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Plant Functional Traits and Ecosystem Functions in Experimental Grassland Stands

Dissertation zur Erlangung des Doktorgrades

Lehrstuhl für Bodenökologie, Prof. Dr. E. Matzner
Universität Bayreuth

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Content

Tables

Appendix

Figures

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Abbreviations and Nomenclature

dm	Dry matter weight
g	Gram
hr	Hour
d	Day
yr / a	Year
Tukey-HSD	Tukey's Honestly Significant Difference
KW-H	Kruskal-Wallis ANOVA
MW-U	Mann-Whitney U-Test
mean	Arithmetic mean
dF	Degree of freedom
F	Distance between distributions (Mean Square of x_i / Mean Square of Error)
p	Probability of error
MS	Average square of the dependent variable
SS	Summation of the square of the dependent variables
nd	Not determined
ns	Not statistically significant (post-Hoc $p > 0.05$)
sd	Standard deviation
N_{accum} / N yield	N accumulated in aboveground dm [g m^{-2} yr^{-1}]
N_{stand}	N accumulated in below- and aboveground dm [g m^{-2} yr^{-1}]
NUE_{bm}	N use efficiency [g dm N_{accum}^{-1}]
WUE_{bm}	Water use efficiency [g dm l $water_{transpired}^{-1}$]
dm %	Percent dry matter
Vol-%	Percent volume
pH	$\log_{10}$ $[H^+]$
eC	Electrical conductivity [µS cm^{-1}]
N concentrations	N soil solution concentrations [mg l^{-1}] in 15, 30 and 90 cm depth
N flux	N loss with seepage [g m^{-2} yr^{-1}]
N_{min}	Inorganic N (Σ NH_4-N + NO_3-N)
Base cations	K, Mg, and Ca
DOC	Dissolved organic carbon
Loss/yield-ratio	Nutrient seepage loss / Nutrient aboveground yield [g m^{-2} yr^{-1}/ g m^{-2} yr^{-1}]
Cab	Competition ability according to WILSON (1988), also chapter 2.4
RYT	Relative Yield Total according to DE WITT (1960), also chapter 2.4
Ref	Reference (bare soil)
stands I-V	Experimental grassland stands on lysimeter facilities
treatments	*Ref* + stands I-V
swards	Rhizodeposit pot cultures (four individuals)
rhizodeposition	DOC / carboxylic acid release [mg C / µM g shoot dm^{-1}]
Corg	Soil organic carbon [mg C g dm^{-1}]
basal respiration	Respiration without root detritus application [µM CO_2-C g $Corg^{-1}$]
mineralisation	Respiration after root detritus application [µM CO_2-C g $Corg^{-1}$]

1 Introduction

1.1 General Introduction

Naturally, grasslands occur under semi-arid climate (steppes, savannas, prairies, pampas; Figure 1), where lack of precipitation impedes growth of woodland communities. Under temperate climate, almost all European grasslands are man made (WHITEHEAD, 1995).

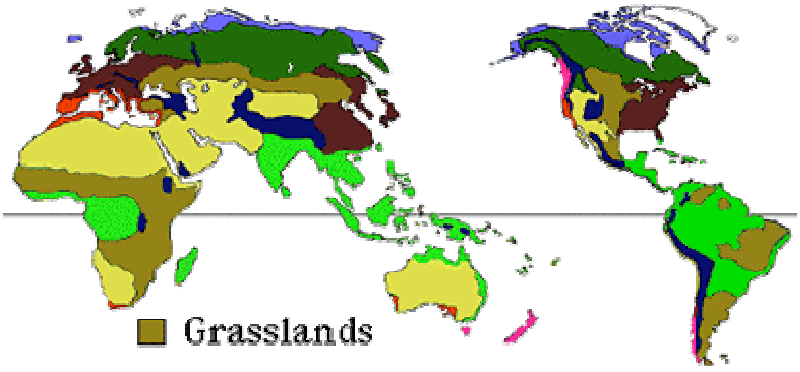


Figure 1 Distrubtion of grasslands world-wide. MISSOURI BOTANICAL GARDEN, 2002 http://mbgnet.mobot.org/sets/grasslnd/world.htm

Many species occurring in recent grasslands were already present in Europe during the Subboreal period (5500 BC). They mostly inhabited woodland margins, floodplains and mountainous areas (DIERSCHKE & BRIEMLE, 2002). 41 grassland species were determined by pollen analysis for the Subboreal in samples from in the Niederrhein area. The number of determined species increased to 77 grasslands species for the Roman and further to 141 species for medieval times (KNÖRZER, 1996).

First plant breeding was proved for the Mesolithic period (4800 BC). The grassland area increased during Bronze period (1800 BC) by beginning of hay harvest with cutting facilities made from metal und further intensified during the Iron period (800 BC) after introduction of the scythe. Woodlands were strained due to human use and Europe shifted towards an open cultural landscape. During medieval times almost all wetlands, steep and mountainous areas, which were unsuitable for agriculture were shifted towards meadow use.

Grasslands on better soils near settlements were used as pastures (DIERSCHKE & BRIEMLE, 2002). Technical improvements of the enlightment in the 18th century, the use of mineral fertilizers after middle of the 19th century and finally the land consolidation of the 20th century changed the use intensity of grasslands drastically. Enhanced soil amelioration, fertilization and use of heavy facilities raised the productivity of grasslands, but also reduced the structural diversity of the landscape as well as species richness in European grasslands to a great extent (DIERSCHKE & BRIEMLE, 2002).

Grassland Management in Germany

In 1992, in western and northern Europe and the former Soviet Republics, grasslands covered to 50-60 % of agricultural land. In central and southern Europe only 35-40 % was used as meadow or pasture (WEISSBACH & GORDON, 1992). In Germany, grasslands covered an area of 5 million ha with a contribution of meadows accounting for 38 % (STATISTISCHES BUNDESAMT DEUTSCHLAND, 2003). The distribution of European grasslands is mainly influenced by climate and topography. Traditionally, grasslands predominantly occupy habitats, which show unsuitable conditions (e.g. high soil moisture, steep slopes) for arable use (WHITEHEAD, 1995).

Table 1 Intensities of grassland management (after BOCKHOLT ET AL. 1996, SCHUMACHER, 1995)

	Management Intensity	Cutting frequency	N-fertilizer application	Stand structure
Fallow			Varying	Dense, often tall growing, species poor, tendency to dominance patterns, high in production of litter
Extensive	Very Low	**Summer cut regime**: Discontinuously cut in summer, continuous cut in autumn	Oligotrophic	Low in productivity, sparse, often species rich
Semi-extensive	Low to Moderate	**Single cut regime**: in July, occasionally extensive grazing after harvest	0-50 kg slightly Mesotrophic	Moderate in productivity, more dense, often species rich
Semi-intensive	Medium	**Two cut regime**: June and August / September, extensive grazing after last harvest	50-150 kg Mesotrophic	High in productivity, tall growing, moderately species rich
Intensive	High	**Three / Four cut regime**: after end of April	150-300 kg Eutrophic	High in productivity, high growing, dense, species poor
Highly intensive	Very High	**Multiple cut regime**: after end of April	› 300 kg Hypertrophic	Highest in productivity, dense, very species poor

In Germany different management practices can be found (Table 1), which are defined by their cut-regime and N fertilizer application. Management intensities are reflected in types of characteristic stand structures. Furthermore stand structures can be distinguished into types of special use (e.g. hay, silage, pasture, and paddock) or temporal aspects (e.g. grazing after last harvest, frequency and length of grazing; DIERSCHKE & BRIEMLE, 2002). As OPITZ VON BOBERFELD (1994) reported, negative correlations between species richness and nutritional value of plant species primarily led to an intensification of management and thus to decreasing phytodiversity in grasslands. Soil availability of phosphorus, potassium and abiotic conditions (climate, soil environment) also show considerable impacts on productivity and the composition of grassland stands (WHITEHEAD, 1995).

1.2 Grassland Ecosystem Functions / Services

The soil surfaces are intensively intertwined with biotic structures such as root systems, micorrhizae, hyphae and microbial biofilms (SCHEFFER, 2002). Since biotic structures contribute to important features of soils (e.g. aggregation by plant or fungal exudates) and perform exchanges of matter with soil constituents (e.g. cation exchange, mineralisation), soils are considered as a part of grassland ecosystems. For the studies, grassland ecosystems are understood following KROHNE (1998), as *the sum of abiotic and biotic components in a defined system or region*.

Table 2 Ecosystem services, processes and main driving factors in grasslands under management

Services	Processes	Driving factors
Food	o Photosynthesis / **Biomass production** ⬇	**Management / Soil functions / Climatic conditions** ⬇
Water retention / purification	o Evapotranspiration (water use) o Sequestration of nutrients and trace metals (nutrient use)	
Mitigation of atmospheric CO_2	o Sequestration of carbon (carbon use)	

Ecosystem functions or processes (Table 2) are used analogous. They refer to *processes or properties of an ecosystem, which are influenced by its biota* (NAEEM ET AL., 2002). In ecosystems different biotic and abiotic compounds are linked through carbon-, water- and nutrient fluxes. These fluxes are affected by plant performed evapotranspiration as well as sequestration of nutrients and carbon in stand biomass and by filter, buffer and transformation processes in soils (soil functions, SCHEFFER, 2002). For this project, ecosystem processes in grasslands are considered as *an outcome of interaction between biotic and abiotic constituents of ecosystems*.

European grasslands are man made with the purpose of using the inherent processes and exploiting them for human needs (ecosystem services, Table 2). The traditional ecosystem services provided by grasslands are to contribute to food production (milk and meat) in form of pastures or meadows (WHITEHEAD, 1995). Grasslands mainly control water fluxes by water acquisition and evapotranspiration and to some extent by precipitation interception and delay of percolating water into soils feeding seepage due to intensively intertwined root layers. Grasslands fulfil an important function as retention space for water during thunder storms. OBRIST ET AL. (2003) found that in dependence on climatic conditions, *Bromus tectorum* (Cheat Grass) stands transpired up to 7 l m^{-2} d^{-1}. This finding reflects a great implication of grassland species on water cycles.

Human activities led to considerable shifts in nutrient and carbon cycles in grasslands. Due to increased population pressure, intensified management practices required heavy fertilization of grasslands for high productivity. Grasslands also served as depositing sites for liquid manure derived from intensive livestock breeding or sewage sludge from waste water treatments.

Atmospheric inputs are additional sources of nitrogen for European grasslands. Due to combustions processes (e.g. mobility, energy supply) NO_x-emissions result. Considerable amounts of NH_3 are emitted from intensified livestock breeding. As a consequence, high NO_3-and NH_4-inputs to grassland ecosystems with wet and dry deposition occur. Total depositions range from 30 to 40 kg N ha^{-1} yr^{-1} in Germany and the UK (FANGMEIER ET AL., 1994; GOULDING, 1990), up to 40 to 80 kg N ha^{-1} yr^{-1} in the Netherlands (VAN BREMEN & VAN DIJK, 1988).

The ability of grasslands to build up biomass rapidly over a great time of the year (- 300 growing days in the UK; LAZENBY, 1988) and to re-growth after harvest, founded their importance in concern of safety net functions for nitrogen. Considerable growth was found for many species at temperatures above 5° C (WHITEHEAD, 1995).

WILMAN (1965) reported of maximum N uptake rates of *Lolium multiflorum* (Italian Ryegrass) amounting 7.5 kg N ha^{-1} d^{-1}, 14-21 days after a fertilizer application of 140 kg N ha^{-1} d^{-1}. In the longer term, daily uptake rates ranged from 1 to 3 kg N ha^{-1} d^{-1} in dependence of species, climate and management (DILZ, 1988). N uptake rates show a pronounced seasonality. ANSLOW & ROBINSON (1986) found uptake rates increasing in spring from nil to 3 to 4 kg N ha^{-1} d^{-1} in late April, before decreasing to about 0.5 kg N ha^{-1} d^{-1} in July and increasing again in late August / September up to 2 kg N ha^{-1} d^{-1}. Mediated by high productivity, grasslands can yield from 8,000 to 15,000 kg biomass ha^{-1} yr^{-1} and sequester enormous amounts of nitrogen (200 to 550 kg N ha^{-1} yr^{-1}; WHITEHEAD, 1995). KUTRA & AKSOMATIENE (2003) confirm high sequestration of N for perennial grass species in crop rotation systems with reduction of N concentrations in seepage two years after sowing. Even as under sown species to *Beta vulgaris* (Sugar Beet), grasses could account for a sequestration of 426 kg N ha^{-1} yr^{-1}.

Since atmospheric CO_2 concentrations have been increasing during the last decades, responses of grassland productivity to elevated CO_2 received considerable attention (VANDERMEER ET AL., 1998; STERNBERG ET AL., 1999; GRIME ET AL., 2000; KÖRNER, 2000; ZAVALETA ET AL., 2003; VERBURG ET AL., 2004). Some studies focussed on morphological or physiological aspects (e.g. water use efficiency) in understanding and predicting responses of grassland plants to elevated CO_2 (LAMBERS, 1993; CASTELLS ET AL., 2002; SHAW ET AL., 2002; WULLSCHLEGER ET AL., 2002).

Other studies focused on the role of grassland soils for carbon sequestration and soil processes (VERBURG ET AL., 1998; VAN NOORDWIJK ET AL., 1998; COLLINS, ET AL., 2000; FONTAIN ET AL., 2004) and on microbial characteristics (CHENG & JOHNSON, 1998; KANDELER ET AL., 1998). Most studies suggested positive implications of elevated CO_2 on productivity due to shifts in water use efficiency and improved production of secondary metabolites (e.g. phenolic compounds, LAMBERS, 1993; CASTELLS ET AL., 2002) with possible effects on carbon sequestration in soils.

All of the above mentioned ecosystem services, attributed to water, nutrient and carbon cycle, are mainly linked to grasslands by their biomass production and soil functions. *Biomass production* is regarded as one of the *key points* in understanding grassland stands, their dynamics and their implications on ecosystem processes.

1.3 Competition and Niche Complementary in Grasslands

Plant functional groups and functional traits serve as basic concepts in understanding functional roles of plant species within their community and towards their role in ecosystem functioning.

1.3.1 Plant Functional Groups / Functional Traits

KÖRNER (1993) referred to functional groups, as *elements that bear a certain set of common structural and / or process features*.

Table 3 Grouping of functional criterions and their specification as single traits after KÖRNER (1993), modified

Functional grouping criterion	Functional traits
Quality	o *Morphological and physiological aspects*: Life form, grass / herb, leaf structure, water / nutrient use efficiencies, nutrition strategies, mutualism, etc.
Spatial arrangement	o Upper, middle and bottom layer, rooting depth, root-system, root/shoot-ratio, horizontal distribution of plants
Temporal appearance	o *Phenological aspects*: seedlings, mature individuals, geophytes, early / late successional species

Functional groups can be distinguished by *qualitative* (structural, physiological or life strategy), *spatial* (arrangement) and *temporal* (appearance or activity) grouping criterions (Table 3). Functional groups are implemented and differentiated by functional *traits* of the given species.

Root systems can be regarded as plant traits in concern of spatial differentiation of grasslands. Grassland plants can be distinguished in groups featuring dense superficial homorhizal root layers (small - medium monocotyledonous), homorhizal systems with great extension (tall monocotyledonous) or allorhizal superficial or deep reaching systems found with dicotyledonous (KUTSCHERA & LICHTENEGGER, 1982, 1992). Since root distribution is specific for a given root system, combinations of different root systems should functionally complement due to spatial avoidance.

Species, however, may also feature synergistic effects due to combination of qualitative traits, by enhancing the availability of soil borne resources. A potential mechanism for increasing nutrient availability may be given through *hydraulic equilibration* (SMITH ET AL., 1999; BURGESS ET AL., 2001). A plant induced increase of soil moisture in nutrient rich patches may enhance nutrient mobility and thus provide greater access to nutrients for plants (VAN NOORDWIJK & CADISCH, 2002).

This mechanism requires the presence of at least one species featuring higher water potentials and greater extension of its rhizosphere that could initiate sufficient hydraulic tension.
Herbaceous vegetation may profit from *root synlocation* with trees or shrubs to some extent. Root synlocation means sharing soil space, (e.g. a macro pore) for better resource access of all species (VAN NOORDWIJK & CADISCH, 2002). In grasslands, species with tap roots build up macro pores which provide preferential penetration paths for other species after their decease.

Nutritional strategies are also qualitative functional traits (see rhizodeposition to plant rhizosphere). Plant species with a lower performance in mobilizing nutrients may profit from the metabolic effort of highly performing species (VAN NOORDWIJK & CADISCH, 2002).

The ability of plants to join rhizobial symbiosis is also regarded as a qualitative functional trait. Legumes often show mutualistic root infections with *Rhizobium* strains providing N fixation ability. Evidence for profiting of non-legume plants from legumes in rhizobial symbiosis due to mineralisation of legume root biomass is given (MAYER ET AL., 2003). Amino acid exudation accounts to a lesser extent to nitrogen facilitation by non-legumes species (PAYNEL ET AL., 2001). There is an on going discussion about the role of rhizobial symbiosis as a functional trait and its implications on species interactions (TILMAN ET AL., 2002; LOREAU & HECTOR, 2001; SCHERER-LORENZEN ET AL., 2003).

Mycorrhizal symbiosis may provide another important mechanism of mutual nutrient use for higher plants. Up to 80% of higher plant species form mutual associations with different soil fungi, which intensively affect the acquisition of phosphorus and trace metals (VAN DER HEIJDEN & CORNELISSEN, 2002). Its importance for plant functional relationships has been widely discussed (KLIRONOMOS ET AL., 2000; HECTOR ET AL., 2002; VAN DER HEIJDEN & CORNELISSEN, 2002). It may also be due to hyphal links and interspecies transport of nutrients and carbon such as nitrogen or phosphorus (SIMARD ET AL., 2002).

Discretely measured traits lack of precision, since many of them can shift due to physiological or morphological plasticity, when abiotic or biotic environmental conditions change. Functional groups or even functional traits of plants often lack of discrete well defined boundaries or thresholds. A certain classification becomes rather difficult, particularly when functional traits may change in response to environmental shifts (KÖRNER, 1993). Hence, broad approaches may provide the best start in revealing impacts of functional diversity of stands on ecosystem functions. Qualitative criterions such as rooting depth can be measured discretely, while the criterion root system is rather difficult to group. Broad approaches to differentiation are likely to be more rational than scrutinized ones.

1.3.2 Competition in Grasslands

European grasslands are man made semi-natural systems, which were created over the last 4 000 years. Besides environmental conditions, management practices proved a deep implication on ecosystem functions of grasslands. The intensification of grassland use brought about considerable increases in biomass production, albeit it led to a decrease in species richness through enhanced competition and thus to a loss of functional diversity.

In concern of nutrient acquisition, VAN NOORDWIJK & CADISCH (2002) regarded competition between plant species as *a process of acquisition of a shared resource, or subsequent consequences for growth and productivity of the competiting plants*.

Competition affects nutrient acquisition through *resource depletion*, *reduction of potential uptake* per unit root length density in presence of other roots and *reduction in mobility of nutrients* by reduced soil moisture (VAN NOORDWIJK & CADISCH, 2002).

Several authors consider competition as determinants of stand composition and grassland productivity (WIJESINGHE ET AL., 2001; CARLEN ET AL., 2002; LAVOREL & GARNIER, 2002). HAUGLAND & TAWFIQ (2001) and HOFMAN & ISSELSTEIN (2004) identified competition as a key component in understanding the establishment of seedlings in grasslands. HOFMAN & ISSELSTEIN (2004) regarded fast growing species with high root to shoot allocation or pronounced plasticity in shoot development as most promising for establishment in grasslands. For example, despite severe reduction in growth when subdued to shading, *Plantago lanceolata* is able to reach upper stratum in grasslands by enhanced biomass allocation to the shoot.

However, slow growing seedlings establish poorly in grasslands (FOSTER, 1999) but often show a greater resilience towards soil draught. CARLEN ET AL. (2002) and HOFMAN & ISSELSTEIN (2004) considered shoot competition as a limiting factor for species growth, whereas HAUGLAND & TAWFIQ (2001) identified root competition as crucial for establishment of seedlings with growing importance of shoot competition with time. They also assumed that root competition is of major importance on soils with nutrient limitations. At abundant nutrient supply, light becomes the limiting resource. CARLEN ET AL. (2002) attributed competitive ability between *Festuca pratensis* (Meadow Fescue) and *Dactylis glomerata* (Barnyard Grass) mainly to their specific performance of aboveground traits.

Root systems, life span, nutrient use efficiency or nutritional strategies were identified as important traits in determining the competition ability of grassland species (SPERRY & HACKE, 2002; WRIGHT & WESTOBY, 2003; WILBY ET AL., 2001; LONERAGAN, 1997).

WIJESINGHE ET AL. (2001) explained plant dominance patterns and competition in grasslands with trade-offs between dominance and nutrient forage precision. Following CAMPBELL ET AL. (1991), *alternative strategies* are assumed for subordinate species featuring a development of smaller root systems with higher precision than dominants. Higher precision in nutrient foraging is understood as a higher focus of root system expansion on nutrient rich patches in soils. In contrast to this strategy, the development of broad root systems leads to exploration of greater soil space without special focus on nutrient rich patches.
Perception and response is also controlled by the scale of soil heterogeneity (WIJESINGHE & HUTCHINGS, 1999). *Arrhenatherum elatius* (Tall Oat Grass) and *Plantago lanceolata* (Narrow Leaf Plantain) give examples for fast growing dominants with broad root systems. Both species are able to enhance their precision in nutrient foraging in mycorrhizal symbiosis. CRAINE ET AL. (2002) reported of additional mechanism of competition for plants either by accessing a unique source (rhizobial symbiosis) or high grades of nutrient conservation (tough, dense, long lived tissues).

LAVOREL & GARNIER (2002) confirmed this point of view. They generally attributed fast growth, broad nutrient foraging and low nutrient conservation in biomass to dominant species on soils without limitation in nutrient supply. Whereas nutrient limited dominants were described as slow growing species with a high resorption of nutrients from senescing tissues.

LAVOREL & GARNIER (2002) revealed differences in physiology of dominant species as main factors in controlling the primary aboveground productivity of different successional sites (compare ELLENBERG, 1977; POORTER & DE JONG, 1999; AERTS, 1989; AERTS & BERENDSE, 1989). On these sites, positive correlations between plant productivity and N mineralisation rates were found and those were associated in considerable shifts from *Erica tetralix* / *Calluna vulgaris* (Cross-leaved / Common Heath) towards *Molinia caerulea* (Tall Moor Grass) dominance (VAN VUUREN ET AL., 1992).

Specific leaf area (SLA) was identified as a *primary trait* correlating with other important factors such as leaf life span, nutrient contents, photosynthetic rates well (LAVOREL & GARNIER, 2002).

1.3.3 Niche Complementary and Phytodiversity in Grasslands

Interspecific relations may also include synergistic or complementary effects if functional traits of species differ. In grasslands differences in *qualitative traits* (e.g. life form, nutritional strategy), *spatial traits* (e.g. microhabitat, growth height, root systems) or *temporal traits* (e.g. phenology) may facilitate complementary use of resources and enable species to settle in a distinct niche and avoid competition. DIERSCHKE (1994) defined a niche as *an n-dimensional hyperspace, whose axes are given by abiotic and biotic factors*. Classical niche theory regards species with similar functions occupying the same niche (GRUBB, 1977), hence two species of the same niche will exclude each other in a habitat (KÖRNER, 1993). Niche differentiation (ND) may enable coexistence of species and may also enhance the overall use resources by complementary.

Segregation of bottom, middle and upper vegetation strata can be referred to as a pattern of ND in grasslands (DIERSCHKE & BRIEMLE, 2002). The upper stratum is often sparse. It mainly consists of flowers and fruits of tall grasses and herbs. The middle stratum is often dominated by species of medium height. The stratum shows considerable leaf areas and thus a maximum of light harvest in grasslands. Hence, the bottom stratum often suffers shading. It consists of sparsely distributed creeping species, rosette plants and geophytes. Herbs show a decline in biomass with height (FLIERVOET, 1984). ND of species in different strata enhances the complementary use of light. A species affiliation to a certain stratum is regarded as a species trait.

Grassland species may elude competition with others by not using the same resources in the same space at the same time as other coexisting species. As a core consensus, species richness or functional diversity is postulated to imply on ecosystem functions through niche complementary.

NAEEM ET AL. (2002) referred to the term 'biodiversity' following HARPER & HAWKSWORTH (1994), as *the extent of genetic, taxonomic and ecological diversity over all spatial and temporal scales*.

Phytodiversity can be regarded as a specification of biodiversity in concern of plant communities. Several authors report of a considerable loss of species richness in ecosystems and their possible implications on ecosystem functions (GRIME, 1973; WHITTAKER, 1975; MC NAUGHTON, 1977; HOOPER & VITOUSEK, 1997; LAWTON, 1994).

Management practices have important implications on grassland composition and species richness. JANSEN ET AL. (1998) found nitrogen and phosphorus fertilization strongly limiting species richness in different European grasslands. BOOTH & GRIME (2003) indicated some stability in phytodiversity due to higher genetic diversity and thus adaptation ability to grazing and trampling. But RYSER ET AL. (1995) and KÖHLER ET AL. (2001) also reported of decreased species richness due to cessation in cutting. The cutting regime is also of relevance, although frequencies higher than three cuts per year tend to decrease species richness, too (ZECHMEISTER ET AL., 2003). Species rich grasslands in Austria tend to show poor profit margins due to lower productivity. ZECHMEISTER ET AL. (2003) questioned the economical value of species richness and considered it only as a factor absorbing agro-environmental subsidies.

Nevertheless, positive relations between taxonomic or functional diversity and ecosystem functions such as productivity are reported by several authors (HECTOR ET AL., 1999; REICH ET AL., 2001; TILMAN ET AL., 2001; VAN RUIJVEN & BERENDSE, 2003). SCHWARTZ ET AL. (2000) reviewed studies about the role of phytodiversity and different ecosystem functions. They confirmed higher productivity at higher levels of phytodiversity, but also pointed out, that many experiments suffer of inflating implications of phytodiversity on ecosystem functions through unrealistic distribution of species abundances (equal species quantities).

WHITTAKER (1965, 1975) suggested that more attention should be given towards functional roles of species (see chapter 1.3.1) in relation to their abundance or productivity. Positive relations between phytodiversity and biomass production require functional complementary (*niche effect*) in respect to resource utilization. A functional approach to understanding phytodiversity, the so called *mass-theory* was developed by GRIME (1998). He attributed biomass productivity predominantely to the performance of *dominant species*. Hence, the diversity of dominant species (ecosystem controllers) representing different functional characteristics is thought to drive ecosystem functions, whereas, *subordinate* and *transient species* are considered accessory for biomass production. Both drive the re-assembly of communities after perturbation by controlling the upcoming of dominant species.

HUSTON (1997) raised attention to the fact that randomly designed experiments show a higher selection probability for the appearance of dominant species in stands of higher phytodiversity. Productivity may hence, be increased by a higher number of dominants and not by increased phytodiversity per se.

TILMAN ET AL. (1997) referred to this "*hidden treatment*" on biomass production in phytodiversity experiments as *sampling effect* and considered it as an intrinsic factor of the relationship between phytodiversity and ecosystem functions (TILMAN, 1996, 1997; NAEEM ET AL., 1994; VAN DER HEIJDEN ET AL., 1998).
This point of view provoked an intensive debate in the following years about the design of phytodiversity experiments. Other authors assumed sampling effects impeding phytodiversity experiments. They stated, that accepting the sampling effect as an intrinsic factor, consequently requires the acceptance of random assembly of semi-natural communities (WARDLE, 1999).

Since studies provided evidence that grassland communities are not randomly assembled (WILSON & ROXBURGH, 1994; GRIME, 1987) and the loss of species is also not at random (KUNIN & GASTON, 1997), sampling effects should be taken into consideration as an additional constraint in interpreting of phytodiversity experiments. Sampling effects may be reduced by expelling gradients between species in respect of the measured ecosystem function and using monocultures as references (WARDLE, 1999). Many authors confirmed this point of view (AARSEN, 1997; GRIME, 1997; HOOPER & VITOUSEK, 1997; GARNIER ET AL., 1997). Species over-yielding in stands of higher diversity above its monoculture biomass was introduced as a tool for avoiding misinterpretation due to sampling effects.

TILMAN ET AL. (2001) gave evidence for considerable over-yielding in grassland stands of higher diversity in comparison to the monoculture level in a long-term experiment. Although, the authors could not show species over-yielding for stands of higher diversity above the monoculture level. Hence, implications of phytodiversity on productivity remained disputable.

Implications of species richness on aboveground productivity (TILMAN, 1997; HECTOR ET AL., 1999; LOREAU ET AL., 2001; REICH ET AL., 2001; VAN RUIJVEN & BERENDSE, 2003) were explained by niche complementary between species traits. Hence, experimental designs focused on functional traits (HOOPER, 1998; TILMAN ET AL., 2001). These authors also found positive correlation between functional diversity and aboveground productivity and claimed niche complementary to be crucial in understanding grassland ecosystem functions.

