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Distribution of plant functional traits in a range of grassland formations differing in water and nitrogen availability

A comparison using the SynBioSys and BiolFlor databases

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Abstract

A database linkage between the BiolFlor and SynBioSys databases was applied to evaluate the general use and application of such linkages for grassland approaches, as well as to investigate the distribution of plant functional traits along environmental gradients. Therefore, eleven plant traits concerning plant morphology, survival strategy and utilization were selected from the German BiolFlor database. The Dutch SynBioSys NL information system was used for the acquisition of data about grassland formations, their specific species composition and the constancy of species within the accordant formations. Eleven formations covering a wide range of environmental conditions and utilization intensities were selected. To build the environmental gradients, the average Ellenberg indicator values for nitrogen [N] and moisture [F], which are the most important environmental factors for plant community composition, were calculated. The non-numerical trait expressions within grassland communities were weighted with the constancies of the correspondent species. They were, furthermore, calculated as percentages of trait expressions within formations. Bar plots were drawn and regression analyses were accomplished to investigate whether there are significant statistical relationships between trait expressions and environmental gradients.

The implementation of the database linkage was comparatively complex, since, for the major part, the common basis, a species reference list, had to be manually adjusted. Nevertheless, the linkage of the databases succeeded with a common basis of 1615 species. Because of the huge amount of provided information about vegetation composition and plant traits, the two databases are predestinated for further grassland approaches. The present investigation shows that database linkages can be characterized as useful instruments in this context.

It could be shown that grassland communities differ in their specific trait composition due to their environmental requirements. For some of the investigated traits, like leaf anatomy, storage organs and strategy types, many considerable relations with [N] and [F] are observable. Other traits show fewer conspicuous relations with the gradients, for example the root and shoot

metamorphoses and leaf persistence. In these cases other influencing variables, which are not considered here, may play a role.

Kurzfassung

Eine Verknüpfung der BiolFlor und SynBioSys Datenbanken dient in dieser Arbeit dazu, die generelle Nutzung und Implementierung solcher Verknüpfungen für Grünlandstudien zu bewerten sowie das Auftreten von unterschiedlichen funktionalen Pflanzenmerkmalen entlang von Umweltgradienten zu untersuchen. Dazu wurden elf Pflanzenmerkmale aus den Bereichen Morphologie, Überlebensstrategie und Nutzung aus der deutschen BiolFlor Datenbank ausgewählt. Aus dem niederländischen SynBioSys NL Informationssystem wurden Daten über Graslandverbände, ihre spezifische botanische Zusammensetzung und die Stetigkeit der Arten innerhalb der entsprechenden Verbände gewonnen. Insgesamt wurden elf Gesellschaften, die ein großes Spektrum an Umwelt- bzw. Nutzungsbedingungen repräsentieren, ausgewählt. Die Umweltgradienten wurden anhand der mittleren Ellenberg'schen Zeigerwerte für Stickstoff [N] und Feuchtigkeit [F] errechnet. Hierbei handelt es sich um die wichtigsten Parameter im Zusammenhang mit der botanischen Zusammensetzung von Grünlandgesellschaften. Die einzelnen nichtnumerischen Merkmalsausprägungen innerhalb der Formationen wurden mit der entsprechenden Stetigkeit der Arten gewichtet und darüberhinaus prozentual dargestellt. Es wurden Säulendiagramme erstellt sowie Regressionsanalysen durchgeführt, die dazu dienten den statistischen Zusammenhang zwischen den Ausprägungen der Merkmale und den Gradienten für Stickstoff und Feuchtigkeit zu überprüfen.

Die Verknüpfung der beiden Datenbanken gestaltete sich relativ komplex, da die gemeinsame Datengrundlage, eine Referenzliste der gemeinsamen Arten, größtenteils manuell erstellt werden musste. Die Verknüpfung gelang jedoch mit einer Datenbasis von 1615 Arten. Die große Menge an wertvollen Informationen über Vegetation und pflanzliche Merkmale, die durch die beiden Datenbanken bereitgestellt wird, prädestiniert diese für die Anwendung in der Grünlandforschung. Diese Arbeit zeigt, dass die Datenbankverknüpfung in diesem Zusammenhang ein wichtiges Instrument darstellt.

Weiterhin konnte gezeigt werden, dass Grünlandgesellschaften sich, je nach ihren Ansprüchen an die Wasser- und Nährstoffversorgung, in ihrer Zusammensetzung von funktionalen Pflanzenmerkmalen unterscheiden. Für manche Merkmale, z.B.

Blattanatomie, Speicherorgane und Strategietypen, konnten viele deutliche Zusammenhänge mit den Gradienten für Feuchtigkeit und Stickstoff identifiziert werden. Bei anderen Merkmalen (Metamorphosen des Sprosses und der Wurzel, Blattdauer etc.) gelang dies in geringerem Umfang. Hier könnten andere, in dieser Arbeit nicht berücksichtigte, Parameter eine Rolle spielen.

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[1] Tables and figures with letter notations instead of Arabic numerals are presented in the appendix

1 INTRODUCTION

1.1 GENERAL INTRODUCTION

Scientific databases are valuable instruments to concentrate results and observations on a national and transnational scale. They can be useful in many disciplines and may provide a large amount of precious information (Montanarella *et al.* 1998, Lepczyk *et al.* 2008). Via modern communication channels information can be extracted and distributed all over the world accordingly. In context with botanical and ecological studies, there are already several databases available. They are usually provided by research institutions and government agencies on a national level. As a result of close collaborations, there will be transnational databases available within a short time (Schaminée *et al.* 2007).

The sensible linkage between different databases can provide further conclusions which cannot be drawn from the single data. For this purpose, individual parts can be combined on a common basis to gain new information. A connection between the German BiolFlor trait database and the Dutch SynBioSys NL information system is used in the present investigation. The common basis is a consolidated species reference list.

With respect to the field of grassland research, up to now, there are few scientific investigations using database linkages (e.g. Lososova *et al.* 2006, Nol *et al.* 2008, Tautenhahn *et al.* 2008). In this regard, an approach that combines vegetation and plant trait databases aiming to create new information about the trait distribution along environmental gradients, like the present study, is so far unique.

During the last years, the functional classification of plant species becomes more and more interesting (Weiher *et al.* 1999) and the subject of functionality of plant attributes has been discussed within several topics, including response to climate change, ecosystem adaptation and exploitation of environmental resources. In the context of plant community structure, the functionality is connected to the life history of plants, e.g. dispersal, expansion and reproduction. Functionality is given when plant attributes are advantageous for the individual species under specific environmental conditions (Kleyer 1999, Weiher *et al.* 1999). Another consideration is to implicate the subject of functionality in context to disturbance responses (McIntyre *et al.* 1999).

Within a community of plants, it is possible to classify several plant functional types. According to Lavorel *et al.* (1997), they can be defined as non-phylogenetic groupings of species which perform similarity in an ecosystem with common biological attributes. They can be grouped on the basis of their contribution to ecosystem processes or responses to environmental changes. The construction of plant functional types is based on the selection of specific plant traits (Lavorel *et al.* 1997, Diaz Barradas *et al.* 1999). They are biological characteristics, e.g. morphological features, which determine whether a plant species is able to establish, persist and develop under specific environmental conditions (Kahmen 2003). A consistently growing list of studies is concerned with the collection of key traits characterising plant functionality (e.g. Diaz *et al.* 1999, McIntyre *et al.* 1999, Diaz *et al.* 2004). The trait sets differ depending on the attached importance of the individual authors (Weiher *et al.* 1999). In context with this investigation, eleven traits concerning plant morphology, survival strategy and utilization are used.

Furthermore, different grassland formations can be characterized by varying environmental conditions, utilization intensity and botanical compositions (Dierschke & Briemle 2002). Eleven formations differing in a wide range of these attributes have been selected. Among the selected syntaxa, there are formations of great agricultural importance, like the *Cynosurion cristati*, but also communities which are threatened with extinction due to utilization abandonment or modification in many landscapes. In the latter formations in particular, for instance the *Caricion davallianae*, usually rare species accommodate and make these formations necessarily worth of protection (Dierschke & Briemle 2002).

Water and nitrogen availabilities can be characterized as the most important environmental gradients influencing the plant sociological structure (Dierschke & Briemle 2002). These two factors, established on the basis of Ellenberg's indicator values for nitrogen [N] and moisture [F], serve as gradients within this study.

Along these gradients, the grassland formations with their different composition of particular trait expressions should be ranged.

It has to be considered that the selected plant communities as well as the Ellenberg indicator values are the results of multivariate classifications and have, therefore, abstract and constructional characteristics. These classifications are not affected by temporal dynamics and evolution (Dierschke & Briemle 2002, Ellenberg 2001).

The present investigation has two main aims. On the one hand, the methodical application and construction of database linkages within the field of grassland research shall be examined and on the other hand, new information shall be gained due to the practical use of the constructed project database.

On the methodical level, the application of database linkages for the creation of valuable information for grassland approaches concerning plant functional traits ought to be evaluated. In this context, it shall be exposed how proper the practical use of the aforementioned databases is and how satisfactory the linkage works. For this purpose, possible problems concerning the connection of the individual parts ought to be identified and potential solutions shall be presented.

Furthermore, the construction of the project database and data analyses shall serve to gain information about the relative occurrence of specific trait expressions within the selected grassland formations and to get an impression of how their distribution changes along the selected environmental gradients of moisture and nitrogen. These questions have not yet been investigated with the application of large database sets. If it succeeds to reach this aim due to database linkages it would, therefore, be a methodical innovation. A further goal is to draw conclusions from these relations with regard to the importance of plant attributes under specific environmental conditions and to examine if there is a possibility to predict changes of the trait distribution under altered environmental conditions. In this regard, there ought to be a small excursus to climate change which has, among others, significant effects on water availability.

1.2 HYPOTHESES

The falsifiable hypotheses of the present investigation are shortly presented in the following.

The BiolFlor and SynBioSys NL databases are suitable for the application within the field of grassland research. A sensible linkage between the two databases is possible.

The linkage between the BiolFlor and SynBioSys NL databases is a useful instrument to analyse and visualize the distribution of plant traits in the field of grassland research.

There is a relation between plant communities and the distribution of plant traits. The composition of trait expressions within grassland formations differs with respect to altering indicator values for moisture and nitrogen.

Changes of the trait composition due to altering environmental conditions, especially in view of climate change, are predictable by the use of database linkage and analysis.

2 MATERIAL AND METHODS

2.1 THE SYNBIOSYS INFORMATION SYSTEM

The information about the occurrence of species within the selected plant communities was obtained from the SynBioSys NL database. SynBioSys is an acronym for ‘Syntaxonomic Biological System’. It is an open-access information system containing data about plant species, vegetation and landscape. It has been developed by the Alterra, a research institute for ecosystem studies in Wageningen (The Netherlands). The information system is based on a GIS platform for the visualisation of various layers of information and connection of functions (Schaminée *et al.* 2007).

In this study, the SynBioSys NL version 1.19 was used for data collection purposes. It has to be mentioned that there is a new version (1.20) available at present. The program can be downloaded free of charge (http://www.synbiosys.alterra.nl/) as a Dutch version. The dataset is available as a database file, which is advantageous for analysis and was, therefore, used for the extraction of data.

The SynBioSys NL provides details about 43 classes of grassland associations (Hennekens 2008) which are located throughout the Netherlands. Within these classes, eleven formations were used for the creation of the project database (simplified database structure is presented in Fig. M).

Furthermore, the information system provides data about 38.940 relevés, which are floristic-sociological approaches in relatively small sample plots in the field including the description of vegetation (Schaminée *et al.* 2007). The relevés can be attached to specific grassland formations by their relevé number. A total of 9872 surveys were used for the present investigation of the eleven selected grassland formations.

In addition, the SynBioSys NL contains 3404 entries about species. Within this species pool, 1615 entries could be used for the development of the project database. For each species, a request of its specific constancy within the considered syntaxon is possible. Constancy can be described as the percentage of plots from a given syntaxon in which the species is present (Wittig & Streit 2004). In combination with the

BiolFlor traits (chapter **2.2**), it was used to quantify the trait expression within a syntaxon.

Several parameters were calculated for the precise characterisation of the SynBioSys Nl version in context with the selected data (an overview is given in **Tab. 1)**. The parameter 'n' is the total number of relevés which belong to the syntaxa (without duplicates). The α-diversity is the average number of species found in the relevés within the syntaxa. It characterises the “within-habitat”- diversity (Wittig & Streit 2004).

The γ-diversity is the total number of species within the syntaxa (without duplicates). The parameter contains several α-diversities which are not obligatorily different from each other. There was a loss of usable species of the γ-diversity due to the adjustment of the species lists (**Tab. 1,** used γ-Diversity [%]).

Tab. 1 Characterization of the SynBioSys NL dataset

SynBioSys Abbreviate	Names	n [1]	α-Diversity	γ-Diversity	Used γ-Diversity	Used γ-Diversity [%]
09BA	*Caricion davallianae*	766	28.90	516	312	60.47
12BA	*Lolio-Potentillion anserinae*	1028	17.21	379	288	75.99
14AA	*Corynephorion canescentis*	1278	15.80	368	151	41.03
15AA	*Mesobromion erecti*	157	38.89	323	210	65.02
16AA	*Junco-Molinion*	849	30.40	399	236	59.15
16AB	*Calthion palustris*	700	29.41	504	337	66.87
16BA	*Alopecurion pratensis*	224	24.23	155	124	80.00
16BB	*Arrhenatherion elatioris*	242	35.11	395	303	76.71
16BC	*Cynosurion cristati*	429	26.90	419	326	77.80
19AA	*Nardo-Galion saxatilis*	3786	23.47	476	280	58.82
32AA	*Filipendulion*	413	20.34	351	249	70.94

[1] total number of relevés within the syntaxa

The varying experience in the development of the SynBioSys NL is currently being integrated in the development of the pan-European information system SynBioSys Europe. This European database shall contain more information than the Dutch version, e.g. species-specific details about plant functional traits (Schaminée *et al.* 2007).

2.2 THE BIOLFLOR DATABASE

In this study, the BiolFlor database was used as a source of information about plant functional traits. It contains data of biological and ecological traits of the vascular flora of Germany, which covers the major part of Central European plant species (Kühn *et al.* 2004) Therefore, it is possible to combine the information with the Netherlands SynBioSys project.

The Department of Community Ecology at the UFZ (Centre for Environmental Research) conducted several research projects in the last ten years. The gained data were brought together to develop the BiolFlor database. It was published by the German Federal Agency for Nature Conservation. The database is available as a book and as a CD-ROM. Furthermore, a beta version in German and English is available on the internet (http://www.ufz.de/biolflor/index.jsp) and continuously expanded by inputs of new data (Kühn *et al.* 2004). For this investigation, the internet version (1.1) was used.

The BiolFlor project provides information about 3659 species, which could be divided into 2743 natives, 40 uncertain archaeophytes, 218 archaeophytes, 470 naturalised neophytes and 185 casual neophytes, which form no steady part of the German flora. The species lists of Wisskirchen & Haeupler (1998) and Schubert & Vent (1990) were used for the collection of the species data. There is also a large number of synonyms available which simplifies the search for single species (Kühn *et al.* 2004). In this study, 1615 species of the whole BiolFlor species pool were used.

Furthermore, queries about 66 different plant traits are possible, which can be classified into status, chromosome number, DNA content, phylogeny, morphology, leaf traits, flowering, phenology, floral and reproductive biology, seed traits, ecological strategy, indicator values for grassland species, range, urbanity, hemeroby, habitats and sociology. For every trait, several states are possible which are mostly accompanied by a qualifier (Krumbiegel 2002). The qualifier can deliver further information about the specific trait expression of a species (Kühn *et al.* 2004).

In context with this investigation, the trait characteristics for life form, life span, leaf anatomy, leaf persistence, root and shoot metamorphoses, rosettes, storage organs, vegetative propagation as well as the several grassland utilization values and strategy types were considered.

2.3 GERMANSL- THE NEW REFERENCE LIST FOR THE GERMAN FLORA

The first step of the development of the project database was the comparison between the species names of SynBioSys and BiolFlor. Otherwise the two databases could not have been effectually connected. For this purpose, the names of the lists were synchronised separately with the GermanSL reference list and then connected in the project database (q.v. Fig. M). Some details about the reference list are given in the following.

The German SL is used to be the new nationwide reference list for the German flora. It is developed and provided online by the section 'Taxonomic Reference Lists within the 'Network Phytodiversity Germany' (NetPhyD). The first version was available in March 2008. It can be downloaded free of charge (Jansen & Dengler 2008).

The German SL includes the information of the previous national standard lists, which were established by Wisskirchen & Haeupler (1998), Koperski *et al.* (2000), Scholz (2000), Schmidt *et al.* (1996), Schories *et al.* (1996) and Mollenhauer & Christensen (1996). The combined dataset was corrected and completed. Furthermore, thousands of new taxa were added. The German SL contains about 30.000 accepted and synonymous names as well as further information, like the red-list status of species (Jansen & Dengler 2008).

Although the GermanSL has only been available for a short time, it is already used in several German databases. Moreover, it ought to be the taxonomical foundation for a pan-European reference list within the SynBioSys Europe project (Schaminée *et al.* 2007) which is currently under development (Jansen & Dengler 2008).

2.4 THE SELECTED GRASSLAND FORMATIONS

Eleven grassland formations were selected on the basis of the German grassland communities and the available associations of the SynBioSys information system. The formations differ in their key aspects of sociology, abiotic properties and utilization in the context of agriculture. Some details about the selected formations are listed below. Nomenclature follows the aforementioned German SL reference list (**2.3**).

The *Corynephorion canescentis* belongs to the rare group of extensively used grassland associations on sandy soils of dunes. They can be characterized as low productivity pastures with a high species richness (Cerny *et al.* 2007). There is an increase in the degeneration of these formations through a steady renouncement of utilization at such non-economical locations. A typical species is *Corynephorus canscens* (Dierschke & Briemle 2002).

The *Mesobromion erecti* occurs on moderately dry, alkaline to neutral soils under atlantic-subatlantic climate conditions. For many centuries under extensive utilization, even without any manuring, it was an important source for forage. The importance of this association in a context of agriculture has been declining during the last decades. The distribution area has been significantly decreased by agricultural management and urban expansion (Willems 1982). According to Willems (1982), faithful species are e.g. *Anthyllis vulneraria, Bromus erectus, Carex caryophyllea, Leontodon hispidus, Pimpinella saxifraga, Plantago media, Scabiosa columbaria.*

The *Arrhenatherion elatioris* can be characterized as a species rich formation at low and relatively warm locations with intermediate growing conditions. It was of great importance previous to the strong intensification of agricultural cultivation during the last decades. The canopy structure is multi-layered with a high proportion of biomass in the lower sections. A high yield is possible even at a low level of fertilization. They can be mown two or three times a year (Dierschke & Briemle 2002). Nowadays, the *Arrhenatherion elatioris* is likely to occur at locations which could not have been made accessible for agriculture. According to the increased application of fertilizer, there is a slow alteration towards species poor grassland communities within the formation (Dierschke & Briemle 2002). According to Dierschke & Briemle (2002) dominant species are *Arrhenatherum eliatus, Campanula patula, Crepis biennis, Daucus carota, Galium album, Veronica arvensis* etc.

The species rich *Nardo-Galion saxatilis* (syn. *Violion caninae*) grows in nutrient poor habitats on mineral soils with a good water supply. In former times, it belonged to the extensively used pastures, e.g. for sheep and goats. Species with low competition abilities can develop through a short and loose canopy structure. Nowadays the formation is threatened by extinction. Faithful species are *Nardus stricta, Polygala vulgaris, Potentilla erecta, Viola canina* etc. (Dierschke & Briemle 2002).

The *Cynosurion cristati* can be characterized as a highly productive and highly yielding grassland association with good forage qualities. It develops at locations with good water and nutrient supply. Compared to meadows, there is a generally poorer species diversity within the pastures at equivalent locations. In general, the average number of species per community is below 30 and decreases with a higher utilization intensity. The species of the *Cynosurion cristati* are usually small growing grasses and herbs with a good vegetative dispersal ability and a good adaptation to grazing, e.g. *Alopecurus pratensis, Bellis perennis, Cynosurus cristatus, Dactylis glomerata, Leontodon autumnalis* and *Trifolium repens* (Dierschke & Briemle 2002). According to their competition ability, species of higher demands grow predominantly in shapes with a lower nutrient and intensity level. Such species rich shapes of the *Cynosurion cristati* have continuously been pushed back by modern grassland management and are still located at a submontane level (Dierschke & Briemle 2002).