In respect of water use in grasslands, CALDEIRA ET AL. (2001) found higher soil moisture in species mixtures than in monocultures on Mediterranean BIODEPTH-sites. The authors attributed this finding to enhanced interception due to higher structural aboveground diversity. However, NAEEM ET AL. (1994) did not find any implication of increased biodiversity on water use of grassland stands.

Lower contents of extractable NO_3-N / NH_4-N (N_{min}) were found in soils with stands of higher species richness (TILMAN, 1996; NIKLAUS ET AL., 2001). The latter also reported a decrease in nitrification due to increased phytodiversity in swiss grasslands. SCHERER-LORENZEN ET AL. (2003) reported of decreased NO_3 losses under stands of higher diversity, but attributed this finding to lower contribution of legumes in these stands. NAEEM ET AL. (1994) did not find effects of biodiversity on N_{min} availability in grassland stands.

In the contrary, HOOPER & VITOUSEK (1997) identified stand composition rather than species richness as crucial in concern of limiting N_{min} availability in grassland stands. In the case of nutrient use, increased biodiversity led to significantly lower availability of phosphorus and potassium in ECOTRON experiments (NAEEM ET AL., 1994). However, the latter experiment integrated other trophic levels (herbivores, predators and decomposers). This might explain the different results of the studies.

No results are available about implications of phytodiversity on DOC fluxes in grasslands. Nutritional strategies and mutual interactions may play important roles in this concern.

Summarizing, the implications of phytodiversity on ecosystem functions such as water or nutrient use and thus limiting the availability in soils remain questionable. Many studies showed the development of dominance patterns and great importance of single species in concern of biomass production. Hence competition is likely the driving factor controlling plant species interactions in grasslands. These findings suggest a greater focus on stand characteristics such as stand composition and functional complementary of dominant species in concern of implications on water, nutrient and DOC in grasslands. Focus on dominant species and their functional traits are needed for a better understanding of stand composition implications on grassland ecosystem functions.

1.4 Fe Acquisition Strategies and Rhizodeposition

Plant rhizodeposition comprise soluble exudates (sugars, carboxylic acids, amino acids, phytosiderophores, etc.), mucilage and sloughed off root cells (MARSCHNER, 2002). Enhanced exudation of carbon compounds is generally a stress response to P or Fe deficiency, Al toxicity or anoxia (JONES, 1998). The responses are highly stress- and plant specific (JONES, 1998; ABADIA ET AL., 2002). GRANSEE & WITTENMEIER (2000) and HERTENBERGER ET AL. (2002) confirm plant specific exudation of sugars, amino acids and carboxylic acids. Plants are able to mobilize nutrients in the rhizosphere such as P (JONES, 1998; NEUMANN & RÖMHELD, 1999; GERKE ET AL., 2000ab), Fe (MARSCHNER, 2002; JONES, 1998; MA & NOMOTO, 1996; SCHMIDT, 2003), Zn (WALTER ET AL., 1994; CAKMAK ET AL., 1998) or Cu (GRIES ET AL., 1998) through a *release of organic compounds*, solubilisation of micronutrients and uptake of metal chelates.

Although Fe is abundant in soils (0.2 to 5 %; SCHEFFER, 2002), Fe deficiency is often found in plants growing on alkaline soils (MARSCHNER, 2002; ZHANG ET AL., 1999). Mass flow requires at least a concentration of 10 µM (MA & NOMOTO, 1996), which can only be achieved at pH 3 for in-organic forms (LINDSAY, 1974). With every unit above pH 4, the Fe solubility decreases to the 1000-fold. Plant Fe uptake can be impaired by high HCO_3^- concentrations (NIKOLIC & RÖMHELD, 2002) or alkalization of rhizosphere due to NO_3^- nutrition as shown for *Juncus acutiflorus* (Sharp-flowered Rush) by SMOLDERS ET AL. (1997). ZOU ET AL. (2001) confirmed lower Fe uptake of *Zea mays* (Corn) supplied when supplied with NO_3^- compared to NH_4^+. Leaf chlorosis and reduction in plant growth are symptoms of Fe deficiency (BERGMANN, 1992).

MARSCHNER (2002) distinguished between dicotyledonous (dicots) or non-graminaceous *Fe-strategy I plants* and graminaceous monocotyledonous (monocots) *Fe-strategy II* plants (also ZHANG ET AL., 1999; SCHMIDT, 2003). Strategy I plants respond to Fe deficiency through enhanced fine root growth, ATPase induced efflux of H^+ (DELL ORTO ET AL., 2002) and exudation of *carboxylic acids* (JONES, 1998; ABADIA ET AL., 2002). Decrease in pH enhance the activity of membrane bound reductases and reductive uptake of Fe from *Fe(III)-org complexes.* (JONES, 1998; DE LA GUARDIA & ALCANTARA, 2002). Enhanced exudation under Fe deficiency is confirmed for malate (SCHULZE ET AL., 2002) and for citrate (KIHARA ET AL., 2003; DELHAIZE ET AL., 2003). For the role of phytohormones in response to Fe deficiency see ROMERA ET AL. (1999) and SCHMIDT ET AL. (2000).

Strategy II plants respond to Fe deficiency by increased exudation of non-proteinogenous amino acid like compounds of the mugineic acid family referred to as *phytosiderophores* (PS; MARSCHNER, 2002; ZHANG ET AL., 1999).
For the re-uptake of Fe Phytosiderophore (PS-Fe) complexes, a specific *active uptake system* at the plasma membrane is required (MA & NOMOTO, 1996; WELCH ET AL., 1997; RÖMHELD & MARSCHNER, 1990; BIENFAIT, 1988,). PS exudation is subdued a strong diurnal rhythm (MARSCHNER, 2002) with a peak during the early morning and a high implications of radiation (CAKMAK ET AL., 1998). For PS metabolism see KAWAI ET AL. (1993); MA ET AL. (1995); SAKAGUCHI ET AL. (1999) and NEGISHI ET AL. (2002).

Strategy II plants likely show competition advantages under Fe deficiency compared to strategy I plants. There is no evidence that strategy I plants feature mechanisms for PS uptake. JOHNSON ET AL. (2002) reported of impaired uptake of Ferrioxim B-Fe[1] by *Cucumis sativus* (Cucumber, strategy I) due to its high stability and thus resistance against reduction of Fe (III). CESCO ET AL. (2000; 2002) also showed that this species is less efficient in Fe acquisition from Fe bound to humic substances leached from peat than *Hordeum vulgare* (Barley, strategy II). Lower performance in Fe acquisition was attributed to limitation of *Cucumis sativus* to a reductive Fe uptake, whereas ligand exchange was suggested for *Hordeum vulgare*. ZHANG ET AL. (1999) found that strategy II plants facilitate higher Fe acquisition from supplied $Fe(OH)_3$ than strategy I plants and attributed this finding to higher Fe efficiency of strategy II under alkaline conditions.
The amounts of PS (RÖMHELD & MARSCHNER, 1990; VON WIREN ET AL., 1995) and their structure determine the efficiency of strategy II plants. VON WIREN ET AL. (2000) found hydroxylated PS with higher affinity to Fe (III) and higher complex stability (e.g. *Hordeum vulgare*) than unhydroxylated species. PS-Fe-complexes with stability constants of 18.1 were found (MA & NOMOTO, 1996), whereas citrate and malate show lower affinity and complex stability of 7.1 to 11.5 (MARTELL & SMITH, 1976-1989). Ligand exchange of Fe from PS-Fe to carboxylic acid-Fe is unlikely.

The mobility of Fe chelates and thus the availability for plant uptake can be limited by sorption processes to solid soil surfaces (JONES, 1998; ABADIA ET AL., 2002). Considerable amounts of DOM can be tightly adsorbed to Fe- and Al-oxyhydrooxides (KAISER & GUGGENBERGER, 2000; KAISER & ZECH, 2000). SIEBNER-FREIBACH ET AL. (2003) showed that *Arachis hypogea* (Peanut), a strategy I plant, lacks of mobilizing ability to Ferrioxime B-Fe adsorbed to Ca-montmorrillonite under alkaline conditions.

[1] Siderophore compound released by actimycetes

STRÖM ET AL. (1997) reported of concentrations in soil solution of calcaric Leptosols amounting up to 4.1 µM for malate and up to 2.5 µM for citrate. Considerable amounts of lactic, oxalic, malic and succininc acid were also found in centrifugates of arable soils (WESTERGAARD-STROBEL ET AL., 1999). 1500 µM of malate were found in *Trifolium repens* (White Clover) rhizosphere (BOLAN, 1994) while formate or acetate can amount to 560 or 630 µM (BAZIMARA-KENGA ET AL., 1995) in a *Agropyron repens* (Couch Grass) rhizosphere.
Since exudates are prone to microbial degradation, they drive biological activity in the rhizosphere. DE NEERGARD ET AL. (2002) found 3 to 9 % of ^{14}C assimilated by *Salix viminalis* (Hemp Willow) translocated to SOM and 0.5 to 2.0 % translocated to microbial biomass after 4 weeks. BUTLER ET AL. (2004) confirmed a translocation of 10 % of ^{14}C assimilated by *Lolium multiflorum* (Annual Ryegrass) to the soil with the greatest contribution to microbial biomass (80 to 90 %). DOMANSKI ET AL. (2001) reported of ^{14}C translocation by *Lolium perenne* (Perennial Ryegrass) up to 11 % to SOM, 1.1 to DOC (exudates) and 4.9 % to microbial biomass. This rhizodeposition means a C input into soil up to 0.4 g C m^{-2} d^{-1}.

Enhanced exudation drives microorganism density (BAUDOIN ET AL., 2003), microbial diversity (GRAYSTON ET AL., 1998; TESFAYE ET AL., 2003) and activity FONTAINE ET AL. (2003). It is established that carboxylic acids are utilized carbon substrates for microorganisms (JONES, 1998; ABADIA ET AL. 2002). Citrate and malate are degraded rapidly by rhizosphere microorganisms within 2-3 hrs (JONES & DARRAH, 1994). VON WIREN ET AL. (1994) also reported of high microbial degradation of non-hydroxylated PS. Microbial degradation of Fe-PS complexes is likely impaired due to high stability. Low degradability has been shown for bacterial and fungal siderophores such as Pseudobaction 358 and Ferrioxime B (DUIJFF ET AL., 1994; CROWLEY ET AL., 1991). Hydroxylated PS are likely utilized by microorganisms to a lesser extent.

Higher respiration in rhizosphere of *Lolium perenne* compared to the bulk soil (BUTLER ET AL., 2004) is assumed to be due to enhanced decomposition of SOM within the rhizosphere (*rhizosphere priming effect*, RPE; KUZYAKOV, 2002). Exudates can act as positive primers. KUZYAKOV ET AL. (2001) calculated a positive RPE for *Lolium perenne* amounting up to 6 g C m^{-2} d^{-1} by temporal separation of $^{14}CO_2$-evolution into fast (root respiration) intermediate (exudate respiration) and slow (root decomposition) fluxes. For *Triticum aestivum* (Common Wheat) a RPE of 1.7 g m^{-2} d^{-1} was determined by ^{13}C- and ^{14}C-techniques on soils containing C_4 plant detritus (KUZYAKOV & CHENG, 2001).

Plant induced priming effects are limited to RPEs due to low diffusion ranges of exudates as found for *Zea mays* (limited to 10 mm from root surface, KUZYAKOV ET AL., 2003) and decreasing soluble/non-soluble ratios of compounds with increasing distance from the root surface (WHIPPS, 1984, 1987). HAMER & MARSCHNER (2002) confirmed positive priming effects induced by additions of oxalic acid. FU & CHENG (2002) found positive RPEs in mixtures of C_3 and C_4 grassland plants. CHENG ET AL. (2003) identified considerably higher RPEs in a strategy I plant than compared to a strategy II plant. These differences in RPEs are likely due to chemical composition of exudates released to the rhizosphere. Since Fe acquisition strategies control the composition of exudates to a great extent, they may also affect RPEs.

Plants suffer Fe deficiency due to high HCO_3^- concentrations in soil solution of alkaline soils (LINDSAY, 1974; MARSCHNER, 2002). Increased HCO_3^- concentrations may also be due to physiological effects of predominantely NO_3^- fed plants (SMOLDERS ET AL., 1997). Two strategies for Fe mobilization are found among plants, which both involve the rhizodeposition of organic compounds for solving, chelating and uptake of the Fe chelates (MARSCHNER, 2002). Strategy I plants (dicotyledonous herbal species) feature rhizodeposition of H^+ and carboxylic acids (malate, citrate, a.o.) for mobilization of Fe. Strategy II plants (monocotyledonous graminaceous species) feature rhizodeposition of phytosiderophores. In dependence to their structure, phytosiderophore Fe chelates show a very high stability (MA & NOMOTO, 1996). Higher stability likely reduces the biodegradability of phytosiderophores Fe chelates in contrast to carboxylic Fe chelates, which are prone to being rapidly utilized by microorganisms. Since strategy II plants feature special active uptake mechanisms for phytosiderophore Fe (MARSCHNER, 2002), the utilization of Fe bound to phytosiderophores by strategy I plants is limited (ZHANG ET AL., 1999). Considerable concentrations of carboxylic acids were found in soil solution and centrifugates from arable soils (WESTERGAARD-STROBEL ET AL. (1999). A transfer of rhizodeposited carbon to soil microbial biomass to 0.4 g C m^{-2} d^{-1} was found for *Lolium perenne* (DOMANSKI ET AL., 2001). Hence, microbial density, diversity and activity are driven by rhizodeposition to a great extent (BAUDOIN ET AL., 2003; TESFAYE ET AL., 2003; FOUNTAINE ET AL. 2003). Positive priming effects were found in plant rhizospheres. Rhizodeposits are assumed to function as positive primers (KUZYAKOV, 2002). Increased priming effects in rhizospheres of strategy I species in comparison to a strategy II hint at implications of Fe acquisition strategy in concern of carbon sequestration in grasslands. Only limited knowledge is available about quantity and quality of rhizodeposited carbon of grassland species and potential consequences of competition between strategy I and II plants on rhizodeposition under Fe deficiency.

1.5 Plant Species Implication on Decomposition of Roots

Plant root biomass is the primary source of detritus for soil organic matter (SOM) in grassland soils (DORMAAR, 1992; BURKE ET AL., 1997). In steppe vegetation, horizontal gradients of SOM were found in soils to 30 cm depth between bunchgrass thickets from the edge to the centre of the interspace (LEE & LAUENROTH, 1994; HOOK ET AL., 1994). As KELLY ET AL. (1996) pointed out, this gradient was also found in absence of aboveground litter inputs. BURKE ET AL. (1998) assume that below 5 cm depth, no significant contribution of aboveground litter occurs in steppe grasslands.
It is certain that such a development of *resource islands* (BURKE ET AL., 1998) is less likely for temperate grasslands due to higher density and entangling of root systems. Nevertheless, the contribution of root biomass inputs to SOM formation will be similar. Hence, the development of root systems and root decomposability are important factors of carbon dynamics for temperate grasslands.

The root life span is a determinant of carbon inputs by plants into soils. Root life spans are plant specific. In general they are closely linked to habitat adaptation of grassland species (VAN DER KRIFT ET AL., 2002). The high fertility species *Lolium perenne* features short root life spans to 14 weeks, whereas *Arrhenatherum elatius* (Tall Oat Grass) roots have lower turnover rates with root life spans to 40 weeks. High fertility species predominately show short root life spans and decreased root diameter with certain implications on carbon and nutrient turnover. GILL ET AL. (2002) confirmed this relationship between root life span and diameter for short-grass steppe plants.

In general, litter quality is a determinant of decomposition for leaf tissues (CONN & DIGHTON, 2000; KOUKOURA ET AL., 2003). Higher leaf litter quality does not also imply high root litter quality per se. Decomposability of roots from some palatable species (MORETTO ET AL., 2001) or high fertility species (VAN DER KRIFT ET AL., 2001a) did not differ in decomposition compared to unpalatable or low fertility species. Roots of the high fertility species *Holcus lanatus* (Common Velvet Grass) did not show higher decomposition rates than roots from other grassland species. Lower decomposition was mainly due to lower N contents compared to roots from low fertility species (VAN DER KRIFT ET AL., 2001a).

FOEREID ET AL. (2004) found negative implications of N fertilizer additions on root decomposition. VAN DER KRIFT ET AL. (2001b) did not find implications of fertilization (14 g N m^{-2}) on decomposition of *Holcus lanatus* and *Anthoxanthum odoratum* (Sweet Vernal Grass) roots. Soil amendments with different plant residues leading to immobilizations to 27 mg N kg^{-1} (HADAS ET AL., 2004) suggest enhanced N demand of microorganisms for decomposition of plant tissues in soils. Additional N supply particularly led to a significant increase in rhizodeposition and decomposability of rhizodeposits from *Holcus lanatus* (VAN DER KRIFT ET AL., 2001b). Enhanced rhizodeposit decomposition indicates fast cycling of fertilizer N by *Holcus lanatus*. Under these conditions, rhizodeposits released to the rhizosphere may act as positive primers for root decomposition (also KUZYAKOV, 2002).

Plant specific implications on rhizosphere microflora are mainly assumed to be attributed to exudates release (GRAYSTON ET AL., 1998; BAUDOIN ET AL., 2002; FONTAIN ET AL., 2003). ROBINSON ET AL. (1999) showed that negative or positive effects on decomposition can occur when root litter of different species are mixed.

AS VAN DER KRIFT ET AL. (2001b) pointed out, is the presence of living plants a distinct factor in affecting the decomposition of root litter. In the rhizosphere of *Festuca ovina* (Sheep Fescue) different implications on litter decomposition could be found. *Festuca ovina* root litter incubated in *Festuca ovina* rhizosphere was decomposed faster as compared to bare soil incubation. On the other hand was decomposition of *Anthoxanthum odoratum* litter reduced in *Festuca ovina* rhizosphere. This suggests a certain implication of the identity of root litter in concern of decomposition within plant rhizospheres. It is likely that rhizosphere microflora is not only adapted to exudate compound profiles but also shows adaptation to recalcitrant compounds, which may affect decomposition performance of root litter.
No information about implications of specific root litter identity on mineralisation in different rhizosphere media is available. Besides rhizodeposition characteristics, the adaptation of rhizosphere community to specific root litter may act as another plant induced factor determining carbon sequestration in grasslands.

1.6 Aim of the Study

Within the framework of the project BIOLOG-Bayreuth, the goal was to investigate implications of *stand composition* (functional traits of dominants) and *functional diversity* (number of functional traits) on ecosystem functions of experimental grassland stands.

Ecosystem functions in focus were *biomass production*, *water use*, *nutrient retention* and implications on the release of *dissolved organic carbon* (DOC). Plants differing in qualitative traits (grass / herb) and spatial traits (growth height, leaf structure, and root system) were chosen to identify potential complementary niche effects between species. The grassland stands consisted of dicultures (stand I-III), and two steps of increasing species richness (2, 4 and 8 species in stand I-III, IV, V) and one step of increasing functional diversity (2 and 4 different root systems in stand I-III; IV-V).

Our study focussed on measurements of water, nutrient and carbon fluxes in solution using 28 lysimeter facilities.

Additional pot experiments were carried out in 2003 to study interactions between species of different nutritional strategies (Fe strategy I / II) and their implications on DOC release to the rhizosphere. In a laboratory experiment, the implications of root tissues identity on mineralisation in different rhizosphere media were investigated.

1.7 Hypotheses

The experiments reported in this thesis were designed to test following hypotheses about implications of stand species traits and composition of experimental grasslands on ecosystem functions:

I Functional group's identity rather than functional diversity determines the use of soil borne resources in grassland stands.

Stands with higher grass contribution show:

I_a Enhanced biomass production

I_b Lower evapotranspiration

I_c Lower sequestration of N, K, Mg and Ca in biomass

I_d Increases in mineralisation of soil organic nitrogen

II Fe acquisition strategies of dominant plant species show implications on DOC quantity and quality in rhizosphere solution.

Grassland swards with herb dominance show:

II_a Higher concentrations of DOC in rhizosphere solution

II_b Differences in composition of organic compounds in rhizosphere solution compared to grass dominated swards

III The rhizosphere micro flora is adapted to "host" plant specific release of carbon compounds. The host plant's rhizosphere community performs**:**

Preferential mineralisation of litter derived from its "host" rather than of litter derived from a different plant

2 Materials & Methods

The following chapter is divided into three main parts comprising information about experimental design, installation and sample treatments (analysis) for three experiments concerned with implications of plant traits on water- nutrient and carbon dynamics carried out during 2001 and 2004.

The first part is dedicated to *Experimental Grassland Stands on Lysimeter Facilities* in 2002 until end of 2003. It focuses on the impact of differences in stand composition on water and nutrient fluxes in the soil.

The second part describes in plant species, maintenance, sampling and analysis of carbon compounds in rhizodeposit solution obtained during the *Rhizodeposit Experiment* in summer 2003.

The third part describes the *Root Mineralisation Experiment* in autumn 2003.

2.1 Lysimeter Experiments 2002 / 2003

The lysimeter experiments were planned to investigate possible impacts of different combinations of plant functional traits, such as growth height and rooting depth, on ecosystem functions.

2.1.1 Experimental Design / Introduction of Species

Holcus lanatus L. (*H. lanatus*) was chosen as a central species that occurs in any experimental grassland stand. It was chosen, because it is abundant in grasslands of northern Bavaria and it features a high productivity when meeting adequate environmental conditions (chapter 2.1.1.1). *H. lanatus* was combined with one functionally complementary species in stands I-III (Table 4). To investigate potential beneficial effects of functional complementary in two-species stands on utilization of soil born resources. The species complemented either in different growth height (stand I/II), or in rooting depth (stand I/III), or in physiological differences (stand II/III). To test whether there is a beneficial impact of increased functional diversity on optimal utilization of soil born resources, all three species of stands I-III were gathered with *H. lanatus* to a four-species stand IV.

Table 4 Composition and functional differentiation of species in experimental grassland stands on lysimeter facilities (max. rooting depth according to KUTSCHERA & LICHTENEGGER, 1982, 1992; average growth height according to ROTHMALER, 1994)

Treatments	**Species No.**	**Species**	**Functional differentiation**		
			Functional Group	Rooting depth [cm]	Growth height [cm]
Reference	0	-			
I	2	***Holcus lanatus***	**Grass**	**45**	**30- 100**
		Arrhenatherum elatius		120	60- 120
II	2	***Holcus lanatus***			
		Geranium pratense	Herb	30	20- 60
III	2	***Holcus lanatus***			
		Plantago lanceolata	Herb	90	5- 50
IV	4	***Holcus lanatus***			
		Arrhenatherum elatius			
		Geranium pratense			
		Plantago lanceolata			
V	8	See IV, additionally:			
		Anthoxanthum odoratum	Grass	25	15- 45
		Taraxacum officinale	Herb	210	5- 40
		Alopecurus pratensis	Grass	60	30- 100
		Ranunculus acris	Herb	30	30- 100

In stand V, *H. lanatus* was grown in combination with the three species from stand IV and additionally four species representing the same functional characteristics, but differing in species identity. Thus, stand V was thought to test, whether there are effects of functional redundancy or rather beneficial effects due to increased species richness.

2.1.1.1 Species Description

Holcus lanatus L. (Common Velvet Grass, Figure 2), enduring Poaceae species, 30-100 cm in height, growth lawn alike or in low cushion shaped sparse thickets with creeping sprouts. *H. lanatus* blades are soft, with numerous 0.02 up to 0.95 mm long hairs. The homorhizal root system reaches depths of about 60 cm. (KUTSCHERA & LICHTENEGGER, 1982). *H. lanatus* blooms from June to August with plain a reddish colour. The species prefers collin (max. 300 m above sea level, ESL) up to mountainous (max. 1600 m) elevation zones (ROTHMALER, 1994). ELLENBERG (1991) characterized *H. lanatus* as an ecophysiological indicator of light habitats of medium warmth (Table 5). *H. lanatus* prefers soils with a good water supply and medium Nitrogen availability. It shows enhanced competition ability under high N availability (KLAPP, 1965). According to KUTSCHERA & LICHTENEGGER (1982), the preferred soil texture is from loamy to rich in clay. *H. lanatus* occurs frequently on Cambisols, Fluvisols and other soils with stagnic and gleyic properties. WILMANNS (1998) referred to *H. lanatus* as a typical species of agronomic grasslands in Europe (*Molinio-Arrhenatheretea*) within the order of rich meadows and pastures (*Arrhenatheretalia*).

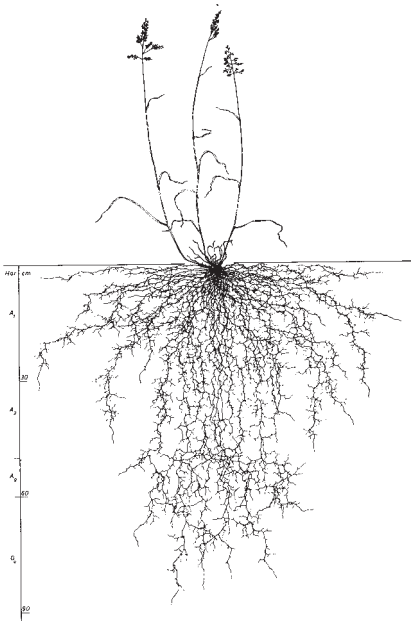


Figure 2 Sectional view of *Holcus lanatus* L. according to KUTSCHERA & LICHTENEGGER (1982), modified

Arrhenatherum elatius L. (Tall Oat Grass, Figure 3), enduring Poaceae species. KUTSCHERA & LICHTENEGGER (1982) described *Arrhenatherum elatius* (*A. elatius*) as a species of 50 up to 180 cm growth height, with a rooting depth of 150 cm up to 250 cm. It grows in huge thickets building up sparse stands. *A. elatius* blooms from June to July with small white coloured flowers. The species occurs in the mountainous elevation zone up to 1600 m ESL (ROTHMALER, 1994). *A. elatius* is described as an indicator of bright habitats of medium warmth.

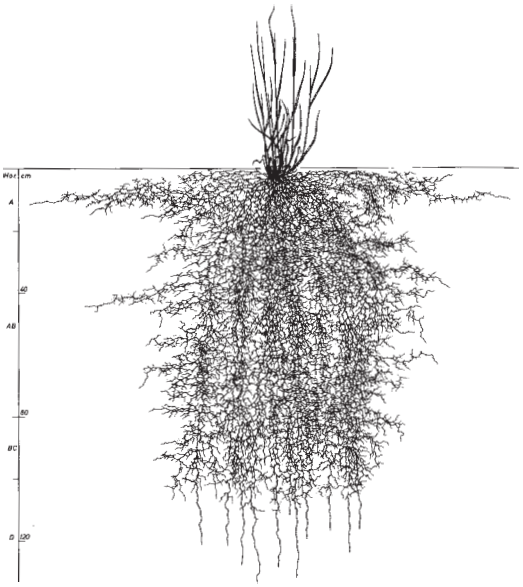


Figure 3 Sectional view of *Arrhenatherum elatius* L. according to KUTSCHERA & LICHTENEGGER (1982), modified

A. elatius is indifferent in concern of soil water supply, but it prefers soils with higher base saturation and N availability (ELLENBERG, 1991, Table 5), where it can acclaim major dominance in grasslands. According to KUTSCHERA & LICHTENEGGER (1982), a sandy soil texture and balanced water supply is preferred. *A. elatius* is the key species of agronomic grasslands in Europe (WILMANNS, 1998). It is name giving for the class of *Molino-Arrhenatheretea* and its orders of dry communities (*Arrhenatheretalia*) including several lower level associations (e.g. *Arrhenatherion elatioris*).

Plantago lanceolata L. (Narrow Leaf Plantain, Figure 4), enduring Plantaginaceae species. KUTSCHERA & LICHTENEGGER (1992) described *Plantago lanceolata* (*P. lanceolata*) as a plant of 5 to 50 cm height. Its leaves are lance-shaped, slightly waxy with some hairs. *P. lanceolata* has a tap-root system with an expansion up to a depth of 90 cm and deeper. It blooms from May to September with small white flowers. It occurs in zone up to sub alpine (max. 2000 m ESL) elevation zones (ROTHMALER, 1994). ELLENBERG (1991) characterized *P. lanceolata* as an ecophysiological indicator of shadow to light habitats of varying warmth (Table 5). It shows no preferences in water supply, reaction and N availability of soils (KLAPP, 1965). According to KUTSCHERA & LICHTENEGGER (1992), the preferred soil texture is sandy. *P. lanceolata* occurs frequently on Cambisols, sandy Fluvisols, profound Leptosols, Calcaric Regosols or Rendzic Leptosols. *P. lanceolata* is a ubiquitous species, which appears on rubble heaps, waysides, meadows and pastures. In Europe, it centres in agronomic grasslands (*Molinio-Arrhenatheretea*) within the order of rich meadows and pastures (*Arrhenatheretalia*) and in dry grasslands associations (*Festuco-Brometea*).

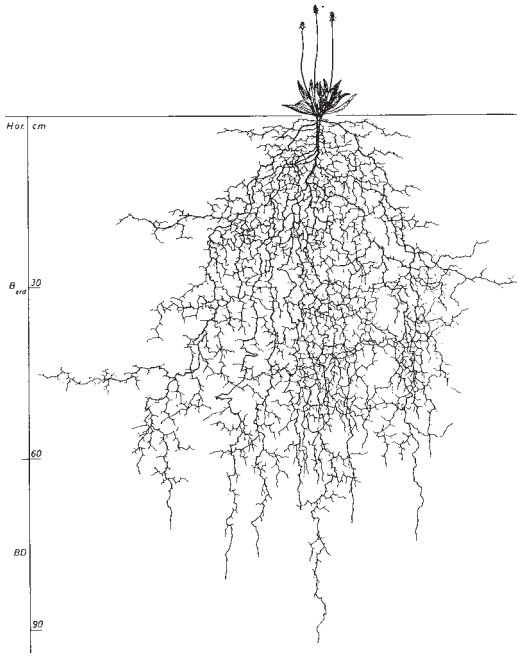


Figure 4 Sectional view of *Plantago lanceolata* L. according to KUTSCHERA & LICHTENEGGER (1992), modified

Geranium pratense L. (Meadow Crane's Bill, Figure 5), enduring Geraniaceae species. KUTSCHERA & LICHTENEGGER (1992) described *Geranium pratense* (*G. pratense*) as a species from 30 up to 80 cm in height. Its root system is cylindrical with one small tap root, branching in several lateral roots. The shallow root system expands merely up to 30 cm depth. The leaf shape is deeply palmately lobed. Their colour is reddish-brown. *G. pratense* blooms from June to August with intensively violet coloured flowers. The species also occurs up to the mountainous zone (ROTHMALER, 1994). *G. pratense* is an indicator of light habitats of higher warmth. It shows lower preferences in concern of soil water supply but demands good base saturation and higher N availability (ELLENBERG, 1991). Its competition ability is highest under higher N availability conditions (KLAPP, 1965). *G. pratense* frequently occurs on Fluvisols with slight gleyic properties and occasionally on Cambisols. WILMANNS (1998) characterizes *G. pratense* as a common species in nutrient rich agronomic grasslands within the association of *Arrhenatherion elatioris*.

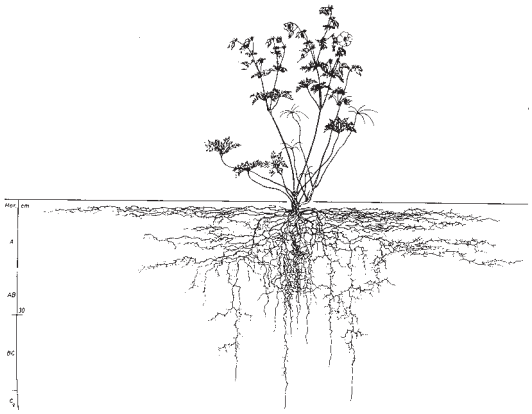


Figure 5 Sectional view of *Geranium pratense* L. according to KUTSCHERA & LICHTENEGGER (1992), modified

Table 5 Ecophysiological indicator values for species used in experimental grassland stands I-IV on lysimeter facilities according to ELLENBERG (1991) and N competition value according to KLAPP (1965)

Species	**L** Light	**T** Temperature	**F** Soil Moisture	**R** Soil Reaction	**N** Soil Nitrogen
Holcus lanatus	7	6	6	x	5
Arrhenatherum elatius	8	5	x	7	5
Plantago lanceolata	6	x	x	x	3
Geranium pratense	8	6	5	8	4
Range of Indicator values	**1-9**	**1-9**	**1-12**	**1-9**	**1-5**

L = 1 shadow indicator – 9 bright light indicator

T = 1 low temperature indicator (alpine conditions) – 9 extreme warmth indicator (Mediterranean conditions)

F = 1 dryness indicator – 12 occasionally or permanently submerged species

R = 1 acidity indicator – 9 base or $CaCO_3$ indicator

N = 1 high competition ability at nil or low N fertilization – 5 high competition ability at high N fertilization (45 g N m^{-2} yr^{-1})

X = indifferent

2.1.1.2 Additional Species of Stand V

Anthoxanthum odoratum L. (Sweet Vernal Grass, Figure 6), enduring Poaceae species. *Anthoxanthum odoratum* (*A. odoratum*) is a species of 15 up to 50 cm height. Its root system is homorhizal, it is shallow with depth up to 30 cm. The blades and roots contain derivates of coumarine, which gives an intensive scent of *Gallium odoratum* (woodruff) (KUTSCHERA & LICHTENEGGER, 1982). *A. odoratum* blooms from Mai to June with small whitish flowers. It occurs up into the sub alpine zone (ROTHMALER, 1994). ELLENBERG (1991) characterized *A. odoratum* as a species with wide ecophysiological amplitude (Table 6). It only shows a preference in soils with at least medium base saturation. *A. odoratum* avoids soils featuring gleyic properties, thus a wide range of European soils can be inhabited (KUTSCHERA & LICHTENEGGER, 1982). It centres within agronomic grasslands in meadows, pastures and waysides of the *Nardetalia* (Mat Grass Meadows) order (ROTHMALER, 1994).

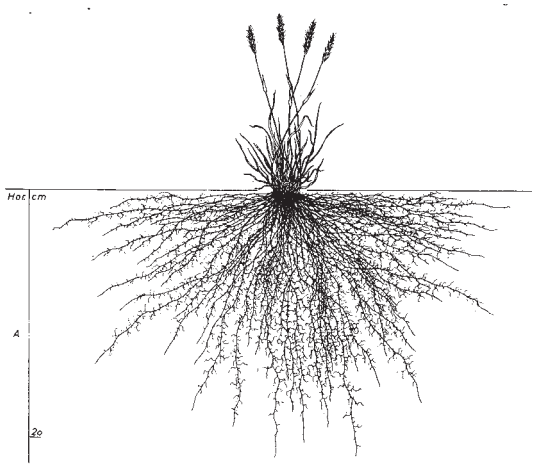


Figure 6 Sectional view of *Anthoxanthum odoratum* L. according to KUTSCHERA & LICHTENEGGER (1982), modified

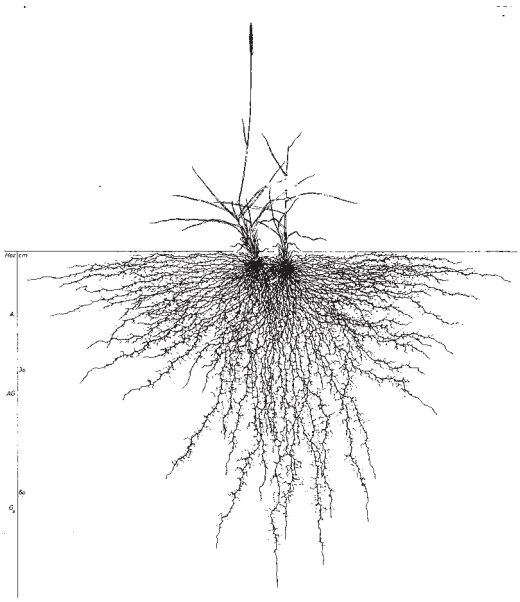


Figure 7 Sectional view of *Alopecurus pratensis* L. according to KUTSCHERA & LICHTENEGGER (1982), modified

Alopecurus pratensis L. (Meadow Foxtail, Figure 7), enduring Poaceae species. *Alopecurus pratensis* (*A. pratensis*) has a growth height from 30 up to 120 cm. Its homorhizal root system expands up to a depth of 60 cm (KUTSCHERA & LICHTENEGGER, 1982). *A. pratensis* blooms from May to June in plain white flowers. It grows up to sub alpine zone and sporadic in the alpine zone (› 2000 m ESL, ROTHMALER, 1994). The species has its centre on habitats in half-shadow up to half-light on soils with good water supply and base saturation with high N availability (ELLENBERG, 1991, Table 6), where it shows pronounced competition ability (KLAPP, 1965) *A. pratensis* prefers sandy up to loamy textured Gleysols, Fluvisols and seldom Cambisols (KUTSCHERA & LICHTENEGGER, 1982). The species occurs in agronomic grassland within moist associations of the *Arrhenatherion* and other orders (ROTHMALER, 1992).

Taraxacum officinale, L. (Common Dandelion, Figure 8), enduring Asteraceae species. *Taraxacum officinale* (*T. officinale*) is grows up to a height of 50 cm. The blades are arranged within a rosette, they contain a milky xylem sap. The root system is allorhizal with a dominating tap root and only less branching. It can occur up to alpine elevation zone (KUTSCHERA & LICHTENEGGER, 1992). The species blooms from April to July in huge and bright yellow coloured flowers (ROTHMALER, 1994). *T. officinale* is characterized as a plant preferring half-light conditions, and high base saturation (ELLENBERG, 1991, Table 6). At high N availability, it shows high competition ability (KLAPP, 1965). It occurs on Gleysols, Fluvisols and on a wide range of Cambisols (KUTSCHERA & LICHTENEGGER, 1992). ROTHMALER (1992) classifies *T. officinale* as belonging to the *Arrhenatherion* and other N rich grassland orders (meadows, pastures, rural sites and waysides).

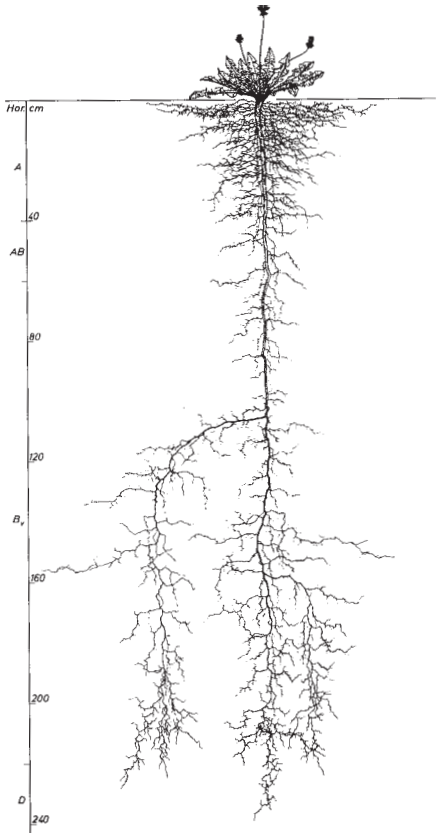


Figure 8 Sectional view of *Taraxacum officinale*, L. according to KUTSCHERA & LICHTENEGGER (1992), modified

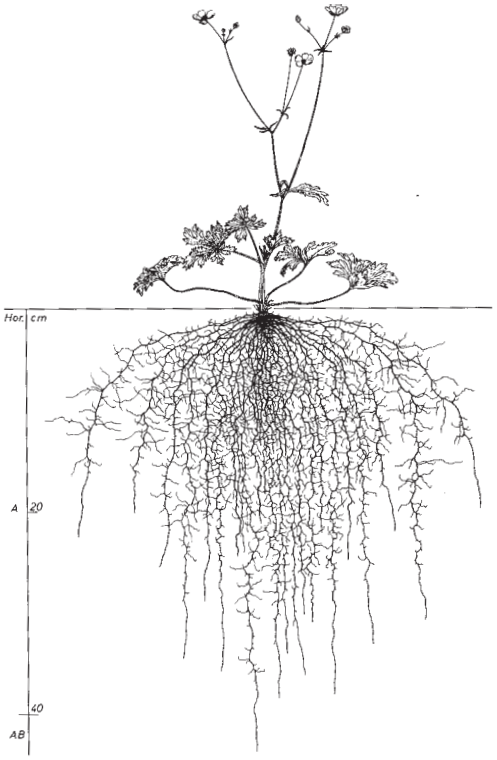


Figure 9 Sectional view of *Ranunculus acris* L. according to KUTSCHERA & LICHTENEGGER (1992), modified

Ranunculus acris, L. (Meadow Buttercup, Figure 9), enduring Ranunculaceae species. *Ranunculus acris (R. acris)* is of a growth height from 30 to 100 cm. It grows in thickets. Its allorhizal root system expands up to 100 cm depth. The leaf shape is palmately lobed. It occurs up to sub alpine elevation zones (KUTSCHERA & LICHTENEGGER, 1992). Blooming is from May to September with whitish-yellow flowers (ROTHMALER, 1994). ELLENBERG (1991) described *R. acris* as an indicator for half-shadow – half-light conditions on soils with good water supply (Table 6). Its occurrence is widespread excluding soils with distinct gleyic properties (KUTSCHERA & LICHTENEGGER, 1992). ROTHMALER (1992) ascribes *R. acris* to meadows, pastures and waysides of *Molinio-Arrhenatheretea*.

Table 6 Ecophysiological indicator values for species used in experimental grassland stand V on lysimeter facilities according to ELLENBERG (1991) and N competition value according to KLAPP (1965)

Species	**L** Light	**T** Temperature	**F** Soil Moisture	**R** Soil Reaction	**N** Soil Nitrogen
Anthoxanthum odoratum	x	x	x	5	n.a.
Alopecurus pratensis	6	x	6	6	5
Taraxacum officinale	7	x	5	8	5
Ranunculus acris	7	x	6	x	3
Range of indicator values	**1-9**	**1-9**	**1-12**	**1-9**	**1-5**

L = 1 shadow indicator – 9 bright light indicator

T = 1 low temperature indicator (alpine conditions) – 9 extreme warmth indicator (Mediterranean conditions)

F = 1 dryness indicator – 12 occasionally or permanently submerged species

R = 1 acidity indicator – 9 base or $CaCO_3$ indicator

N = 1 high competition ability at nil or low N fertilization – 5 high competition ability at high N fertilization (45 g N m^{-2} yr^{-1})

X= indifferent

n.a. no account

2.1.2 Installation & Maintenance

2.1.2.1 Lysimeter Facilities

Figure 10 Part of lysimeter facilities in spring 2002

The lysimeter facilities (Figure 10 – Figure 12) used for the establishment of experimental grassland stands are situated in the *Ecological-Botanical Garden* of the University of Bayreuth (49° 55′45′′ N; 11° 35′10′′ E). The Ecological-Botanical Garden (ÖBG) lies on 360 m above sea level (BOD/gartenuebersicht.html; 2004-10-23). The climatic conditions are classified as temperate with moist summers (HÄCKEL, 1993).

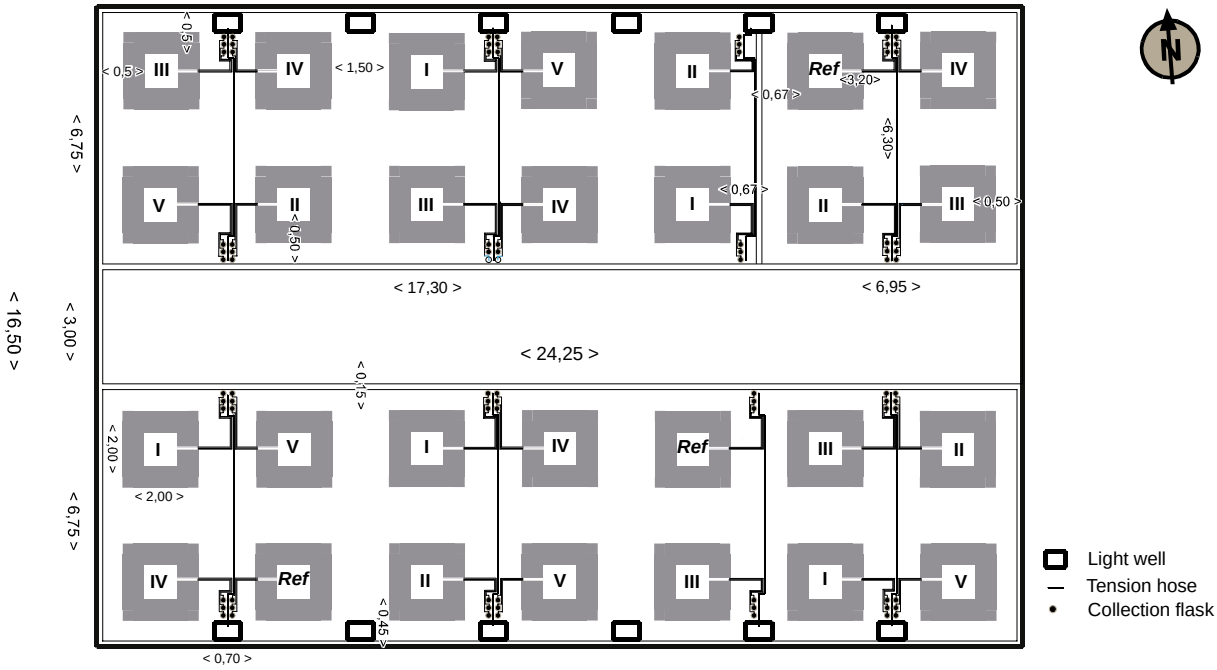


Figure 11 Overview and arrangement of stands on the lysimeter facilities in the Ecological Botanical Garden of the University of Bayreuth

The 28 lysimeter facilities were made from concrete. Before filling, the concrete walls had been smoothened with metal brushes and a special coating (INERTOL 49W) for drinking water protection was applied. The application of the coating was repeated two times. The lysimeter enclose a soil volume of 1.3 x 1.3 x 1m (1.69 m^3) and approximately 0.23 m^3 of drainage.

The layer of drainage gravel is subdivided into an upper layer of 15 cm containing small sized gravel (⊘ 2 to 6.3 mm) and a lower layer of 25 cm containing medium sized gravel (6.3 to 20 mm). The gravel layers were separated by a Geotextile (Opti-flor H 7013, Figure 12).

2.1.2.2 Soil Characterization / Soil Treatments

The filling of the lysimeter facilities with grassland soil was done in summer 2001. For this purpose about 50 Mg of subsoil and 18 Mg of topsoil from nearby the former BIODEPTH-site were excavated and brought to the Ecological Botanical Garden. Within a soil survey, DIEZ (1972) classified the soils which are referred to as poor Cambisols (WRB, 1998) with occasionally appearing stagnic properties. They were derived from silty sandy materials brought in a vast floodplain in upper Triassic age (kmBm, *Mittlerer Burgsandstein mit Basisletten*; EMMERT, 1977). Due to the arid climate in upper Triassic, sediments were delivered periodically by catastrophic flooding and long periods of drying up. These dry periods caused even clay to sediment and led to a build up of lenses and layers of deeply red clay. For recent hydrology of the area, lateral water flows within the soil are of major importance (DIEZ, 1974).

The soil at the excavation site had the following properties: The topsoil layer up to 26 cm depth was subdued ploughing, it is classified as *Ap* (according to AG BODEN, 1996) or as *mollic horizon* (according to WRB, 1998). The Munsell colour was 2.5 YR 5:4. The particle size distribution for this horizon was loamy silt (Table 7).
The horizon below was from 26 to 50 cm depth. Its Munsell colour was 2.5 YR 7:8 derived from iron oxides such as haematite and ferrihydrite. The parent material was characterized by a chaotic side by side of sandy layers, clay lenses and silty layers. The mean particle size distribution was 7 / 68 / 25 mass-%. The bulk density was medium (1.40 Mg m^{-3}). Signs of clay weathering and goethite formation were apparent. Fe and Mn-reduction occurred occasionally, mostly in form of concretions and red mottles in *BvSw* horizon or according to WRB (1998) classified as a *cambic horizon* with *endostagnic properties*.

The Munsell colour in the horizon from 50 to 150 cm was 2.5 YR 8:4. Showing the same variety of particle size distributions, it differed by a distinctly higher bulk density (1.80 Mg m^{-3}). Intensive greyish mottling caused by anoxic processes dominated the horizon. It was classified as *CvSd*. In the lower part of the profile a layer with blocks of accumulated SiO_2 occurred. Both characteristics contribute to its stagnic properties. The soil type was classified as *Pseudogley Braunerde* (AG-BODEN, 1996) or as an *Endostagnic Cambisol* (WRB, 1998).

A mixture of the subsoil horizons (*BvSw*/*CvSd*) was used for filling the lysimeter facilities. After excavation, the subsoil was homogenized by a rotor tiller. Three different grades of compaction were established to find the optimal compaction grade. This grade should prevent water from running down at the lysimeter walls, albeit water should infiltrate easily into the soil. So, each 10 cm of loose subsoil was compacted by a hand tamper to 5 cm depth. The subsoil was filled in 14 single layers. Each surface layer was scratched after compaction to enable better contact to upper layers. The topsoil was steamed for 12 hrs at 100° C for sterilization. After cooling the soil was carefully filled in and slightly compacted by trampling.

One month after filling seed mixtures were sown ensuring even relations in individual seedling numbers of each species. The seedlings were watered, when necessary. Weeds have been removed every month in 2001. In late October the stands were harvested after excessive growth of *H. lanatus* and *P. lanceolata*. All other species seedlings were barely detectable at this time.

Physicochemical Soil Parameters

Soil samples were taken for initial physicochemical parameters. The particle size distribution (Table 7) of the topsoil was silt medium in clay (Ut3, according to AG BODEN, 1996), in subsoil it was Ut4, silt high in clay. The bulk density was very low (Ld 1) for top and low (Ld 2) for the subsoil (according to AG BODEN, 1996).

Table 7 Mean (sd) physical parameters of a Stagnic Cambisol top- and subsoil filled in lysimeter facilities in 2001

Parameter	**Topsoil (0 - 30 cm)**	**Subsoil (30 - 100 cm)**
Particle size distribution [mass-%]		
Sand (63 – 2000 µm)	7 (0)	7 (0)
Silt (2 – 63 µm)	78 (0)	69 (0)
Clay (< 2 µm)	16 (0)	25 (1)
Bulk density [Mg m^{-3}]	1.30 (0.01)	1.49 (0.01)

The pH in topsoil (Table 8) is slightly higher than in subsoil, which is classified as highly acidic (according to AG BODEN, 1996). In grassland soils a pH of 5.6 up to 6.3 should be aimed at (LFL, 2003). The electrical conductivity was significantly higher in the topsoil. This finding indicated higher extractable salt contents in the topsoil.

Table 8 Mean (sd) chemical parameters and contents of extractable nutrients of a Stagnic Cambisol top- and subsoil filled in lysimeter facilities in 2001

Parameter	**Topsoil (0 - 30 cm)**	**Subsoil (30 - 100 cm)**
pH ($CaCl_2$)	4.9 (0.2)	4.2 (0.3)
eC [µS cm^{-1}]	120 (1)	49 (1)
	----------[mg kg^{-1}]----------	
NH_4-N (1 M KCl)	19.6 (9.9)	n. m.
NO_3-N (1 M KCl)	27.0 (9.2)	n. m.
PO_4-P (CAL)	38.2 (0.2)	8.1 (0.2)
K (1 M NH_4Cl)	254.0 (23.6)	279.7 (30.6)
Mg (1 M NH_4Cl)	81.8 (10.2)	297.0 (37.8)
Ca (1 M NH_4Cl)	888.7 (49.8)	835.1 (122.7)

The total content of extractable N (N_{min}) amounted up to 47 mg kg^{-1} (Table 9). SCHEFFER (2002) gave N_{min} ranges in Ah-horizons of 21.8 up to 99.5 mg N_{min} kg^{-1} for grassland soils. Since grasslands can absorb huge quantities of applied Nitrogen, distinct content classes for evaluation N_{min} are not reasonable. According to LFL (2003) inputs should not exceed N removal by far. For CAL-extracts, LFL (2003) gave a range of level B (low) from 22 up to 40 mg PO_4-P mg kg^{-1}.

Table 9 Mean (sd) nutrient stocks in soil used for lysimeter filling in 2001

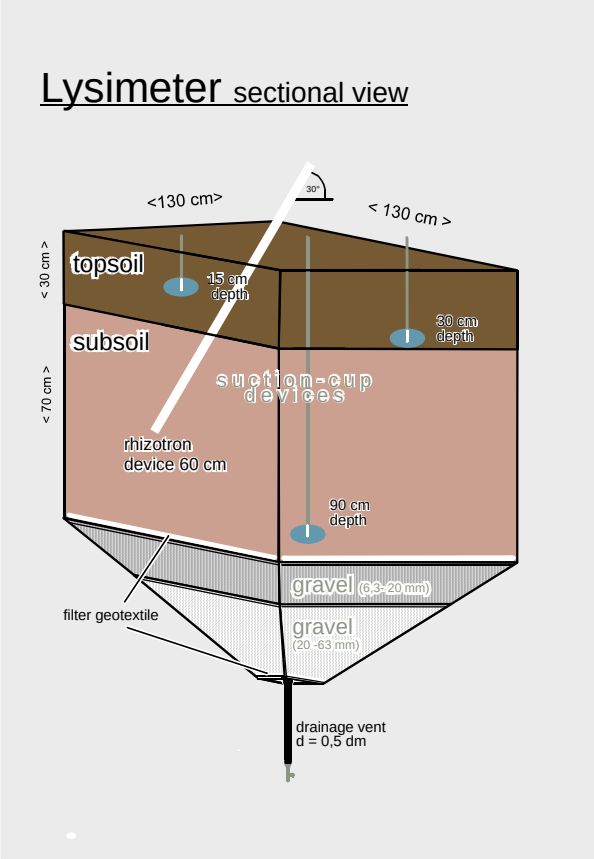
Stock	**Topsoil (0 - 30 cm)**	**Subsoil (30 – 100 cm)**
	[g m^{-2}]	
N_{min}	18.2 (0.7)	n. m.
P	14.9 (0.1)	8.5 (0.1)
K	101.1 (9.4)	297.7 (32.6)
Mg	32.0 (4.0)	620.8 (79.1)
Ca	346.6 (19.4)	871.0 (128.0)

Since K^+, Mg^{2+} and Ca^{2+} have been extracted with1 M NH_4Cl only vague interpretation can be drawn from fertilization suggestions given by LFL (2003). Based on CAL extraction, K availability of 250 mg kg^{-1} is regarded as very high (E). Based on $CaCl_2$ extraction, topsoil contents of available Mg are regarded as low (B), whereas subsoil contents are high (D). The cation exchange capacities (CEC_{act}) of the top- and subsoil (59 / 118 $mmol_c$ kg^{-1}) are regarded as low (SCHEFFER, 2002). AG BODEN (1996) classifies the base saturation of the topsoil (99 % CEC_{act}) as saturated (BS5) and for the subsoil (63 % CEC_{act}) as high base saturation (BS4).

With exception of PO_4-P, huge amounts of nutrients (Table 9) were easily available for plant nutrition and may to some extent be prone of leaching with seepage.

2.1.2.3 Installation and Maintenance

In 2001 one suction cup device per lysimeter was installed in 15 and 30 cm depth (Figure 12). The suction cups are made of acrylic glass (Perspex) on which a ceramic head was attached. This ceramic had a pore size of 100 µm. A capillary (⦰ 1.5 mm) was connected to an evacuated flask, which sampled the soil solution. Two air-pumps were used for evacuation of the flasks. The pumps maintained a permanent tension of 300 hPa. In October 2002 additional suction cups in 90 cm depths were installed and connected to the existing tension device.



Seepage was collected after leaving the lysimeter through a drainage vent using 60 l vessels. These vessels were attached to the drainage vent by a hose.

In October 2002 the subsidiary projects ROOT and SOIL installed rhizotrons made from Perspex (⦰ = 4.6 cm). In respect to requirements for root observation, the facilities were installed at an angle of 30° up to a depth of 60 cm. Subsidiary project SOIL used the rhizotrons were used for probing volumetric soil moisture with aid of a TDR-tube probe (trime RS44). The probe was calibrated to the Perspex material and tested in the laboratory.

Figure 12 Sectional view of a lysimeter device with installed suction cups and rhizotron

The depth of measurement was calculated according to (sin (α) × rhizotron length (subsurface). Since a TDR measurement integrated over a depth of ± 10 cm, three depths (0-20, 20-40 and 40-60 cm) were chosen for determination of soil moisture.

For assessing a conversion factor between measured volumetric soil moisture and gravimetric soil moisture, a small box was filled with subsoil which had been compacted the same manner as in the lysimeters (Figure 13). Six measurements were made for comparison of volumetric and gravimetric soil moisture with a TDR measurement in the vertical middle of the box and three replicated soil samples taken with a drilling rod (⦰ 0.5 cm) close to the rhizotron.

Figure 13 Reference box filled with subsoil for assessment of conversion factors between volumetric soil moisture measured with trime RS44 tube probe and gravimetric soil moisture

A wide but significant correlation between volumetric soil moisture (TDR) and gravimetrical moisture content (Figure 14) was found for calculation of water stored in layers from 0- 20, 20- 40 and 40- 60 cm depth of the lysimeter facilities.