The grassland communities of the *Alopecurion pratensis* are widespread and located under a moderate nutrient and water availability, e.g. in floodplains. Although there is a continuous discussion about the true taxonomical classification among experts, the association can be assigned to the class of *Molinio-Arrhenatheretea* (Dierschke & Briemle 2002). According to a good adaptation to flooding and low temperatures, it can also occur in Eastern Europe. Very constant species of the association are e.g. *Agrostis stolonifera, Alopecurus pratensis, Elymus repens, Festuca pratensis, Holcus lanatus, and Taraxacum officinale.* The species richness is generally below that of *Arrhenatherion elatioris* (Dierschke & Briemle 2002).

The plant communities of *Lolio-Potentillion anserinae* develop in flood plains and are frequently affected by flood water, which leads to a high dynamic in vegetation development. During these periods, the respiration is limited according to oxygen deficiency (particularly in winter). The nutrient supply through mineralisation under periods of drought is good. Within the utilized grassland, the formation can be grouped among the humid and wet meadows and pastures (Dierschke & Briemle 2002). The species of the *Lolio-Potentillion anserinae* have a well adapted dispersal ability by vegetative growth and show a generally low response to disturbance. Due to the difficult growing conditions, many species have developed morphological adaptations, like aeration tissues, e.g. *Rumex crispus* and *Rumex obtusifolius* (Dierschke & Briemle 2002).

The species rich plant communities of *Junco-molinion* occur in periodically wet and acidic habitats with a fluctuating groundwater level. Extensive agricultural use as meadows includes low manuring and infrequent mowing (Havlová 2006). To the diagnostic species of the *Junco-molinion* belong e.g. *Molinia caerulea*, *Scorzonera humilis* and *Succisa pratensis.* Moreover the formation contains species typical for acidic habitats, like *Luzula campestris* and *Nardus stricta* (Havlová 2006).

The *Calthion palustris* can be described as moderately yielding meadows of high variability at the species level. It becomes abundant at moist towards wet sites with low acidity and humus rich, partially even swampy soils. It develops under a moderate nutrient availability. The species composition, which is related to the *Caricion davallianae*, is very variable depending on the fertilization level. The meadows of *Calthion palustris* are usually mown once or twice during the vegetation period. There are few species describing the main focus of the formation, e.g. A*grostis canina, Caltha palustris, Carex acuta, Juncus acutiflorus* and *Lychnis flos-cuculi* (Dierschke & Briemle 2002).

Tall forbs become very important in habitats with a good water and nutrient availability and they grow in several different grassland associations. Within this group, the formation of *Filipendulion* is associated with the highest humidity. There is a deep temporal and spatial relation to the marshes at the species level. In general, the species richness of the populations is low (Dierschke & Briemle 2002). The local conditions can be characterized as humid to wet according to regular short-time floodings. The nitrogen availability is moderate. In the present agricultural landscape the *Filipendulion* occur as margins like populations at the borders of meadows and e.g. along lakes and moats. A characteristic species of the *Filipendulion* is meadowsweet (*Filipendulia ulmaria*) which is very well adapted to the prevalent conditions according to its morphological traits. Meadowsweet is often dominant in the canopy structure and therefore eponymous to the formation. According to Dierschke & Briemle (2002), there are further diagnostic species in the context of *Filipendulion*, like C*alystegia sepium, Cirsium palustre, Euphorbia palustris, Senecio paludosus* and *Lysimachia vulgaris*.

The *Caricion davallianae* belongs to plant communities of extensive utilization. Nowadays, it becomes very rare in many landscapes. It develops in chalk regions which are constantly influenced by flooding. The productivity of this grassland formation as well as the forage quality are low (Dierschke & Briemle 2002). Associations with high species diversity and colourful flowering aspects can be located in Southern Europe in particular. Getting further north, the species richness decreases. Moreover, the *Caricion davallianae* includes a multiplicity of endangered species. According to Dierschke & Briemle (2002) associated species are e.g. *Carex davalliana, C. flava, Dactylorhiza incarnata, Eriophorum latifolium* and *Parnassia palustris*.

Abbreviations of the selected grassland formations were used for the graphical display of the results (**Tab. 2**).

Tab. 2 Abbreviations of grassland formations used in the present study

Abbreviation	Entire denotation of the syntaxon
AloPr	*Alopecurion pratensis*
ArrEl	*Arrhenatherion elatioris*
CalPa	*Calthion palustris*
Carda	*Caricion davallianae*
CorCa	*Corynephorion canescentis*
CynCr	*Cynosurion cristati*
Filip	*Filipendulion*
JuncMo	*Junco-Molinion*
LolPo	*Lolio-Potentillion anserinae*
MesEr	*Mesobromion erecti*
NarGa	*Nardo-Galion saxatilis*

2.5 THE SELECTED TRAITS ACCORDING TO THE BIOLFLOR DATABASE

The selected traits in the context of this investigation were already mentioned in chapter **2.2**. They are available in the BiolFlor database and belong to the subjects of plant morphological traits, utilization and survival strategy. A description of the single traits is given in the following (an overview is given in **Tab. 3**).

Life form provides information about the strategy of persistence in periods of unfavourable conditions. The trait is assigned to the vertical position of vegetative buds towards to the soil surface during winter and dry periods, respectively. The buds are mostly regeneration buds and also seeds within the group of annual plants. The range of plant life forms (hemicryptophytes, geophytes, chamaephytes, therophytes, phanerophytes and hydrophytes) differs significantly according to the predominant climate conditions in specific regions (Raunkiaer 1934, Ellenberg 1996) (**Tab. 3**).

Life span is the time in which a plant species usually completes its life cycle and finally dies. The BiolFlor information predominantly refers to the classes of actual life span like annuals, biennials and perennials. Furthermore, the usual number of generative reproductions of a perennial species is regarded. The pluriennial-hapaxanthic types only have one generative reproduction event but grow for longer than one year, whereas the pluriennial-pollakanthic plants have more than one generative step in their life (Krumbiegel 2002) (**Tab.3**).

The trait **leaf anatomy** reflects main structures within a leaf to fulfil specific tasks, e.g. aeration tissues under oxygen deficiency or tissues for water storage. Such morphological-anatomical attributes provide information about living conditions in a specific environment (Ellenberg 1996). There are several trait characteristics specified (mesomorphic, hygromorphic, succulent, scleromorphic, helomorphic and hydromorphic plants) (**Tab. 3**).

Leaf persistence is the time from the emergence of a leaf until its cast. It is of great importance for plant metabolism and biomass production. Therefore, it has a high influence on the competitive ability of plants. Persistent green plants have leaves throughout the whole year. Overwintering green plants replace their old leaves in spring time whereas summer green plants only build their leaves during the vegetation period (Ellenberg *et al.* 2001) (**Tab. 3**).

A metamorphose can be characterized as a modification of plant shape according to an adaptation to the mode of living or environmental conditions (Nultsch 2001). This modification includes the development of different structures for special tasks like dispersal and storage from surrounding tissues (Krumbiegel 2002). In the context of this thesis, the **root and shoot metamorphoses** of plants were considered (**Tab. 3**).

Rosettes develop through the absence of shoot elongation between the nodes. Therefore, all the foliar leaves grow in a circular arrangement at the shoot base. Only the flower stalks or the peduncles consist of long internodes. Rosettes have a protective function. Beside the rosette plants, the trait includes information about erosulate plants with long internodes and hemirosette plants which have either long or short internodes (Krumbiegel 2002) (**Tab. 3**).

Perennials and persistent plants, respectively, need storage tissues for nutrients or water within periods of interrupted or limited photosynthesis. The occurrence of such **storage organs** is usually associated with the ability of vegetative propagation and dispersal. Roots, rhizomes and parts of the shoot predominantly serve as storage organs of graminaceous plants, whereas dicotyledons mostly generate storage organs through swelling of root sections. Especially the primary root can swell up to a remarkable size (e.g. *Rumex obtusifolius*). The location of storage organs has an important effect on the species-specific response to utilization, e.g. there is a risk of nutrient loss through mowing and grazing when the organs are located close to the soil surface (Voigtländer & Jacob 1987) (**Tab. 3**).

The mode of dispersal is crucial for the capability of a plant species to capture new habitats and, therefore, expand its distribution area. Dispersal can occur with or without external support. In addition to the generative propagation and the dispersal with generative diaspores, many plant species are able to disperse asexually. The **vegetative propagation** happens by development of runners, rhizomes, shoot tubers etc. (Nultsch 2001, Krumbiegel 2002) (**Tab. 3**).

In comparison to the indicator values of Ellenberg, there are several **grassland utilization values** available. They provide information about the mowing, grazing and trampling tolerance of plant species as well as the foraging value for livestock. The available utilization values from the BiolFlor information system are based upon the classification of Briemle *et al.* (2002). The dataset provides information about 660 plant species of central-European grasslands. The data only contain species which are directly connected to pastures or meadows (Briemle *et al.* 2002) (**Tab. 3**).

The occurrence of a plant species within a specific plant community not only depends on external factors such as environmental conditions or competition aspects but also on the numerous attributes of the single plant species, which can be summarised as the ecological strategy of a species (Wittig & Streit 2004). The ecological **strategy types** of BiolFlor follow the system of Grime (2001). He develops the CSR-model based on the theory of island biogeography of MacArthur and Wilson (1967). The main strategy types are competitors (C-types), stress-tolerators (S-types) and ruderals (R-types). Most plant species cannot be dedicated to one of the three main groups without difficulty, since there are rather smooth transitions between the main strategy types. For this reason, Grime defines transition types (CR-, CS-, SR- and CSR-types) which allow a proper classification (Klotz & Kühn 2002a) (**Tab. 3**).

Tab. 3 Overview of the selected traits, trait expressions and used abbreviations

Trait	Abbreviation	Trait expression
Life form	Ther	therophytes
	Phan	combination of macrophanerophytes, nanophanerophytes, pseudophanerophytes and hemiphanerophytes
	Hemc	hemicryptophytes
	Geop	geophytes
	Cham	chamaephytes
	Hydr	hydrophytes
Life span	plup	pluriennial-pollakanthic
	pluh	pluriennial-hapaxanthic
	bienn	biennial
	annu	annual
Leaf anatomy	hydr	hydromorphic
	helo	helomorphic
	hygr	hygromorphic
	meso	mesomorphic
	scle	scleromorphic
	succ	succulent
Leaf persistence	persist	persistent green
	overwin	overwintering green
	summer	summer green
	spring	spring green
Root metamorphoses	others	combination of buttress root, adhesive root, rootless and pleiocorm
	rshoot	root shoot
	rtuber	root tuber
	secstor	secondary storage root
	primstor	primary storage root
Shoot metamorphoses	others	combination of runner-like rhizome, assimilating shoot, runner with bulbous tip, bulbil, brood shoot, pleiocorm, shoot tuber, shoot tendril, shoot succulence, turio, bulb
	shthor	shoot thorn
	rhizpl	rhizome-like pleiocorm
	rhizo	rhizome
	runtub	runner with tuberous tip
	runner	runner
Rosettes	roset	rosette plants
	hemir	hemirosette plants
	erosul	erosulate plants

Trait	Abbreviation	Trait expression
Storage organs	others	combination of runner with tuberous tip, runner-like rhizome, runner with bulbous tip, bulbil, hypocotyl bulb, shoot tuber, succulence, secondary storage root, turio, root tuber, bulb
	rhizpl	rhizome-like pleiocorm
	rhiz	rhizome
	pristor	primary storage root
Strategy type	sr	stress-tolerators/ruderals
	s	stress-tolerators
	r	ruderals
	csr	competitors/stress-tolerators/ruderals
	cs	competitors/stress-tolerators
	cr	competitors/ruderals
	c	competitors
Vegetative propagation	others	combination of runner with tuberous tip, runner-like rhizome, runner with bulbous tip, bulbil, brood shoot, fragmentation, gemma, innovation bud with storage root, innovation bud with root tuber, phyllogenous shoot, shoot tuber, turio, bulb
	rootsh	root shoot
	rhizplei	rhizome-like pleiocorm
	rhizo	rhizome
	runner	runner
Grassland utilization values		Foraging value
		Grazing tolerance
		Trampling tolerance
		Mowing tolerance

2.6 THE GRADIENTS

To emphasise the differences between the selected grassland formations according to their distribution of selected traits, the formations were allocated to gradients of water and nitrogen availability. These two factors have the most important influence on the floristic shape of grassland (Dierschke & Briemle 2002).

The resource water is crucial concerning the utilization of grassland locations. Although grassland communities can establish under a wide range of environmental conditions, it is well known that process and intensity of biomass production are closely related to water availability (Voigtländer & Jacob 1987). Apart from climatic requirements, water availability predominantly depends on the soil conditions. In general, intermediate conditions deemed to be best for utilization, whereas extreme conditions (wet or dry) are regarded as disadvantageous. A wide range of water regimes leads to a broad diversity of grassland ecosystems and formations in Central Europe (Dierschke & Briemle 2002).

Nitrogen is the most important nutrient for plants. It has a significant influence on the vitality and productivity of grassland species and, therefore, a strong effect on the botanical composition. Nowadays, the anthropogenic enhancement of nitrogen availability takes place on the majority of used grassland locations (Dierschke & Briemle 2002).

The Ellenberg indicator values for moisture [F] and nitrogen [N] were used to develop the gradients. The indicator values do not provide information about the specific requirements of a certain species, but about its occurrence along gradients of environmental factors underlying natural competition (Ellenberg *et al.* 2001).

The indicator value for **moisture** describes the appearance of a plant species along a gradient of soil humidity running from shallow-dry precipice to swampy soils. The values run from '1' to '9', with '1' describing an indicator for heavy drought and '9' characterising an indicator for extremely wet conditions, mostly associated with oxygen deficiency (Ellenberg *et al.* 2001).

The indicator value for **nitrogen** describes the occurrence of a species along a gradient of mineral nitrogen availability during the vegetation period. It runs from '1' to '9' respectively. The lowest value ('1') indicates extreme nutrient-poor locations, which are very rare nowadays, whereas the highest value ('9') stands for exorbitant high nutrient-rich locations (Ellenberg *et al.* 2001).

For this investigation, a list of Ellenberg indicator values was added to the species database in order to develop the two gradients (q.v. Fig. M). Selective queries allowed an assignment of indicator values to the majority of species (79%). Afterwards, the average indicator values of the grassland formations were calculated according to the available values for individual species. The calculation of the mean from Ellenberg indicator values is intrinsically considered to be incorrect, but in ecological studies it is commonly applied (e.g. Ewald 2007, Samonil & Vrska 2008, Simonova & Lososova 2008). There was no weighting according to the species constancy.

2.7 DATA ANALYSIS AND CALCULATION

2.7.1 CREATION OF THE PROJECT DATABASE AND USE OF SOFTWARE

The common software (MS Office) was applied for the linkage between the BiolFlor and SynBioSys databases. The first step was an adjustment of the species names in consideration of the GermanSL reference list (q.v. **2.3**) using a database software (MS Access). The adjusted species list represented the foundation for further queries. The results of the trait-concerning queries in BiolFlor were exported, processed and, afterwards, added to the project database, which contained all data collections. The files of the SynBioSys source concerning grassland formations were directly integrated to the project database (the simplified database structure is presented in Fig. M).

The software environment '**R**' (R Development Core Team 2008) was used for the statistical analysis and the graphical display of the results.

2.7.2 CALCULATION

The considerations and approaches for the analysis and calculation are described in the following.

The trait information was available for most species of the project database. Hence, for some traits the whole species cluster of a syntaxon could be considered, whereas for some others, not all species could be used. For each species, many trait expressions are possible, for instance plant species can have several ways of vegetative propagation (Krumbiegel 2002).

Furthermore, a qualifier was available for the majority of traits. It represents whether an expression of trait is always present or merely sometimes (Krumbiegel 2002). Only the regularly present (typical) expressions of traits were used for this investigation. The constancy of species within a syntaxon was used to enable a weighting of the different trait expressions. It was partitioned according to the number of trait expressions of a species and then assigned to them. For example, a species has a constancy of 0.9 within the formation 'XY'. For the trait vegetative propagation it shows three expressions (e.g. runner, runner with tuberous tip and innovation bud with root tuber). Each of the trait expressions gets the same proportion of constancy. Hence, for this example, each expression gets 0.3. After weighting, the values for each trait expression within a syntaxon were summed up. To reach comparability between the datasets of the different grassland formations, the percentage quotations were calculated (a further example of the weighting is given in Tab. C).

Besides, also numerical traits were selected, like the grassland utilization values. They were not weighted according to the constancy (q.v. **2.1**). In this case, the means were calculated directly.

In addition to the analysis of the strategy types provided by BiolFlor, the proportion of the single components of ‘C’ (competitors), ‘R’ (ruderals) and ‘S’ (stress-tolerators) within the individual grassland formations were calculated. Their proportions were established on the basis of the values for the BiolFlor strategy types (sr, s, r, csr, cs, cr and c) via partitioning into the single components. The proportions of these components are comparable to the C-S-R-signatures of Hunt *et al.* (2004), who created a spreadsheet tool to calculate and compare the relevance of the single C-, S- and R- components within the CSR-model of Grime.

With the software environment **R,** the graphical display in form of bar plots was done first. The bars (grassland associations) were ordered according to their average indicator values for moisture and nitrogen, respectively. When a trait showed too many trait expressions, those that had low percentage values were merged to a group called 'others' (q.v. **Tab. 3**).

A causal relation between the selected indicator values for moisture and nitrogen, which were regarded as explanatory variables, and trait expressions was assumed. Therefore, in a second step, a regression analysis was done to investigate the statistical relationship between the trait expressions and environmental gradients. This was done for the most important trait expressions (56 individual calculations). For this purpose, the relative values for the trait expressions (dependent variables, y_i) were plotted against the environmental indicator values (independent variables, x_i). The normal distribution of data was assumed and additionally verified with the Shapiro-Wilk normality test. Simple linear regressions were calculated and drawn. In four cases, quadratic relations were additionally tested. In these cases the quadratic model $lm\ (y \sim x + I\ (x^2))$ was applied. Here, it is searched for a second-degree polynomial (parabola, $f(x) = ax^2 + bx + c$) fitting the data as good as possible.

Within the individual analyses, the t-test for the correlation coefficient (r) was applied. It verifies if there is a significant statistical relation between the variables 'x' and 'y'. In each calculation, there are eleven pairs of values, so the degree of freedom is nine in each case ($df = n-2$).

3 RESULTS

3.1 THE GRADIENTS

The eleven selected grassland formations were characterised by mean Ellenberg indicator values (**Tab. 4)**. The formations covered a wide range of indicator values for moisture [F] and nitrogen [N]. The *Corynephorion canescentis* and *Mesobromion erecti* represented the formations occurring under the driest conditions with an indicator value for moisture of 4.41 in each case. The *Caricion davallianae* represented the most humid conditions (F = 7.37). The average indicator value for nitrogen was also lowest in the formation of *Corynephorion canescentis* (N = 3.39), whereas it was highest in the formation of *Filipendulion* (N = 5.39). The average Ellenberg indicator values for light [L], temperature [T], continentality [K] and reaction [R] were not considered in the further investigation.

Tab. 4 Ellenberg's indicator values (Ellenberg *et al.* 2001) for light [L], temperature [T], continentality [K], moisture [F], reaction [R] and nitrogen [N]. Values are the unweighted mean of species indicator values averaged across the grassland formations

	[L]	[T]	[K]	**[F]**	[R]	**[N]**
Alopecurion pratensis	6.99	5.61	3.52	**6.63**	5.93	**4.88**
Arrhenatherion elatioris	7.05	5.73	3.68	**4.93**	6.54	**5.01**
Calthion palustris	7.03	5.66	3.38	**7.24**	5.92	**4.74**
Caricion davallianae	7.35	5.54	3.36	**7.37**	5.81	**3.84**
Corynephorion canescentis	7.38	5.75	3.45	**4.41**	5.00	**3.39**
Cynosurion cristati	7.13	5.63	3.51	**5.72**	6.26	**4.63**
Filipendulion	6.76	5.56	3.60	**7.25**	6.06	**5.39**
Junco-Molinion	7.22	5.46	3.23	**7.14**	5.17	**3.59**
Lolio-Potentillion anserinae	7.37	5.79	3.52	**6.98**	6.50	**5.37**
Mesobromion erecti	7.10	5.71	3.60	**4.41**	6.69	**3.78**
Nardo-Galion saxatilis	7.10	5.50	3.40	**5.66**	5.14	**3.42**

Additionally, a simple linear regression analysis was applied to investigate the relationship between the selected gradients for moisture [F] and nitrogen [N]. They were positive, but not significantly related (R^2= 0.15, p= 0.245).

3.2 LEAF ANATOMY

The mesomorphic, scleromorphic and helomorphic types were the most important classes within the six expressions of the trait leaf anatomy (**Fig. 1**). On rather dry locations, e.g. within the formations of *Corynephorion canescentis* and *Mesobromion erecti,* the scleromorphic and mesomorphic types represented the largest part of leaf anatomy types (>96%), whereas the helomorphic types were of little importance. The latter types revealed considerable increases with an ascending gradient for moisture, accompanied by relative declines of scleromorphic and mesomorphic types. Thus, within the formation of *Caricion davallianae* the proportion of scleromorphic and mesomorphic types was below 44%, whereas the proportion of helomorphic types was above 43%.

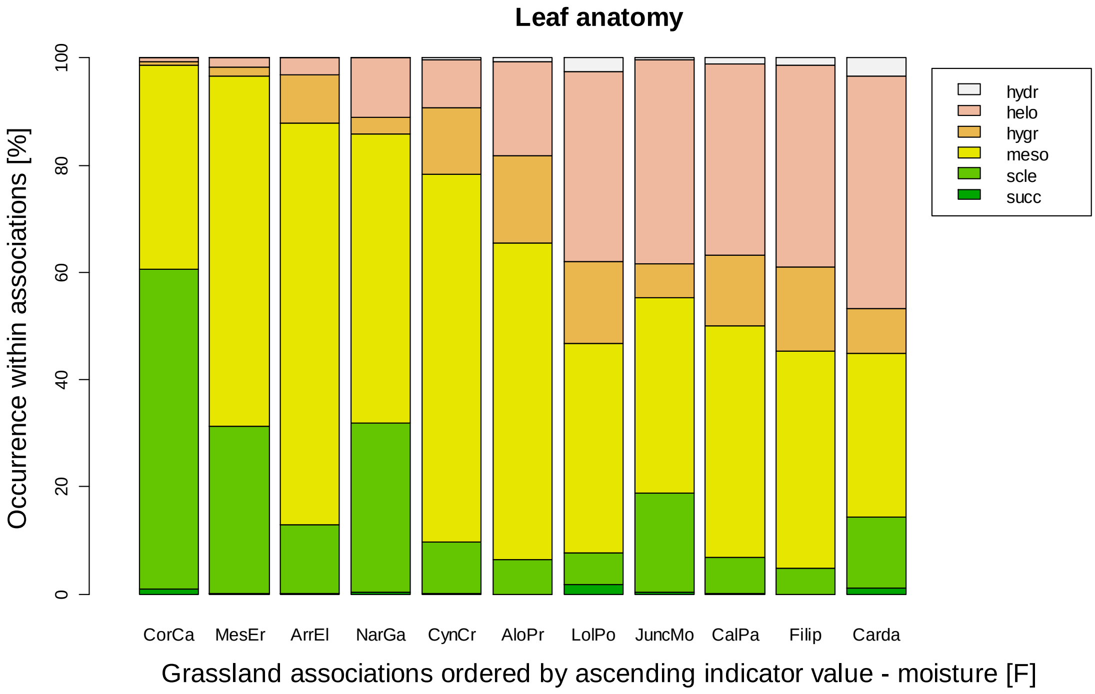

Fig. 1 Occurrence of leaf anatomy types within selected grassland formations, ordered by ascending Ellenberg indicator value for moisture [F]. Descriptions of abbreviations corresponding to syntaxa are given in Tab. 2, hydr = hydromorphic types, helo = helomorphic types, hygr = hygromorphic types, meso = mesomorphic types, scle = scleromorphic types, succ = succulent types

The hygromorphic types had a relatively small proportion of the trait expressions which was below 17% among the selected formations. A linear regression analysis showed the highly significant (p<0.001) relation between the proportion of hygromorphic types and nitrogen availability (**Fig. 2**). Whereas the hygromorphic types were extremely rare under nitrogen-poor conditions, e.g. in the formation of *Corynephorion canescentis* (0.6%), their occurrence increased with an ascending nutrient availability. On the nutrient-rich locations of the *Filipendulion* they reached more than 15%.

The helomorphic types were extremely rare under dry conditions, e.g. their proportion within the formations of *Corynephorion canescentis* and *Mesobromion erecti* was below 2% in each case. The more humid the environmental conditions became, the higher was the proportion of helomorphic types (**Fig. 3**). Therefore, their proportion within the *Caricion davallianae* was up to 43%. It is the syntaxon presenting the highest moisture conditions within this investigation.

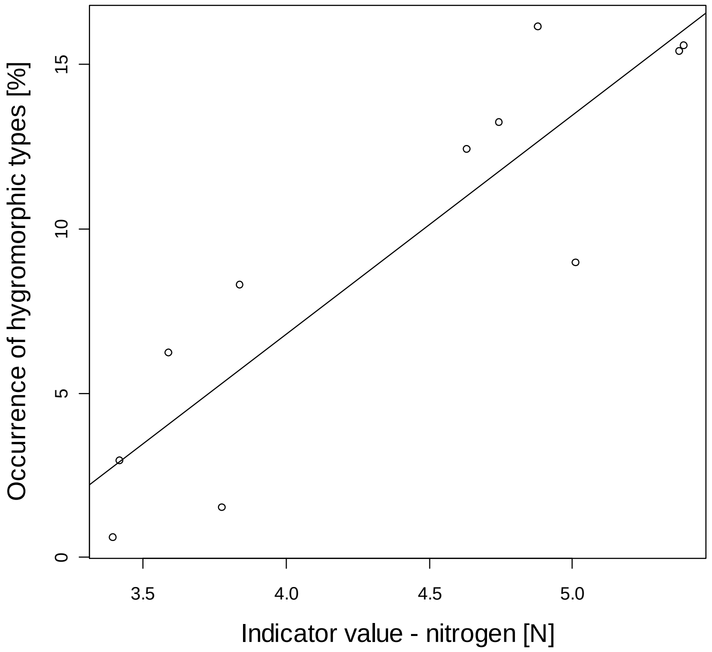

Fig. 2 Leaf anatomy - Relative occurrence of hygromorphic types within the selected grassland formations plotted against Ellenberg indicator value for nitrogen [N], Results of regression analysis for simple linear regression: R^2=0.80, p<0.001

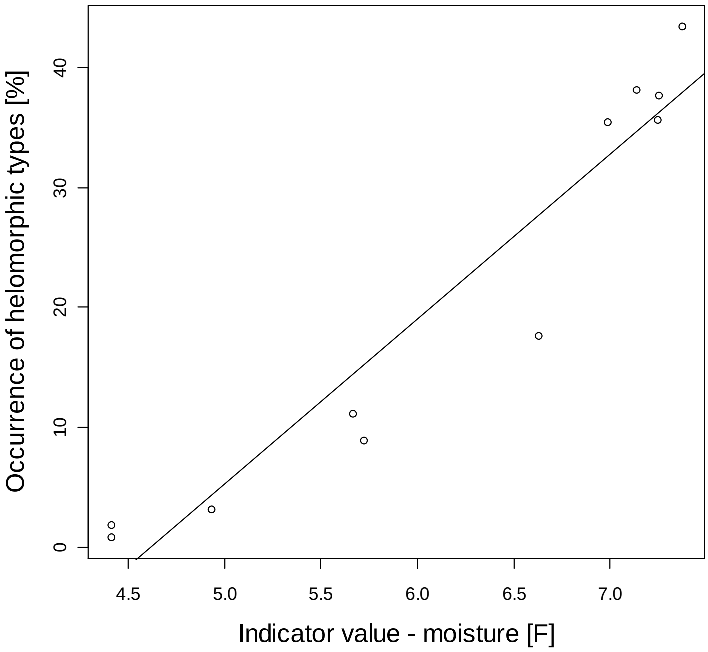

Fig. 3 Leaf anatomy - Relative occurrence of helomorphic types within the selected grassland formations plotted against Ellenberg indicator value for moisture [F], Results of regression analysis for simple linear regression: R^2=0.92, p<0,01; Furthermore the quadratic model *lm (helo ~ F + I (F ^{2}))* was tested, Results of the regression analysis of the further model: R^2=0.97, p<0.001

Further linear regression analyses of the relations between helomorphic, hygromorphic, mesomorphic and scleromorphic types and the gradients for moisture [F] and nitrogen [N] were done. The proportion of scleromorphic types was significantly decreasing from 59.6 to 4.7% with ascending nitrogen availability (p<0.01). Furthermore, their occurrence declined with increasing moisture (p<0.05). Moreover, the proportion of hygromorphic types (0.6- 16.2%) increased significantly with ascending moisture (p<0.05) (q.v. **Tab. 5**, Fig. A-C).

The proportion of mesomorphic types, which was generally high (30.5- 74.9%), decreased with increasing moisture (p<0.1) (Fig. D). The other calculations concerning the trait leaf anatomy did not show significant relations with [F] and [N] (q.v. **Tab. 5**).

Tab. 5 **Results of the regression analyses (simple linear regressions)** [1]

	Response variable	**Explanatory variables**					
		Gradient moisture [F]			**Gradient nitrogen [N]**		
Trait	**Trait expression**	**+/-** [2]	**R^2**	**p**	**+/-** [2]	**R^2**	**p**
Life form	hemicryptophytes [%]	-	0.23	0.138	+	0.09	0.370
	hydrophytes [%]	+	0.67	0.002 [3]	+	0.13	0.272
	geophytes [%]	+	0.69	0.002	+	0.03	0.621
Life span	annual types [%]	-	0.34	0.058	+	0.00	0.975
	pluriennial-pollakanthic types [%]	+	0.53	0.011	+	0.01	0.775
Leaf anatomy	helomorphic types [%]	+	0.92	0.004 [3]	+	0.07	0.416
	hygromorphic types [%]	+	0.46	0.022	+	0.80	0.000
	mesomorphic types [%]	-	0.36	0.050	+	0.04	0.578
	scleromorphic types [%]	-	0.51	0.014 [3]	-	0.60	0.005
Leaf persistence	summer green types [%]	+	0.19	0.187	+	0.01	0.726
	persistent green types [%]	-	0.09	0.375	-	0.02	0.675
Root metamorphoses	plants with primary storage roots [%]	-	0.04	0.571	+	0.44	0.025
Shoot metamorphoses	rhizome building plants [%]	-	0.09	0.360	-	0.15	0.240
Rosettes	hemirosette plants [%]	-	0.47	0.019	±	0.00	0.999
	erosulate plants [%]	+	0.50	0.016	+	0.00	0.880
Storage organs	rhizome building plants [%]	+	0.62	0.004	-	0.04	0.570
	runner building plants [%]	+	0.73	0.001	+	0.56	0.008
	tuft building plants [%]	-	0.46	0.021 [3]	-	0.20	0.169
Vegetative propagation	rhizome building plants [%]	+	0.27	0.104	-	0.15	0.237
	runner building plants [%]	+	0.01	0.769	+	0.52	0.012
Grassland utilization indicator values	Foraging value	-	0.22	0.144	+	0.14	0.255
	Grazing tolerance	-	0.08	0.415	-	0.01	0.834
	Mowing tolerance	-	0.00	0.850	+	0.35	0.055
	Trampling tolerance	-	0.63	0.004	-	0.22	0.146

	Response variable	Explanatory variables					
		Gradient moisture [F]			Gradient nitrogen [N]		
Trait	**Trait expression**	**+/- [2]**	**R²**	**p**	**+/- [2]**	**R²**	**p**
Strategy type	strategy type C [%]	+	0.00	0.846	+	0.53	0.012
Strategy type-partitioned into C-S-R-components	Component C [%]	+	0.01	0.759	+	0.40	0.036
	Component S [%]	+	0.04	0.546	-	0.45	0.024
	Component R [%]	-	0.32	0.069	-	0.00	0.892

---

[1] An overview of the coefficients *a* and *b* of the 56 linear equations $(\hat{y}=a+bx)$ is given in Tab. B

[2] ' **+** ' = positive relation, ' **-** ' = negative relation

[3] in this cases the model $lm\ (y \sim x + I\ (x^2))$ was additionally applied, the results are given in Tab. 6

Tab. 6 Results of the regression analyses for the quadratic model $lm\ (y \sim x + I\ (x^2))$

	Response variable	Explanatory variable		
		Gradient moisture [F]		
Trait	**Trait expression**	**+/- [1]**	**R²**	**p**
Life form	hydrophytes [%]	+	0.83	0.001
Leaf anatomy	helomorphic types [%]	+	0.97	$5.45x10^{-7}$
Leaf anatomy	scleromorphic types [%]	-	0.62	0.022
Storage organs	tuft building plants [%]	-	0.48	0.076

---

[1] ' **+** ' = positive relation, ' **-** ' = negative relation

3.3 STORAGE ORGANS

Runners (23.3– 47.8%) and rhizomes (16.0- 37.0%) were the most abundant groups of storage organs among the selected grassland formations, although tuft building plants played a certain role under dry conditions. The proportions of the different trait expressions were comparatively balanced under dry and nutrient-poor conditions. The more humid the environmental conditions were and the higher the nutrient availability was, the lower was the proportion of other trait expressions for the benefit of runner and rhizome building plants (latter only for moisture). The linear regression analysis showed that the proportion of tuft building plants declined from 31.9 to 5.4% with an increase of moisture ($p<0.05$) (q.v. **Tab. 5**, Fig. E).

The particular proportion of runner and rhizome building plants was below 25% within grassland formations belonging to dry locations (e.g. *Corynephorion canescentis* and *Mesobromion erecti*). It increased significantly with ascending moisture up to 48% and 37%, respectively (**Fig. 4** and **Fig. 5**)

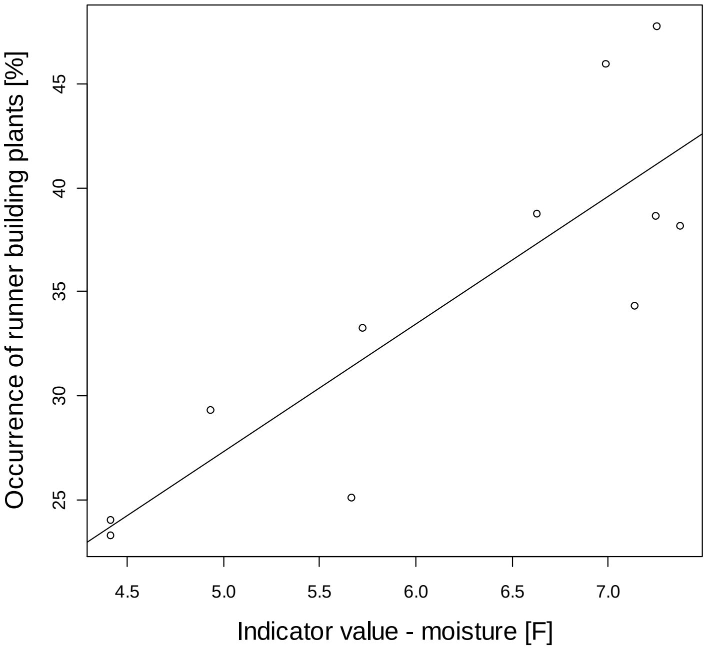

Fig. 4 Storage organs - Relative occurrence of runner building plants within the selected grassland formations plotted against Ellenberg indicator value for moisture [F], Results of regression analysis for simple linear regression: $R^2=0.73$, $p<0,001$

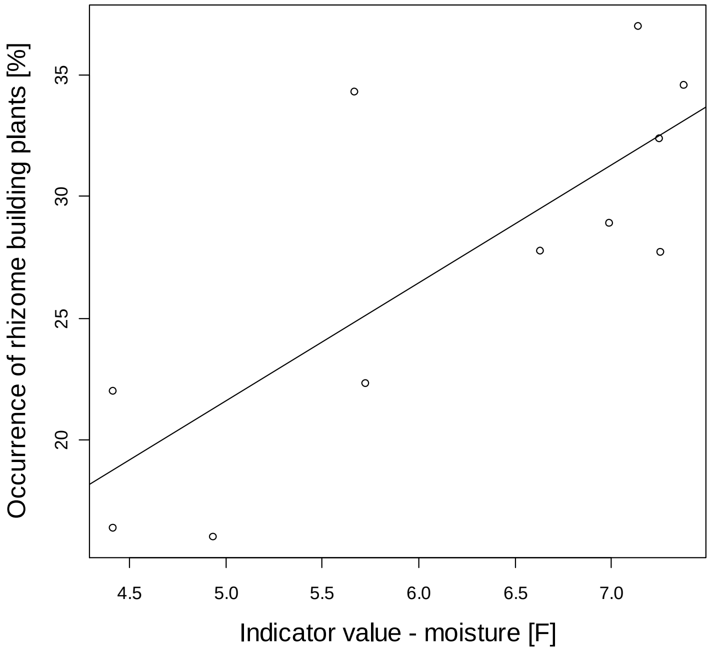

Fig. 5 Storage organs - Relative occurrence of rhizome building plants within the selected grassland formations plotted against Ellenberg indicator value for moisture [F], Results of regression analysis for simple linear regression: R^2=0.62, p<0.01

As mentioned before, the proportion of runner building plants increased significantly with an ascending nutrient availability (p<0.01) (**Fig. 6**). It was highest in the formation of *Filipendulion.*

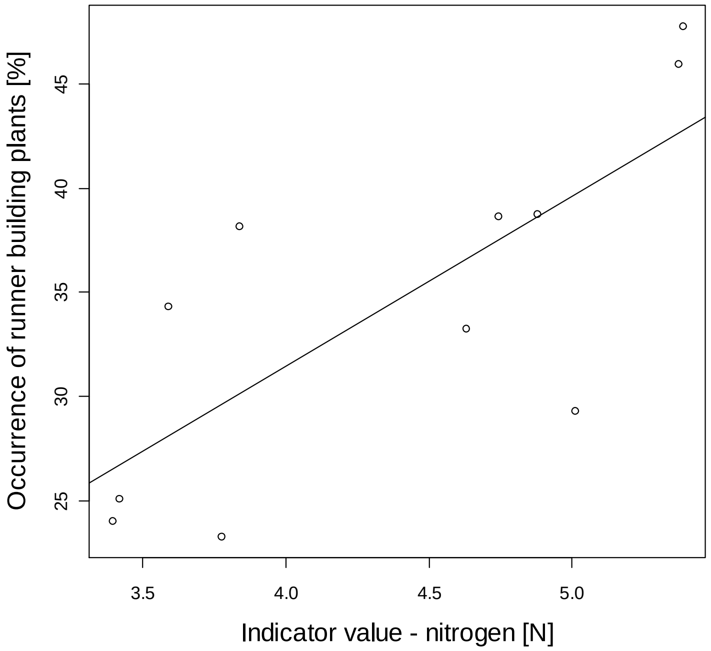

Fig. 6 Storage organs - Relative occurrence of runner building plants within the selected grassland formations plotted against Ellenberg indicator value for nitrogen [N], Results of regression analysis for simple linear regression: $R^2=0.56$, $p<0.01$

Furthermore, other linear regression analyses concerning the trait storage organs were done. There were no significant interactions between tuft and accordingly rhizome building plants with the indicator value for nitrogen [N].

3.4 STRATEGY TYPES

The different groups of strategy types delivered by the BiolFlor database were analyzed in view of their relations with nutrient availability and moisture. The linear regression analysis showed a significant increase of the proportion of competitors (strategy type C) from 10.5 to 47.0% with an ascending nitrogen availability ($p<0.05$) (**Fig. 7**).

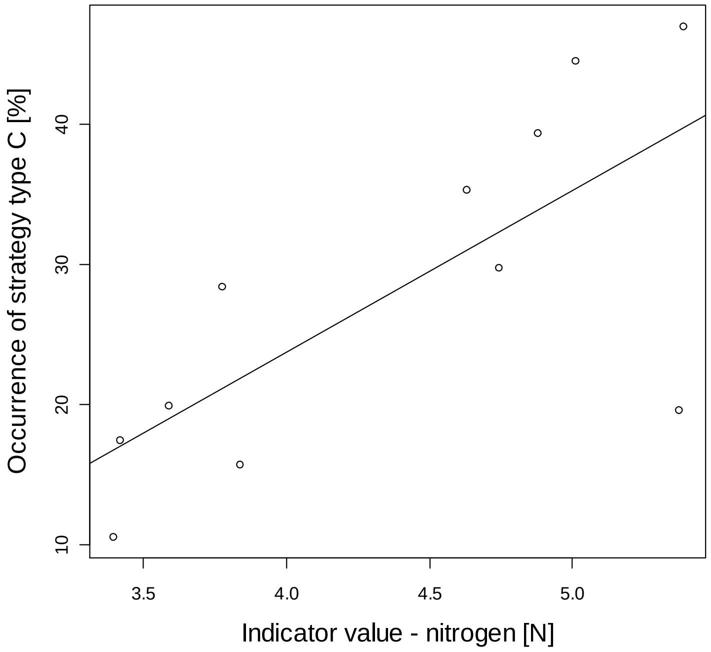

Fig. 7 Strategy types - Relative occurrence of competitors (strategy type C) within the selected grassland formations plotted against Ellenberg indicator value for nitrogen [N]. Results of regressions analysis for simple linear regression: $R^2=0.53$, $p<0.05$

Moreover, the strategy types were partitioned into single C-, S- and R-components within the syntaxa and analyzed in view of their relationships with the gradients. The linear regression analysis showed a significant increase of the proportion of component 'C' (component of competitors) from 42.5 to 69.8% with an ascending gradient for nitrogen ($p<0.05$) (**Fig. 8**).