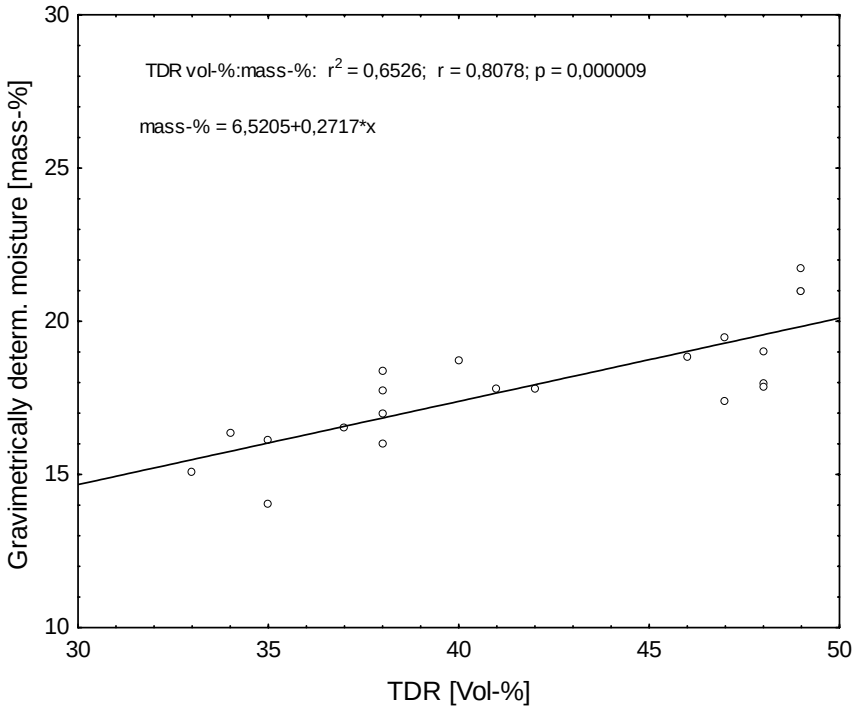


Figure 14 Regression between volumetrical soil moisture and gravimetrical soil moisture content of soil tested in a Reference box in 2002 / 2003

Maintenance

The maintenance of the grassland stands included watering of the stands, periodically weeding of alien plant species and further planting of species end of 2002. Table 10 shows mean climatic parameters for the investigation site. In 2002, irrigation was based on shape of *P. lanceolata* (turgor). In 2002, the mean monthly temperature met the means from 1992 - 2001, whereas the mean precipitation was increased by 234 mm in 2002 (LUEERS, personal notice).

Table 10 Mean temperature and precipitation in the Ecological Botanical Garden for the period 1992 - 2001 and in 2003 according to EBG/klimadaten.html; [1] micrometeorology, LUEERS, personal notice

	Temperature 1992 - 2001 [°C]	**Precipitation 1992 - 2001** [mm]	**Temperature 2003[1]** [°C]	**Precipitation 2003[1]** [mm]
annual mean / sum	7.9	723.6	8.7	476.7
January	- 1.0	60.8	-1.2	83.3
February	- 0.1	45.0	-3.8	17.2
March	3.7	54.6	4.5	10.6
April	6.8	45.7	7.9	26.2
May	12.0	56.3	14.3	73.3
June	14.9	78.9	20.0	23.3
July	17.1	85.7	18.6	49.3
August	16.5	57.3	20.6	20.7
September	12.8	55.6	12.6	40.1
October	8.3	56.3	5.2	63.1
November	3.2	56.9	4.9	19.3
December	0.4	70.5	0.7	50.3

In 2003, the mean monthly temperature was distinctly higher from May to August. The precipitation in spring and summer months was distinctly lower, thus the annual sum matched 248 mm less compared to the mean of 1992 - 2001.

Figure 15 Container for storing precipitation water, collected from the roof of a greenhouse

After installation of the rhizotrons, volumetric soil moisture was used for irrigation control. A minimum threshold was defined as 18 Vol-% in topsoil from 0-20 cm depth (permanent wilting point ≈ 12 %). For irrigation, precipitation was collected and stored in two polythene containers (Figure 15). Irrigation was applied in the evening by using watering cans with a sprinkler to ensure an even distribution of water on the soil surface.

Plant species, which failed to establish in 2002, such as *R. acris*, *G. pratense* and *A. pratensis* (chapter 3.1.2) were cultivated during summer and planted in November 2002 (REUTER, 2005).

In 2002, herbs, especially *T. officinale* showed severe signs of N-deficiency such as dwarf growth, small and crippled young leaves and pail colour. Fertilization was applied in order to compensate for nutrient removal by harvest.

Table 11 Nutrient input by fertilization (Favorit Blau) in 05 and 09, 2002/ 2003

Year	NH_4-N	NO_3-N	PO_4-P	K^+	Mg^{2+}	Ca^{2+}	Na^+	SO_4^{2-}	Cl^-
	[g m^{-2} yr^{-1}]								
2002	7.0	4.7	4.8	1.5	1.4	0.5	0.3	2.6	2.2
2003	6.1	4.3	4.4	1.1	0.6	0.5	0.3	1.9	0.4

The overall N removal with aboveground biomass was estimated 11 g m^{-2} yr^{-1}. After harvest and sampling, in May and September 2002 / 2003 mineral fertilizer (Favorit Blau N / PO / K / Mg, Humuswerk Westerbeck) was applied to the stands (Table 11) in the evening. Due to the dry climate in 2003 (Table 10), stands received further irrigation approximately half an hour before fertilizer application. The fertilizer was solved in water and applied with watering cans onto the stands. After first fertilization the signs of N-deficiency vanished.

2.1.3 Sample Treatment / Analysis

2.1.3.1 Measurements / Sample Treatment

Precipitation was obtained using three Hellmann precipitation gauges situated in the centre of the lysimeter facilities in 2 m height. Sampling took place at weekly frequency. Weekly samples of each gauge were merged and kept in polythene bottles at 5° C until end of the month. Irrigation water and nutrient solution were also stored this way.

Soil moisture was measured at a weekly interval at three depths.

Soil solution was obtained continuously in 15, 30 and additional in 90 cm depth in 2003. The solution was sampled once a month, when possible. In dry summer months often collection times of 2 to 3 months had to be tolerated in order to obtain sufficient sample volume. Seepage was obtained in 100 cm depth. The vessels for collection were sampled weekly. An aliquot was taken and merged in a monthly mixed sample, which was stored in polythene bottles at 5° C.

All precipitation, irrigation water, fertilizer solution, soil solution and seepage solution samples were filtered through cellulose nitrate (Schleicher & Schuell, 0.45 µm) filter pads and stored at 2° C until analysis.

Subsequently to the biomass harvest in May and September, three N_{min}-samples were taken with the help of a drilling rod (⦰ = 1.8 cm). The samples were taken in a depth of 0-15 and 15-30 cm. They were stored in polythene bags and stored at 5° C until further procession. The samples were passed through a sieve (mesh width = 2 mm) and extracted with KCl solution (chapter 2.1.3.2).

In 2002 / 2003 subsidiary project SHOOT harvested aboveground ground biomass at a height of 5 cm above the ground. The samples were dried at 60° C for three days and weighed for dry matter. Subsidiary project ROOT took in-growth core samples for estimation of belowground biomass. The belowground biomass was washed out, dried at 60° C for three days and weighed.

2.1.3.2 Extraction Methods / Analysis

For assessing general soil parameters such as pH, eC and contents of available nutrients following methods and analytical facilities were implemented.

pH_{CaCl2} was measured according to VDLUFA (1991) in a 1 M $CaCl_2$ extract. The electrical conductivity was measured according to SCHLICHTING & BLUME (1995) in a dihydrogen-oxide extract. pH and electrical conductivity were determined potentiometrically.

Cation exchange capacity (CEC_{act}) was measured as Ca^{2+}, K^+, Mg^{2+}, Na^+ und Al^{3+} in an NH_4Cl-extract according to MEIWES ET AL. (1984). Metal cations either in solution samples, extracts or digestion solution (biomass analysis) were detected with the aid of ICP-AES (GBC Integra XMP). NH_4^+ was determined in solute samples or KCl-extracts with help of Flow Induced Analysis (MLE FIA-LAB) with an ammonium indicator. Anions such as NO_3^-, SO_4^{2-} und Cl^- in solution samples were detected with ion chromatography (DIONEX DX 500).

For N_{min} determination, 20 g of sieved soil samples were extracted with 200 ml of 1 M KCl in the overhead tumbler for 1 h. The extraction solution was filtered through a paper filter pad (Schleicher & Schuell 589[3] Blauband, aschefrei) and stored at 2° C until analysis. Another 20 g were incubated at 20° C in a 250 ml syringe for four weeks. The water content of the sample was adjusted to field capacity during the incubation time. The further procedure was in analogy to extraction of fresh N_{min} samples. NH_4^+ in KCl-extracts was converted into NH_3, dissoluted in a dye according to DIN 11732. The extinction of the solution was measured photometrically at a wavelength 259 nm using a FIA (MLE FIA-LAB). NO_3^- in KCl-extracts was converted to a diazonium salt and measured according to DIN 13395 at a wavelength of 546 nm with aid of FIA.

Dissolved organic carbon (DOC) in solute samples was split thermally in synthetic air, Dissolved inorganic carbon (DIC) was removed by HCl and CO_2 was detected by IR-detection (ELEMENTAR highTOC). The determination of solute Total dissolved nitrogen (TN) was done after thermal digestion in O_2-current in form of NO_X with a chemo-luminescence detector. Plant available PO_4 was detected colourmetrically in CAL-extract (VDLUFA, 1991) using FIA (MLE FIA-LAB) after reduction as molybdenum blue dye.

Above- and belowground biomass samples were dissolved by HNO_3 pressure digestion. For this, 100 mg of biomass and 1 ml of HNO_3 s.p. was given into 50 ml quartz digestions flasks and digested at 170° C for 8 hrs. K, Mg and Ca were determined with aid of ICP-AES. Carbon and Nitrogen contents were determined after combustion by Flash EA1112 (Thermo Finnigan).

2.2 Rhizodeposit Experiment 2003

During autumn 2002 four grassland species were germinated in organic growth medium under greenhouse conditions in the Ecological Botanical Garden of the University of Bayreuth (ÖBG) as described by REUTER (2005) and kept until transplantation 2003 into planting pots.

2.2.1 Experimental Design

The experimental design was conceived to test for intra- and interspecific competition under Fe-deficiency. Plant species chosen for this experiment represent two grass and two herb species out of the pool of the eight species planted on lysimeter facilities (Table 12).

Table 12 Species and functional differentiation used for rhizodeposit pot experiments in 2003

Species	**Functional differentiation**		
	Physiology	**Fe Strategy**	**Competitiveness**[2]
Holcus lanatus	Grass	II	+
Anthoxanthum odoratum	Grass	II	--
Plantago lanceolata	Herb	I	+
Ranunculus acris	Herb	I	--

A highly competitive and a species of minor competitiveness of each physiological group and Fe-strategy (MARSCHNER, 2002) were chosen to be grown either in monoculture (4 individuals per species) or in dicultures (2 individuals per species). The plants were transplanted in April within their growth medium pots to ensure optimal taking roots in the hostile quartz sand provided in the experimental pots.

Table 13 Nomenclature for species combinations of the rhizodeposit pot experiments, (n = 4)

Species Combinations	***H. lanatus***	***A. odoratum***	***P. lanceolata***	***R. acris***
Ref	Bare sand	Bare sand	Bare sand	Bare sand
Monoculture	***H. lanatus***	***A. odoratum***	***P. lanceolata***	***R. acris***
Diculture (***Di***)	+ ***A. odoratum***	+ ***P. lanceolata***	**+ *R. acris***	
	+ ***P. lanceolata***	+ ***R. acris***		
	+ ***R. acris***			

Each plant species was combined with each other species in dicultures. The species combinations are shown in Table 13. The design served for identification of intra- and interspecific effects on rhizodeposition. The different species combinations were replicated four times (n = 4).

[2] Competitiveness for biomass build up as observed in experimental grasslands stands in 2001 and 2002

2.2.2 Installation / Maintenance

The planting pots (Figure 16) were made of perspex, they contained a volume of 3405 cm^3 (h = 15 cm, r = 8.5 cm). To sustain UV-protection for plant roots, an aluminium foil was attached to the planting pots. Quartz sand (∅ 200-800 µm; $d_B \approx 1.55$ g cm^{-3}) was used as a growth medium (rhizosphere sand). In order to remove DOC absorbing iron and aluminium oxides, the sand was cleaned with HCl (5 Vol-%) and subsequently purged with demineralised H_2O until the eC was ‹ 10 µS cm^{-1}. A polythene material (Poroplast, cleaned as growth medium) with a pore width of 100 µm was used as filter plate.

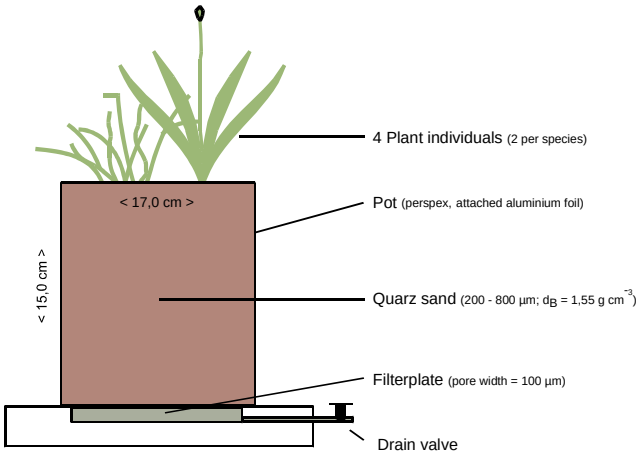


Figure 16 Planting pot used for culture of 4 plant individuals for rhizodeposit experiment

The germination of plant species was initiated in a heated greenhouse under artificial light. During winter 2002 / 2003, the plants were transplanted to approximately 80 cm^3 seized pots made from growth medium. After sufficient penetration with roots, the pots were transported to a cool greenhouse of the ÖBG with ambient temperature and no artificial illumination. The plants were finally transplanted to the experimental planting pots on 04/03/2003. To ensure sufficient growth of microbial species, the sand was inoculated with a sample of 2.5 g of topsoil taken from lysimeter stand V. This stand contained the four grassland species, thus was likely to contain the typical micro flora under these species. Due to that organic growth medium and inoculation supplement, the mean total carbon content of the sand amounted 0.6 to 0.9 mass-%.

Since the experiment was done under open field conditions merely protected by a PVC foil slant, mesoclimatic and radiation effects due to varying exposition had to be taken into account. To avoid flawing of results by position bias, species combination were arranged randomly within a column (Figure 16). A favoured illumination in some parts of the aisle by slanting radiation was reduced by shadings.

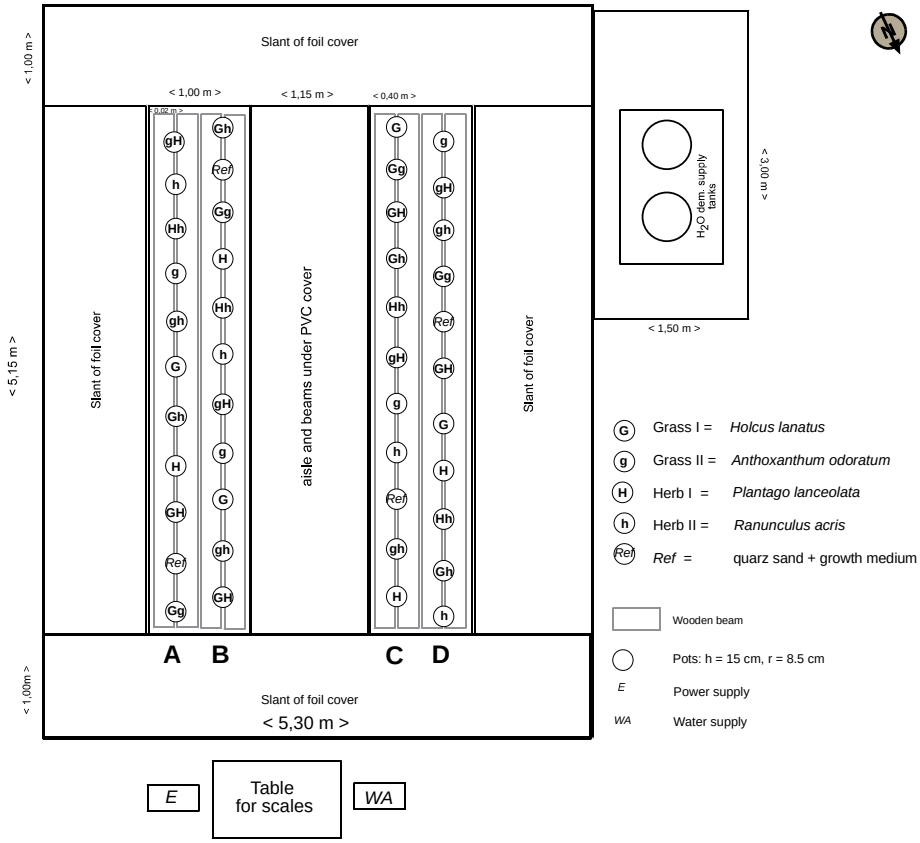


Figure 17 Overview of the arrangement of different species compositions for rhizodeposit pot experiments in the backyard of the BITÖK

Irrigation / Fertilization

The water content was adjusted three times a week with nutrient solution (Table 14) until 100 % field capacity (≈ 900 cm^3). Water losses by evapotranspiration were determined gravimetrically and compensated. The Hoagland solution contained essential nutrients with exception of Fe.

Table 14 Composition of nutrient solution according to Hoagland (modified)

Salt	$Ca(NO_3)_2$	KNO_3	$MgSO_4$	KH_2PO_4	H_3BO_3	$MnSO_4$	$ZnSO_4$	$CuSO_4$	$NH_4MO_7O_{24}$
[µM l^{-1}]	10000	5000	4000	1000	24	15	2	1	1

NH_4^+ was only added in traces ($NH_4MO_7O_{24}$) to avoid physiological acidification of the rhizosphere by NH_4^+ antiport uptake by plants. To avoid osmotic stress, the pots were purged with demineralised H_2O every fortnight. For this, 500 ml H_2O were added twice to produce brief logging. After that, nutrient solution was added and drained off until field capacity (FK) was achieved.

Starting after the 1st harvest, end of July 2003 $FeCl_3$ was added to the nutrient solution to a concentration of 3 µM.

2.2.3 *Sample Treatments / Analysis*

2.2.3.1 Rhizodeposit Sampling

Sampling of rhizodeposits was carried out mid of month. Due to short half life times of many rhizodeposit compounds (e.g. carboxylic acids, sugars), metabolites accumulated since the last sampling had to be purged out of the quartz sand. Purging reduced possible organic compound precipitation due to high cation concentrations. The pots were logged with H_2O-dem. for 20 min, collected in polythene bottles at 2° C until further processing. The logging procedure was repeated and after 20 min the solution was repeatedly percolated and the pots were logged for further 5 min. The solution was drained off into polythene bottles and sterilized by a sodium Ag chloride salt (Micropur, 1 Tabl. = 0.1 g Ag l^{-1}).

Samples for DOC, DON and ion analysis were filtered through cellulose nitrate filter pads (Schleicher & Schuell, 0.45 µm). Samples for HPLC rhizodeposit samples were filtered through glass fibre filter (Whatman GF3) and stored at 20° C until freeze drying.

2.2.3.2 Analysis

In a monthly routine pH and electrical conductivity was determined potentiometrically in purge and rhizodeposit solution. DOM was determined quantitatively as C_t und N_t (LiquiTOC, ELEMENTAR HighTOC). Qualitative analysis was carried out with aid of specific UV-absorbance at 280 nm and emission spectra (E2/E1 435-480 / 300-345 nm, UVIKON 930, BIO-TEK Instruments). Technical problems led to a bias of C and N measurements. Due to low sample volume left, only DOC concentrations were repeatedly measured with HighTOC. (Chapter 2.4.2, Figure 20) shows the regression equation for calculation of spectral analyses.

HPLC Determination of Organic Acids

Analysis of organic acids was conducted by reversed phase HPLC in the ion suppression mode as described by NEUMANN ET AL. (1999), using a reversed-phase C-18 column (GROM-SIL 120 ODS-5 ST; 5 µm particle size, length 250 mm, ID 4 mm, GROM, Herrenberg, Germany) and a guard column (length 20 mm, ID 4 mm;) with the same column material. Isocratic elution was performed at a flow rate of 0.5 ml min^{-1} and a column temperature of 35° C with 18 mM KH_2PO_4, pH 2.25 (adjusted by addition of 85 % o-phosphoric acid). A sample volume of 20 µl (lyophilized sample re-dissolved in HPLC elution buffer and centrifuged for 5 min at 14000 x g) was injected into the flow of the eluent. Organic acids were detected spectrophotometrically at 215 nm. Identification and quantification of the organic acids was performed by comparing the retention times, absorption characteristics at 215 and 250 nm and peak areas with those of known standards.

Determination of Nutrients and Trace Metals

In solution, $Fe^{2+/3+}$, Zn^{2+}, Cu^{2+}, Mn^{2+}, K^{+}, $Mg^{2+}$and Ca^{2+} were detected with aid of ICP-AES (GBC Integra XMP). NH_4^{+}, PO_4^{3-} was determined coloumetrically with Flow Induced Analysis (MLE FIA-LAB). Ion chromatography (DIONEX DX 500) was used for detection of NO_3^{-} and SO_4^{2-}.

Aboveground and belowground biomass was dried at 60° C for three days, and subsequently ground in a zirconium ball mill. The samples were dissolved by HNO_3 pressure digestion. For this, 100 mg of biomass and 1 ml of HNO_3 s. p. was given into 50 ml quartz digestions flasks and digested at 170° C for 8 hrs. Metals and trace metals were also determined by ICP-AES (GBC Integra XMP).

Chlorophyll contents in leaves of *H. lanatus* and *P. lanceolata* were measured colormetrically with a N-Test (Hydro-Agri GmbH Dühmen).

2.3 Root Mineralisation Experiment 2003

After finishing the rhizodeposit pot experiment, root tissue biomass and rhizosphere sand were obtained to test for respiratory parameters. For this purpose, tissues of a grass (*H. lanatus*) and a herbal species (*R. acris*) were incubated in different types of rhizosphere sand also obtained at the rhizodeposit experiment. The species differed in root biometrical characteristics (Figure 18, Table 15). The rhizosphere sands comprised of different rhizospheres of *H. lanatus*, *R. acris* and *H. lanatus*/*R. acris* diculture (*Di*) as well as *Ref.*

Sample Treatments / Analysis

The obtained biomass was thoroughly washed out over a sieve of 630 µm mesh width. One part of the root biomass was stored at 2° C, the other was dried for three days at 60° C. Fresh biomass was biometrically analysed. A. REUTER (subsidiary project ROOT) carried out determination of root length densities, total surface area and total volume of root biomass, using an optical scanner and WINRhizo software.

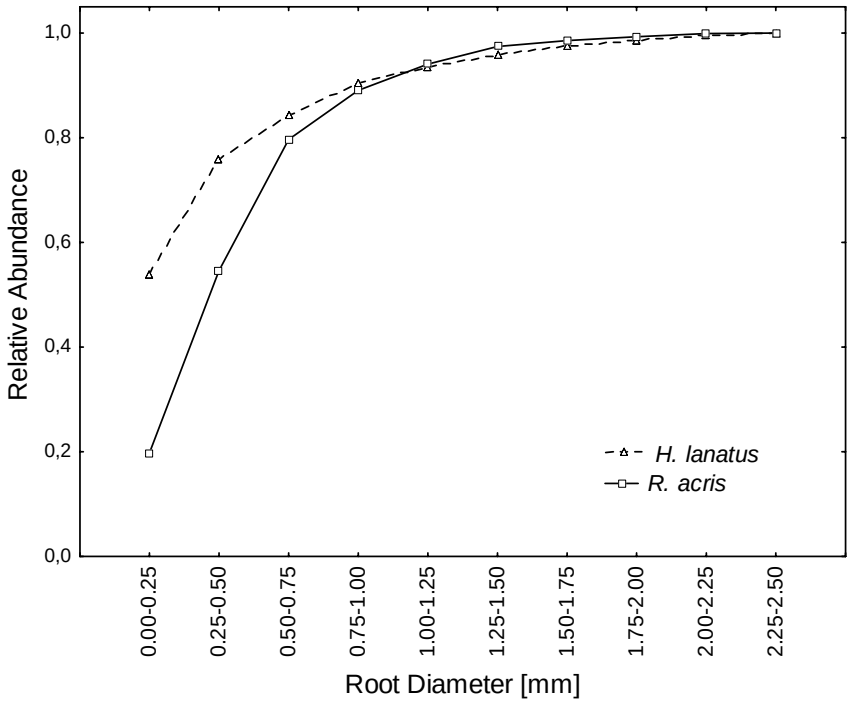


Figure 18 Median relative abundance of root diameter classes for *H. lanatus* and *R. acris* biomass
(A. REUTRER, personal notice)

For both species, most root biomass was found within the diameter classes below 0.75 mm. Due to its homorhizal root system, *H. lanatus* showed a higher relative abundance in fine roots to 0.25 mm than *R. acris*. 50 % of *H. lanatus* roots had a diameter of to 0.25 mm, whereas *R. acris* showed the main amount of roots within the class 0.25 to 0.50 mm.

Root length density, root surface area and root volume were significantly higher for *H. lanatus* than for *R. acris* (Table 15). These differences allowed to test whether morphological root parameters show impacts on root mineralisation.

Root tissue C/N was determined at the *Chair of Plant Nutrition of the Alexander von Humboldt University* Berlin with aid of a C/N Elementanalyzer (varioMAX-CNS).

Table 15 Median (25th /75th Percentile) of root biometrical parameters used for root mineralisation experiments

Parameter	*H. lanatus*	*R. acris*	MW-U	KW-H	*P*
Root length density [cm 100 mg^{-1}]	1038 (985/1150)	220 (190/222)	*	5.30	0.021
Root surface area [cm^2 100 mg^{-1}]	133 (125/153)	37 (36/38)	*	5.30	0.021
Root volume [cm^3 100 mg^{-1}]	1.4 (1.3/1.6)	0.5 (0.5/0.6)	*	5.40	0.020

(Kruskal-Wallis-ANOVA, Mann-Whitney U-Test; dF = 3)
A. REUTER, personal notice

The median C and N contents (Figure 19) did not differ significantly between root of *H. lanatus*, *R. acris* and dicultures of both species. The median C/N-ratio was tendentiously higher for *H. lanatus* (27.2) than for *R. acris* (14.9) and diculture root biomass (19.6, Kruskal-Wallis-ANOVA: dF = 2, F =3.73, *p* =0.155, N=12).

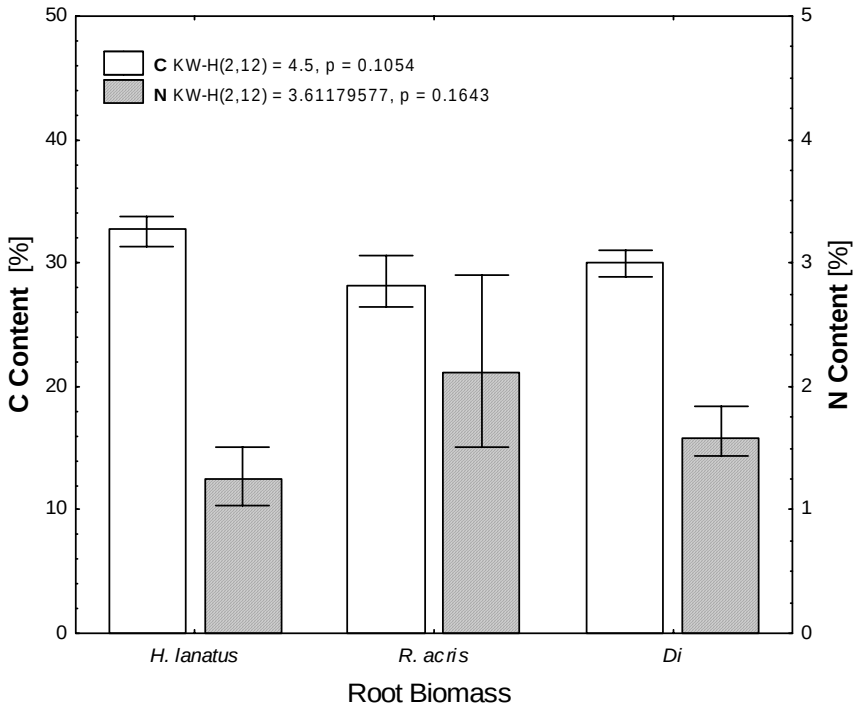


Figure 19 Median (25th / 75th Percentile) of C and N contents for *H. lanatus*, *R. acris* and diculture root biomass

C Kruskal-Wallis H (2,12) = 4.5, *p* = 0.105
N Kruskal-Wallis H (2,12) = 3.6, *p* = 0.164

The rhizosphere sand was analysed for contents of C_t by combustion (Table 16). DOC was extracted with 0.01 M $CaCl_2$. For this 10 g of rhizosphere sand were extracted with 50 ml $CaCl_2$ for 1 hr in an overhead-tumbler. Total DOC was detected by Shimadzu TOC 5050. UV-Absorbance of extracts was determined at 254 and 280 nm wavelength by Perkin & Elmer Lambda 5000. No significant differences between growth media could be detected, with exception of slightly lower C_t contents in *Ref*.