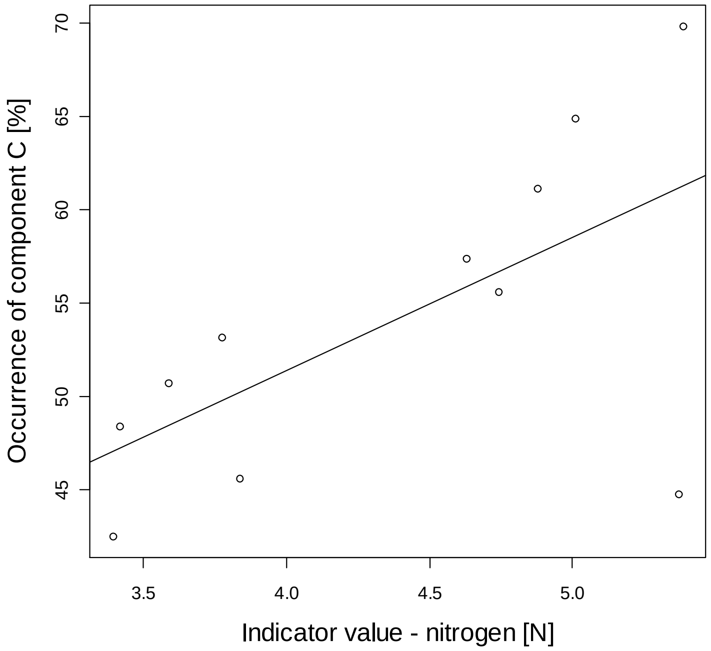

Fig. 8 Strategy types - Relative occurrence of component C (component of competitors within the trait strategy types) within the selected grassland formations plotted against Ellenberg indicator value for nitrogen [N]. Results of regressions analysis for simple linear regression: $R^2=0.40$, $p<0.05$

Furthermore, a significant decline of the proportion of component 'S' (component of stress-tolerators) (15.4- 38.4%) with increasing nutrient availability ($p<0.05$) was observed (**Fig. 9**). No further significant relations were identified due to the analyses of the relation between the single components of the strategy types provided by BiolFlor and the gradients for moisture and nitrogen.

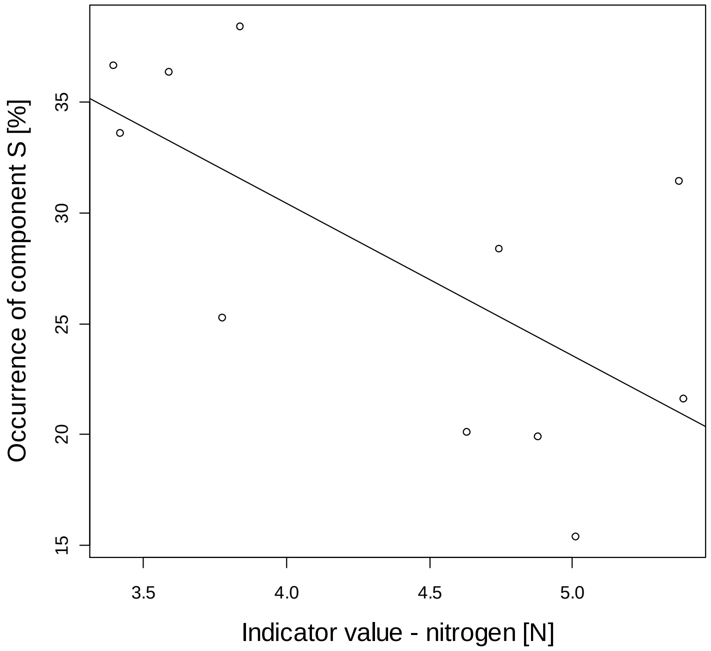

Fig. 9 Strategy types - Relative occurrence of component S (component of stress-tolerators within the trait strategy types) within the selected grassland formations plotted against Ellenberg indicator value for nitrogen [N]. Results of regressions analysis for simple linear regression: $R^2=0.45$, $p<0.05$

3.5 LIFE FORM

The hemicryptophytes were the largest group of life forms. Their proportion varied between 61.8 and 82.9% among the selected syntaxa of this investigation. Very high proportions were associated with dry or moderately humid conditions. The second largest group were the geophytes, whose proportion was generally below 21%.

A bar plot of the proportions of the several life forms within the selected grassland formations, ordered by ascending indicator value for moisture [F] offered the great importance of the hemicryptophytes and the comparatively small relevance of the other life form types (**Fig. 10**). Nevertheless, there was an increase of the proportion of geophytes with increasing moisture, accompanied by a light decrease of the main group. The combined group of phanerophytes played a certain role in few grassland formations, e.g. the *Nardo-Galion saxatilis* and *Caricion davallianae*. These circumstances resulted from the increased proportion of nanophanerophytes within the accordant formations. Their proportion was generally below 4.2%.

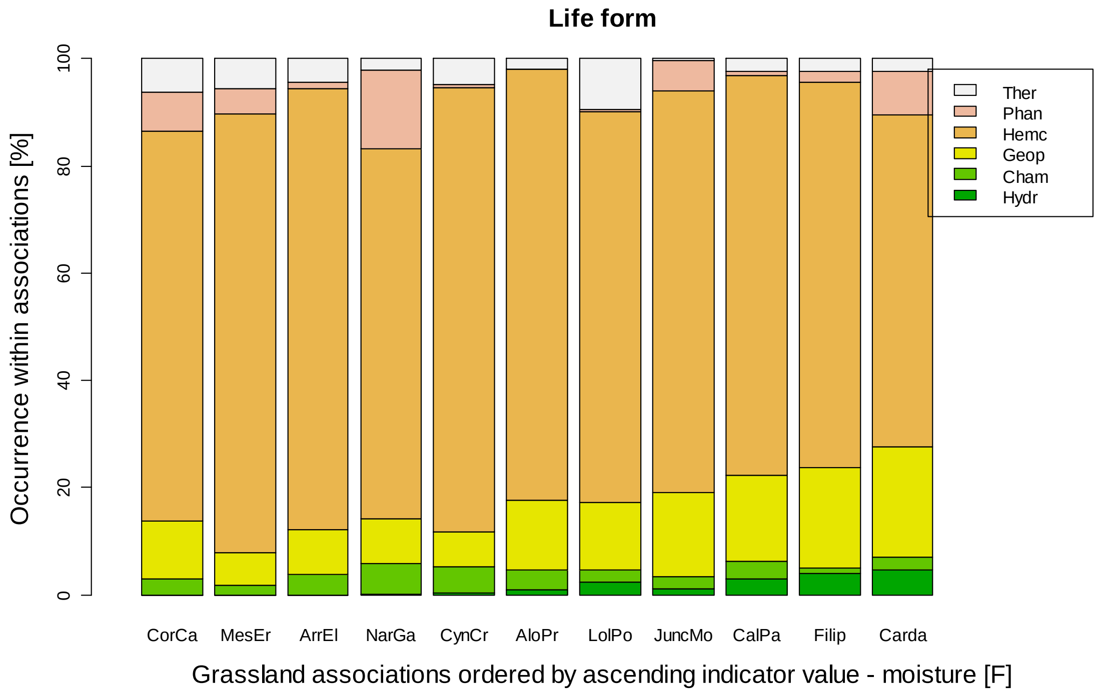

Fig. 10 Occurrence of life forms within selected grassland formations, ordered by ascending Ellenberg indicator value for moisture [F]. Descriptions of abbreviations corresponding to syntaxa are given in Tab. 2., Ther= therophytes, Phan= combination of macrophanerophytes, nanophanerophytes, pseudophanerophytes and hemiphanerophytes, Hemc = hemicryptophytes, Geop= geophytes, Cham = chameaphytes, Hydr= hydrophytes

The linear regression analysis of the relation between the proportion of geophytes (6.2- 20.6 %) and the gradient for moisture showed a significant increase of this life form type with increasing moisture (p<0.01) (**Fig. 11**).

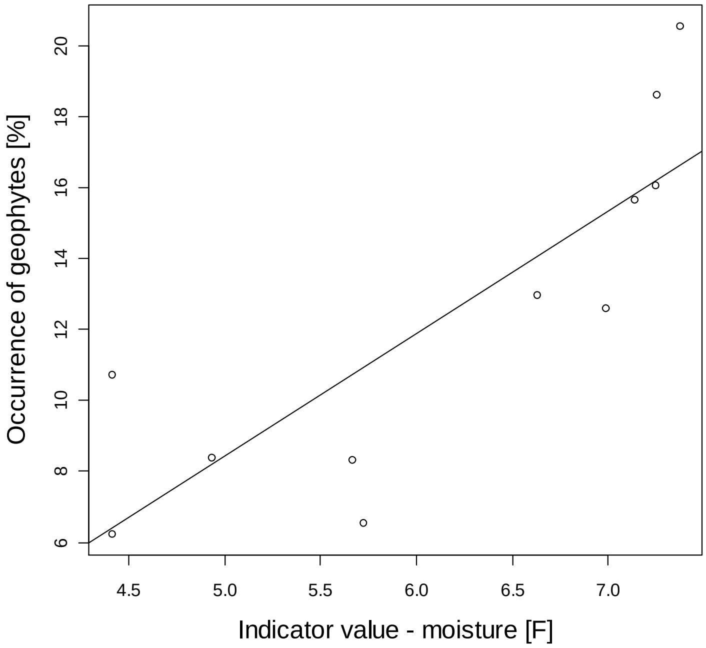

Fig. 11 Life form - Relative occurrence of geophytes within the selected grassland formations plotted against Ellenberg indicator value for moisture [F]. Results of regression analysis for simple linear regression: $R^2=0.69$, $p<0.01$

A regression analysis of the proportion of hydrophytes, a relatively small group within the life forms (0.0- 4.6%), and the indicator value for moisture [F] was done. Hydrophytes did not occur in grassland formations which were associated with dry environmental conditions, e.g. the *Mesobromion erecti*. The more humid the conditions were, the higher was their proportion (**Fig. 12**). A quadratic increase of the proportion of hydrophytes with ascending moisture was suggested on the basis of the distribution of values. A corresponding regression analysis showed the highly significant relationship ($p<0.001$) (q.v. **Tab. 6**).

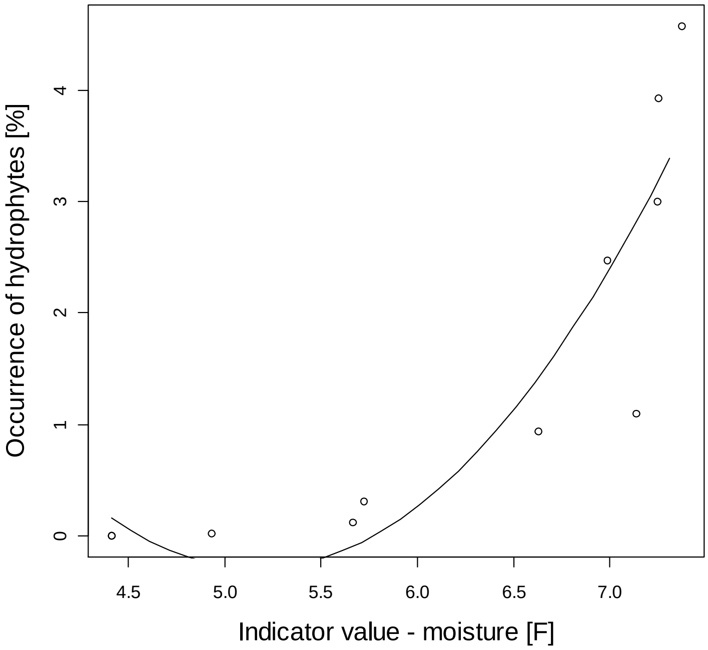

Fig. 12 Life form - Relative occurrence of hydrophytes within the selected grassland formations plotted against Ellenberg indicator value for moisture [F]. Results of regression analysis for the quadratic model *lm (Hydr ~ F+I (F²))*: R^2=0.83, p<0.001

Other regression analyses of life form types with the gradients of moisture [F] and nitrogen [N] did not show significant relations.

3.6 GRASSLAND UTILIZATION VALUES

Several grassland utilization values (foraging, grazing, mowing and trampling tolerance) were calculated as average means and plotted against the indicator values for moisture [F] and nitrogen [N]. Via linear regression analysis, only one highly significant relation was identified. It was the decrease of the indicator value for trampling tolerance with increasing moisture ($p<0.01$) (**Fig. 13**). The value varied between 4.62 and 3.79 among the selected syntaxa.

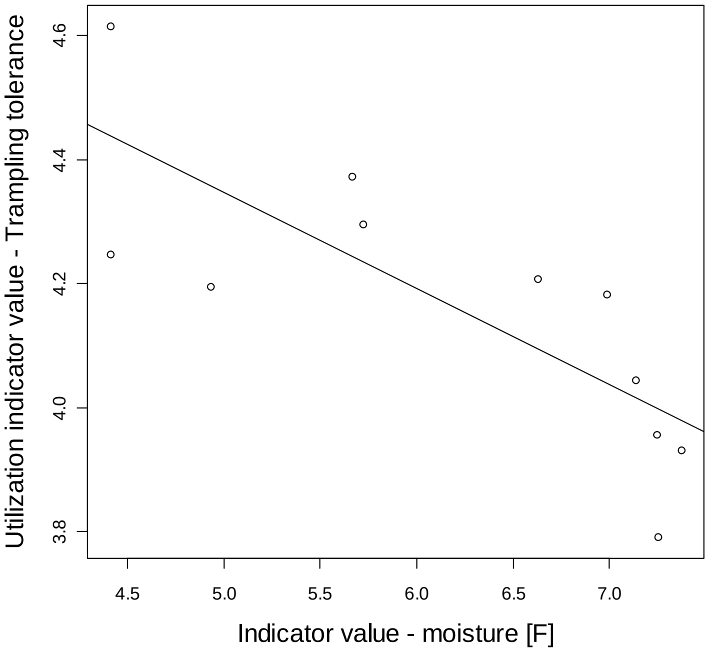

Fig. 13 Grassland utilization values - Average grassland utilization indicator value for trampling tolerance within the selected grassland formations plotted against Ellenberg indicator value for moisture [F]. Results of regression analysis for simple linear regression: R^2=0.63, $p<0.01$

Moreover, the mowing tolerance increased with an ascending nitrogen availability ($p<0.1$) (Fig. F).

3.7 ROSETTES

A bar plot was drawn for the three trait expressions of rosettes within the selected grassland formations, ordered by ascending indicator value for moisture [F] (**Fig. 14**). The hemirosette plants represented the greatest group. Their proportion varied between 43.9 and 67.4% among the selected syntaxa. The second largest group were the erosulate plants (21.4- 48.6%). The bar plot revealed an increase of the proportion of erosulate plants with ascending moisture, accompanied by a descent of hemirosette plants. The proportion of rosette plants marginally changed with altering moisture.

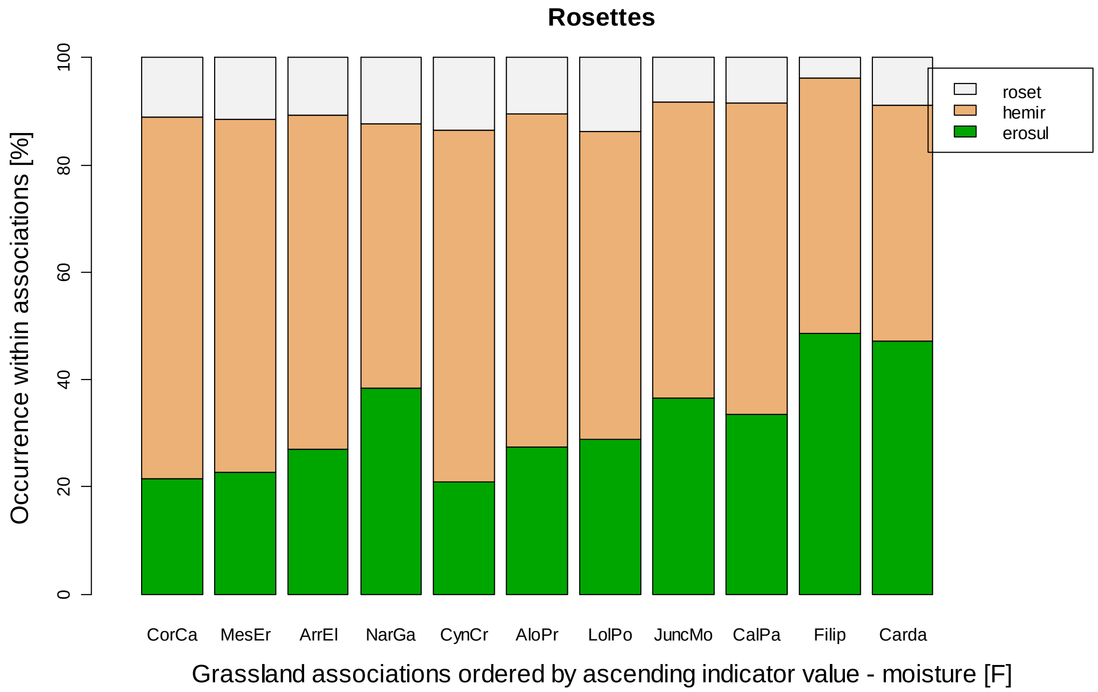

Fig. 14 Occurrence of rosette types within selected grassland formations, ordered by ascending Ellenberg indicator value for moisture [F]. Descriptions of abbreviations corresponding to syntaxa are given in Tab. 2, roset= rosette plants, hemir= hemirosette plants, erosul= erosulate plants

The results of the linear regression analyses corresponded with the pattern given by the bar plot (**Fig. 14**). The proportion of hemirosette plants decreased significantly with an ascending gradient for moisture ($p<0.05$) (Fig. G), accompanied by a significant increase of erosulate plants ($p<0.05$) (Fig. H). The results did not show an effect of nitrogen availability (q.v. **Tab. 5**).

3.8 VEGETATIVE PROPAGATION

Runner building plants represented the greatest group within the trait expressions of vegetative propagation. Their proportion varied from 41.8 to 60.2% among the selected syntaxa. The second largest group were the rhizome building plants (15.9-45.4%). The other trait expressions, e.g. generation of rhizome-like pleiocorms and root shoots, were of relatively small importance. The regression analyses of the relationship between the occurrence of runner and rhizome building plants and the selected gradients for moisture [F] and nitrogen [N] only showed one significant relation. It was the significant increase of the proportion of runner building plants with an ascending nitrogen availability ($p<0.05$) (q.v. **Tab. 5,** Fig. I).

3.9 LIFE SPAN

The perennial plants (pluriennial-pollakanthic plants) were the by far largest group within the trait expressions of life span. Their proportion varied between 79.4 and 95.8% among the selected syntaxa. Annual and biennial plants were, therefore, of little importance. The linear regression analyses were done for the relationship of annuals and pluriennial-pollakanthic types with the gradients for moisture [F] and nitrogen [N]. The proportion of pluriennial-pollakanthic plants showed a significant increase with ascending moisture ($p<0.05$) (Fig. J), whereas the nitrogen availability had no effect on their proportion. Moreover, the proportion of annuals decreased with ascending moisture ($p<0.1$) (q.v. **Tab. 5**, Fig. K). Their proportion varied between 0.4 and 15.2% among the selected syntaxa.

3.10 ROOT AND SHOOT METAMORPHOSES

Plants with primary storage roots represented the largest group within the trait expressions of root metamorphoses. Their proportion varied between 43.3 and 78.4% among the selected syntaxa. Moreover, plants with root shoots (5.5- 28.9%) and root tubers (0- 40.3%) had a certain meaning. The regression analyses concerning the trait root metamorphoses only showed one significant relationship with the selected gradients. It was the significant increase of the proportion of plants with primary storage roots with an ascending nitrogen availability ($p<0.05$) (q.v. **Tab. 5**, Fig. L).

The two largest groups within the trait expressions of shoot metamorphoses were represented by plants with runners with tuberous tips (0.1- 54.5%) and rhizome-like pleiocorms (2.7- 44.4%). A certain meaning, but not in every grassland formation, had rhizome building plants (2.8- 38.9%). There was no significant relationship between the proportions of the several trait expressions and the selected gradients ([F] and [N]). Moreover, it was visible that the formation of *Caricion davallianae* showed a different pattern of trait expression compared to the other formations. Within this syntaxon, the proportion of runner building plants was comparatively high (44.9%, in other syntaxa <5%), whereas the proportion of the two main groups was very small (<3%).

3.11 LEAF PERSISTENCE

The persistent and summer green types were the most important groups of trait expressions within the trait leaf persistence. Their proportion varied between 30.9-65.9% and 21.4- 66.8%, respectively. The other two groups of trait expression (spring green and overwintering green) were of little importance (<13%). There were no significant relationships between the several trait expressions of leaf persistence and the gradients for moisture [F] and nitrogen [N] (q.v. **Tab. 5**).

A bar plot of the leaf persistence types within the syntaxa, ordered along the gradient of moisture was drawn (**Fig. 15**). Apart from the formation of *Corynephorion canescentis*, which showed a comparatively deviant trait expression, the bar plot revealed a slight increase of the proportion of persistent green leaf types towards moderate moist conditions. The proportion of the persistent green types decreased towards the wet and accordingly dry grassland formations.

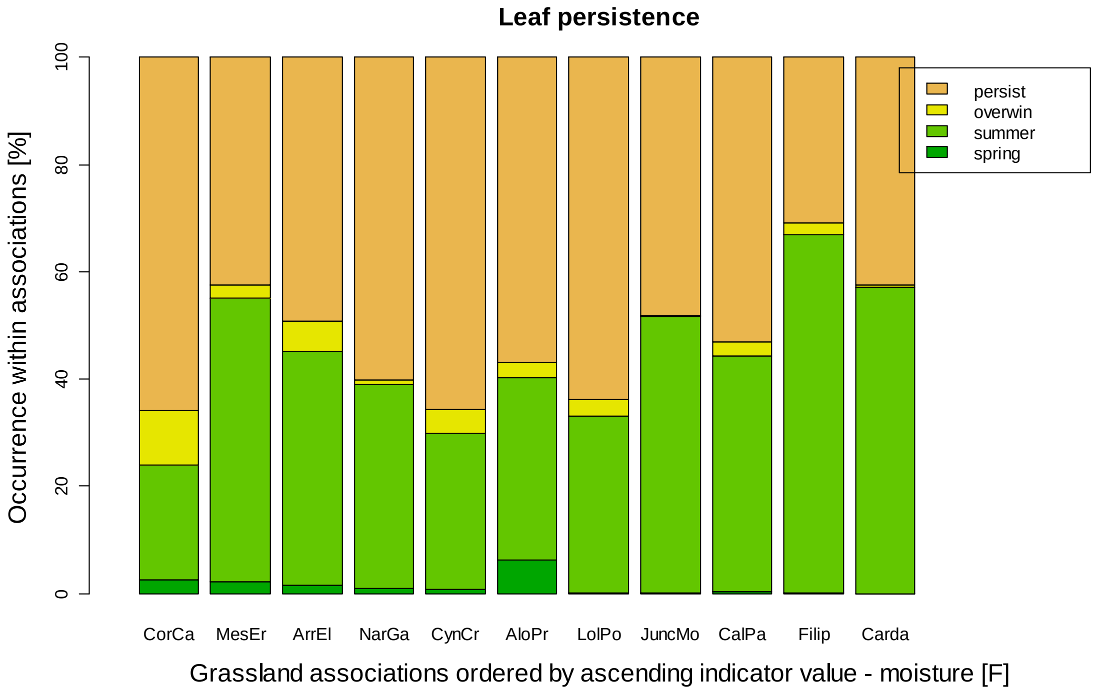

Fig. 15 Occurrence of leaf persistence types within selected grassland formations, ordered by ascending Ellenberg indicator value for moisture [F]. Descriptions of abbreviations corresponding to syntaxa are given in Tab. 2, persist= persistent green, overwin= overwintering green, summer= summer green, spring= spring green

4 DISCUSSION

4.1 COMMON REFERENCE TO THE HYPOTHESES

At first it can be assumed that the connection between the BiolFlor and SynBioSys NL databases is practicable with the common software and that the large individual data sets are predestinated for approaches within the field of grassland research. Different aspects of the utilization and linkage between the two databases are given below (chapter **4.2**). Therefore, the difficulties during the creation of the common basis in form of a species reference list will be presented as well as a potential solution for further investigations.

Moreover, the linkage between the two databases turned out to be a useful instrument to analyse and visualize the distribution of plant traits. A precondition is that the database information has to be sensible connected.

Furthermore, the results show that the composition of trait expressions within grassland formations differs with respect to altering indicator values for moisture and nitrogen and the corresponding relations become clear. As it was mentioned before, the distribution of plant traits along environmental gradients has not yet been investigated with the linkage of large databases. The here presented utilization of a database linkage can, therefore, be characterized as methodical innovation for the clarification of questions concerning the distribution of plant functional traits along environmental gradients. The individual results of the trait distributions will be explained and discussed in detail in the following sections (**4.4**). In this context the relevance of the individual traits with regard to altering environmental conditions will be discussed, respectively.

In a short excursus to climate change (**4.5**) a possible prediction of the changes in trait composition due to altered environmental conditions will be discussed.

4.2 EVALUATION OF THE DATABASE USE, LINKAGE AND CONSTRUCTION

The BiolFlor and SynBioSys NL databases can be characterized as comparatively easy to handle. Due to a clear data structure, it is easy to make a great amount of data accessible and to screen for the relevant information. As it was mentioned before, a reference list of common species had to be created first. All species entries of each database were considered for the adjustment. This step was comparatively complex. At first the two databases included two different vegetations, the German and the Dutch flora, which certainly have differences in their composition of plant species. Furthermore, the taxonomical nomenclature was not congruently used. For instance, abbreviations of some author names or within the species names were handled in different ways. Moreover, there were a couple of special signs (e.g. '*') within the SynBioSys species data set. Most likely, these circumstances were connected with the approaches of the individual contributors of the data entries. For these reasons, the majority of species had to be adjusted manually. In this context, the GermanSL reference list as foundation for the comparison was an indispensable support.

All species of BiolFlor could be successfully adjusted with the GermanSL list. Within the SynBioSys species pool, there was a considerable loss of entries during the adjustment. Thus, for many entries, there were only classifications to genera performed (677 entries), which were of no use in context with this investigation, since the use of BiolFlor requires the full species name. Furthermore, many species names were quite simply not available among the almost 30.000 entries of the GermanSL (266 entries). These species partially originated from the Mediterranean region and had generally low constancies. There was no inclusion of questionable matches (63 entries), so that the adjusted reference list used in this investigation is free of doubt. Nevertheless, the number of unusable entries represents a loss of valuable information.

The individual databases represent a large amount of valuable information for ecological studies in general. To make the information useful for investigations using database linkages it would be better to apply a standard reference list for the taxonomical nomenclature as well as consistent designations (e.g. for common structural elements of the database). Even though, the implementation is likely to be complicated, it can enhance the quality of such linkages, since the loss of information due to adjustments can be minimized and it is possible to accelerate the process. The first step is already done with the employment of the GermanSL reference list in different German databases (Jansen & Dengler 2008).

4.3 THE APPLICABILITY OF THE SELECTED GRADIENTS

Even when, the average Ellenberg indicator values for moisture and nitrogen were not calculated on the basis of the whole species pool, since they are not available for every species, a capable allocation of the grassland formations to the environmental gradients succeeded. At this point, it has to be mentioned that the Ellenberg indicator values are not empirical and they are temporally and spatially independent (Fanelli *et al*. 2007). Furthermore, the calculation of the mean from Ellenberg indicator values is intrinsically considered to be incorrect, but in ecological studies it is common practice (e.g. Ewald 2007, Samonil & Vrska 2008, Simonova & Lososova 2008). The calculation of average Ellenberg indicator values and, therefore, the synthetic creation of environmental parameters, as it was performed in the present investigation, is commonly applied as a useful tool in ecological bioindication (Fanelli *et al.* 2007).

On the basis of common descriptions (Dierschke & Briemle 2002, Ellenberg 1996) concerning the ecological framework and environmental conditions under which individual grassland formations occur, it is possible to ratify the allocation of the eleven syntaxa along the gradients for moisture and nitrogen. As a matter of fact, there is a multiplicity of further determining factors and possibilities for a classification, but water and nitrogen are the most important factors in this context (Lauenroth & Dodd 1978, Dierschke & Briemle 2002). Their availability is influenced by anthropogenic causes (drainage, fertilization etc.) as well as non-anthropogenic effects (floodings, climate, geologic realities etc.) (Stout & Schnabel 1994, Ford *et al.* 2008, Borken & Matzner 2009, McIntyre *et al.* 2009).

4.4 THE DISTRIBUTION OF TRAITS

4.4.1 GENERAL COMMENT ON TRAIT EXPRESSIONS

Plant functional traits are defined as biological characteristics, e.g. morphological features, which determine whether a plant species is able to establish, persist and develop under specific environmental conditions (Kahmen 2003). The composition of a trait set describing plant functionality is currently discussed among experts (e.g. Diaz *et al.* 1999, McIntyre *et al.* 1999, Diaz *et al.* 2004). As described before, the BiolFlor derived plant traits consist of several trait expressions (Kühn *et al.* 2004). The data set of BiolFlor is mainly based on literature, e.g. PHD theses and ecological papers. At this point, it has to be mentioned that the quality of the species trait data differs according to the quality of input information, since some species are well investigated and others to a lesser extend (Krumbiegel 2002). For this reason, the authors of the BiolFlor database concede that the allocation of trait expressions is not always absolutely certain (Krumbiegel 2002). Nevertheless, since the BiolFlor database provides a large amount of valuable information, which is incommensurable among German trait databases, its utilization was considered to be justified.

The results show the differences in the several trait expressions among the selected grassland formations, as well as the connections of these variations with the water and nutrient availability. Several of the investigated traits show a clear relationship with the environmental factors, whereas others are marginally influenced. Furthermore, it has to be mentioned that the expressions of traits are often related to each other (Krumbiegel 2002). Therefore, it is not advisable to consider the individual results separately from each other (Crawley 2000).

The most important results of this investigation will be discussed in the following sections. Therefore, the individual trait expressions will be explained and their role in context with altering environmental gradients will be discussed. If possible, the potential connections between the trait expressions will be explained.

4.4.2 LEAF ANATOMY

The most significant relations with the gradients for moisture and nitrogen were observed within the several trait expressions of leaf anatomy. The trait characterizes the transport and regulation of water and nutrients within the plant (Klotz & Kühn 2002b, Ghannoum 2009, Novick *et al.* 2009). The results allow a multiplicity of conclusions regarding adaptation mechanisms to environmental requirements.

Hygromorphic species are delicate plants and therefore very sensitive to low humidity and drought (Klotz & Kühn 2002b, Wittig & Streit 2004). Therefore, the hygromorphic plants predominantly grow in shade and semi-shade (e.g. ferns) and play a minor role in central-European flora (Ellenberg 1996, Klotz & Kühn 2002b). Within this investigation their proportion was indeed below 17%. The results show that their proportion within the selected syntaxa increases with ascending nitrogen availability and moisture. The latter result can be explained by the adaption of hygromorphic plants to rather humid locations and sensitivity against dryness (Ellenberg 1996, Klotz & Kühn 2002b, Leuschner 2002). Their increase with ascending nutrient availability can be ascribed to an accompanied change of the competition situation and microclimate properties at lower vegetation layers. With an ascending nutrient availability, the fast and tall growing plants have an advantage (Grime *et al.* 1997, Kleyer 1999, Weiher *et al.* 1999). In these cases, the shade tolerant species, especially the hygromorphic plants, still find suitable growing conditions under the dense canopy of the tall growing plants (Weiher *et al.* 1999). It should be considered that the protective function of the tall growing plants actually enables the establishment of hygromorphic plants, which depend on shadowy and moist conditions. Coomes *et al.* (2009) found comparable explanations in their investigation of shade-tolerant species in nutrient rich forest ecosystems.

Moreover, an increase of **helomorphic** plants with ascending moisture was observed. This can be explained by their good adaptation to swampy locations. Specific reasons are the high abundances of stomata and vascular bundles per leaf area, as well as aeration tissues (aerenchyms, lacunae) in the subterranean plant organs, which allow them to establish at oxygen deficient soils (Ellenberg 1996, Klotz & Kühn 2002b).

Therefore, the helomorphic plants have, compared to species with another leaf anatomy, a great advantage at locations, which are exposed to periodical floodings and stagnant moisture, e.g. in the formation of *Caricion davallianae*. Striker *et al. (*2006) and Pierik *et al. (*2009) support this assumption.

Scleromorphic plants have firm and stiff leaves, a thickend epidermis and cuticula. They are able to limit their transpiration during periods of dryness, but under favourable conditions, they can revive their transpiration comparatively fast (Klotz & Kühn 2002b). A strong decrease of their proportion with ascending moisture and nitrogen availability was observed. These circumstances can be explained due to their slow aboveground growth (development of the root and stiffening of cell wall require most of assimilates), which leads to an inferiority to other species at locations with a good water and nitrogen supply (Ellenberg 1996). The results suggest that the trait expressions for the protection against loss of water become less important, or rather disadvantageous, the more favourable the environmental conditions get. This relation is supported by Schreiber & Riederer (1996).

Furthermore, a decrease of **mesomorphic** types with ascending moisture was observed. They have no particular morphological characteristics for environmental adaptation (Ellenberg 1996). Since helomorphic leaf types have a great advantage under humid and wet conditions the proportion of mesomorphic types declines in the course of their increase.

4.4.3 STORAGE ORGANS

As mentioned before, the ability to develop storage organs is crucial for the survival of adverse periods (Puijalon *et al.* 2008). Perennial grassland species store assimilates for the maintenance of metabolism during winter and dry periods, for the regeneration of shoot biomass after winter or disturbance (e.g. by utilization) and for periods of high assimilate requirements (e.g. during shoot elongation) (Voigtländer & Jacob 1987). In the context of this investigation, an increase of the proportion of **runner** building plants with ascending water and nitrogen availability was observed.

Runners are lateral shoots with long internodes and adventitious roots (Nultsch 2001). Furthermore, an increase of **rhizome** building plants with ascending moisture could be observed. Rhizomes are subterranean, horizontally growing and thickend shoot axes with shoot-borne roots (Nultsch 2001). In the majority of cases, they have cataphyllary leaves (Voigtländer & Jacob 1987).

An increase in water and nitrogen availability is considered to facilitate fast growing species and to enhance productivity (Klapp 1971, Voigtländer & Jacob 1987, Knox & Clarke 2005). Especially the competitors, which are closely explained in the chapter about strategy, benefit from these conditions. They usually develop storage organs, especially runners and rhizomes (Klotz & Kühn 2002a). A precondition for storage procedures is an assimilate accumulation which is beyond the internal consumption (Klapp 1971, Monson *et al.* 2006). This condition can be fulfilled at locations with an elevated resource supply (Voigtländer & Jacob 1987).

Also Tylova *et al.* (2008) observed an increase in storage procedures among competitors with ascending nitrogen availability at moist locations. Comparable results are also provided by Steinbachova-Vojtiskova *et al.* (2006) and Grover (2009).

A further reason for the increase with ascending moisture is that clonal growth is considered to be the dominant mode of plant growth in wet grassland (Pauliukonis & Gough 2003). Runners and rhizomes have an outstanding role in this context (Krumbiegel 2002). For instance the eponymous species *Filipendulia ulmaria* in the formation of *Filipendulion* propagates via rhizomes. Also prominent species within the formation of *Carex davalliana*, like *Epipactis palustris*, *Parnassia palustris* and *Mentha aquatica* develop runners and rhizomes for storage and vegetative propagation (Dierschke & Briemle 2002, Krumbiegel 2002). The latter context will be discussed in more detail in chapter **4.4.8**.

An increase of rhizome biomass with increasing moisture was also observed by Srutek (1997).

4.4.4 STRATEGY TYPES

Within the present study, the proportion of **stress tolerators** decreased with increasing nutrient availability. These circumstances can be explained by their environmental adaptations and requirements. The stress tolerators are often perennials with a generally low biomass production and reproduction rate. They occur under extreme environmental conditions (e.g. at saline or dry locations) and are able to exploit resources of poor availability (Nagy & Proctor 1997, Klotz & Kühn 2002a). Compared to the other strategy types they have, therefore, a clear advantage at the dryer and lowly fertilized locations, e.g. in the formations of *Corynephorion canescentis, Mesobromion erecti* and *Nardo-Galion saxatilis*. Under more productive conditions, when environmental factors hardly got any limiting effects, they lost their advantages for the benefit of competitors, as Walker & Preston (2005) described.

In opposition to the decrease of the stress tolerators, the proportion of **competitors** increased with ascending nitrogen availability. They are perennial, highly competitive species at favourable locations, e.g. in the formation of *Filipendulion*. They generally develop storage organs and have a low seed production. Competitors are considered to be very sensitive to a high grade of disturbance and stress, thus, they can barely develop at locations which are favourable for the stress tolerators. In the majority of cases, they are perennial forbs, shrubs and trees (Klotz & Kühn 2002a).

Also Liancourt *et al.* (2009) observed an increase of competitors with increasing resource availability.

Interestingly, there was no significant change of the **ruderals** with an altering nitrogen and water availability. They are short-living mostly herbaceous species with high growing rates and occur at locations which are frequently disturbed, e.g. by anthropogenic influences (Klotz & Kühn 2002a). Disturbance is an event that destroys biomass and, therefore, frees up space for colonisation (Lavorel *et al.* 1997). Within the agricultural grassland, the ruderals are generally of little importance, since there are usually few locations unsettled by plants (Klotz & Kühn 2002a). Nevertheless, the proportion of ruderals was highest within the *Cynosurion cristati* and *Lolio-Potentillion anserinae*, which represent the most frequently disturbed formations in this investigation (Dierschke & Briemle 2002).

4.4.5 LIFE FORM

The results of this investigation show an increase of the proportion of **geophytes** with ascending moisture. This can be explained by their pronounced protection of regeneration buds, which is best among the several life forms. The buds are located beyond the soil surface. Hence, they are protected from summer drought and winter coldness (Ellenberg 1996). Obviously, the subterranean protection of regenerative tissues is advantageous under humid conditions, e.g. in the formation of *Caricion davallianae*. Also Carni *et al.* (2005) observed an increase of the occurrence of geophytes with ascending moisture. The observed increase of their proportion towards moist conditions is, furthermore, unmistakably connected with the increase of the amount of storage organs (q.v. chapter **4.4.3**) (Krumbiegel 2002).

Depending on the competition for light, geophytes can only establish at locations where the hemicryptophytes, with their usual long leaf persistence, have been pushed back and the canopy structure is relatively loose (Ellenberg 1996). The proportion of hemicryptophytes was indeed comparatively low within the selected grassland formations presenting a high moisture, although it remained the most important group.

The **hydrophytes** are herbaceous water plants with regeneration buds beyond the water surface (Krumbiegel 2002). Within the vegetation of the utilized grassland, they are naturally of little importance. Nevertheless, the results show a strong increase of the proportion of hydrophytes with ascending moisture. Due to their environmental requirements, they cannot develop under dry conditions, so they are completely absent within the formations of *Corynephorion canescentis* and *Mesobromion erecti*. Within the *Caricion davallianae*, the formation presenting the highest moisture, their proportion reached nearly 5%.

An increase of the proportion of hydrophytes can serve as an indicator for highly wet conditions in grasslands, probably accompanied by long-term problems of utilization through permanent water logging. Very wet locations, which are usually characterized by low productivity, cannot be mechanically mown or grazed with high stocking rates since this implicates long-term damages of the sward (Voigtländer & Jacob 1987). Such wet conditions lead more and more to a complete abandonment of the utilization at these sites (Dierschke & Briemle 2002).