Table 16 Median (25th /75th Percentile) carbon characteristics of rhizosphere sand used for mineralisation experiments

Parameter	***Ref***	***H. lanatus***	***R. acris***	***Di***	MW-U	KW-H	*P*
C_t [mg C g dm^{-1}]	5.7 [b] (5.2/5.8)	8.3 [a] (8.0/8.8)	7.6 [a] (7.3/8.3)	8.0 [a] (7.0/ 8.2)	*	10.41	0.015
DOC [mg C l^{-1}]	2.8 (2.7/4.8)	4.0 (4.0/4.1)	4.5 (3.5/4.6)	3.2 (2.4/3.5)	n. s.	4.43	0.218
Absorbance 254 nm	0.03 (0.03/0.03)	0.03 (0.02/0.03)	0.03 (0.02/0.03)	0.027 (0.023/0.028)	n. s.	0.44	0.931
Absorbance 280 nm	0.02 (0.02/0.03)	0.02 (0.02/0.23)	0.02 (0.02/0.03)	0.02 (0.02/0.04)	n. s.	0.32	0.955

(Significant differences are indicated by different letters; Kruskal-Wallis-ANOVA, Mann-Whitney U-test, n = 3)

Measurements of rhizosphere sand respiratory parameters (Table 17) were carried out according to ANDERSON & DOMSCH (1978). CO_2 was determined by Gas Chromatography (Hewlett-Packard 6890) at 20° C. Sand samples were equilibrated for 3 hrs in 120 ml glass flasks. The determination of microbial biomass and mineralisation rates was carried out with sugar addition.

Table 17 Median (25th/75th Percentile) of respiratory parameters of rhizosphere sand used for mineralisation experiments

Parameter	***Ref***	***H. lanatus***	***R. acris***	***Di***	MW-U	KW-H	*P*
Basal respiration [CO_2-C µM g^{-1} dm h^{-1}]	0.15 (0.11/0.32)	0.18 (0.17/0.24)	0.19 (0.16/0.25)	0.19 (0.12/ 0.25)	n. s.	0.44	0.933
Microbial biomass [mg g^{-1}]	0.60 (0.58/0.62)	0.72 (0.72/0.79)	0.77 (0.74/0.79)	0.62 (0.61/0.63)	n. s.	0.44	0.933
qCO2 [µM C g $Cmic^{-1}$]	256 (180/511)	248 (209/337)	245 (209/339)	310 (198/417)	n. s.	0.13	0.988

(Significant differences are indicated by different letters; Kruskal-Wallis-ANOVA, Mann-Whitney U-test, n = 3)

For calculation of microbial biomass 23 µM CO_2 g dm^{-1} hr^{-1} were taken as equivalent to 20.6 mg C_{mic} g dm^{-1} (ANDERSON & DOMSCH, 1978). Metabolic quotient (qCO_2) was determined according to ANDERSON & DOMSCH (1990). No significant differences in respiratory parameters were observed, thus the requirements for further incubation were given.
For element analysis, dried biomass was ground by a zirconium ball mill and digested by HNO_3 pressure digestion. For this purpose, 100 mg of biomass and 1 ml of HNO_3 s.p. was given into 50 ml quartz digestions flasks and digested at 170° C for 8 hrs. P, K, Mg and Ca were determined with aid of ICP-AES (GBC Integra XMP).

Carbon and Nitrogen contents were determined after combustion by ELEMENTAR, highTOC.

The rhizosphere sand was also stored at 2° C until further procession. After first evaluation of suitability of the rhizosphere sand, sand and root samples were transferred to a Respicond devise at *Chair of Soil Geography and Soil Ecology of the Ruhr University Bochum*. CO_2-evolution was measured continually once an hour (Respicond apparatus, Nordgren Innovations, Bygdea, Sweden). CO_2 was accumulated in 10 ml of a 0.6 M KOH and changes in electrical conductivity were used for calculating CO_2-evolution per hour. The whole measurement period of 236 hours was supervised by U. Hamer. After 90 hrs KOH solution was exchanged by fresh solution.

For decomposition measurements, 2.5 g fresh matter root biomass was inoculated in 10 g of moist (FK) rhizosphere sand. The addition of *H. lanatus* root biomass increased the carbon content of the growth medium by 1.6 mg C to 8.3 mg C g dm^{-1}; whereas *R. acris* root biomass increased the carbon contents by 0.9 g C top 7.6 mg C g dm^{-1}.

2.4 Calculations of Indices / Statistics / Computing

Indeces used for assessment of grassland stands (Lysimeter experiment)

The ratio between annual nutrient loss with seepage and aboveground yield was used to differentiate productive grassland stands with high nutrient seepage loss from productive stands with low nutrient seepage loss.

$$\textbf{Loss/yield-ratio} = \Sigma_{\text{nutrient loss}} / \Sigma_{\text{nutrient yield}} \qquad \text{(Equation 1)}$$

Nutrient loss = nutrient loss with seepage [g m^{-2} yr^{-1}]
Nutrient yield = nutrient aboveground yield [g m^{-2} yr^{-1}]

Indices used for determination of plant competition (Rhizodeposit Experiment)

Relative yield total (RYT, DE WITT, 1960) was calculated for identifying interspecific competition in dicultures by RYT. The competition ability of single species was calculated by Cab (WILSON, 1988). Both competition indices were used for determining competition in concern of species biomass, individual biomass and for Fe contents in species and individual biomass according following equations:

$$\textbf{RYT} = 0.5 \times [(dm_{ab} / dm_{aa}) + (dm_{ba} / dm_{bb)}] \qquad \text{(Equation 2)}$$

$$\textbf{Cab} = \log_e [(dm_{ab} / dm_{aa}) / (dm_{ba} / dm_{bb)}] \qquad \text{(Equation 3)}$$

dm_{aa}, dm_{bb} = biomass [3] / Fe content [4] of species a/b in intraspecific competition (monoculture) [g dm pot^{-1}]
$dm_{ab,}$ dm_{ba} = biomass / Fe content of species a/b in interspecific competition (diculture) [g dm pot^{-1}]

Table 18 Interpretation of competition indices relative yield total (RYT, DE WITT 1960) and Competition ability (Cab, WILSON, 1988)

Index		Interpretation
RYT	**≈ 1**	Complementarity between species a and b
	‹ 1	Competition between species a and b
Cab	**≈ 0**	Complementarity between species a and b
	› 0	Species a with higher competition ability
	‹ 0	Species b with higher competition ability

[3] [g dw species m^{-2}, g dw $individual^{-1}$]
[4] [mg Fe g^{-1}, mg Fe $individual^{-1}$]

2.4.1 Explorative / Statistical Procedures

Kohonen's self organizing maps

A *self organising map* procedure (KOHONEN, 2001) was used for a first explorative analysis and visualization of soil solution data (attributes, such as pH, eC, N_{min}, K^+, Mg^{2+}, Ca^{2+} and DOC) of grassland stands in lysimeter facilities for 2003.

This artificial neuronal network was computed according to WAGNER ET AL. (2004). Data were z-standardized [(x_i – arithmetic mean)/ sd] and similarity between replicates was calculated as Euclidean distance. Since data distribution is not of importance for *Kohonen's maps*, no normalization procedure was applied.

The neuronal network consists of multiple nodes arranged within a regular formation. A node is represented by a vector, which dimensions are set by the number of attributes entering the analysis. The first phase of computing *Kohonen's maps*, the training phase starts with a random arrangement of nodes. Data node vectors are compared to attribute vectors and are adjusted to the most similar data vector.
For a given attribute the most similar node vector is called the *winning node*. Adjusting to attribute vectors was also carried out for the next neighbour nodes with a decrease in weight in proportion to the distance to the winning node. The training phase was repeated multiple times to optimize adjusting of multidimensional node vectors to the given attribute vectors. At the end of the training, at least each data vector was similar to a node vector. Nodes of high similarity were next neighboured to each other with a increase in distance with decreasing similarity. Data were assigned and thus classified to trained winning nodes.
Due to the fix network grid, the distances between single nodes were regular. In order to enhance the visual interpretation, coordinates of nodes were shifted iteratively. *Sammon's mapping* (SAMMON, 1969) allowed to shift node vectors in inverted proportionality to their similarity. The regular network is shifted towards a "elastic" net which reflected similarity of nodes by distances between the nodes more effectively.

For graphic visualization, nodes, which were not assigned to attributes during the training, were erased. The winning nodes were visualized in a topological map for single attributes (layer of components) as well as aggregated for different grassland stand replicates. To identify multiple assignations and avoid loss of information, the origin of samples was checked. Topological distances between replicates of each stand were tested for significance using a *Kolmogorov-Smirnov Z-test*.

Univariate / Multivariate Parametric Procedures

Data obtained on the lysimeter facilities were predominantly not normally distributed (*Kolmogorrow-Smirnov / Shiparo-Wilk-Test*). They were log-transformed to bring them near normality. Since data were log-transformed, any average value given in Table 20 - 53 and Figure 21 – 40 is a re-transformed arithmetic mean ($\bar{x}$) without measure of deviation. Log-normalised data were screened with a *multi factorial ANOVA* (*MANOVA*) for implications of depth, stand and depth×stand on soil solution concentrations or soil moisture. *One way ANOVA* was used to test for differences between treatments (*Ref* / stand I-V) for identification of significant differences *Tukey's Honestly Significant Difference Test* (*HSD-Test*) was performed as post hoc test for identification of significant differences between group means.

Univariate Parameter Free Procedures

Data of rhizodeposit pot and root mineralisation experiments also lacked normality. Since log-transformation did not result in appropriate closure to normality, data were calculated parameter free. In Table 54–76 and Figure 41-52 means are given as median values with 25^{th} and 75^{th} Percentile. Significant differences within populations were calculated with help of *Kruskal-Wallis-ANOVA*. *Mann-Whitney U-Test* was used as a post hoc test for identification of significant differences between group medians.

2.4.2 Conversion of DOC Concentrations / Outlier Definition

Due to technical problems, DOC measurements of rhizodeposit with our LiquiTOC device had to be repeated from sterilized samples, which were stored at 20° C below zero. Since no solution was left for further measurements of NO_3^-, DON-calculations were rejected.

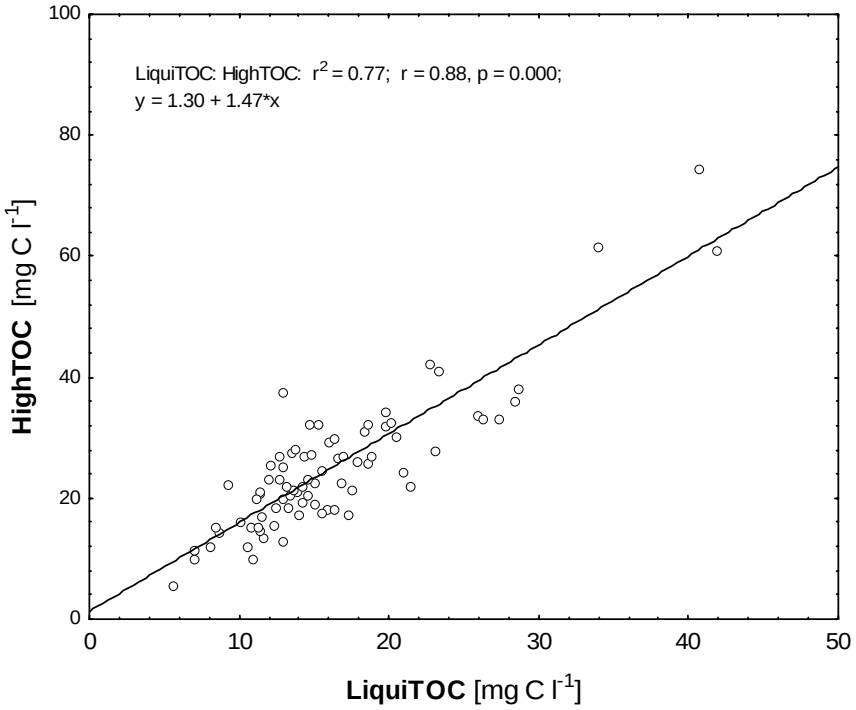


Figure 20 Regression between LiquiTOC and HighTOC C concentration data

Synchronous Fluorescence and Emission spectra were conversed by a regression function (Figure 20). A comparison between un-conversed LiquiTOC and conversed HighTOC data is given in Appendix, Table XIX – XXI.

Outlier Definition

For the mineralisation experiment, intolerable deviation (*outliers*) was defined as *remaining of a replicate below 50 % of the 25th Percentile treatment median* or *exceeding* of a replicate the *treatment's 75th Percentile more than two-fold.* One replicate of following treatments were excluded from statistical calculation: *Ref*, Di and *R. acris* in *H. lanatus rhizosphere sand*. A comparison between original and processed data is given in Appendix, Table XXII – XXIII.

2.4.3 Computing

- Data were computed under OS *MS Windows XP* multilingual, using *Excel*, *Access* and *Word* of the *MS Office 2003* English package.
  (http://www.msn.com)

- Statistics were calculated with aid of *Statistica 6.1* German (StatSoft, Inc., 2004). STATISTICA für Windows [Software-System für Datenanalyse]
  (http://www.statsoft.com)

- Sectional views and overviews were created with aid of *Freehand 10.0* (Macromedia, Inc.(http://www.macromedia.com)

- Kohonen's maps were computed using the software *SOM_PAK*, supplied by Neural Networks Research Centre, Helsinki University of Technology, Finland.
  (http://www.cis.hut.fi/research/som-research/)

  Subsequently, data were transferred to *MS Excel 2000* by implementing a *Fortran Routine* (G. LISCHEID, personal notice) and were visualized with aid of *Statistica 6.1*.

3 Results & Discussion

The following chapter presents results of the lysimeter experiments in 2002 and 2003, results obtained from the rhizodeposit pot experiment and the root mineralisation experiment in 2003.

3.1 Experimental Grassland Stands on Lysimeter Facilities in 2002 / 2003

3.1.1 Stand Composition / Biomass Characteristics

In 2002, the aboveground composition of our experimental grassland stands I-V showed distinct dominance patterns with a single or, in co dominance two species prevailing (Figure 21).

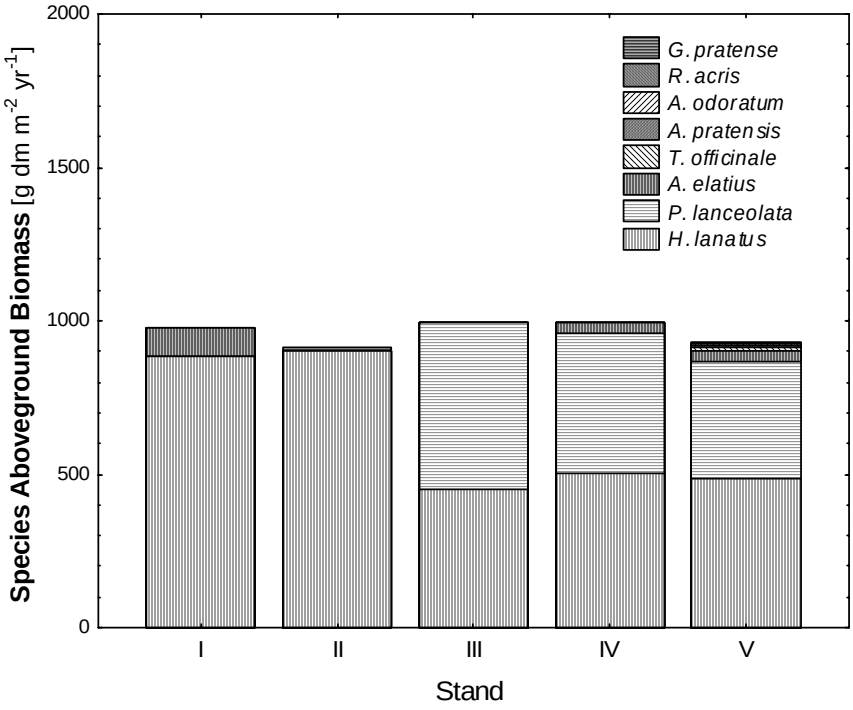


Figure 21 Mean species aboveground composition of experimental grassland stands I-V in 2002 (Raw data: NEßHÖVER & BEIERKUHNLEIN, unpublished)

Stand I and II were dominated by *H. lanatus* and stands III-V were co dominated by *H. lanatus* and *P. lanceolata* with almost equal contribution of both species (Table 19). All other species, with exception of *A. elatius* (subordinate), contributed less than 5 % to aboveground biomass yield in 2002. This finding is likely explained by rapid growth and dense biomass layers of the dominant species, which hindered germination and establishment of the other species as reported for *T. officinale* (OPITZ VON BOBERFELD, 1994).

MARIOTT ET AL. (2003) reported of fallow grasslands, which shifted towards *H. lanatus* dominance within seven years of succession at high precipitation (to 1000 l m^{-2}) without fertilizer application. *H. lanatus* and *P. lanceolata* are both well known to spread rapidly in early successional phases and in sparse grassland stands (OPITZ VON BOBERFELD, 1994; DIEPOLDER, 2001).

In 2003, the species aboveground biomass composition of our experimental grassland stands changed drastically during spring (Figure 22). Dominating *H. lanatus* sprouted very early in the end of January. Subsequent stress due to reappearing frost, led to a die back of aboveground biomass of *H. lanatus* to a large extent.

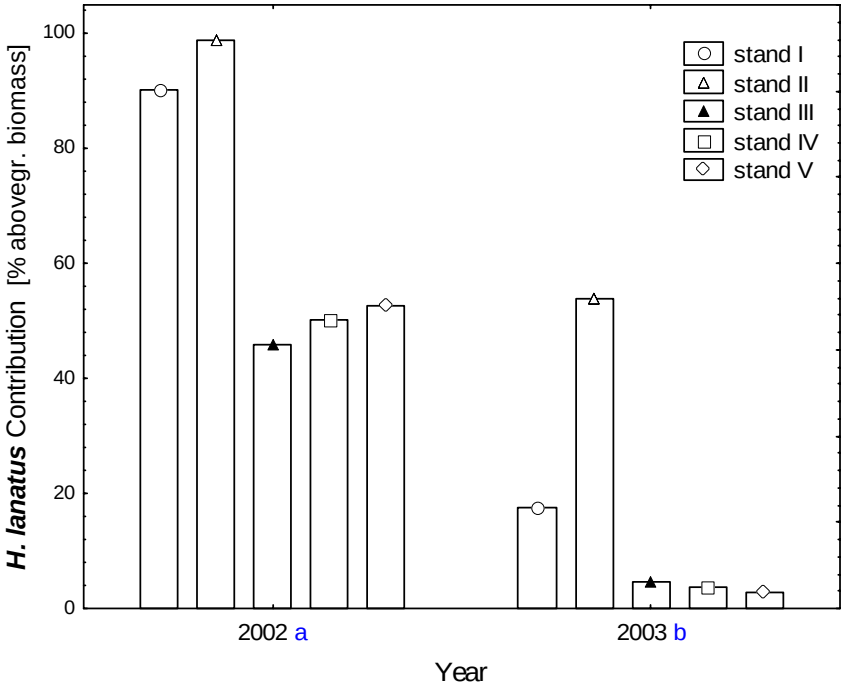


Figure 22 Comparison of *H. lanatus* contribution to aboveground biomass of experimental grassland stands I–V between 2002 and 2003

Significant distinctions between years for all stands are indicated by different letters (multifactoral-ANOVA: dF = 4, F: 4.17, p ‹ 0.01; Tukey HSD **; stand I-V n = 5; raw data 2002: NEßHÖVER & BEIERKUHNLEIN; 2003: TÜNTE & BEIERKUHNLEIN, unpublished)

OPITZ VON BOBERFELD (1994) characterized *H. lanatus* as a species preferring oceanic climates. In Bavarian grasslands, *H. lanatus* is known to be sensible when exposed to water stress induced by drought or frost (DIEPOLDER, personal notice).

Necrotizing of *H. lanatus* biomass, very likely led to increased input of belowground detritus in spring 2003. In stand I, *A. elatius* replaced dead *H. lanatus* entirely and provided considerable aboveground biomass (Figure 23). *G. pratense* substituted dead *H. lanatus* biomass to a great extent in stand II. The composition of stand III shifted considerably to almost a monoculture of *P. lanceolata*.

In analogy to 2002, dominant and subordinate species determined the stand composition of our grassland stands in 2003 (Figure 23, Table 19). *A. elatius* substituted *H. lanatus* as dominant grass species in stands I and III-V.

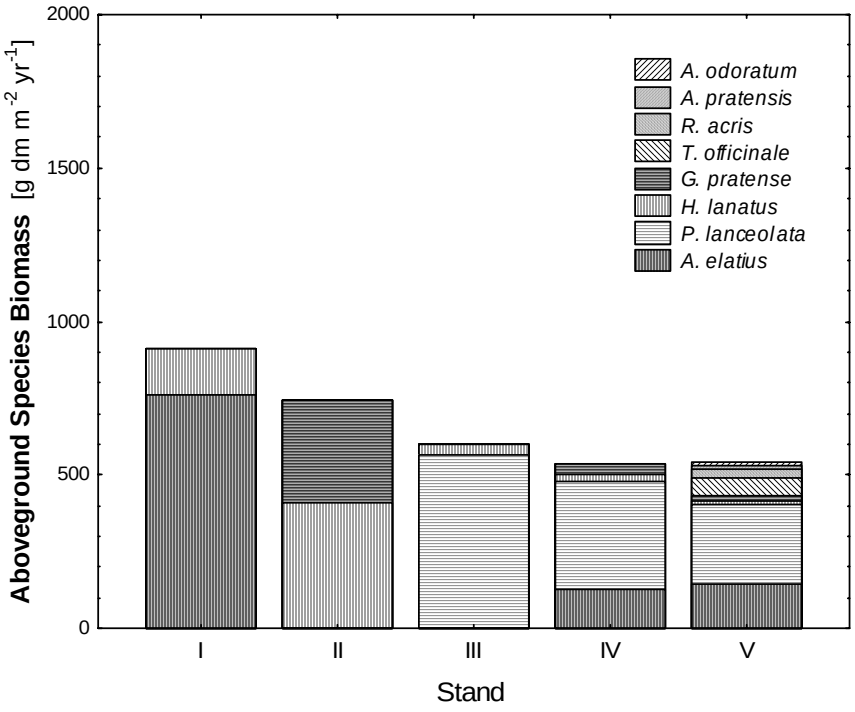


Figure 23 Mean species aboveground composition of experimental grassland stands I-V in 2003 (raw data: TÜNTE & BEIERKUHNLEIN, unpublished)

P. lanceolata dominated stand III entirely and remained co dominant with *A. elatius* in stand IV and V. Stand IV and V were distinguished by accompanying subordinate species *G. pratense* or *T. officinale*. Higher contribution of *T. officinale* (10 % of biomass) in stand V was associated with a decreased contribution of *P. lanceolata*.

Competition among species seemed to play a more important role for the performance of dominant species, rather than complementary relations. Decreased *P. lanceolata* biomass in stand V may hint at a somehow controlling role of subordinate species on biomass production of dominant species as suggested by GRIME (1998) for the establishment of dominant species in early successional phases.

3.1.1.1 Distinguishing Grassland Stands in 2002 / 2003

In 2002, our grassland stands were distinguished grass diculture of *H. lanatus* (stand I) a *H. lanatus* monoculture (stand II) and grass/herb mixture stands (*H. lanatus* and *P. lanceolata*, stand III-V, Table 19). All other species remained rather accessory ("transient" species) in terms of biomass contribution.

Table 19 Species dominance in experimental grassland stands (species with biomass contribution › 5 %)

Year	I	II	III	IV	V
	Species dominance				
2002	o *H. lanatus* ^{d} o *A. elatius* ^{so}	o *H. lanatus* ^{d}	o *H. lanatus* ^{cd} o *P. lanceolata* ^{cd}	o *H. lanatus* ^{cd} o *P. lanceolata* ^{cd}	o *H. lanatus* ^{cd} o *P. lanceolata* ^{cd}
2003	o *A. elatius* ^{d} o *H. lanatus* ^{so}	o *H. lanatus* ^{cd} o *G. pratense* ^{cd}	o *P. lanceolata* ^{d}	o *P. lanceolata* ^{cd} o *A. elatius* ^{cd} o *G. pratense* ^{so}	o *P. lanceolata* ^{cd} o *A. elatius* ^{cd} o *T. officinale* ^{so}

d = dominant: aboveground biomass › 60 %; cd = co dominant 20-60 %, so subordinate: › 5 - ‹ 20 %
raw data 2002: NEßHÖVER & BEIERKUHNLEIN, unpublished; 2003: TÜNTE & BEIERKUHNLEIN, unpublished

Hence, the implications of our grassland stands on ecosystem functions were mainly determined by dominant species' functional traits. Implications of functional diversity on ecosystem functions could on be monitored at a mere scale of species presence and absence.

H. lanatus showed very low biomass contribution in stand IV and V. It was regarded a transient species in these stands. In analogy to 2002, *G. pratense*, *A. odoratum* and *R. acris* were also regarded as transient species in stand V. The establishment of *A. pratensis* failed since individuals could be found only in some replicates of stand V.

From 2002 to 2003, the composition of our grassland stands shifted and *A. elatius* and *G. pratense* and to some extent *T. officinale* gained higher contribution to stands aboveground biomass. A grass diculture (stand I), a grass/herb co dominant diculture (stand II), a herb monoculture (stand III) and two grass/herb dicultures accompanied by subordinate herbs (stand IV and V) were distinguished.

3.1.1.2 Biomass Yields

In 2002, the mean aboveground biomass yields of our grassland stands (Figure 21, Table 20) ranged slightly from 913 to 996 g dm m^{-2} yr^{-1}. Since the contribution of subordinate and transient species to aboveground yields was marginal, the performance of dominant species *H. lanatus* and *P. lanceolata* rather than functional diversity determined biomass yields in 2002.

Table 20 Mean above- and belowground biomass dry matter yields of experimental grassland stands I-V in 2002

Parameter	I	II	III	IV	V	Tukey HSD	F	*P*
	[g m^{-2} yr^{-1}]							
Aboveground dm^	978	913	994	996	929	ns	1.98	0.136
Belowground dm°	1099	971	1129	1012	994	ns	2.91	0.047
	[g g^{-1}]							
Root/Shoot-ratio	1.1	1.1	1.1	1.0	1.1	ns	1.07	0.396

Significant distinctions between stands are indicated by different letters (one way-ANOVA: dF = 5; Tukey HSD-Test; stand I-V n = 5).
^ raw data: NEßHÖVER & BEIERKUHNLEIN, unpublished ° raw data: REUTER (2005)

The mean belowground yields of our grassland stands ranged from 971 to 1129 g dm m^{-2} yr^{-1}. Stand II (*H. lanatus*) and IV (*H. lanatus* + *P. lanceolata*) had tendentiously lower belowground biomass yields. The mean root/shoot-ratios of our grassland stands ranged marginally from 1.0 to 1.1 g g^{-1}.

Table 21 Mean above- and belowground biomass yields of experimental grassland stands I-V in 2003

Parameter	I	II	III	IV	V	Tukey HSD	F	*P*
	[g m^{-2} yr^{-1}]							
Aboveground dm^	910 ^{a}	747 ^{a}	597 ^{b}	537 ^{b}	543 ^{b}	*	22.14	0.000
Belowground dm°	1157 ^{a}	841 ^{ab}	889 ^{ab}	834 ^{b}	863 ^{ab}	*	3.18	0.036
	[g g^{-1}]							
Root/shoot-ratio	1.3 ^{ab}	1.1 ^{b}	1.5 ^{ab}	1.6 ^{ab}	1.6 ^{a}		3.88	0.018

Significant distinctions between stands are indicated by different letters (one way-ANOVA: dF = 5; Tukey HSD-Test; stand I-V n = 5)
^ raw data: TÜNTE & BEIERKUHNLEIN, unpublished ° raw data: REUTER (2005)

In 2003, the mean aboveground biomass ranged considerably from 537 to 910 g dm m^{-2} yr^{-1}. Necrotizing of *H. lanatus* during spring led to a decline in aboveground biomass yields.

Stand II- V had significantly lower yields in 2003 compared to 2002 (MANOVA: dF 4, F: 14.83, $p < 0.001$; Tukey HSD *). Higher *H. lanatus* detritus inputs in spring of 2003 (Figure 22) likely led to enhanced N availability in stand I (*A. elatius* + *H. lanatus*) and II (*H. lanatus* + *G. pratense*) than in stand III-V (chapter 3.1.3.2). Higher biomass production in stand I and II is likely explained by higher N availability.

The mean belowground biomass yields of our grassland stands (Table 21) ranged from 834 to 1157 g m^{-2} yr^{-1}. Implications of functional diversity between stand III-V on belowground biomass yield could not be found. Compared to 2002, stand I (*A. elatius* + *H. lanatus*) showed higher yields, whereas stand II had considerably lower yields in belowground biomass (MANOVA dF 4, F: 1.66, $p > 0.05$). Higher belowground biomass in stand I is explained by the enhanced growth of *A. elatius*. *A. elatius* was the only species which substituted the decline of *H. lanatus* biomass to a full extent. OPITZ VON BOBERFELD (1994) confirmed high competition ability under extensive cutting for *A. elatius* in established meadows.

In 2003, stand IV and V showed significantly higher root/shoot-ratios compared to 2002 (MANOVA dF 4, F: 3.72, $p < 0.05$, Tukey HSD **). The root/shoot-ratios were higher in stands containing *P. lanceolata* (III-V) than in stand I-II. The differences were only significant for stand III (*P. lanceolata*). In general, higher contribution of stands with herbs featuring pronounced tap roots (*P. lanceolata, T. officinale*) seem to be reflected in higher root/shoot-ratios.

Neither in 2002 nor in 2003, belowground biomass data confirmed theoretical belowground complementary due to different root architecture as shown by KUTSCHERA & LICHTENEGGER (1982, 1992). No limitation of rooting depth occurred for instance for stand II in 2002. Since this stand comprised a *H. lanatus* monoculture, root expansion was expected to be limited to shallow soil depths. Analogous, stand III (*P. lanceolata*) did not show lower belowground biomass in greater depth in 2003 (REUTER, 2005). Root system plasticity enabled species to exhaust their soil environment irrespective of assumed root architecture types. Hence differences in root systems were expected to be in biometrical parameters such as root diameter or root length density (REUTER, 2005).

3.1.1.3 Nutrient Accumulation in Biomass

In 2002, the mean N accumulation in above- and belowground biomass (N_{stand}) of our grassland stands (Table 22) ranged from 18.2 to 20.4 g N m^{-2} yr^{-1}. Grass/herb mixtures (stand III-V) showed a slightly higher N_{stand} than grass dominated stands I and II. The contribution of N accumulated in aboveground biomass to N_{stand} was higher in stand III-V. This finding was mainly attributed to species traits of *P. lanceolata* (Appendix, Table III-IV).

Table 22 Mean nutrient accumulation in above- and belowground biomass of experimental grassland stands I-V in 2002

Nutrients	I	II	III	IV	V	Tukey HSD	F	*P*
	----------[g m^{-2} yr^{-1}]----------							
N_{stand} ^°	18.3	18.2	20.4	20.0	18.5	ns	2.36	0.088
K_{stand} ^°	28.2 ^{b}	27.4 ^{b}	37.8 ^{a}	37.0 ^{ab}	32.2 ^{b}	*	14.64	0.000
Mg_{stand} ^°	3.1 ^{b}	2.9 ^{b}	4.0 ^{a}	3.7 ^{a}	2.9 ^{b}	*	19.71	0.000
Ca_{stand} ^°	4.0 ^{c}	3.7 ^{c}	8.4 ^{a}	7.5 ^{a}	6.7 ^{b}	***	72.11	0.000

Significant distinctions between stands are indicated by different letters (one way-ANOVA: dF = 5; Tukey HSD-Test; stand I-V n = 5)
^ raw data aboveground biomass: NEßHÖVER & BEIERKUHNLEIN, unpublished ° raw data belowground biomass: REUTER (2005)

The mean K accumulation (K_{stand}) ranged from 27.4 to 37.8 g K m^{-2} yr^{-1}. Grass/herb mixtures showed a higher K_{stand} than stand I and II. However, these differences were only significant for stand III. Stand II (*H. lanatus*) showed significantly higher K accumulation in aboveground biomass (84 % K_{stand}) than stand III (*H. lanatus* + *P. lanceolata*, 77 % K_{stand}, Appendix, Table IV). This finding indicates a higher storage of K in belowground biomass for *P. lanceolata*.

The mean Mg accumulation in biomass (Mg_{stand}) of the stands ranged from 2.9 to 4.0 g Mg m^{-2} yr^{-1}, the mean Ca accumulation (Ca_{stand}) ranged considerably from 3.7 to 8.4 g Ca m^{-2} yr^{-1}. Stand I, (*H. lanatus* + *A. elatius*) II (*H. lanatus*) and V (*H. lanatus* + *P. lanceolata*) showed significantly lower Mg_{stand} and Ca_{stand} than stand III (*H. lanatus* + *P. lanceolata*) and IV (*H. lanatus* + *P. lanceolata*). The Mg accumulation in aboveground biomass was higher in stand II (42 % Mg_{stand}) compared to stand III (37 % Mg_{stand}, Appendix, Table IV). A slightly higher storage of Mg in belowground biomass was indicated for *P. lanceolata*. The Ca accumulation in aboveground biomass of stand I was slightly lower than compared to the other stands. This finding hints at lower storage of Ca in belowground biomass of grass dominated stands.

In 2003, the mean N_{stand} of our grassland stands (Table 23) ranged from 14.7 to 21.4 g N m^{-2} yr^{-1}. N_{stand} was predominately affected by higher *H. lanatus* detritus in stand I (*A. elatius* + *H. lanatus*) and II (*H. lanatus* + *G. pratense*). These stands had significantly higher N_{stand} than stand III-V.

In contrast to *H. lanatus* dominated stand I in 2002, under *A. elatius* dominance in 2003, stand I showed a tendentiously higher contribution of N aboveground accumulation to N_{stand} aboveground biomass than stand III (Appendix, Table IV).

Table 23 Mean nutrient accumulation in above- and belowground biomass of experimental grassland stands I-V in 2003

Nutrients	**I**	**II**	**III**	**IV**	**V**	Tukey HSD	F	*P*
	----------[g m^{-2} yr^{-1}]----------							
N_{stand} ^°	21.4 [a]	20.1 [a]	16.2 [b]	14.7 [b]	14.8 [b]	**	10.97	0.000
K_{stand} ^°	24.8 [a]	23.9 [a]	23.3 [a]	19.1 [b]	19.9 [b]	*	5.10	0.005
Mg_{stand} ^°	3.2	3.5	3.8	3.2	3.3	Ns	1.89	0.152
Ca_{stand} ^°	4.3 [b]	7.6 [a]	9.0 [a]	6.8 [a]	7.2 [a]	*	10.58	0.000

Significant distinctions between stands are indicated by different letters (one way-ANOVA: dF = 5; Tukey HSD-Test; stand I-V n = 5).
^ raw data aboveground biomass: TÜNTE & BEIERKUHNLEIN, unpublished ° raw data belowground biomass: REUTER (2005)

The mean K_{stand} ranged from 19.1 up to 24.8 g K m^{-2} yr^{-1}. K_{stand} was significantly higher for stand I-III (dicultures) than for stand IV-V. A higher biomass production in stand I and II likely led to increased K_{stand} compared to the other grassland stands. Species traits of *P. lanceolata* were likely responsible for a higher K_{stand} in comparison between stand III and stand IV and V. In comparison to stand I, stand III showed significantly lower K aboveground contribution to K_{stand} (Appendix, Table IV). This finding suggests, analogous to 2002, a greater storage of K in belowground biomass of *P. lanceolata* than for the dominant grass species *H. lanatus* and *A. elatius*.

The mean Mg_{stand} ranged from 3.2 to 3.5 g Mg m^{-2} yr^{-1}. Analogous to K_{stand}, implications of species traits for Mg_{stand} were found. Stand III (*P. lanceolata*) showed a tendentiously higher Mg_{stand} than any other stand. The differences in Mg in above- and belowground biomass between stand I and III were rather low (Appendix, Table IV).

The mean Ca_{stand} ranged from 4.3 to 9.0 g Ca m^{-2} yr^{-1}. Despite of higher biomass yields, stand I showed significantly lower Ca_{stand} than any other grassland stands. The contribution of Ca aboveground accumulation to Ca_{stand} was slightly lower in grass dominated stands (70-72 / 76-79 % Ca_{stand}) in 2002 and 2003 (Appendix, Table IV).

3.1.1.4 Grassland Stand Implications on Biomass Yields and Nutrient Accumulation in 2002 / 2003

For both years, aboveground biomass yields were in the range of data reported of two-cut regimes in European grasslands (SCHERER-LORENZEN, 1999; GASTINE ET AL., 2003a; MARIOTT ET AL., 2003). DIERSCHKE & BRIEMLE (2002) gave biomass yields of 550 g dm m^{-2} yr^{-1} for mesotrophic two-cut regimes grasslands in Bavaria. SCURLOCK ET AL. (2002) gave an average yield of 150 to 1000 g dm m^{-2} yr^{-1} for a variety of 31 grassland communities spread worldwide. In respect to the applied mesotrophic two-cut regime, the biomass yields can be considered high.

The dominance patterns found in grassland stands in 2002 and 2003 confirmed the *mass theory* of GRIME (1998) that almost dominant species are of relevance in concern of biomass production. Theoretical belowground complementary (KUTSCHERA & LICHTENEGGER, 1982; 1992) of plants or functional diversity at the presence / absence scale did not seem to play an important role in productivity in 2002 and 2003.

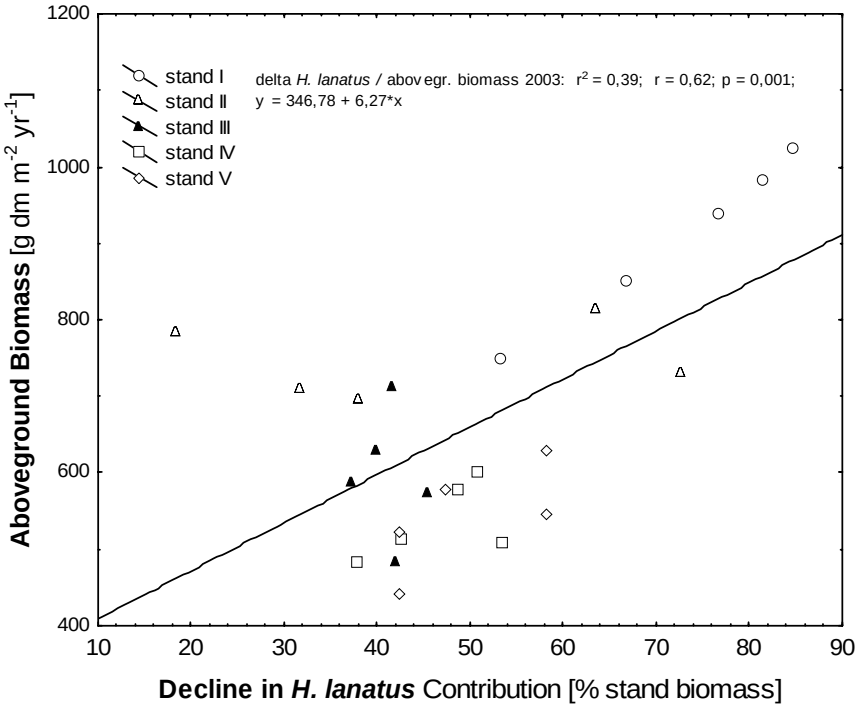


Figure 24 Correlation between the decline in *H. lanatus* biomass and aboveground biomass of experimental grassland stands I-V in 2003 (raw data: NEßHÖVER & BEIERKUHNLEIN, unpublished, TÜNTE & BEIERKUHNLEIN, unpublished)

Higher aboveground biomass yields in stand I and II could not be attributed to differences in functional diversity. Significant correlations between the decline in *H. lanatus* contribution and aboveground yields in 2003 (Figure 24) strongly suggest nutritional implications on biomass yields.

The artificial conditions on the lysimeter facilities likely accelerated the development of grassland in concern of nutrient availability. Filling of the lysimeters increased mineralisation of organic matter and thus enhanced nutrient availability to underpin initial *Ley-phase* (OPITZ VON BOBERFELD, 1994) of high biomass production in the first years after establishment. Due to low soil resources, high nutrient acquisition by our grassland stands and losses with seepage, the *Starvation-phase* with declines in biomass production was likely entered rapidly (also chapter 3.1.6.3).

No considerable differences in belowground yields and no limitation in rooting depth were found for *H. lanatus* or *G. pratense,* which could confirm root architectures given by KUTSCHERA & LICHTENEGGER (1982, 1992). REUTER (2005) found that root diameter was the only morphological parameter, distinguishing the grassland stands. Grass dominated stands featured lower root diameters compared to grass/herb mixtures. Root system plasticity led almost equal distribution of root biomass in the experimental grassland stands (REUTER, 2005). Differences in belowground complementary could only be detected as a combination of homorhizal or allorhizal root systems of grass and herb species.

During the course of 2003 *A. elatius* and *P. lanceolata* supplanted *H. lanatus*. The decline of the latter may be induced to higher sensibility towards draught stress for this species with oceanic climate preferences (OPITZ VON BOBERFELD, 1994). Theoretical complementary in above- and belowground traits in stand III did not lead to niche differentiation for *H. lanatus* and *P. lanceolata*. However, the belowground traits may have developed differently due to root plasticity induced by a pot-like alien lysimeter environment. Other traits may have become limiting factors (e.g. nutritional strategy, radiation resistance) and may have shifted competition in favour of *P. lanceolata*.

Functional traits of dominant species have also affected the productivity of stand II. Since almost equal amounts of *H. lanatus* detritus accumulated under stand I and II, tendentiously lower productivity in stand II may be attributed to a lower physiological activity of *H. lanatus* and *G. pratense*.

In temperate grasslands, belowground biomass can vary from 180 to 1400 g dm m^{-2} at a depth of 10 cm (FITTER ET AL., 1998; RAJANIEMI ET AL., 2003). In established European grasslands root production can range from 410 to 560 g m^{-2} yr^{-1} (WHITEHEAD, 1995). The major amounts of belowground biomass (86 %) are found within the upper 15 cm of clover rye-grass swards (WHITEHEAD, 1995). In our grassland stands 65 to 70 % of root biomass was found within the upper 25 cm of soil (REUTER, 2005).

SCHERER-LORENZEN (1999) found fine root biomass (Ø < 1 mm) from 250 to 1500 g dm m^{-2} in the topsoil to 30 cm in established grassland plots (BIODEPTH-site, Bayreuth). Regarding these ranges, belowground biomass in our grassland stands is considered high for both years.

Functional diversity at the presence / absence scale did not affect belowground biomass in 2002 and 2003. GASTINE ET AL. (2003b) also did not find consistent implications of functional diversity on belowground biomass in grasslands in BIODEPTH-sites. Higher N availability (chapter 3.1.3.2) played an important role in biomass production for stand I (*A. elatius + H. lanatus*), but it did not affect belowground biomass in stand II (*H. lanatus + G. pratense*). This finding also hints at low physiological activity of *H. lanatus* and *G. pratense*.

The root/shoot-ratio varied only slightly between different grassland stands. It corresponded with the range given by DUKES & HUNGATE (2002) for annual grasslands (0.2 to 1.4) or given by HOOPER (1998) for Mediterranean type grasslands (0.3 to 1.1). Hence, the root/shoot-ratio of our grassland stands was considered high. Higher root/shoot-ratios suggest higher belowground competition between participating species for stand III-V. MOONEY & WINNER (1991), SIMANE ET AL. (1993) and KALAPOS ET AL. (1996) reported of increased root/shoot-ratios under moderate water stress conditions. Tendentiously higher root/shoot ratios in stand III - V may indicate enhanced competition for nitrogen amongst the species. MARSCHNER (2002) reported of root/shoot-ratio as an important indicator for nitrogen, phosphorus or magnesium deficiency. They may also reflect increasing abundances of *P lanceolata* (Appendix, Table I/II) with allorhizal tap root belowground systems.

In 2002, mixtures of *H. lanatus* and *P. lanceolata* (stand III-V) showed a tendency towards higher nutrient accumulation in above- and belowground biomass. Higher nutrient accumulation was only significant for base cations in stands with higher contribution of *P. lanceolata*. Since higher nutrient accumulation seems to be attributed to higher contribution of *P. lanceolata* to stand biomass, species traits rather than belowground complementary or functional diversity played an important role for nutrient use of our grassland stands.

A significant general decline in N accumulation in aboveground biomass in our grassland stands from 73 % N_{stand} to 53 % N_{stand} from 2002 to 2003 reflects increasing contribution of *P. lanceolata* from 47 to 69 % of grassland stand biomass to some extent (Appendix, Table II-III).

Since stand I also showed a decline in contribution of N aboveground accumulation to N_{stand} (Appendix, Table II-III), N shortage or advers implications of draught on N translocation to aboveground biomass have also to be assumed for the stands. Enhanced translocation of K was expected as a response to the hot and dry climate in spring / summer 2003 rather than shifts in N translocation patterns. Since stands were irrigated severe draught stress was unlikely to occur.

In 2003, the nutrient use was determined by input of *H. lanatus* detritus. Stand I and II showed significantly higher N_{stand} and $K_{stand.}$ Despite of higher biomass yields in stand I, Mg_{stand} was almost equal and C_{stand} was significantly lower than in stand III-V. These findings indicate a high plasticity in Ca and Mg demand for *H. lanatus* and *A. elatius.* Ca and Mg contents may also be affected by high K^+ concentrations in soil solution from 30 and 90 cm depth due to cation competition SCHIMANSKY (1981). Nevertheless, higher contribution of accumulated K in aboveground biomass to K_{stand} seems to reflect another physiological difference between grass and herb species used for the experiments.

3.1.2 Water Use

The mean soil moisture and seepage rates were used to determine implications of stand composition on evapotranspiration of our grassland stands. The mean soil moisture in our grassland stands measured in October 2002 (Table 24) ranged from 32 to 41 Vol-%.

3.1.2.1 Soil Moisture

The soil moisture increased significantly with depth in 2002 and 2003. In 2002, significant differences were found between treatments (*Ref* / stand I -V) at particular depths. (Appendix, Table VIII). Stand II (*H. lanatus*) had significantly higher soil moisture in 0-20 cm depth than other grassland stands.

Table 24 Mean soil moisture in 0-20, 20-40 and 40-60 cm depth of *Ref* and experimental grassland stands I-V in 10, 2002

Depth [cm]	***Ref***	**I**	**II**	**III**	**IV**	**V**	Tukey HSD	F	*p*
	----------Vol-%]----------								
0 – 20	35 ^{b}	37 ^{ab}	40 ^{a}	37 ^{ab}	37 ^{ab}	32 ^{b}	*	3.49	0.018
20 – 40	41	37	38	35	36	38	Ns	1. 30	0.300
40 – 60	40	38	40	41	38	40	Ns	0.67	0.653

Significant distinctions between stands are indicated by different letters (one way-ANOVA: dF = 5; Tukey HSD-Test; *Ref* n = 3, stand I-V n = 5)

In 2003, the soil moisture was measured from April to December. The mean soil moisture of the stands ranged from 23 to 40 Vol-% (Table 25). Significant differences were also found between treatments (*Ref* / stand I-V) and between treatments at particular depths (Appendix; Table IX).

Table 25 Mean soil moisture in 0-20, 20-40 and 40-60 cm depth of *Ref* and experimental grassland stands I-V in 04-12, 2003

Depth [cm]	***Ref***	**I**	**II**	**III**	**IV**	**V**	Tukey HSD	F	*P*
	----------Vol-%]----------								
0 - 20	26	23	23	23	22	23	ns	2.11	0.102
20 - 40	38 ^{a}	30 ^{b}	34 ^{ab}	31^{b}	30 ^{b}	31 ^{b}	**	7.89	0.000
40 - 60	43 ^{a}	35 ^{b}	40 ^{a}	36 ^{b}	35 ^{b}	37 ^{b}	*	13.70	0.000

Significant distinctions between stands are indicated by different letters (one way-ANOVA: dF = 5; Tukey HSD-Test; *Ref* n = 3, stand I-V n = 5)

Stand II (*H. lanatus + G. pratense*) showed tendentiously higher soil moisture in 20-40 cm depth. The differences between stand II and any other stand were significant for 40-60 cm depth.

3.1.2.2 Seepage Rates / Evapotranspiration

In 2002, the mean annual seepage rates under our grassland stands (Figure 25) ranged slightly from 552 l m^{-2} yr^{-1} to 572 l m^{-2} yr^{-1}. Stand II (*H. lanatus*) showed tendentiously higher seepage fluxes than the other grassland stands. Due to evapotranspiration (ET), the seepage under experimental grassland stands amounted only 70 % of the water fluxes under *Ref*.

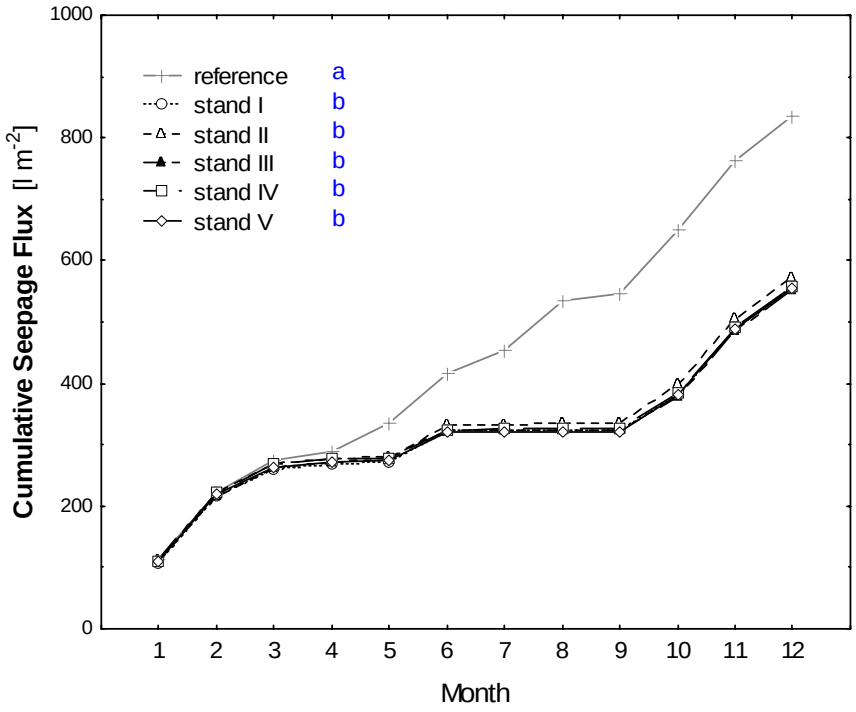


Figure 25 Mean cumulative seepage flux in 100 cm depth under *Ref* and experimental grassland stands I-V for 01-12, 2002

Significant distinctions between stands are indicated by different letters (one way-ANOVA: dF: 5, F: 86.00, $p < 0.000$; Tukey HSD ***, *Ref* n = 3 stand I-V n = 5)

ET was calculated as difference between water input (precipitation, irrigation) and seepage output from the lysimeters.

Table 26 Mean evapotranspiration of experimental grassland stands I-V in 2002

	I	II	III	IV	V	Tukey HSD	F	*P*
	----------[l m^{-2} yr^{-1}]----------							
Evapotranspiration	387	371	391	386	388	Ns	0.92	0.4703

Significant distinctions between stands are indicated by different letters (one way-ANOVA: dF = 5; Tukey HSD; stand I-V n = 5)

In 2002, the ET of our grassland stands (Table 26) ranged only slightly from 371 to 387 l m^{-2} yr^{-1}. Stand II (*H. lanatus*) showed only tendentiously lower ET than the other grassland stand. These slight differences may hint at implications of lower aboveground biomass in stand II on water use.

In 2003, the mean seepage rates under our grassland stands (Figure 26) ranged from 267 to 318 l m^{-2} yr^{-1}. Stand II (*H. lanatus* + *G. pratense*) showed significantly higher rates (38 to 51 l m^{-2} yr^{-1}) than any other grassland stand. This finding indicates a lower water use due to physiological species traits of *H. lanatus* and *G. pratense*. The mean seepage rates under the grassland stands accounted for 80 % of the rates under *Ref*.

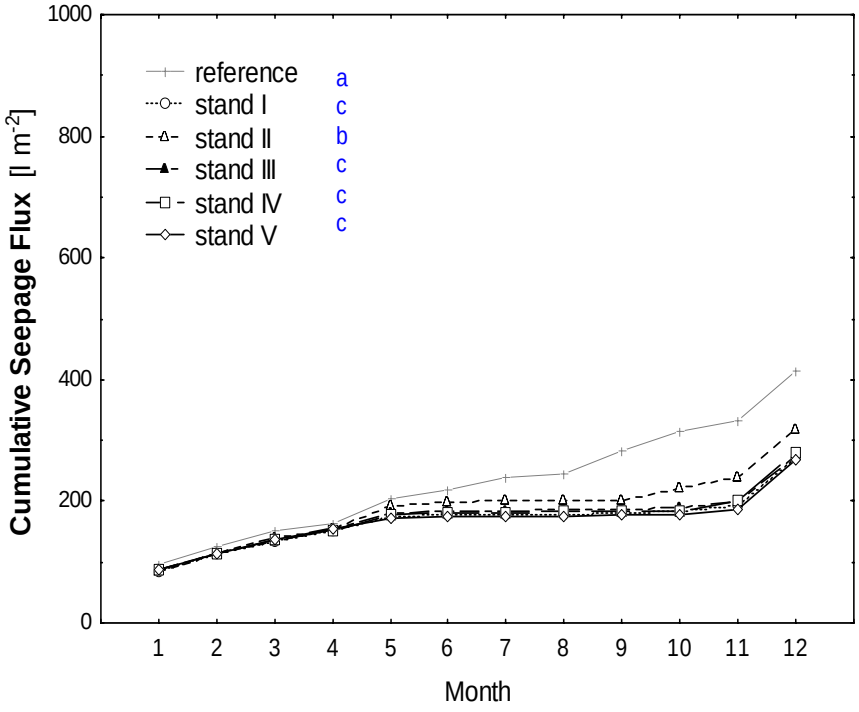


Figure 26 Mean cumulative seepage flux in 100 cm depth under *Ref* and experimental grassland stands I-V for 01-12, 2003

Significant distinctions between stands are indicated by different letters (one way-ANOVA: dF: 5, F: 39.59, $p < 0.000$; Tukey HSD **, *Ref* n = 3 stand I-V n = 5)

Due to the hot and dry spring and summer in 2003 (Chapter 2.1.1), evapotranspiration of our grassland stands (Table 27) was distinctly higher compared to 2002.

Table 27 Mean evapotranspiration of experimental grassland stands I-V in 2003

Parameter	I	II	III	IV	V	Tukey HSD	F	*p*
	----------[l m^{-2} yr^{-1}]----------							
Evapotranspiration	551 [a]	505 [b]	548 [a]	543 [a]	556 [a]	**	9.68	0.000

Significant distinctions between stands are indicated by different letters (one way-ANOVA: dF = 5; Tukey HSD; stand I-V n = 5)

ET ranged considerably between the grassland stands from 505 to 556 l m^{-2} yr^{-1}. Evapotranspiration was significantly lower in stand II (*H. lanatus* + *G. pratense*) compared to any other grassland stand.

3.1.2.3 Grassland Stand Implications on Water Use 2002 / 2003

Stand II showed slightly lower water use in 2002 and significantly lower water use in 2003. No implications of functional diversity on the presence / absence scale could be found. Combinations of grasses and herbs did not differ generally from grass dominated stands in water use.

Lower water use in stand II in 2002 (*H. lanatus*) could be ascribed to slightly lower biomass of this stand in 2002. In 2003 (*H. lanatus + G. pratense*) biomass yields were significantly higher than in stand III-V, though the water use was considerably lower. Lower water use in stand II could not be ascribed to lower belowground biomass or root length densities at any depths in 2003 (REUTER, 2005). Water use may be affected by higher availability of nitrogen as reported by OPITZ VON BOBERFELD (1994) for *A. elatius* grassland stands or for *Hordeum vulgare* by SCHINDLER ET AL. (1998). High K^+ supply with soil solution (7.7 -13.2 mg l^{-1} in 30 and 90 cm depth) may also have reduced ET of stand II (LINDHAUER, 1983).

Investigations concerning implications of functional diversity and water use of grassland stands are rare and contradictory. GASTINE ET AL. (2003b) also did not find differences in soil moisture (0-10 cm) between monocultures and plant mixtures in grassland. Whereas, CALDEIRA ET AL. (2001) found higher soil moisture in 0-15 cm depth of plant mixtures compared to monocultures. The authors attributed higher soil moisture to enhanced interception due to higher structural aboveground diversity. However, dew water interception unlikely played an important role in water use of our grassland stands in 2003. The differences in water use found in 2003 rather hint at implications of physiological species traits or nutrient availability in case of *H. lanatus + G. pratense*.