4.4.6 GRASSLAND UTILIZATION VALUES

The results show that the tolerance against trampling decreases with an ascending moisture and is lowest in the formations of *Filipendulion* and *Caricion davallianae*, which represent the most humid conditions among the selected syntaxa. The **trampling tolerance** is a so far little attended attribute of grassland. The trampling tolerance has an important influence on the sociological composition of vegetation. Plant attributes of outstanding relevance in this context are growth height, growth form and life form (Briemle *et al.* 2002). It is generally known that the higher a herbaceous plant grows the more sensitive it is towards trampling. A small growing plant is, therefore, well protected against damage through trampling (Dierschke & Briemle 2002). The aforementioned relation is supported by other observations of this investigation. So the results concerning the trait rosettes show that the proportion of erosulate plants, which have long internodes, is highest within the syntaxa in which the trampling tolerance is lowest. Further results show an increase of the proportion of delicate, hygromorphic plants with ascending moisture. Hence, the species composition evidently changes towards plants with a higher sensitivity against trampling. Also, the investigations of Arnesen (1999) and Stancic *et al.* (2008) show a decrease of the trampling tolerance towards moist grassland.

In the context of trampling tolerance on moist soils, Striker *et al.* (2006) suggest that the constitution of the root plays an important role, in addition to the exposure of the aboveground biomass. The higher the soil moisture is the deeper is the penetration of the animal hoof into the soil, accompanied by a higher exposure of the root. The authors observed that the root structure can influence the damage. For instance the development of aerenchyma tissues under moist conditions, which was observed in this investigation (q.v. **4.4.2**), increases root weakness.

Furthermore, the **mowing tolerance** increased with ascending nitrogen availability. It is an individual, morphologic-ecophysiological trait of vascular plants and is closely related to regeneration ability (e.g. by development of storage organs) and growth rate (Briemle *et al.* 2002). These two parameters are positively influenced by fertilization, as Klapp (1971), Lauenroth & Dodd (1978) and Voigtländer & Jacob (1987) described. Therefore, the mowing tolerance increases as well.

4.4.7 ROSETTES

During the development of a rosette, the internodes are so profoundly shortened that the leaf-carrying nodes become closely clustered. Therefore, the leaves are basally-arranged forming a rosette (Franke 1992). Within the trait expressions of rosettes provided by BiolFlor, it is differentiated between **rosette**, **hemirosette** and **erosulate plants**. The classification resulted from the flowering behaviour of the plant species. The terminal bud of hemirosette plants develops partially elongated internodes during flowering, so that the rosette becomes loose. Entire rosette plants keep their rosulate habitus throughout their lifetime. Their inflorescence has no leaves. Erosulate plants have elongated internodes. Their leaves are arranged in an equally-spaced distance to each other on the shoot axes (Franke 1992, Krumbiegel 2002).

The results of this investigation show that the proportion of hemirosette plants decreases with ascending moisture, while the proportion of erosulate plants increases. Under wet conditions, the protective aspect of a tall plant growth might be an explanation for the higher abundance of erosulate plants (Lenssen *et al.* 2000, Colmer & Voesenek 2009). During short floodings and under stagnant water they can protect the largest part of their shoot from the water, while rosette plants might be entirely covered with water. This might have influences on assimilation and plant metabolism (e.g. respiration) so that an erect growing with elongated internodes is advantageous. Also Lenssen *et al.* (2000) Osmanova (2008) and Pierik *et al.* (2009) observed an increase of elongated shoots under humid conditions.

Furthermore, the extensive utilization of wet grassland locations leads to advantageous conditions for high growing (erosulate) plants, which ordinarily show a higher sensitivity against frequent utilization (Dierschke & Briemle 2002).

There was no clear change of the proportion of entire rosette plants along the gradient of moisture. Reasons might be other adaptation mechanisms to wet conditions concerning leaf anatomy, storage organs and dispersal etc.

4.4.8 VEGETATIVE PROPAGATION

In addition to the dispersal by seeds and progenies, many plants are able to propagate asexually (Franke 1992). Via vegetative components of the shoot and the root (runners, bulbils, innovation buds, rhizomes, bulbs etc.) the plants can occupy free spaces within the sward comparatively fast. Such uncovered patches result from disruptive events (anthropogenically or non-anthropogenically caused) (Lorenzen 1972, Franke 1992, Dierschke & Briemle 2002).

One possibility of vegetative dispersal is the clonal growth by **runners** and **rhizomes**, which represent the most important forms of vegetative propagation in the German flora (Krumbiegel 2002). They have already been discussed in connection with the subject of storage organs. Within this investigation, they were the most important trait expressions of vegetative propagation, comparable to the results concerning the trait storage organs. Also in this case, an increase of the proportion of runners with ascending moisture was observed.

Compared to generative dispersal (e.g. by seeds), the vegetative propagation is commonly supposed to be advantageous under wet conditions (Pauliukonis & Gough 2003). This is, amongst others, connected with the shorter persistence of seeds (of several grassland species) within wet habitats (Mickelson & Grey 2006, Long *et al.* 2009). Furthermore, with a decrease of disturbance events, which is expectable in regards to extensive production at wet locations, the dispersal by seeds and the development of persistent seed banks, respectively, becomes less useful (Kahmen & Poschlod 2004)(q.v. **4.4.9**).

4.4.9 LIFE SPAN

The results show that the proportion of the **perennial** (pluriennial-pollakanthic) plants, which have more than one generative phase in their lives, increases with ascending moisture. They represented the by far largest group within the trait expressions of life span. Since perennial plants depend on storage organs for regeneration, it can be assumed that there is a linkage between the increasing development of storage organs and the higher abundance of perennial plants under wet conditions (Voigtländer & Jacob 1987). The results of Lenz & Facelli (2005) and Elmore *et al.* (2006) support this relation.

The increase of the proportion of perennials with ascending moisture was accompanied by a decrease of **annuals**. The annual plants are completely dependent upon flowering and seed production in each year to ensure the survival of the population (Hovenden et al 2008). Their seedling success can be limited due to the great amount of established high-growing plants and perennials at wet sites which form a close canopy, e.g. in the formation of *Filipendulion* (Bruun & Brink 2008). Moreover, periodical floodings may have negative effects on flowering and seed production (Cho *et al.* 2006) so that the proportion of annuals decreases.

Moreover, Holzel & Otte (2004) described that germination requirements and dormancy cycles of individual species determine the proportion of perennials and annual plants in context with floodings and high moisture.

4.4.10 ROOT AND SHOOT METAMORPHOSES

Modifications of the shoot can be so dramatic, that only a systematic morphological-anatomical analysis can provide information about the real morphological origin of the present organ. For instance, it is possible that the shoot as primary plant organ takes the shape of another organ, e.g. a leaf (Nultsch 2001). Numerous modifications are possible, e.g. runners and rhizomes which have already been discussed, yet no significant relation with the selected gradients was observed in conjunction with the trait shoot metamorphoses.

Moreover, the root can be the subject of various modifications of the inner and outer structure of this primary organ. The development of root tubers and primary storage roots illustrates the adaptation to the geophytical mode of life. They are storage organs and beneficial for overwintering. Similar to the shoot metamorphoses, there are numerous further possible modifications (Nultsch 2001). An increase of the proportion of **plants with primary storage roots** with ascending nitrogen availability was observed. Primary storage roots are thickened primary roots including a thickened hypocotyl and epicotyl (originated from secondary growth) which have a storage function (Nultsch 2001). Representative dicotyledonous species are for instance *Trifolium pratense, T. repens, Cirsium vulgare* and *Rumex crispus*. The possible explanations for an increase of storage procedures under advantageous nutrient conditions have already been discussed in chapter **4.4.3.**

4.4.11 LEAF PERSISTENCE

As it has been mentioned before, the leaf persistence has an important influence on the assimilation rate and biomass production of meadows and pastures (Diepenbrock *et al.* 1999). The trait expressions provided by BiolFlor contain general classifications of plant species (spring green, summer green, overwintering green and persistent green). The results show no significant relations between the leaf persistence types and the gradients of nitrogen and water availability. Nevertheless, there was a slight increase of the proportion of **persistent green** leaf types towards moderate moist conditions, which represent favourable conditions for agricultural usage and forage production (Dierschke & Briemle 2002). So the proportion of persistent leaf types decreased towards the wet and accordingly dry grassland formations of usually extensive utilization. The highly productive formation of *Cynosurion cristati* showed (except for *Corynephorion canescentis,* which showed a comparatively deviant trait expression) the highest proportion of persistent green types. Potentially, not the environmental gradients of moisture and nitrogen are the decisive factors for leaf persistence, but rather other parameters concerning the utilization or disturbance (e.g. frequency of mowing).

4.5 A SHORT EXCURSUS TO CLIMATE CHANGE

The subject of climate change and the potential consequences for ecosystems have heavily been discussed during the last years. The hypotheses of climate researchers provide estimates of how strong the important parameters, like mean sea level and average annual temperature, will change (e.g. Craft *et al.* 2009, Meinhausen *et al.* 2009) but the true dimension will probably become clear over the years.

Since this thesis is, amongst others, concerned with the consequences of altering moisture in agricultural grassland, it is aimed to establish a relationship to the potential consequences of climate change on grassland. The questions are how the environmental conditions may change and what kind of traits will be advantageous under correspondent conditions.

Deposition and atmospheric humidity highly influence the water balance. Furthermore, the annual temperature conditions deeply influence the water availability and, therefore, the species composition within grassland associations (Dierschke & Briemle 2002, Engel *et al.* 2009). Climate researchers have observed an average increase of the annual temperature of about 0.74°C during the last century and suppose a possible increase of up to 6.4°C until 2100 (Greenpeace 2009). This temperature rise will probably lead to an increase of summer droughts (Borken & Matzner 2009). When grassland communities undergo periodical water-stress, plant species with particular environmental adaptations, e.g. due to their morphological traits, are likely to have an advantage on the long run, as Karatassiou *et al.* (2009) described. This thesis has shown that associations from dry locations (e.g. the *Corynephorion canescentis* or the *Mesobromion erecti*) can be characterized by specific traits, like a comparatively high abundance of scleromorphic leaf types and stress-tolerators etc. which are of little importance at moist locations. Probably, such traits will be observable in the future within grassland communities which are increasingly exposed to summer droughts (Leuschner 2000, Van der Veken *et al.* 2004).

Furthermore, Hovenden *et al.* (2008) observed an influence of warming on seed mortality which probably changes vegetation dynamics and dispersal within the sward.

In contrast to drought, climate change will probably lead to an increase in wet periods in other regions (Borken & Matzner 2009). This thesis has shown a great amount of traits eminently occurring under moist conditions, e.g. helomorphic anatomy, runners and rhizomes for storage and vegetative dispersal, geophytical and hydrophytical life forms. Associations undergoing increased wettings will probably show an increase in traits like that over the years (Colmer & Voesenek 2009).

In general, such changes in trait composition will be slow processes and are not entirely predictable since climate change and dynamics within grassland associations are not entirely predictable, as Hulme (2005) and Marshall *et al.* (2008) described.

Furthermore, climate change will have economical influences on forage production (Hopkins & Wilkins 2006, McKeon *et al.* 2009). Maybe pastures cannot be used for the usual time spans since they provide less forage for livestock or conditions are unsuitable for grazing. Probably meadows have to be mown less frequently since the productivity is to low or flooding events hinder mowing for a certain time (McKeon *et al.* 2009). Moreover, the increasing occurrence of fires, especially in the drier Mediterranean regions, potentially destroys great areas for forage production (Borken & Matzner 2009).

The impacts of increasing droughts are currently visible in the Mediterranean regions, e.g. Spain and Portugal. A great amount of arable land has already been lost due to desertification and many regions are threatened by this loss (Spiegel online 2005). Thus, the useable agricultural land becomes more and more precious, especially in view of the increasing world population. Certainly, with this knowledge, the forage production on grassland might be more interesting in the future (Hopkins & Wilkins 2006).

It can be assumed that the distribution of plant functional traits can provide an informative basis for the understanding of plant community ecology in grassland with regard to climate change (McIntyre *et al.* 1999, Diaz *et al.* 2004). A database linkage, like the present one, can serve as a basis to predict possible consequences for trait composition, especially with respect to changes in soil moisture.

5 CONCLUSION

The present thesis shows that the two databases (SynBioSys NL and BiolFlor) are predestinated for the application in the field of grassland research and that a linkage of vegetation databases is a useful instrument to gain information about the distribution of plant functional traits along environmental gradients. In this context, nitrogen and water availability, which are the two most important gradients for plant community composition, were used. Calculated on the basis of Ellenberg's indicator values, they proved to be suitable for the applied method.

It was possible to demonstrate that grassland communities differ in their specific trait composition due to their environmental requirements. For some of the investigated traits, like leaf anatomy, storage organs and strategy types, many considerable relations with [N] and [F] were observed. Other traits showed less obvious relations with the two gradients, for example root and shoot metamorphoses and leaf persistence. In these cases, other influencing variables, which were not considered here, may play a role.

In general, the specific trait expressions are certain adaptations to environmental conditions and provide an advantage for the individual species. The distribution of functional traits within several grassland formations differing in resource availability can provide valuable information for the understanding of dynamics in plant community ecology.

Time will show how the distribution of traits will change due to altered parameters. The ongoing changes in grassland management, like intensification on the one hand and utilization abandonment on the other will be of great importance. Further cause variables are climate change and its potential influence on resource supply, especially water.

6 FUTURE PROSPECTS

In context with this investigation, a German trait database and a Dutch vegetation database were connected to gain general information on the composition of traits along environmental gradients. A fully developed information system like SynBioSys NL is not yet available for the German flora. In the near future there is going to be a pan-European information system in the form of a cooperative project of several European countries and national institutions, called SynBioSys Europe. This project will provide valuable information to an unprecedented extent. It would be interesting to expand the present way of database research to a larger scale, since a broader spectrum of environmental gradients could be observed on a European level. Furthermore, the range of available grassland formations will then be much higher.

Moreover, it would be interesting to investigate further functional traits as, for instance plant attributes connected with seed dispersal and flowering.

In context with the present investigation, several other databases, concerning the field of vegetation and plant traits, like LEDA, BASECO, FLORAWEB, BIOPOP, CLO-PLA and FLORKART were spotted. For the most part, these are still in the process of development. Their applicability for database linkages in the field of grassland research may be evaluated in the future.

7 SUMMARY

In this study, a database linkage has been applied to evaluate the general use and application of such linkages for grassland approaches and to investigate the distribution of plant functional traits along environmental gradients. The German BiolFlor database was used for the acquisition of data about plant functional traits. The selected traits used in this study were life form, life span, leaf anatomy and persistence, root and shoot metamorphoses, rosettes, storage organs, strategy types, vegetative propagation and several grassland utilization values. Each of the plant traits consists of several trait expressions differing with regard to the individual plant species. The Dutch SynBioSys NL information system was used for the acquirement of data about grassland formations, their specific species composition and the constancy of species within the accordant formation. Eleven formations covering a wide range of environmental conditions and utilization intensity were selected (*Alopecurion pratensis, Arrhenatherion elatioris, Calthion palustris, Caricion davallianae, Corynephorion canescentis, Cynosurion cristati, Filipendulion, Junco-Molinion, Lolio-Potentillion anserinae, Mesobromion erecti* and *Nardo-Galion saxatilis*). The SynBioSys and BiolFlor databases were linked on the basis of a common species reference list. The adjustment of the species names occurred with the aid of the German SL, a new taxonomical list for the German flora. A total of 1615 plant species could successfully be adjusted and were, therefore, available for individual database queries. To build the environmental gradients, the average Ellenberg indicator values for nitrogen [N] and moisture [F], which are the most important factors for plant community composition, were calculated.

The individual trait expressions within grassland communities were weighted with the constancy of the correspondent plant species. For further analyses and display, the percentages of trait expressions within formations were calculated. The means of grassland utilization values (numerical data) were directly calculated without weighting. Bar plots of the trait expressions within the selected grassland communities along the environmental gradients were drawn. Furthermore, regression analyses were done to investigate whether there are significant statistical relationships between trait expressions and environmental gradients. Linear regression analyses were done for the most important trait expressions (56 calculations). In four cases, quadratic regressions were additionally tested.

On the methodical level, it could be said that the adjustment of species names for the creation of the common species reference list was comparatively complex. It has to be manually done for the most part, since a different nomenclature as well as different abbreviations were used within the two databases. An advice for the future could, therefore, be the standardized application of taxonomical lists, like the German SL and common designations.

The BiolFlor and SynBioSys databases can be characterized as easy to handle. The huge amount of valuable information about vegetation composition and plant traits makes them predestinated for grassland approaches. The database linkage on the foundation of the adjusted species list worked, and a project database could be created on the basis of the provided information.

The created project database provides all data required for the analysis of the relationships between the trait expressions within formations and gradients for moisture and nitrogen. Based on the regression analyses, several important relationships were identified. It is supposed that there are connections between the individual trait expressions.

Within the trait leaf anatomy, there was a significant increase of the proportions of helomorphic and hygromorphic leaf types with increasing moisture, whereas the proportion of scleromorphic types declined. Moreover, the proportion of hygromorphic types increased with ascending nitrogen availability, accompanied by a decrease of scleromorphic types. Within the trait storage organs, there was a significant increase in rhizome and runner building plants with increasing moisture. The proportion of the latter types increased, furthermore, with an ascending gradient for nitrogen. Concerning the analyses of strategy types, it was conspicuous that the proportion of stress tolerators (S) decreased with increasing nutrient availability, whereas the proportion of competitors (C) increased. Moreover, the proportions of hydrophytes and geophytes increased with ascending gradient for moisture. In context with utilization of grassland, it could be said that trampling tolerance declined with ascending moisture. This occurred accompanied by an increase of the proportion of erosulate plants, while hemirosette plants got slightly pushed back. In general, the proportion of perennial (pluriennial-pollakanthic) plants increased with ascending moisture. Concerning the trait vegetative propagation, it was demonstrated that the dispersal by runners increased with rising nitrogen availability. No significant relationship could be observed concerning the trait leaf persistence.

In a short excursus to climate change, it was attempted to predict changes in the distribution of plant traits with regard to changes in soil moisture. It was assumed that traits which predominantly occurred within formations from dry locations (e.g. scleromorphic anatomy and stress-tolerators) will be observable in the future within grassland communities which are increasingly exposed to droughts. Moreover, it was assumed that associations undergoing increased wettings will show an increase in traits, which predominantly occurred within formations from moist locations (e.g. helomorphic anatomy, runners and rhizomes), over the years.