Greater structural aboveground diversity in grassland stands may have had effects on water use. A higher structural diversity provided additional surfaces for transpiration, which might raise the ET from stands of higher diversity. Leaf area index (LAI) can be used as a measure of surfaces in grassland stands. The mean LAI differed only slightly on a high level (3.5 to 3.9; NEßHÖVER & BEIERKUHNLEIN, TÜNTE & BEIERKUHNLEIN, unpublished data). The differences might have been to small for promoting any distinctions in water use between the stands. They may also have been overlain by decreasing soil evaporation at LAI › 3 (OBRIST ET AL., 2003). Soil evaporation might account to a greater implication on ET of grasslands than differences in transpiration due to differences in structural diversity.

OBRIST ET AL. (2003) identified radiation intensity and water vapour deficit as important factors for grassland ET. Higher aboveground diversity in grasslands also improved plant shading by broadleaved species and stabilized very likely the stand canopy humidity. CENTRITTO ET AL. (2000) reported of increased water use efficiency (WUE) and growth of *Prunus avium* (Wild Cherry) saplings at moderate shading. Enhanced shading in stands of higher diversity was indicated by lower temperatures in superficial soil layers of grassland stands (2° C at maximum, SPEHN ET AL., 2000). However, the authors could not find direct implications of plant diversity on soil moisture.

The canopy temperature is another factor determining ET in grassland stands. EBDON ET AL. (1997) showed a strong increase in ET with canopy temperature beyond a threshold of 23° C. Stands containing species with pronounced differences in water use efficiency (WUE) may benefit from cooling effects provided by species of lower WUE as suggested by HOGH-JENSEN & SCHJOERRING (1997). Hence, an increased structural diversity may also reduce water use of grassland stands and may compensate for greater transpiration surfaces.

It becomes evident, that several structural and physiological mechanisms can be attributed to combinations of different species traits. These combinations can even show antagonistic implications on water use of grassland stands. Hence a deduction of general implications of species traits combinations on water use of grassland stands is rather questionable.

3.1.3 Nutrient Use

Kohonen's self organizing maps (Figure 27, 28) were used as a first approach to soil solution chemistry. This multidimensional procedure includes data of pH, eC and concentrations of N_{min} (NH_4-N + NO_3-N), K^+, Mg^{2+}, Ca^{2+} and Na^+ for every single lysimeter in 15, 30 and 90 cm depths.

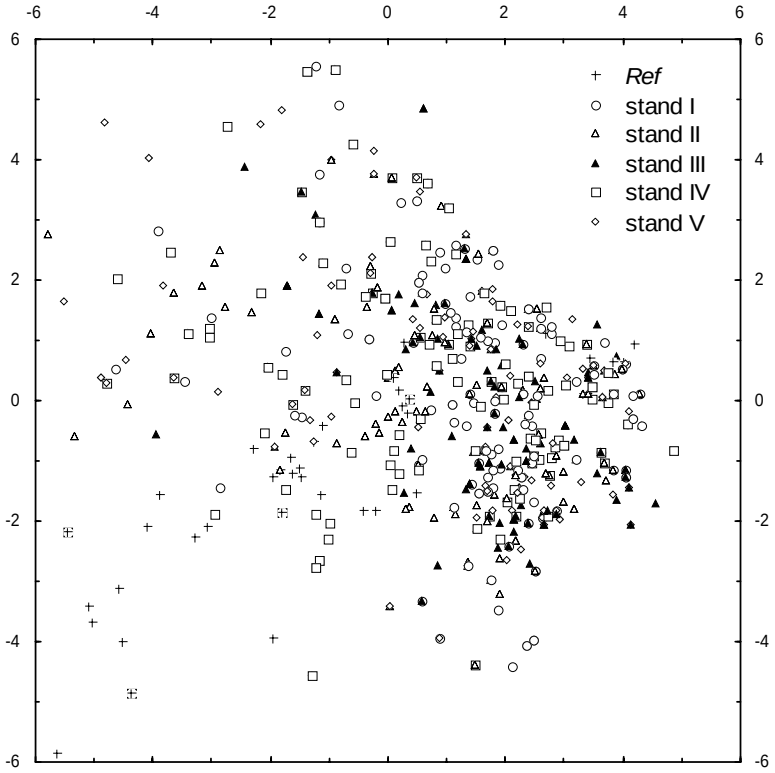


Figure 27 Self organising map of soil solution chemical parameters for *Ref* and grassland stands I–V in 2003 representing 90.5 % of variance

(G. LISCHEID, personal notice)

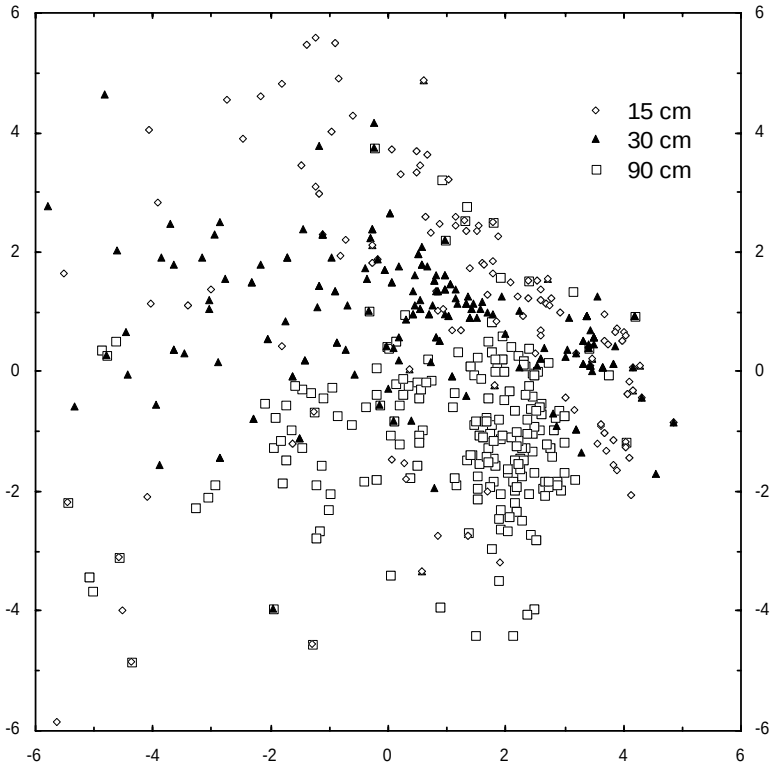


Figure 28 Self organising map of soil solution chemical parameters for 15, 30 and 90 cm depth under treatments for 2003, representing 90.5 % of variance

(G. LISCHEID, personal notice)

It visualises cluster formations of samples similar in concern of solution chemistry in a topological map, in which one signature represents all chemical parameters of one sample. Lysimeter with similar solution chemistry were plotted next neighboured. A decrease in similarity is indicated by increasing distance between sample dots. In 2002, only very slight differences between grassland stands. Therefore, self organizing charts were only calculated for 2003.

In 2003, no obvious cluster formation was found for soil solution samples. However, pronounced differences between treatments (*Ref* / stand I-V) were observed. *Ref* could be separated from the grasslands stands in concern of soil solution chemistry. General differences between the experimental grasslands were rather small. They were significant for stand II (*H. lanatus* + *G. pratense*) and V (*P. lanceolata* + *A. elatius* + *T. officinale*) compared to stand I and III ($p < 0.01$, Kolmogorow-Smirnov-Z test). This finding hints at implications of *H. lanatus* detritus input as well as differences in physiological activity between stand I and II. Stand V differed from stand III and IV by slightly lower contribution of *P. lanceolata* (Figure 3). Significant differences in concern of nutrient concentration may hint at a outstanding role of this species for nutrient use.

Significant differences ($p < 0.001$, Kolmogorow-Smirnov-Z test) between sampling depths were found (Figure 28). These differences reflect higher mineralisation of soil solution with depth. Such gradients were generally expected to occur independently of treatment identification. But their shape was expected to underlie implications of different roots systems. Thus, differences in soil solution chemistry were tested for statistical significance between depths, stand identities and depth×stand.

3.1.3.1 General Chemical Parameters in Soil Solution and Seepage

pH and electrical conductivity (eC) were measured besides nutrient and DOC concentrations in soil solution and seepage of our grassland stands. In 2002, the mean pH (Table 28) ranged in soil solution from pH 5.7 to 6.5 (medium - slightly acid) and in seepage sampled at the drainage vent of lysimeter facilities from pH 7.9 to 8.0 (slightly alkaline).

Table 28 Mean pH and electrical conductivity in soil solution from 15 and 30 cm and seepage from 100 cm depth of *Ref* and experimental grassland stands I-V in 2002

Depth [cm]	***Ref***	**I**	**II**	**III**	**IV**	**V**	Tukey HSD	F	*p*
	----------pH----------								
15	6.1 ^{b}	6.5 ^{a}	6.5 ^{a}	6.4 ^{a}	6.4 ^{ab}	6.3 ^{ab}	*	4.00	0.001
30	5.4	5.9	5.9	5.9	5.7	5.8	ns	1.66	0.186
100	7.8	7.9	7.9	8.0	8.0	7.2	ns	1.00	0.421
	----------[µS cm^{-1}]----------								
15	157	123	134	146	117	145	ns	0.665	0.653
30	212 ^{a}	116 ^{ab}	132 ^{ab}	86 ^{b}	114 ^{ab}	129 ^{ab}	*	3.42	0.020
100	595	515	515	450	468	451	ns	0.97	0.460

Significant distinctions between stands are indicated by different letters (one way-ANOVA: dF = 5; Tukey HSD; Ref n = 3 stand I-V n = 5)

A significant decline in soil solution pH from 15-30 cm depth was found. pH in soil solution was significantly lower than in seepage solution. Significant differences in pH were also found between treatments (*Ref* / stand I-V, Appendix, Table X). Stand I-III (*dicultures*) showed tendentiously higher pH than stand IV-V in 15 and 30 cm depth. However, the differences between stands amounted for merely 0.2 µM H^{+} l^{-1} at maximum. Grassland stands I-III showed a significantly higher pH than *Ref* in soil solution from 15 and 30 cm depth.

The mean eC in solution of our grasslands (Table 28) ranged from 86 to 145 µS cm^{-1} in soil solution and from 450 to 515 µS cm^{-1}in seepage. Significant differences were found between soil solution and seepage and between treatments (*Ref* / stand I-V, Appendix; Table X). Stand II (*H. lanatus*) showed tendentiously lower eC in 30 cm soil solution and seepage solution than any other grassland stand. Our grassland stands had tendentiously lower eC in soil solution and seepage than *Ref*.

Since the pH_{CaCl2} of soil samples ranged from 4.2 to 4.9 (chapter 2.1.2.2), pH in soil solution seemed to be rational. The high pH in seepage solution could not be explained with impacts of soil processes alone. Soil samples taken in 2001 showed eC ranges from 49 to 120 µS cm^{-1}. Considering this range, eC in seepage seemed also far too high, to be explained by soil processes alone. pH and eC in seepage were likely affected by contamination due concrete dissolution from lysimeter walls.

Table 29 Comparison of chemical parameters and solute concentrations in soil solution from 90 cm and seepage from 100 cm depth of *Ref* for 01-05, 2003

Parameter	**Soil solution**	**Seepage**	Tukey HSD	F	*P*
pH	5.5	7.9	***	154.89	0.000
eC [µS cm^{-1}]	266	437	***	96.64	0.000
	----------[mg l^{-1}]----------				
N_{min}	16.1	10.8	*	4.26	0.049
K^+	13.2	22.2	**	11.55	0.002
Mg^{2+}	6.3	8.4	*	6.75	0.015
Ca^{2+}	20.6	52.6	***	113.36	0.000
HCO_3^-	2.8	132.5	***	357.99	0.000
DOC	4.2	3.2	ns	1.97	0.172

Significant distinctions between stands are indicated by different letters (one way-ANOVA: dF = 1; Tukey HSD; *Ref* n = 3)

In order to trace potential implications of concrete dissolution on seepage solution, additional suction cups were installed in 90 cm depth to obtain soil solution of deepest soil layers, which was unlikely affected by dissolution products.

A comparison between soil solution from 90 cm depth and seepage from 100 cm of *Ref* for the period 01-05, 2003 (Table 29), revealed significant differences in mean chemical parameters, nutrient and HCO_3^- concentrations. These differences can be traced back to concrete dissolution in the drainage of the lysimeters. Since all parameters of interest such as $N_{min,}$ K^+, Mg^{2+}, Ca^{2+} and DOC in solution were affected by contamination to some extent, seepage solution was excluded from analyses in 2003. Instead, soil solution from 90 cm depths, representative for actual seepage solution, was used for further interpretation.

In comparison to 2002, the mean pH in soil solution from 15 and 30 cm depth (pH 5.6) of our grassland stands was significantly lower than in 2002 (pH 6.1). The mean eC in soil solution from our grassland stands was significantly was increased two-fold to 256 µS cm^{-1} (Appendix, Table XIII). Lower pH may indicate a higher biological activity for grassland stands in 2003. Higher eC can be explained by enhanced ET due to the hot and dry summer 2003.

Table 30 Mean pH and electrical conductivity in soil solution from 15 and 30 cm and seepage from 100 cm depth of *Ref* and experimental grassland stands I-V in 2003

Depth [cm]	***Ref***	**I**	**II**	**III**	**IV**	**V**	Tukey HSD	F	*p*
	----------pH----------								
15	5.8	5.7	5.9	6.2	6.0	5.7	ns	1.29	0.304
30	4.9	5.5	5.3	5.5	5.2	5.1	ns	1.75	0.166
90	5.3 ^{b}	6.3 ^{a}	6.0 ^{ab}	6.3 ^{a}	6.1 ^{ab}	6.2 ^{a}	*	24.34	0.000
	----------[µS cm^{-1}]----------								
15	326	293	252	249	252	327	ns	0.57	0.721
30	357	209	249	170	238	264	ns	2.20	0.091
90	340 ^{a}	145 ^{b}	150 ^{b}	119 ^{b}	151 ^{b}	152 ^{b}	***	14.81	0.000

Significant distinctions between stands are indicated by different letters (one way-ANOVA: dF = 5; Tukey HSD; *Ref* n = 3, stand I-V n = 5)

The mean pH and eC of soil solution from 15, 30 and 90 cm depth of our grassland stands (Table 30) varied only slightly. pH in soil solution in our grassland stands ranged from 5.1 to 6.2 (medium - slightly acid). In solution from 30 cm, pH was significantly lower than in 15 or 90 cm depth. Slightly lower pH in soil solution from 30 cm suggests enhanced biological activity for this depth. The mean pH in soil solution showed significant differences between treatments (*Ref* / stand I–V) and between treatments at particular depths (Appendix; Table XI). Stand III (*P. lanceolata*) showed tendentiously higher pH than *Ref* in 15 and 30 cm depth. In 90 cm depth, pH in solution from grassland stands was higher than in solution from *Ref* (4.5 µM H^{+} l^{-1}, at maximum). The differences were significant for stand I (*A. elatius* + *H. lanatus*), III and V (*P. lanceolata* + *A. elatius* + *T. officinale*).

The mean eC in soil solution of our grasslands (Table 30) ranged from 119 to 327 µS cm^{-1}. The mean eC in topsoil solution was significantly higher than in subsoil solution. Significant differences between treatments (*Ref* / stand I-V) and between treatments at particular depths were also found (Appendix, Table XI). Stand III showed tendentiously lower eC in 30 and 90 cm depth.

3.1.3.2 Nitrogen Use

Nitrogen (N) concentrations in soil and seepage solution, N fluxes with seepage and contents of KCl-extractable N were taken as indicators for N use of our experimental grassland stands. Concentrations of mineral N were calculated as Σ NH_4-N and NO_3-N and will be referred to as N_{min}.

a N_{min} Concentrations in Soil Solution

In 2002, the mean N_{min} concentration in soil solution (Table 31) ranged from 0.2 to 0.7 mg N_{min} l^{-1} and up to 1.0 mg N_{min} l^{-1} in seepage solution. Grass dominated stands showed slightly higher N_{min} concentrations than grass/herb mixtures.

Table 31 Mean N_{min} concentrations (Σ NH_4-N + NO_3-N) in soil solution from 15 and 30 cm and seepage from 100 cm depth of *Ref* and experimental grassland stands I-V in 2002

Depth [cm]	***Ref***	**I**	**II**	**III**	**IV**	**V**	Tukey HSD	F	*p*
	----------[mg N_{min} l^{-1}]----------								
15	7.9 [a]	0.4 [b]	0.7 [b]	0.3 [b]	0.2 [b]	0.3 [b]	***	8.43	0.000
30	14.2 [a]	0.4 [b]	0.3 [b]	0.2 [b]	0.2 [b]	0.4 [b]	***	17.26	0.000
100	21.0 [a]	0.7 [b]	1.0 [b]	0.3 [c]	0.4 [c]	0.3 [c]	*	86.86	0.000

Significant distinctions between stands are indicated by different letters (one way-ANOVA: dF = 5; Tukey HSD-Test; *Ref* n = 3, stand I-V n = 5)

Significant differences in N_{min} concentrations between depths could not be found. Significant differences were found between treatments (*Ref* / stand I-V) and between treatments at particular depths (Appendix, Table XII). Stand II (*H. lanatus*) showed tendentiously higher N_{min} concentrations than any other grassland stand in soil solution of 15 cm depth. In seepage, the N_{min} concentrations were significantly higher for stand I (*H. lanatus* + *A. elatius*) and II than for the other grassland stands.

This finding suggests implication of a grass species (*H. lanatus*) on N use in grasslands. Tendentiously lower N_{stand} in grass dominated stands indicate lower N use. Higher N_{min} concentrations in soil solution may also be affected by high root turnover-rates (REUTER, 2005). Tendentiously higher potential mineralisation rates of samples from grass dominated stands (Table 33) confirm a certain importance of root turnover on N_{min} concentrations in soil solution.

N_{min} concentrations in grassland stands were considerably lower than compared to concentrations in solution from *Ref*.

In 2003, N_{min} concentrations were measured in soil solution of 15, 30 and 90 cm depth. The mean N_{min} concentration in soil solution from 15 and 30 cm depth of our grasslands increased significantly from 0.5 to 1.7 mg N l^{-1} from 2002 to 2003 (Appendix, Table XIII). The mean N_{min} concentrations in soil solution (Table 32) ranged from 0.2 to 3.0 mg N_{min} l^{-1}. Significant differences were found between treatments (*Ref* / stand I-V), but not at particular depths.

Table 32 Mean N_{min} concentrations (Σ NH_4-N + NO_3-N) in soil solution from 15, 30 and 90 cm depth of *Ref* and experimental grassland stands I-V in 2003

Depth [cm]	***Ref***	**I**	**II**	**III**	**IV**	**V**	Tukey HSD	F	*p*
	----------[mg N_{min} l^{-1}]----------								
15	20.2 [a]	1.0 [b]	2.4 [b]	1.0 [b]	1.2 [b]	1.8 [b]	*	5.83	0.001
30	23.6 [a]	0.8 [b]	3.0 [b]	0.6 [b]	1.1 [b]	1.2 [b]	*	7.87	0.000
90	22.9 [a]	1.0 [b]	2.1 [b]	0.2 [c]	1.1 [b]	0.7 [bc]	**	25.02	0.000

Significant distinctions between stands are indicated by different letters. (one way-ANOVA: dF = 5; Tukey HSD-Test; Ref n = 3, stand I-V n = 5)

Stand III and V showed a decrease in N_{min} concentration with depth, but this was not consistent for all grassland stands (Appendix, Table XIII). Implications of functional diversity on N_{min} concentrations could not be found. High inputs of *H. lanatus* detritus (Figure 22) were not reflected in N_{min} soil solution concentrations of stand I (*A .elatius* + *H. lanatus*). But they were reflected well by higher N_{min} concentrations in stand II (*H. lanatus* + *G, pratense*). Higher soil moisture in stand II could also have led to enhanced N mineralisation and thus higher N concentrations in soil solution. The mean N_{min} concentrations in solution from grassland stands were far lower than in solution from *Ref*.

Nitrogen concentrations in soil solution under European grasslands

MAGID ET AL. (1994) found ranges from 2 to 4 mg NO_3-N l^{-1} in soil solution of 90 cm depth under unfertilized grasslands. SCHERER-LORENZEN ET AL. (2003) reported maximum concentrations of 80 mg NO_3-N l^{-1} under plots at the BIODEPTH-site in Bayreuth without fertilization. N concentrations in soil solution under fertilized grasslands can range from 3 to 19 mg NO_3-N l^{-1} (RYAN & FANNING, 1999; DIEPOLDER, 2000; SCHEFFER, 2002). Since the grassland stands received fertilizer application of 11 / 10 g N m^{-2} yr^{-1}. However, N_{min} concentrations in soil solution of our grassland stands are rated very low for 2002 and low for 2003.

b N_{min} Fluxes with Seepage

In 2002, N_{min} fluxes in seepage were calculated from N_{min} concentrations in seepage of 100 cm depth and seepage water fluxes. The mean N_{min} flux under our grasslands stands (Figure 29) ranged slightly from 0.1 to 0.4 g N_{min} m^{-2} yr^{-1}.

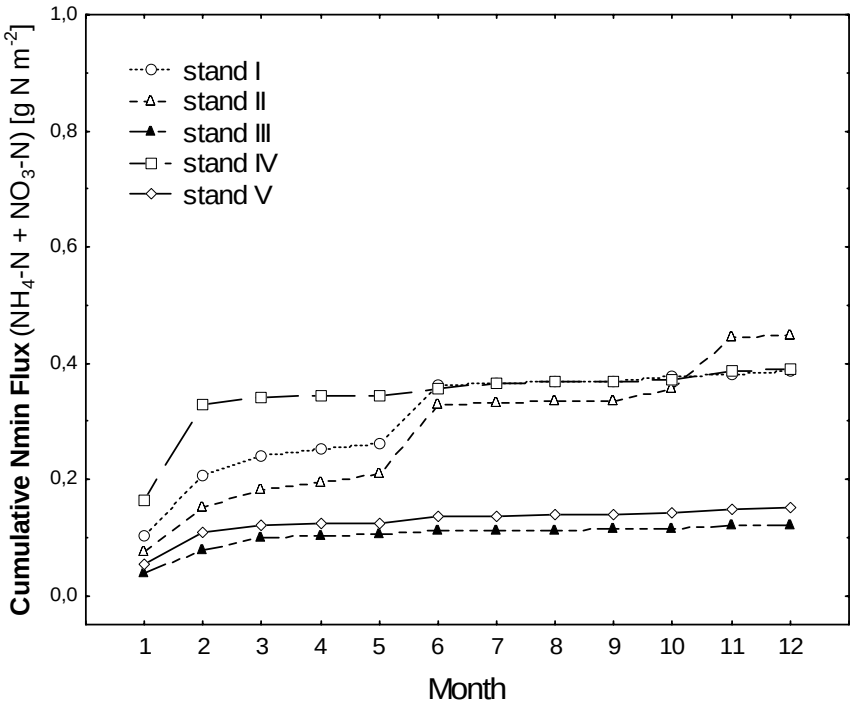


Figure 29 Mean cumulative N_{min} flux (Σ NH_4-N + NO_3-N) with seepage in 100 cm depth of experimental grassland stands I-V in 2002

Significant distinctions between stands are indicated by different letters (one way-ANOVA: dF: 5, F: 30.86, p < 0.000; Tukey HSD ***, stand I-V n = 5)

The differences between N fluxes with seepage from our grassland stands were not significant. Stand I (*H. lanatus* + *A. elatius*) and II (*H. lanatus*) showed tendentiously higher N_{min} fluxes than stand III-V (*H. lanatus* + *P. lanceolata*). N_{min} fluxes of stand III-V occurred predominantely from 01 to 03, 2002. Stand I and II showed one peak in N_{min} fluxes in 05, 2002 (approx. 25 % of annual flux) and for stand II another peak occurred in 10, 2002 amounting approximately 20 % of the annual flux. Peaks in N_{min} fluxes coincided with increased water fluxes (Figure 25), which presumably purged the grassland soils to some extent.

In 2003, the mean N_{min} fluxes under our grassland stands in 2003 (Figure 30) ranged from 0.04 to 0.79 g N_{min} m^{-2} yr^{-1}. Implications of species traits on N_{min} fluxes were found. Stand II (*H. lanatus* + *G. pratense*) had significantly higher N_{min} fluxes than any other grassland stand. N_{min} fluxes were significantly lower for stand III (*P. lanceolata*) than for the other stands.

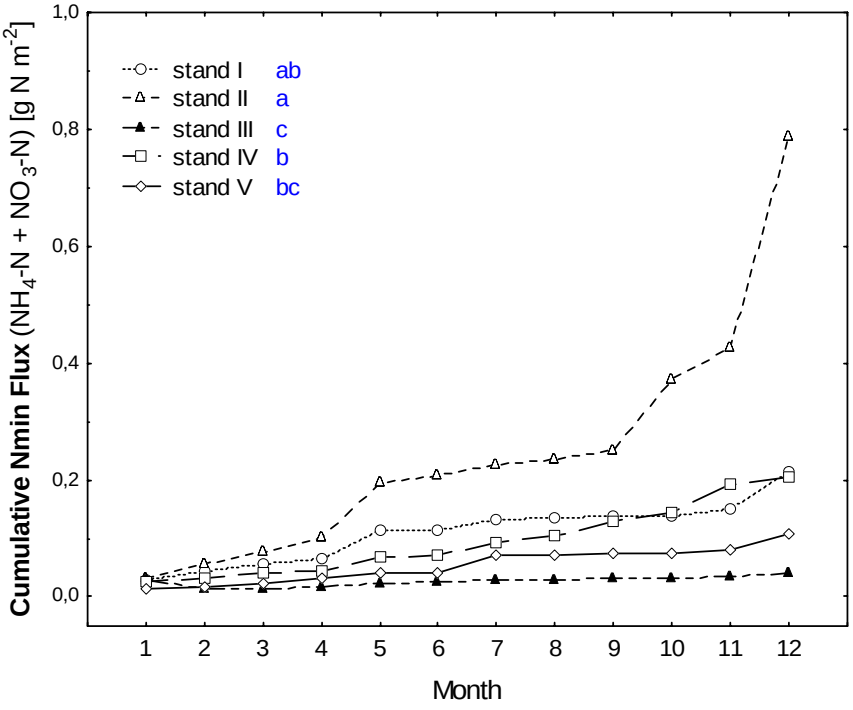


Figure 30 Mean cumulative N_{min} flux (Σ NH_4-N + NO_3-N) with seepage in 100 cm depth experimental grassland stands I-V in 2003

Significant distinctions between stands are indicated by different letters. (one way-ANOVA: dF: 5, F: 29.46, $p < 0.000$; Tukey HSD **, stand I-V n = 5)

Higher N_{min} fluxes under stand II are likely due to higher soil moisture and higher N mineralisation (Table 33) in comparison to stand I. Lower N_{min} fluxes in stand III reflect implications of *P. lanceolata* species traits, which are overlain by co dominant, and to some extent subordinate species in stand IV and V. Fluxes under grassland stands accounted for 5 % of fluxes under *Ref* (13.8 g N_{min} m^{-2} yr^{-1}) at maximum.

Nitrogen fluxes under European grasslands

N seepage fluxes under European grasslands seldom exceed 2 g m^{-2} yr^{-1}, even when fertilizer is applied (WHITEHEAD, 1995). Enhanced fluxes occur generally after fertilization and heavy precipitation (BARRACLOUGH ET AL., 1983). SCHERER-LORENZEN ET AL. (2003) reported of N-losses with seepage ranging from 0.1 to 1 g NO_3-N m^{-2} yr^{-1} at the BIODPETH-site in Bayreuth. Grasslands are able take up about 25 to 40 g N m^{-2} yr^{-1} maintaining N losses below 2 g N m^{-2} yr^{-1} (WHITEHEAD, 1995). At application of 30 g N m^{-2} yr^{-1} *Lolium perenne* (Perennial Ryegrass) swards showed N loss ranging from 0.7 to 1.4 g N m^{-2} yr^{-1} (RYAN & FANNING, 1999). Regarding these ranges, N_{min} fluxes with seepage under our grassland stands were rated medium for 2002 and 2003. For stand II (*H. lanatus* + *G. pratense*), the N_{min} fluxes were rated high for 2003.

c KCl-extractable N_{min}

In 2002, soil contents of KCl-extractable N_{min} (NH_4-N and NO_3-N) were determined in samples taken subsequently to biomass harvest in June and September in 0-15 and 15-30 cm depth. Since deviation between depths was negligible for grassland stands (Appendix, Table XIV), means are given for 0 - 30 cm depth.