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III. APPENDIX

Tab. A Relative occurrence of trait expressions within selected grassland formations [%]

	Caricion davallianae	*Lolio-Potentillion anserinae*	*Corynephorion canescentis*	*Mesobromion erecti*	*Junco-Molinion*	*Calthion palustris*	*Alopecurion pratensis*	*Arrhenatherion elatioris*	*Cynosurion cristati*	*Nardo-Galion saxatilis*	*Filipendulion*
	09BA	12BA	14AA	15AA	16AA	16AB	16BA	16BB	16BC	19AA	32AA
	Carda	LolPo	CorCa	MesEr	JuncMo	CalPa	AloPr	ArrEl	CynCr	NarGa	Filip
Leaf anatomy											
succulent	1.23	1.68	0.99	0.12	0.27	0.13	0.00	0.13	0.09	0.25	0.02
scleromorphic	13.12	5.94	59.59	31.15	18.58	6.82	6.50	12.75	9.71	31.67	4.72
mesomorphic	30.53	39.04	37.97	65.35	36.40	43.01	58.98	74.94	68.52	53.95	40.58
hygromorphic	8.29	15.41	0.62	1.54	6.24	13.24	16.16	8.99	12.43	2.97	15.58
helomorphic	43.44	35.42	0.83	1.84	38.07	35.60	17.64	3.19	8.92	11.13	37.65
hydromorphic	3.39	2.51	0.00	0.00	0.44	1.21	0.72	0.00	0.33	0.04	1.45

Storage organs	Carda	LolPo	CorCa	MesEr	JuncMo	CalPa	AloPr	ArrEl	CynCr	NarGa	Filip
Runner	38.16	46.00	24.01	23.26	34.35	38.67	38.77	29.33	33.24	25.06	47.81
Runner with tuberous tip	0.10	0.03	0.00	0.01	0.08	0.48	0.00	0.07	0.01	0.03	2.22
Runner-like rhizome	0.60	0.18	0.00	2.76	0.11	0.48	0.15	1.24	0.97	0.37	0.49
Runner with bulbous tip	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Bulbil	0.32	0.01	0.01	0.06	0.17	0.11	1.27	0.69	0.16	0.12	0.12
questionable	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Tuft	5.39	7.83	31.90	9.24	11.94	9.13	9.96	15.12	19.77	16.06	5.77
Hypocotyl bulb	0.00	0.00	0.00	0.05	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Pleiocorm	2.88	3.25	9.62	17.28	4.05	4.34	4.39	13.53	7.41	10.95	1.78
Primary storage root	3.18	7.04	8.02	10.58	2.14	5.02	6.12	12.38	8.09	3.95	5.86
Rhizome	34.61	28.94	22.00	16.41	37.03	32.37	27.78	16.03	22.33	34.31	27.72
Rhizome-like pleiocorm	2.70	3.60	3.60	16.32	4.19	5.16	5.27	7.65	6.23	4.21	6.20
Shoot tuber	3.01	0.79	0.21	0.94	2.75	0.99	0.39	1.68	0.95	2.29	0.93
Succulence	0.31	0.55	0.61	0.06	0.00	0.01	0.00	0.05	0.04	0.00	0.01
Secondary storage root	0.27	0.32	0.01	0.95	0.00	0.24	0.28	1.42	0.56	0.25	0.30
Turio	5.47	1.02	0.00	0.03	1.16	0.51	0.00	0.00	0.01	0.35	0.43
Root tuber	2.76	0.02	0.00	2.03	2.02	2.34	1.06	0.04	0.08	2.05	0.22
Bulb	0.24	0.41	0.01	0.06	0.02	0.15	4.57	0.76	0.15	0.02	0.14

Strategy type	Carda	LolPo	CorCa	MesEr	JuncMo	CalPa	AloPr	ArrEl	CynCr	NarGa	Filip
c	15.70	19.58	10.54	28.43	19.94	29.70	39.32	44.51	35.27	17.49	46.97
cr	0.83	3.94	0.90	3.12	0.28	2.35	4.15	10.40	6.59	1.32	3.64
cs	32.12	14.10	40.73	13.65	36.22	22.38	6.80	7.25	6.80	29.40	29.35
csr	40.17	48.51	33.41	49.10	37.51	40.49	48.94	34.56	46.17	46.65	19.10
r	1.52	4.77	5.17	1.98	0.20	1.22	0.55	2.95	3.73	1.16	0.27
s	8.31	7.37	1.04	0.51	5.63	3.51	0.20	0.19	1.19	2.76	0.52
sr	1.34	1.73	8.21	3.22	0.21	0.35	0.05	0.14	0.25	1.23	0.14

Life form	Carda	LolPo	CorCa	MesEr	JuncMo	CalPa	AloPr	ArrEl	CynCr	NarGa	Filip
Hydrophyte	4.58	2.47	0.00	0.00	1.10	3.00	0.94	0.02	0.31	0.12	3.93
Chamaephyte	2.44	2.08	2.97	1.71	2.29	3.27	3.67	3.81	4.84	5.80	1.14
questionable	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Geophyte	20.57	12.59	10.73	6.23	15.66	16.08	12.98	8.39	6.56	8.33	18.62
Hemicryptophyte	61.78	73.01	72.79	81.66	74.94	74.38	80.45	82.07	82.91	68.96	71.89
Macrophanerophyte	0.93	0.04	1.64	1.77	1.01	0.25	0.00	0.42	0.23	2.83	0.13
Nanophanerophyte	3.93	0.13	2.62	2.15	2.16	0.34	0.00	0.48	0.27	4.17	0.51
Pseudophanerophyte	0.39	0.04	0.47	0.53	0.03	0.09	0.05	0.36	0.04	0.49	0.83
Hemiphanerophyte	2.93	0.06	2.62	0.38	2.43	0.10	0.00	0.01	0.00	7.07	0.59
Therophyte	2.45	9.57	6.16	5.57	0.39	2.48	1.91	4.45	4.84	2.23	2.36

Rosettes	Carda	LolPo	CorCa	MesEr	JuncMo	CalPa	AloPr	ArrEl	CynCr	NarGa	Filip
Erosulate plant	47.08	28.84	21.42	22.77	36.60	33.41	27.42	26.93	20.86	38.29	48.55
Hemirosette plant	43.92	57.44	67.35	65.66	55.15	58.08	62.01	62.37	65.48	49.39	47.68
Rosette plant	9.00	13.73	11.23	11.56	8.25	8.51	10.57	10.70	13.66	12.32	3.77

Vegetative propagation	Carda	LolPo	CorCa	MesEr	JuncMo	CalPa	AloPr	ArrEl	CynCr	NarGa	Filip
Runner	46.84	60.24	54.03	43.07	43.27	49.59	51.30	52.59	53.58	41.81	53.82
Runner with tuberous tip	0.06	0.03	0.00	0.01	0.06	0.32	0.00	0.01	0.00	0.03	0.88
Runner-like rhizome	0.61	0.20	0.00	3.97	0.12	0.55	0.17	1.84	1.30	0.41	0.51
Runner with bulbous tip	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Bulbil	0.66	0.01	0.04	0.08	0.36	0.15	1.41	1.02	0.21	0.18	0.12
Brood shoot	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
questionable	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Fragmentation	0.25	0.04	0.00	0.04	0.00	0.04	0.00	0.01	0.00	0.00	0.06
Gemma	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Innovation bud with storage root	0.00	0.02	0.00	0.00	0.00	0.14	0.63	2.11	0.22	0.00	0.57
Innovation bud with root tuber	0.03	0.01	0.00	0.05	0.00	0.05	1.18	0.06	0.05	0.08	0.09
Phyllogenous shoot	3.18	0.52	0.00	0.00	0.48	0.13	0.35	0.00	0.00	0.69	0.07
Rhizome	36.62	27.89	35.25	15.88	45.37	39.79	31.90	20.14	30.41	43.80	31.55
Rhizome-like pleiocorm	2.78	6.00	6.14	25.80	4.51	6.66	7.25	11.83	9.03	4.65	8.44
Shoot tuber	0.96	0.14	0.53	2.58	4.24	0.43	0.00	1.99	1.08	4.40	0.16
Turio	5.68	1.47	0.00	0.04	1.23	0.62	0.00	0.00	0.02	0.38	0.46
Root shoot	2.09	2.99	4.01	8.40	0.36	1.36	0.72	7.30	3.90	3.54	3.11
Bulb	0.24	0.46	0.00	0.08	0.02	0.17	5.09	1.12	0.20	0.02	0.15

Life span	Carda	LolPo	CorCa	MesEr	JuncMo	CalPa	AloPr	ArrEl	CynCr	NarGa	Filip
questionable	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
annual	2.48	10.71	15.23	5.97	0.42	2.81	2.73	7.27	6.18	2.66	3.28
biennial	2.82	1.60	2.91	6.94	2.25	3.75	1.32	5.31	2.67	1.76	2.29
pluriennial-hapaxanthic	1.65	0.16	2.45	2.30	1.72	2.41	0.16	1.64	0.84	1.13	1.99
pluriennial-pollakanthic	93.05	87.53	79.42	84.78	95.61	91.03	95.79	85.78	90.31	94.45	92.44

Root metamorphoses	Carda	LolPo	CorCa	MesEr	JuncMo	CalPa	AloPr	ArrEl	CynCr	NarGa	Filip
Buttress root	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
questionable	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Adhesive root	0.00	0.00	0.00	0.19	0.00	0.00	0.00	0.00	0.05	0.00	0.00
Rootless	0.00	0.14	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.93	0.20
Pleiocorm	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Primary storage root	43.25	77.68	71.22	62.91	52.29	65.32	78.37	70.52	76.68	47.11	68.79
Secondary storage root	3.34	2.94	0.20	6.79	0.00	3.42	1.90	7.87	5.58	4.34	2.67
Root tuber	29.29	0.18	0.00	7.36	40.29	19.97	14.19	0.28	0.60	18.72	2.47
Root shoot	24.12	19.07	28.57	22.74	7.42	11.29	5.54	21.33	17.08	28.91	25.87

Shoot metamorphoses	Carda	LolPo	CorCa	MesEr	JuncMo	CalPa	AloPr	ArrEl	CynCr	NarGa	Filip
Runner	44.90	0.43	0.02	0.06	0.02	0.16	4.87	0.89	0.18	0.02	0.15
Runner with tuberous tip	0.12	54.51	45.27	31.30	40.49	45.73	48.66	40.67	46.54	35.30	52.98
Runner-like rhizome	0.59	0.03	0.00	0.01	0.08	0.51	0.00	0.08	0.01	0.04	2.33
Assimilating shoot	0.01	0.19	0.00	2.97	0.11	0.51	0.16	1.47	1.16	0.37	0.52
Runner with bulbous tip	0.00	0.00	0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Bulbil	0.41	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Brood shoot	0.00	0.00	0.02	0.06	0.25	0.09	0.22	0.77	0.17	0.24	0.03
questionable	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Pleiocorm	3.27	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Rhizome	38.87	4.58	14.55	24.86	4.47	6.05	7.45	22.40	12.76	12.23	2.81
Rhizome-like pleiocorm	2.72	31.78	32.56	17.40	44.40	38.86	31.30	20.02	28.85	41.52	31.19
Shoot thorn	1.24	5.74	5.31	19.31	4.32	6.29	6.93	9.69	8.07	4.21	8.48
Shoot tuber	3.45	0.30	0.82	2.00	0.39	0.01	0.00	1.14	0.61	1.62	0.00
Shoot tendril	0.00	0.88	0.54	1.97	4.82	1.27	0.41	2.79	1.61	4.27	1.06
Shoot succulence	0.30	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Turio	3.87	0.58	0.89	0.06	0.00	0.01	0.00	0.07	0.04	0.00	0.01
Bulb	0.24	0.98	0.00	0.01	0.64	0.51	0.00	0.00	0.01	0.18	0.45

Leaf persistence	Carda	LolPo	CorCa	MesEr	JuncMo	CalPa	AloPr	ArrEl	CynCr	NarGa	Filip
spring green	0.00	0.03	2.64	2.08	0.12	0.43	6.22	1.46	0.76	0.94	0.17
summer green	57.19	33.04	21.36	53.06	51.48	43.93	33.94	43.72	29.06	37.98	66.77
overwintering green	0.41	3.05	10.07	2.45	0.18	2.51	2.86	5.63	4.48	0.84	2.15
persistent green	42.40	63.88	65.92	42.41	48.22	53.13	56.97	49.19	65.70	60.24	30.91

Grassland utilization value	Carda	LolPo	CorCa	MesEr	JuncMo	CalPa	AloPr	ArrEl	CynCr	NarGa	Filip
Mowing tolerance	4.23	4.79	4.57	4.62	4.42	4.64	5.52	4.93	4.74	4.39	4.68
Grazing tolerance	4.60	5.03	5.26	4.59	4.73	4.71	5.01	4.76	4.73	4.88	4.67
Trampling tolerance	3.93	4.18	4.62	4.25	4.04	3.96	4.21	4.19	4.29	4.37	3.79
Foraging value	3.00	3.22	3.23	3.62	3.08	3.20	3.73	3.60	3.42	3.13	3.31

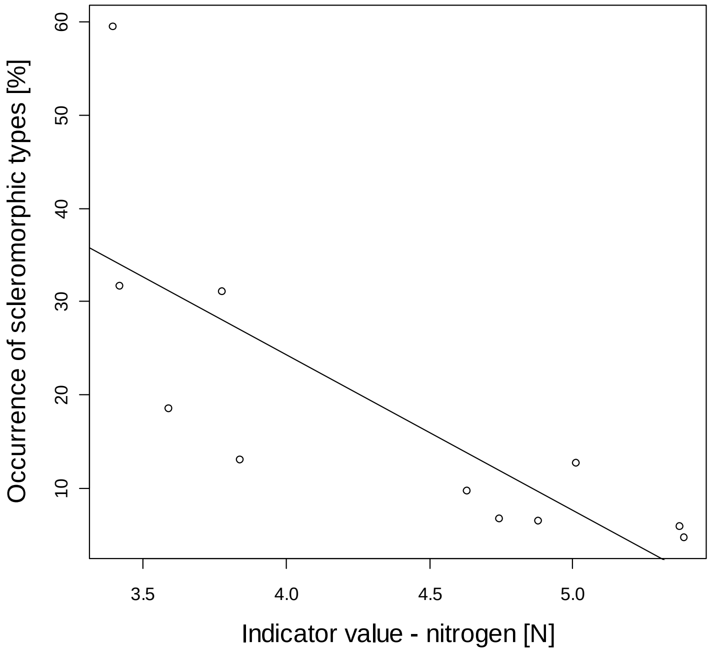

Fig. A Leaf anatomy - Relative occurrence of scleromorphic types within the selected grassland formations plotted against Ellenberg indicator value for nitrogen [N]. Results of regressions analysis for simple linear regression: $R^2=0.60$, $p<0.01$

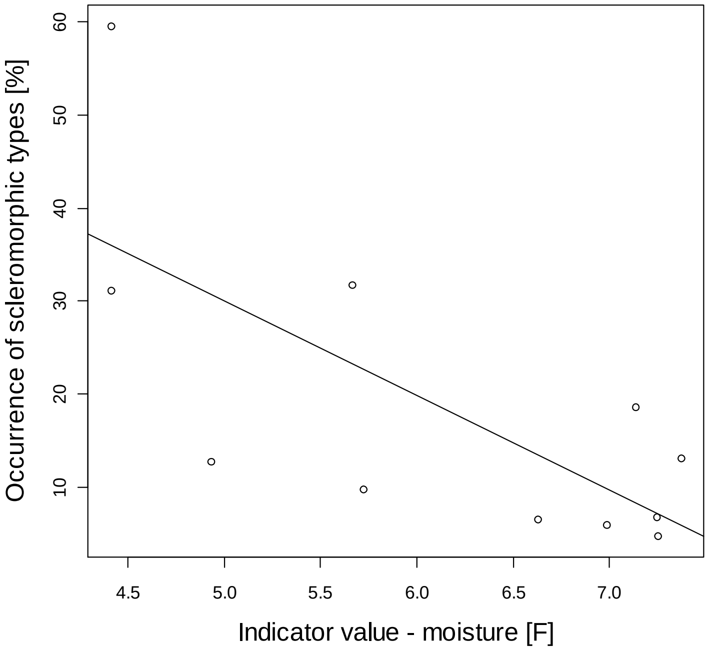

Fig. B Leaf anatomy - Relative occurrence of scleromorphic types within the selected grassland formations plotted against Ellenberg indicator value for moisture [F]. Results of regressions analysis for simple linear regression: $R^2=0.51$, $p<0.05$

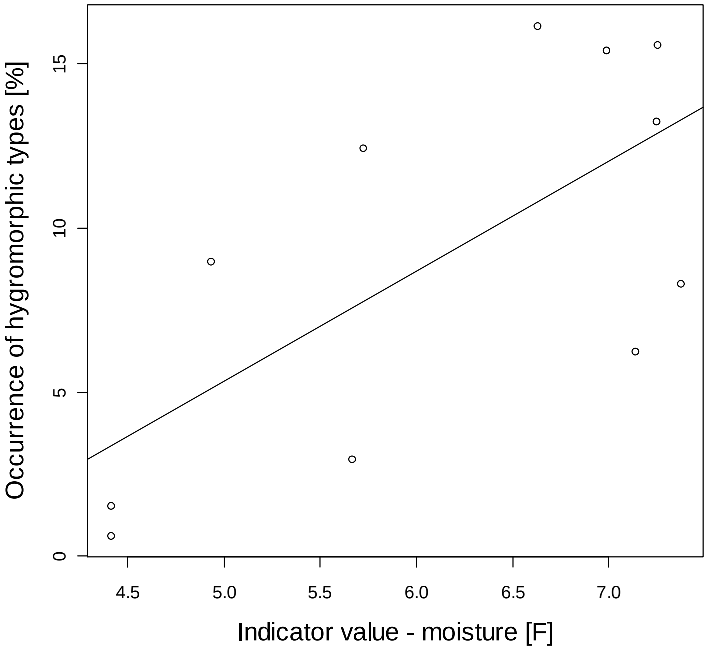

Fig. C Leaf anatomy - Relative occurrence of hygromorphic types within the selected grassland formations plotted against Ellenberg indicator value for moisture [F]. Results of regressions analysis for simple linear regression: $R^2=0.46$, $p<0.05$

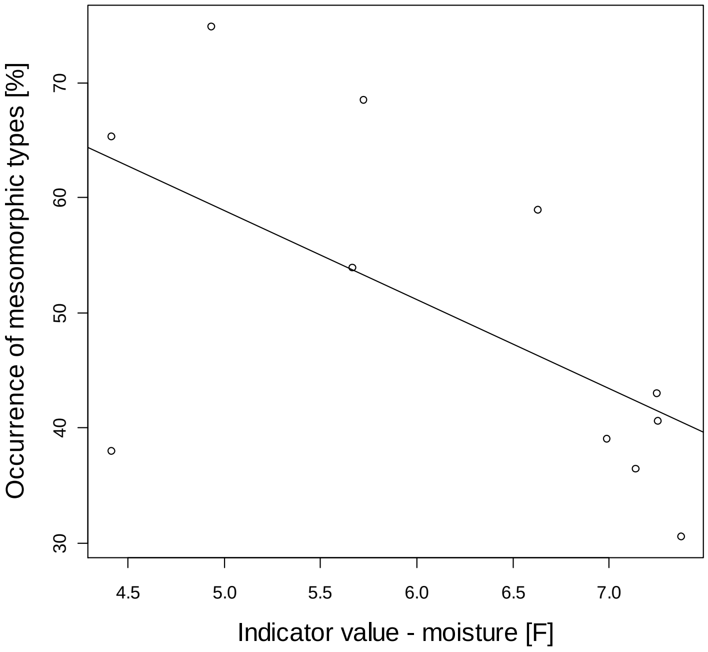

Fig. D Leaf anatomy - Relative occurrence of mesomorphic types within the selected grassland formations plotted against Ellenberg indicator value for moisture [F]. Results of regressions analysis for simple linear regression: $R^2=0.36$, $p<0.1$

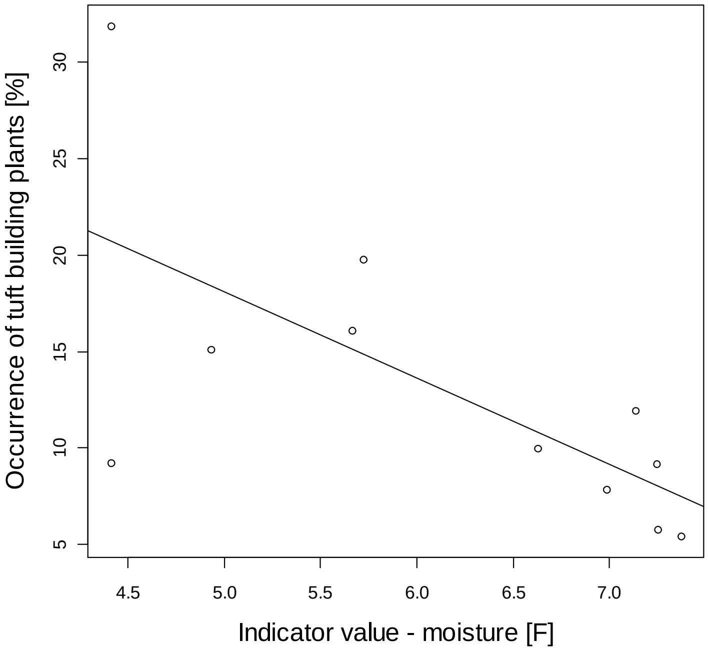

Fig. E **Storage organs - Relative occurrence of tuft building plants within the selected grassland formations plotted against Ellenberg indicator value for moisture [F]. Results of regressions analysis for simple linear regression: $R^2=0.46$, $p<0.05$**

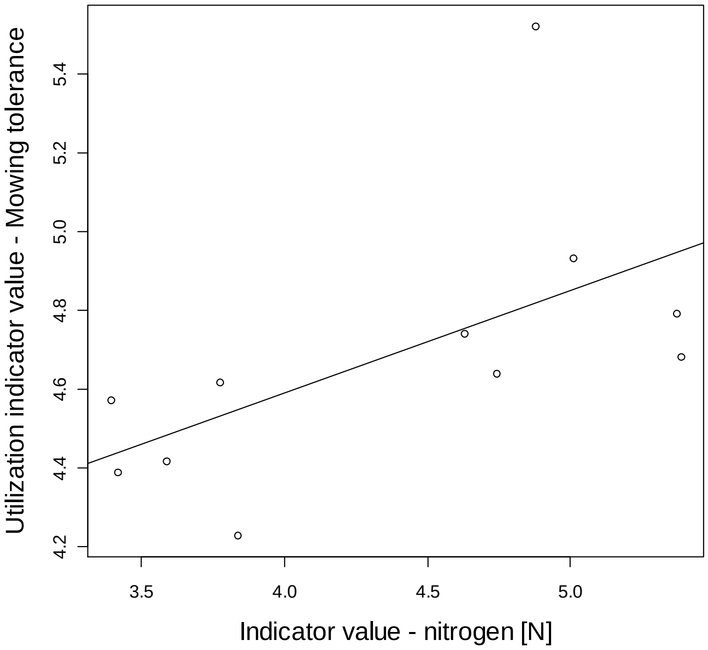

Fig. F **Grassland utilization values - Average grassland utilization indicator value for mowing tolerance within the selected grassland formations plotted against Ellenberg indicator value for nitrogen [N]. Results of the regressions analysis for simple linear regression: $R^2=0.35$, $p<0.1$**

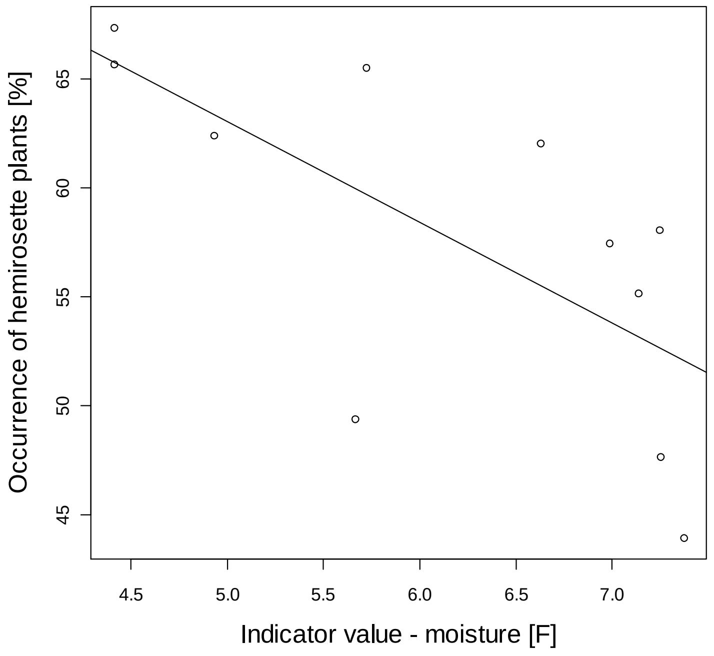

Fig. G Rosettes - Relative occurrence of hemirosette plants within the selected grassland formations plotted against Ellenberg indicator value for moisture [F], Results of regressions analysis for simple linear regression: R^2=0.47, p<0.05

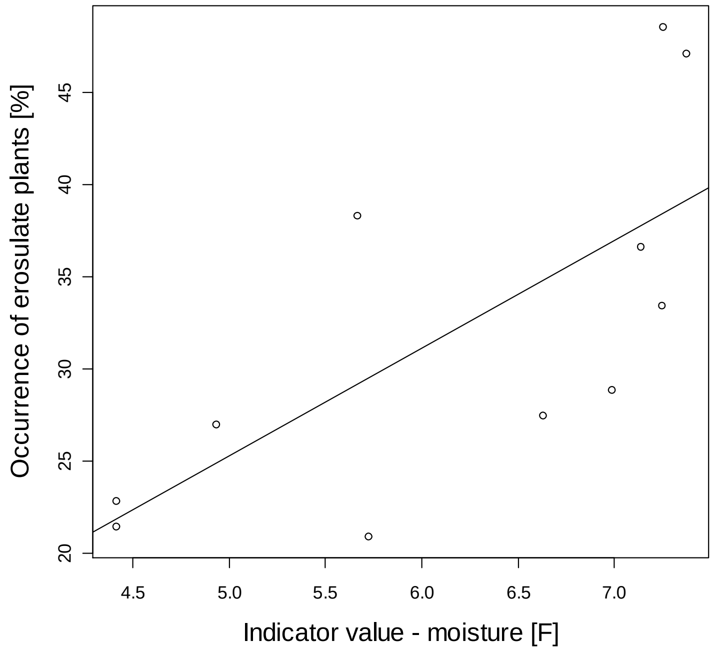

Fig. H Rosettes - Relative occurrence of erosulate plants within the selected grassland formations plotted against Ellenberg indicator value for moisture [F], Results of regressions analysis for simple linear regression: R^2=0.50, p<0.05

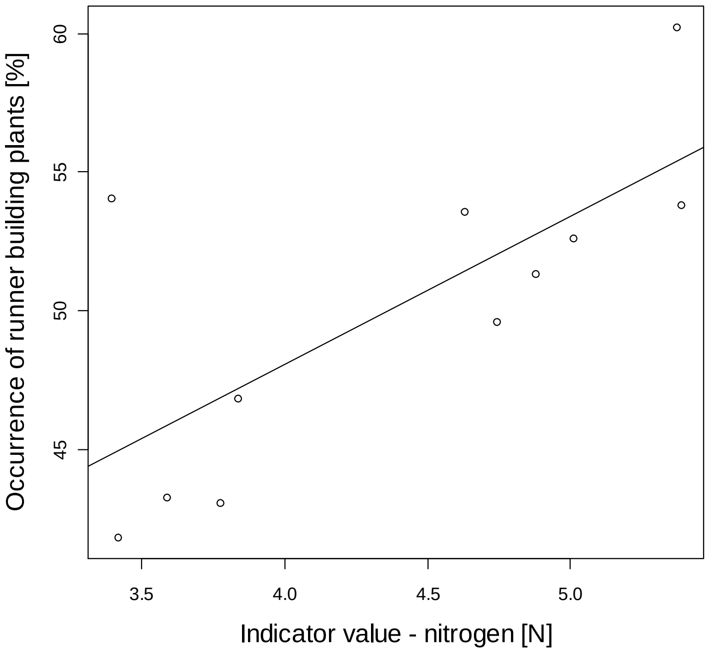

Fig. I Vegetative propagation - Relative occurrence of runner building plants within the selected grassland formations plotted against Ellenberg indicator value for nitrogen [N], Results of regressions analysis for simple linear regression: $R^2=0.52$, $p<0.05$

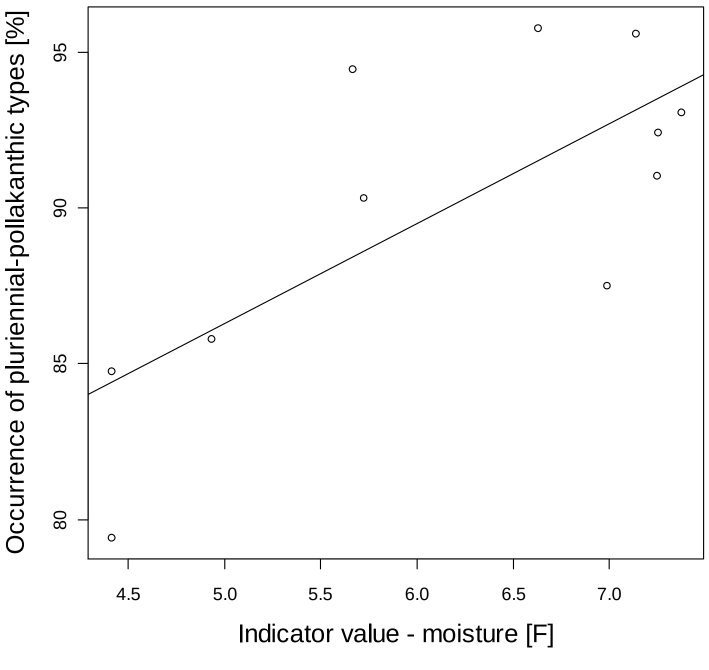

Fig. J Life span - Relative occurrence of pluriennial-pollakanthic types within the selected grassland formations plotted against Ellenberg indicator value for moisture [F], Results of regressions analysis for simple linear regression: $R^2=0.53$, $p<0.05$

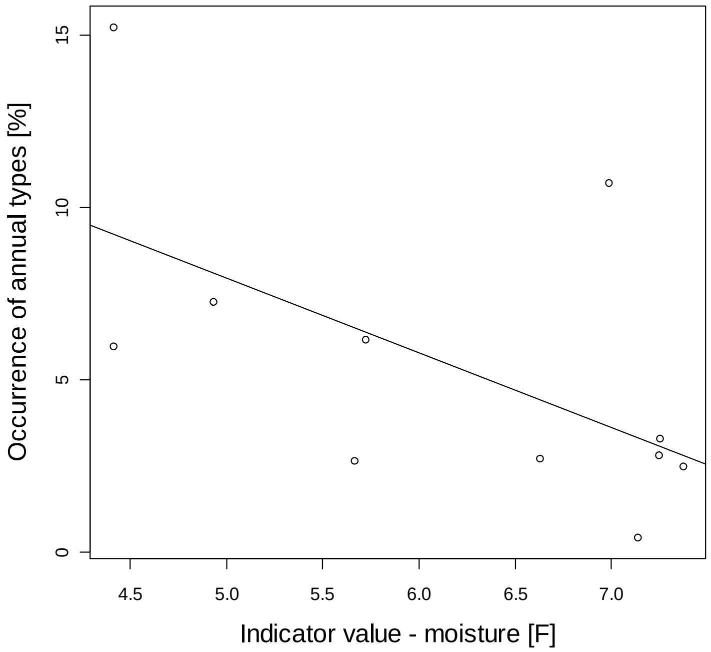

Fig. K **Life span - Relative occurrence of annual types within the selected grassland formations plotted against Ellenberg indicator value for moisture [F], Results of regressions analysis for simple linear regression: R^2=0.34, $p<0.1$**

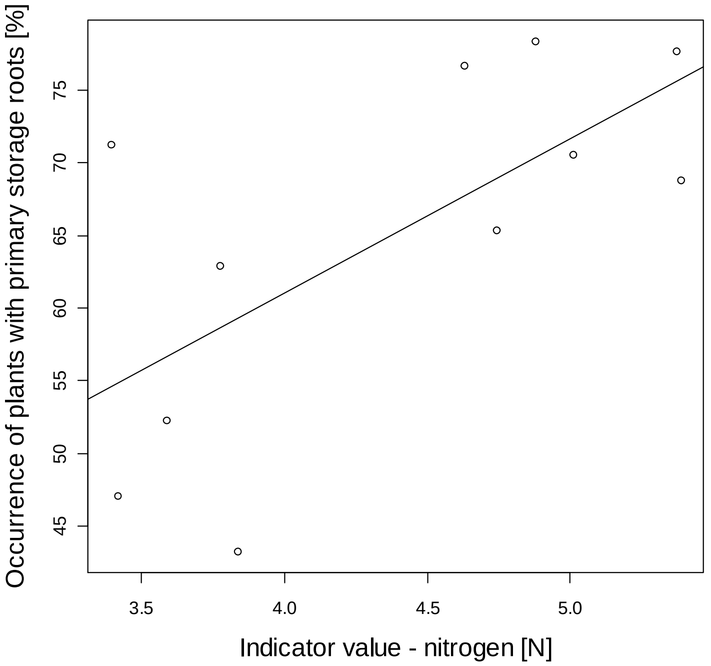

Fig. L **Root metamorphoses - Relative occurrence of plants with primary storage roots within the selected grassland formations plotted against Ellenberg indicator value for nitrogen [N], Results of regressions analysis for simple linear regression: R^2=0.44, $p<0.05$**

Tab. B Overview of the coefficients *a* and *b* of the 56 linear equations ($\hat{y}=a+bx$). The values were calculated in context with the linear regression analyses

Trait	Environm. gradient (*x*)	Trait expression (*y*)	intercept (*a*)	gradient (*b*)
Life form	moisture [F]	hemicryptophytes [%]	91.17	-2.63
	moisture [F]	hydrophytes [%]	-5.85	1.19
	moisture [F]	geophytes [%]	-8.83	3.45
	nitrogen [N]	hemicryptophytes [%]	64.09	2.49
	nitrogen [N]	hydrophytes [%]	-1.98	0.80
	nitrogen [N]	geophytes [%]	7.82	1.06
Life span	moisture [F]	annual types [%]	18.80	-2.17
	moisture [F]	pluriennial-pollakanthic types [%]	70.27	3.21
	nitrogen [N]	annual types [%]	5.16	0.06
	nitrogen [N]	pluriennial-pollakanthic types [%]	87.19	0.65
Leaf anatomy	moisture [F]	helomorphic types [%]	-63.40	13.74
	moisture [F]	hygromorphic types [%]	-11.40	3.35
	moisture [F]	mesomorphic types [%]	97.45	-7.71
	moisture [F]	scleromorphic types [%]	80.80	-10.16
	nitrogen [N]	helomorphic types [%]	-4.67	5.94
	nitrogen [N]	hygromorphic types [%]	-19.87	6.66
	nitrogen [N]	mesomorphic types [%]	33.93	3.67
	nitrogen [N]	scleromorphic types [%]	91.04	-16.67
Leaf persistence	moisture [F]	persistent green plants [%]	70.16	-2.85
	moisture [F]	summer green types [%]	12.47	4.94
	nitrogen [N]	persistent green types [%]	61.67	-2.07
	nitrogen [N]	summer green types [%]	33.81	2.07
Root metamorphoses	moisture [F]	plants with primary storage roots [%]	77.38	-2.02
	nitrogen [N]	plants with primary storage roots [%]	18.68	10.59
Shoot metamorphoses	moisture [F]	rhizome building plants [%]	31.51	-2.89
	nitrogen [N]	rhizome building plants [%]	37.79	-5.51
Rosettes	moisture [F]	hemirosette plants [%]	86.22	-4.63
	moisture [F]	erosulate plants [%]	-3.89	5.83
	nitrogen [N]	hemirosette plants [%]	57.70	0.00
	nitrogen [N]	erosulate plants [%]	29.18	0.65

Trait	**Environm. Gradient (*x*)**	**Trait expression (*y*)**	**intercept (*a*)**	**gradient (*b*)**
Storage organs	moisture [F]	rhizome building plants [%]	-2.67	4.86
	moisture [F]	runner building plants [%]	-3.37	6.14
	moisture [F]	tuft building plants [%]	40.49	-4.48
	nitrogen [N]	rhizome building plants [%]	35.08	-1.79
	nitrogen [N]	runner building plants [%]	-1.26	8.17
	nitrogen [N]	tuft building plants [%]	32.25	-4.43
Vegetative propagation	moisture[F]	rhizome building plants [%]	7.92	4.01
	moisture[F]	runner building plants [%]	46.99	0.49
	nitrogen [N]	rhizome building plants [%]	52.51	-4.56
	nitrogen [N]	runner building plants [%]	26.70	5.34
Grassland utilization indicator values	moisture [F]	Foraging value	3.92	-0.10
	moisture [F]	Grazing tolerance	5.11	-0.05
	moisture [F]	Mowing tolerance	4.80	-0.02
	moisture [F]	Trampling tolerance	5.12	-0.15
	nitrogen [N]	Foraging value	2.81	0.12
	nitrogen [N]	Grazing tolerance	4.90	-0.02
	nitrogen [N]	Mowing tolerance	3.55	0.26
	nitrogen [N]	Trampling tolerance	4.77	-0.14
Strategy types	moisture [F]	strategy type C [%]	23.65	0.70
	nitrogen [N]	strategy type C [%]	-22.34	11.52
Strategy types-partitioned into C-S-R-components	moisture [F]	Component C [%]	49.17	0.78
	moisture [F]	Component S [%]	19.39	1.39
	moisture [F]	Component R [%]	31.44	-2.17
	nitrogen [N]	Component C [%]	22.79	7.14
	nitrogen [N]	Component S [%]	57.95	-6.87
	nitrogen [N]	Component R [%]	19.26	-0.27

Tab. C Example of the 'weighting' of trait expressions, 'a' and 'b' are trait expressions of the same trait, the syntaxon 'XY' includes four species with given constancies. Qualifier = 1 indicates that the trait is always present (typical), Qualifier =2 indicates that the trait is not always present (not regarded in this investigation)

Syntaxon XY

							Trait 1		Trait 2	
Species NO.	Constancy	Trait 1	Qualifier 1	Trait 2	Qualifier 2	∑ trait expressions	a	b	a	b
1	0.4	a	1	~~b~~	~~2~~	1	0.4			
2	0.8	b	1			1		0.8		
3	0.5	b	1	a	1	2		0.25	0.25	
4	0.12	a	1			1	0.12			
∑	1.82					∑	0.52	1.05	0.25	0

∑ trait expression 'a' = 0.77 (in %= 42.30769 = relative occurrence of the trait expression 'a' within syntaxon 'XY')
∑ trait expression 'b' = 1.05 (in %= 57.69231 = relative occurrence of the trait expression 'b' within syntaxon 'XY')
∑ weighted trait expressions = 1.82

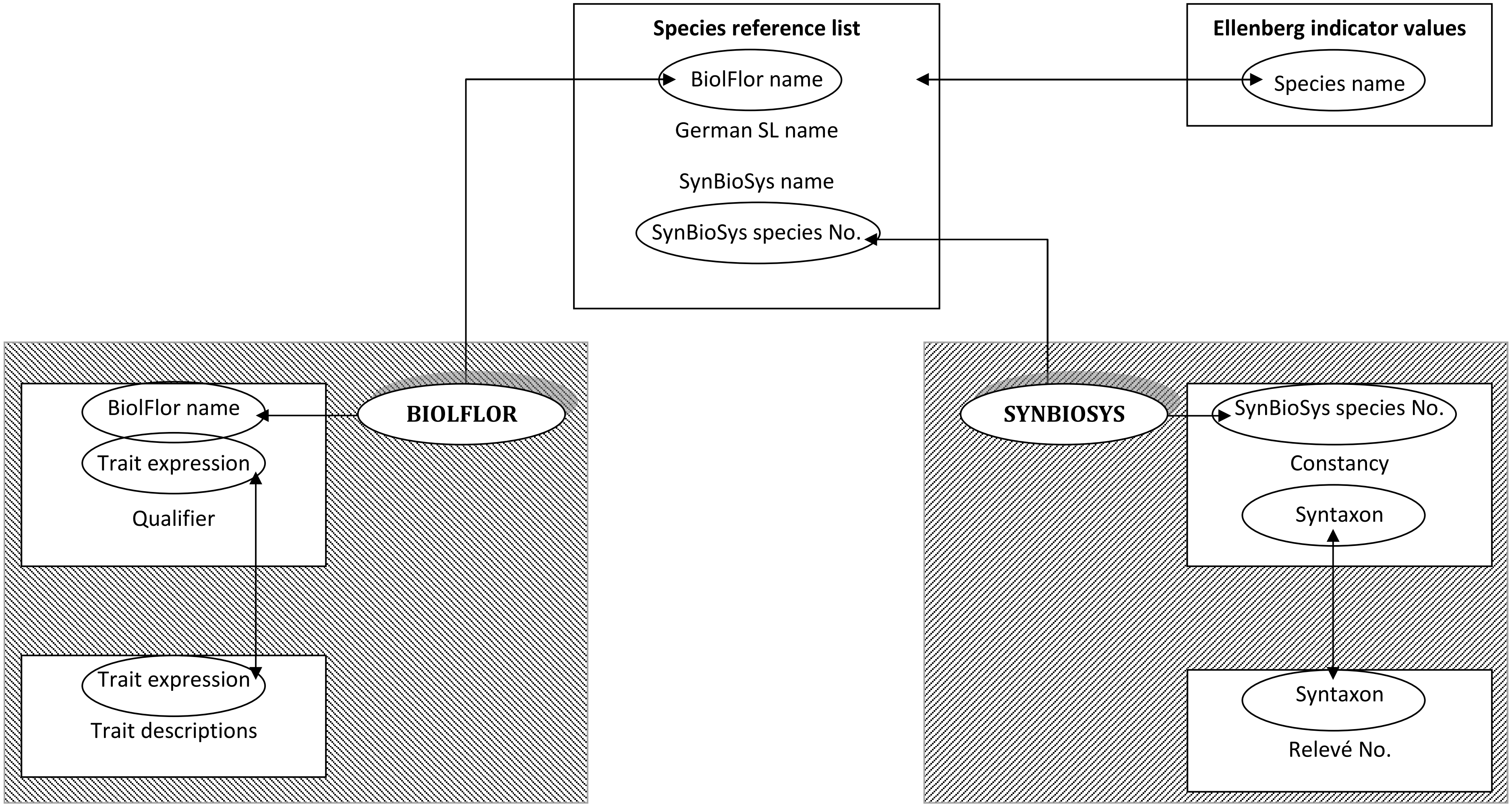

Fig. M Simplified database structure

Eidesstattliche Erklärung

Hiermit versichere ich an Eides statt, die vorliegende Arbeit selbständig verfasst zu haben und keine anderen als die hier angegebenen Quellen und Hilfsmittel benutzt zu haben.

Göttingen, den 21.08.2009

Ort, Datum	Unterschrift (Eva-Maria Kuhl)