Since no significant differences were found for extractable N_{min} between the sampling depths, data were pooled and contents are given for topsoil 0-30 cm depth (Appendix, Table XV). The mean contents of KCl-extractable NH_4-N in soil samples from our grassland stands (Figure 31) ranged from 0.7 to 1.1 mg N kg^{-1}. The mean content of extractable NO_3-N ranged from 0.6 to 0.9 mg N kg^{-1}.

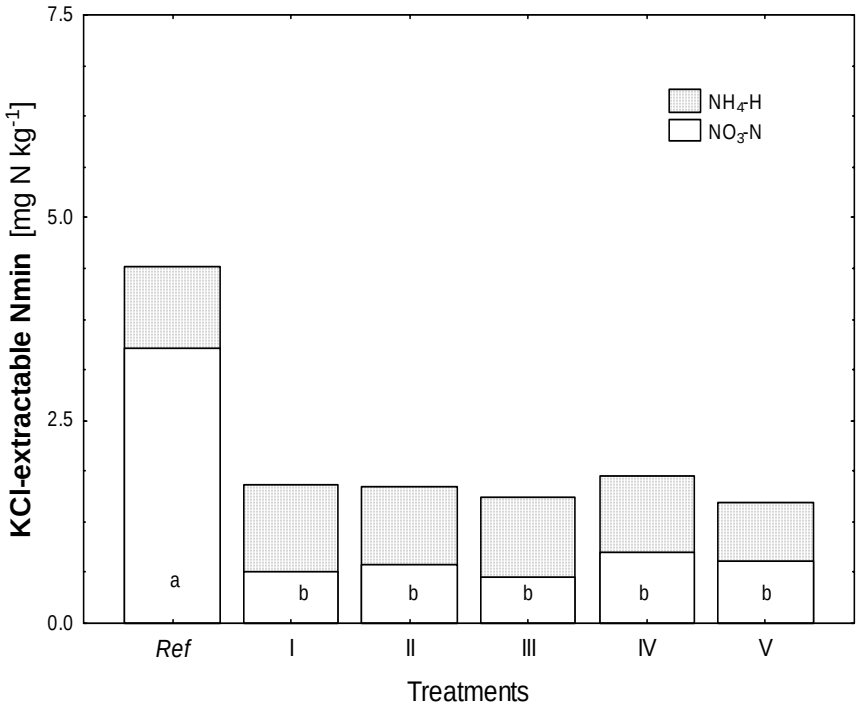


Figure 31 Mean contents of KCl-extractable NH_4-N and NO_3-N in samples taken in 06 and 09, 2002 from topsoil (0 – 30 cm) in *Ref* and experimental grassland stands I-V

Significant distinctions between stands are indicated by different letters (one way-ANOVA; dF: 5;

NH_4-N F: 0.54, p = 0,743 NO_3-N F: 14.30, $p < 0.000$; Tukey HSD ***
Ref n = 3, stand I-V n = 5

NO_3-N accounted for almost half of extractable N_{min} in grassland stands, whereas in *Ref* it was to a four-fold higher than NH_4-N. This finding may be attributed to higher nitrification in *Ref* or to preferential uptake of NO_3-N by grassland plants.

Samples from *Ref* showed significantly higher contents of extractable N_{min} in 15-30 cm compared to 0-15 cm depth. The mean contents of extractable N_{min} in topsoil samples from the grassland stands accounted for 23 % of contents in *Ref* samples at maximum (one way-ANOVA: dF = 5, F = 10.91, $p < 0.001$; Tukey HSD ***).

In 2003, additional soil samples were taken in March for N_{min} determination. The mean KCl-extractable NH_4-N in soil samples from our grassland stands (Figure 32) ranged from 0.7 to 2.3 mg NH_4-N kg^{-1}. The mean KCl-extractable NO_3-N ranged from 0.4 to 0.9 mg NO_3-N kg^{-1} in samples from grassland stands. Stand I (*A. elatius* + *H. lanatus*) and II (*H. lanatus* + *G. pratense*) showed tendentiously higher N_{min} than stand III-V (one way-ANOVA: dF = 5, F = 3.28, $p < 0.05$; Tukey HSD *).

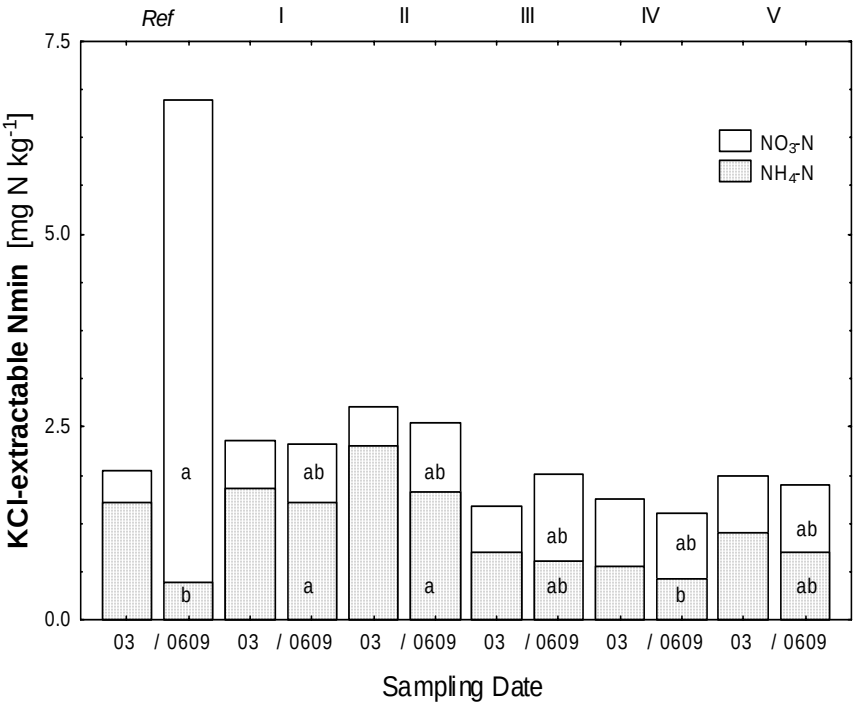


Figure 32 Comparison of mean contents of KCl-extractable N_{min} (Σ NH_4-N + NO_3-N) in samples taken from 0–30 cm depth under *Ref* and experimental grassland stands I-V in 03 and 06/09, 2003

Significant distinctions between stands are indicated by different letters
(one way-ANOVA 03, 2003: dF: 5, NH_4-N F: 1.81, p = 0,127; NO_3-N F: 1.40, p = 0.239

one way-ANOVA 06/09, 2003: dF: 5; NH_4-N F: 6.59, p = 0.000, Tukey HSD ** NO_3-N F: 14.56; *p = 0.000;* Tukey HSD ***; *Ref* n = 3, stand I-V n = 5)

In 0609 samples, the contribution of NO_3-N to N_{min} was considerably lower for *Ref*, stand I and II (to 27 %) than for stand III-V (to 55 %).

In respect to marginal differences between summer and autumn samples in concern of N_{min} contents (Appendix, Table XV), data were pooled. Analogous to spring samples, stand I and II showed higher contents of N_{min} than stand III-V. However, these differences were only significant in comparison to stand IV (one way-ANOVA: dF = 5, F = 11.23, $p < 0.001$; Tukey HSD *). They reflect *H. lanatus* detritus inputs in stand I and II to some extent. The contribution of NO_3-N to extractable N_{min} in stand I and II (to 35 %) was again considerably lower than in stand III - V (to 62 %).

The contents of KCl-extractable N_{min} differed tendentiously between grassland stands and *Ref* for the particular dates. N_{min} in stand I and II accounted for 133 or 100 % respectively of *Ref* in spring; whereas contents from stand III-V accounted for 66 % of N_{min} at maximum. In summer / autumn, N_{min} contents of grassland stands accounted to 28 % of *Ref* at maximum (one way-ANOVA: dF: 5, F: 11.23, p < 0.001, Tukey HSD *).

WHITEHEAD (1995) stated that N_{min} contents in unfertilized European grasslands seldom exceed 15 mg N kg^{-1}. NIKLAUS ET AL. (2001) found extractable NO_3-N in poor grasslands without fertilization ranging from 0 to 2.5 mg kg^{-1}. SCHERER-LORENZEN (1999) gave amounts of 11.3 mg NH_4-N kg^{-1} and 4.2 mg NO_3-N kg^{-1} for soils at BIODEPTH-site in Bayreuth. With fertilizer application (26 g N m^{-2} yr^{-1}), *Lolium perenne* swards can contain 7.7 to 13.1 mg NH_4-N kg^{-1} and 0.2 to 3.4 mg NO_3-N kg^{-1} (WHITEHEAD, 1995). WEDIN & TILMAN (1996) confirmed extractable NO_3-N ranging from 0.1 to 10 mg kg^{-1} at N application of 28 g m^{-2} yr^{-1}. The contents of extractable N_{min} in our grassland stands were rated low - medium in 03, 2003 and low in 06/09, 2002/03 for our grassland stands.

HART ET AL. (1993) reported a pronounced seasonality in extractable N_{min} with lowest amounts in summer months. In our grassland stands only slight differences in extractable N_{min} were found between different sampling dates. This finding suggests a balance between mineralisation processes and plant uptake throughout early spring and autumn. REUTER (2005) found considerable NO_3-N acquisition of grassland plants even during winter months.

Higher contributions of NO_3-N were often found in summer and dominance of NH_4-N in winter and spring (WHITEHEAD, 1995). Dominance of NH_4-N in late spring was confirmed for KCl-extracts (MENYAILO ET AL., 2002a) and soil solution obtained by centrifugation (WILLIAMS ET AL., 1999). Shifts in contribution of NH_4-N and NO_3-N to KCl-extractable N_{min} could not be confirmed for our grassland stands. Solely *Ref* showed a considerable higher contribution of NO_3-N in N_{min} in summer and autumn samples. Lower contribution of NO_3-N to extractable $N_{min,}$ may hint at preferential acquisition of mobile NO_3^- by grassland plants.

Significant correlations between grass contribution to stand biomass [%] and KCl-extractable N_{min} in 2002 and 2003 ($r = 0.42 – 0.46$, $p < 0.05$) hint at certain implications of grass species for mineralisation processes. Due to higher root turnover rates (REUTER, 2005), grass species likely enhance mineralisation processes. Due to rapid N acquisition by grass species, implications of higher root turnover and mineralisation are likely overlain to some extent as suggested for grass species adapted to nutrient rich habitats (BERENDSE, 1998).

d Potential N Mineralisation

The potential N mineralisation rates in soil samples were determined by four weeks incubation under laboratory conditions. In 2002, the mineralisation in samples from grassland stands (Table 33) ranged from 1.3 to 2.3 mg N_{min} kg^{-1} $month^{-1}$. Differences in mineralisation between depths or treatments (*Ref* / stand I-V) at particular depths were found (Appendix, Table XIV).

Table 33 Mean potential N mineralisation rates in soil samples taken from 0 - 30 cm depth from *Ref* and experimental grassland stands in I-V in 06 and 09, 2002

Parameter	*Ref*	I	II	III	IV	V	Tukey HSD	F	*P*
	----------[mg N kg^{-1} $month^{-1}$]----------								
NH_4-N	0.5	0.6	0.8	0.6	0.9	0.8	ns	0.69	0.629
NO_3-N	1.7 ^{a}	1.7 ^{a}	1.3 ^{ab}	0.8 ^{b}	0.8 ^{b}	0.9 ^{ab}	*	4.43	0.001

Significant distinctions between stands are indicated by different letters (one way-ANOVA: dF = 5; Tukey HSD-Test; Ref n = 3, stand I-V n = 5)

Stand I and II (*H. lanatus*) showed tendentiously higher N mineralisation than the other stands. The mineralisation rates were lower for grassland stands than for *Ref* (one way-ANOVA: dF = 5, F = 1.92, $p < 0.05$; Tukey HSD ns). The rates were used to calculate potential in-situ mineralisation[5]. They were assessed at 0.9 to 1.5 g N_{min} m^{-2} $month^{-1}$ for the topsoil of grassland stands in 2002.

In 2003, the mean mineralisation rates (Table 34) in samples taken from grassland stands in 03, 2003 (spring) ranged considerably from 1.7 to 20.1 mg N_{min} kg^{-1} $month^{-1}$. The mineralisation was lower in samples taken in 06/09, 2003 (summer / autumn) with a range of 1.5 to 2.8 mg N_{min} kg^{-1} $month^{-1}$ (Appendix, Table XV).

Table 34 Comparison of mean potential N mineralisation rates in soil samples taken from 0- 30 cm depth taken from *Ref* and experimental grassland stands I-V in 03 and 06/09, 2003

Parameter	*Ref*	I	II	III	IV	V	Tukey HSD	F	*P*
	----------[mg N kg^{-1} $month^{-1}$]----------								
				-spring-					
NH_4-N	16.2	10.3	15.6	1.0	1.9	2.0	*	10.71	0.000
NO_3-N	4.7 ^{ab}	2.8 ^{b}	4.5 ^{ab}	0.7 ^{c}	1.1 ^{bc}	1.4 ^{bc}	*	8.86	0.000
				-summer/autumn-					
NH_4-N	0.6	1.0	0.8	1.0	0.8	1.5	ns	0.96	0.448
NO_3-N	1.5	1.0	2.0	1.0	0.7	0.9	ns	2.05	0.077

Significant distinctions between stands are indicated by different letters (one way-ANOVA: dF = 5; Tukey HSD-Test; *Ref* n = 3, stand I-V n = 5)

The differences between stands were due to higher *H. lanatus* detritus inputs in stand I and II.

[5] In-situ mineralisation = *N Mineralisation rate* [g m^{-2} $month^{-1}$] × *Period between samplings* [month] × d_B [1.30 Mg m^{-3}] × *Soil volume* [0.3 m×1.3 m×1.3 m]

The potential N mineralisation in soil samples taken in spring differed significantly from mineralisation in samples taken in summer / autumn for all stands (Appendix, Table XVI). The potential mineralisation rates decreased from spring to autumn for grassland stands. The differences between samples from 06 and 09, 2003 were only tendentious (one way-ANOVA: dF = 1, F = 4.83, $p < 0.001$; Tukey HSD ns).

In spring, N mineralisation for stand I (*A. elatius* + *H. lanatus*) and II (*H. lanatus* + *G. pratense*) was significantly higher than for stand III (*P. lanceolata*) and IV (*P. lanceolata* + *A. elatius* + *G. pratense*) and tendentiously higher than for stand V (*P. lanceolata* + *A. elatius* + *T. officinale*). Compared to *Ref*, mineralisation rates were significantly lower for stand III-V (one way-ANOVA: dF = 5, F = 8.81, $p < 0.001$; Tukey HSD *). Higher mineralisation rates also reflect higher *H. lanatus* detritus input in stand I and II. However, significant correlations between decline in *H. lanatus* contribution and potential mineralisation could not be found.

In summer / autumn samples, the N mineralisation was only tendentiously higher for stand II compared to stand III (*P. lanceolata*). Stand I showed even lower N mineralisation than the other grassland stands. Thus, effects of *H. lanatus* detritus inputs on mineralisation were rather short termed.

Significant correlations were found between grass contribution and mineralisation rates ($r = 0.41$, $p < 0.05$).

The mineralisation was tendentiously lower for grassland stands I, III-V compared to *Ref*. (one way-ANOVA: dF = 5, F = 0.41, $p > 0.05$). The potential mineralisation rates suggest an in-situ mineralisation ranging from 1.1 to 13.2 g N_{min} m^{-2} $month^{-1}$ for spring samples and from 1.0 to 1.8 g N_{min} m^{-2} $month^{-1}$ for topsoil taken in summer / autumn 2003.

Potential mineralisation in 2002 / 2003

The potential N mineralisation in soil samples was slightly higher for grass dominated stands. Significant correlations between grass contribution and potential mineralisation in 2002 and summer / autumn 2003 ($r_{2002} = 0.65$ / $r_{2003} = 0.43$, $p < 0.05$) indicate the implication of grass species on N dynamics in grasslands (Figure 33).

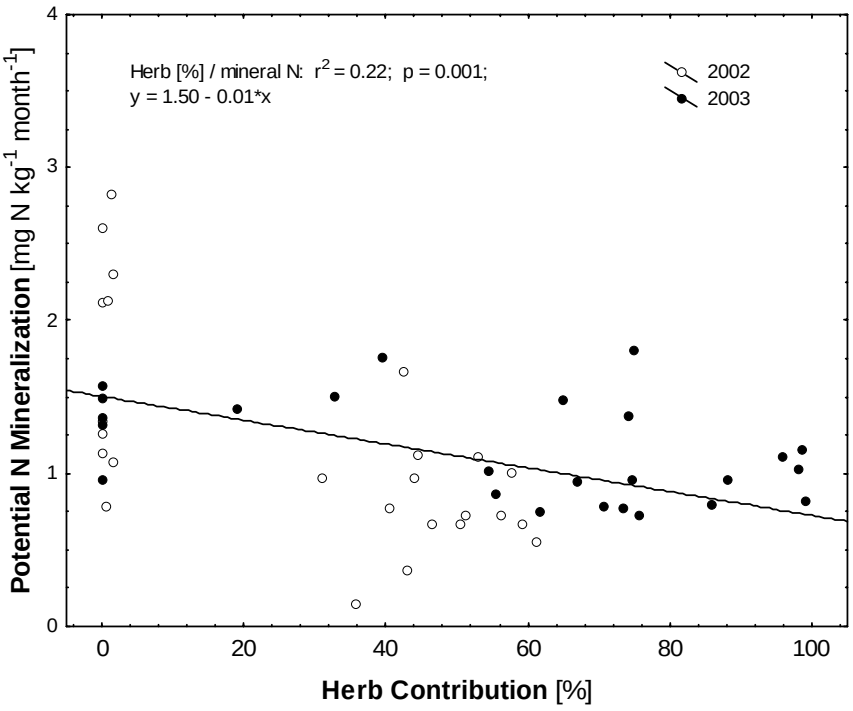


Figure 33 Correlation between herb contribution and potential N mineralisation in topsoil samples (0 -30 cm) from experimental grassland stands I-V for summer/autumn 2002/03

Since grass species had lower N contents (Appendix, Table V-VII), litter quality was unlikely a driving factor of higher mineralisation, rather than amounts of root detritus and morphological parameters. REUTER (2005) found high root turnover and lower root diameter in grass dominated stands. Incubation of *H. lanatus* root biomass (Chapter 3.3) confirmed high mineralisation for grass root biomass (chapter 3.3). In 2003, stand I and II showed considerably higher mineralisation, which can be traced back onto higher *H. lanatus* detritus inputs. Possible implications of functional group or species traits were very likely overlain by this.

SCHERER-LORENZEN ET AL. (2003) gave nitrification rates for samples from 15 cm depth of 0.05 to 1.10 g m^{-2} $month^{-1}$. BERENDSE (1998) found mineralisation rates of less than 1 g N m^{-2} yr^{-1} in topsoil of poor heath land sites, which succeeded in grasslands with subsequent increase in mineralisation to 13 g N m^{-2} yr^{-1}. MENYAILO ET AL. (2002b) gave rates of 7.5 to 64 mg N_{min} kg^{-1} $month^{-1}$, which accounts for a mineralisation of 15 g m^{-2} $month^{-1}$. WEDIN & TILMAN (1996) gave in-situ mineralisation of fertilized grasslands (28 g N m^{-2} yr^{-1}) ranging from 2 to 20 g m^{-2} yr^{-1}. The N mineralisation in soil samples from our grassland stands were rated medium.

e Grassland Stand Implications on Nitrogen Use in 2002 / 2003

In 2002, higher N_{min} availability (concentrations in soil solution and seepage and fluxes) in stand I (*H. lanatus* + *A. elatius*) and stand II (*H. lanatus*) are traced back to lower N_{stand} and higher root turn-over and N mineralisation rates in grass dominated stands.

In 2003, despite of higher N_{stand}, higher N_{min} availability in stand I and II compared to the other grassland stands was due to higher mineralisation processes induced by inputs of *H. lanatus* detritus in these stands (Figure). Application of mineral fertilizers presumably led to priming effects (KUZYAKOV, 2002) which overcame microbial immobilization of N. Such effects may have been reduced in stand III-V by lower availability of root detritus. Furthermore, rapid and sufficient acquisition and storage of fertilizer N in root biomass could have additionally limited mineralisation in stand III-V .

Despite of higher availability of N_{min}, biomass production and N accumulation were considerably lower in stand II compared to stand I. Higher biomass production of stand I was mostly due to *A. elatius* performance. However, REUTER (2005) found no differences in root-length densities between the grassland stands. The root-length density (1 to 6 cm cm^{-3}) is assumed to be sufficient for complete removal of NO_3^- from the soil (CLAASSEN & STEINGROBE, 1999) at any depth. This finding suggests competition implications on physiological processes in plants. Root activity was likely lower in stand II compared to stand I.

Differences in N_{min} concentrations could not be traced back to differences in plant diversity in both years. SCHERER-LORENZEN ET AL. (2003) confirmed the absence of plant diversity impacts on NO_3^- concentrations in soil solution at the BIODEPTH-site in Bayreuth. Stand I and II were both dominated by *H. lanatus* (› 92 % aboveground biomass, BEIERKUHNLEIN, personal notice). Higher N_{min} concentrations in seepage indicated lower use of N_{min} at greater depth for *H. lanatus*. A focus on nutrient use at shallow depths for *H. lanatus* agreed with root architectures given by KUTSCHERA & LICHTENEGGER (1982). In contrary, REUTER (2005) did not find differences in root biomass between different stands in in-growth-cores at greater depths. Hence, lower use of N_{min} is likely due to lower physiological activity rather than attributed to differences in root architectures.

NIKLAUS ET AL. (2001) found lower contents of extractable NO_3-N in stands that contained 31 species than in stands with 5 species. However, no differences occurred between intermediate (12 species) stands and the stands of lower phytodiversity. TILMAN ET AL. (1996) as well as HOOPER & VITOUSEK (1997) found decreasing NO_3^- contents in topsoil and beneath in the presence of legumes, which may have affected N availability to a great extent. GASTINE ET AL. (2003a) did not find any differences between monocultures and dicultures in concern of extractable N_{min} in soils.

In 2002, stand I and II had tendentiously higher mineralisation rates than the other stands. Differences in N mineralisation could not be attributed to phytodiversity differences of the grassland stands. They were likely induced by specific characteristics of dominant *H. lanatus* in stand I and II. They may be affected by higher root turnover rates of *H. lanatus* compared to other species. NIKLAUS ET AL. (2001) also did not find differences between stands of high and low diversity in concern of N mineralisation.

In samples from stand I and II the *H. lanatus* detritus inputs likely enhanced the N mineralisation and thus led to higher N availability. The mean loss of *H. lanatus* biomass was considerably higher in stand I (736 g dm m^{-2} than in stand II, IV and V (495, 481 and 470 g dm m^{-2}) and lowest for stand III (423 g dm m^{-2}). However, no significant correlations between biomass loss and mineralisation rates could be found. Stand III and IV neither had increased mineralisation rates, nor was the N_{min}-availability increased. Nitrogen appeared to be immobilized in stand III and IV (Table 49).

Enhanced potential mineralisation did not lead to higher contents of extractable N_{min} under stand V and it did not lead to higher N_{min} concentrations in soil solution of stand I. Plant acquisition balanced additional N input by mineralisation processes in case of stand I.

REUTER (2005) also pointed out, that lower ET in stand II (chapter 3.1.2.2) may have affected NO_3^--acquisition due to lower mass flow towards plant roots in stand II. SMETHURST (2000) confirmed transpiration induced mass flow as an important mechanism in acquisition of mobile nutrients. Hereby, nutrient mass flow in soils is dependent on soil moisture, plants water use and the degree of interaction with exchanging sites.

No correlations were found between biomass, N_{stand} and N_{min} concentrations in soil solution or N_{min} fluxes. Besides grassland stands control of N_{min} by direct uptake of NO_3^- and NH_4^+, grassland stands likely control mineralisation processes indirectly through ET processes. Positive correlations between soil moisture parameters and N_{min} concentrations or N_{min} fluxes (Table 35) also suggest ET processes as a factor determining differences in N cycle between grassland stands.

Table 35 Correlation matrix for mean soil moisture parameters, mean N_{min} concentrations in seepage and mean N_{min} fluxes under grassland stands I-V in 2003

Parameter	**N_{min}** [mg N l^{-1}]	**N_{min} flux** [g N m^{-2} yr^{-1}]
Soil moisture 20 cm	-0.15	0.14
Soil moisture 40 cm	0.35	0.49 *
Soil moisture 60 cm	0.41 *	0.62 *
Seepage rates	0.55 *	

* Significant correlations between parameters ($p < 0.05$)

Higher N_{min} availability in stand II compared to stand I also show the importance of higher soil moisture for in concern of N_{min} fluxes.

3.1.3.3 Base Cation Use

Soil solution concentrations and fluxes of K^+, Mg^{2+} and Ca^{2+} with seepage were obtained as indicators for base cation use of the experimental grassland stands. In 2002, soil solution was taken in from 15 and 30 cm depth and additionally from 90 cm in 2003.

a Base Cation Concentrations in Soil Solution and Seepage

In 2002, K^+ concentrations in soil solution of the grassland stands (Table 36) ranged from 3.0 to 7.0 mg K^+ l^{-1} and in seepage from 18.6 mg K^+ l^{-1} to 28.9 mg K^+ l^{-1}. The K^+ concentrations increased significantly with depth. Also, significant differences were found between treatments (*Ref* / stand I-V) and between treatments at particular depths (Appendix, Table XVI).

Table 36 Mean K^+ concentration in soil solution from 15 and 30 cm depth of *Ref* and experimental grassland stands I-V in 2002

Depth [cm]	***Ref***	**I**	**II**	**III**	**IV**	**V**	Tukey HSD	F	*P*
	[mg K^+ l^{-1}]								
15	8.1 [a]	4.9 [ab]	4.9 [b]	3.3 [b]	3.0 [b]	4.5 [ab]	*	4.18	0.001
30	11.0	6.8	6.8	5.9	5.9	7.0	Ns	2.34	0.076

Significant distinctions between stands are indicated by different letters (one way-ANOVA: dF = 5; Tukey HSD-Test; Ref n = 3, stand I-V n = 5).

Stand III and IV (*H. lanatus* + *P. lanceolata*) showed tendentiously lower K^+ concentrations in soil solution than any other grassland stand. The mean K^+ concentrations in soil solution from 15 and 30 cm increased significantly from 5.5 to 7.6 mg K l^{-1} from 2002 to 2003 (Appendix, Table XVII). In 2003, K^+ in soil solution (Table 37) ranged from 3.5 to 13.2 mg K^+ l^{-1}.

Table 37 Mean K^+ concentration in soil solution from 15, 30 and 90 cm depth of *Ref* and experimental grassland stands I-V in 2003

Depth [cm]	***Ref***	**I**	**II**	**III**	**IV**	**V**	Tukey HSD	F	*p*
	[mg K^+ l^{-1}]								
15	12.9	4.3	3.5	5.6	4.5	6.7	ns	2.48	0.063
30	14.8	9.9	11.8	7.7	11.3	13.2	ns	2.77	0.043
90	16.4 [a]	9.2 [b]	9.1 [b]	8.7 [b]	9.5 [b]	9.5 [b]	***	8.84	0.000

Significant distinctions between stands are indicated by different letters (one way-ANOVA: dF = 5; Tukey HSD-Test; Ref n = 3, stand I-V n = 5).

Significant differences were also found between treatments (*Ref* / stand I-V) and between treatments at particular depths (Appendix, Table XVII). A significant increase in K^+ concentrations with depth was found for soil solution from 15 and 30 cm. No implications of functional diversity on K^+ were found. Stand III (*P. lanceolata*) showed tendentiously lower K^+ concentrations in 30 and 90 cm soil solution than the other grassland stands.

Mg^{2+} Concentrations

The mean Mg^{2+} concentrations in soil solutions of our grassland stands (Table 38) ranged from 1.8 to 2.9 mg Mg^{2+} l^{-1} and from 8.5 to 10.1 mg l^{-1} in seepage in 2002. Significant differences in Mg^{2+} concentrations were found between treatments (*Ref* / stand I-V) and between soil solution and seepage (Appendix, Table XVI).

Table 38 Mean Mg^{2+}- concentration in soil solution from 15 and 30 cm depth of *Ref* and experimental grassland stands I-V in 2002

Depth [cm]	***Ref***	**I**	**II**	**III**	**IV**	**V**	Tukey HSD	F	*P*
	----------[mg Mg^{2+} l^{-1}]----------								
15	2.3	2.1	2.4	2.9	2.2	2.2	ns	0.75	0.595
30	4.2 ^{a}	1.9 ^{b}	2.3 ^{ab}	1.8 ^{b}	2.1 ^{ab}	2.2 ^{ab}	*	3.19	0.030

Significant distinctions between stands are indicated by different letters (one way-ANOVA: dF = 5; Tukey HSD-Test; *Ref* n = 3, stand I-V n = 5).

The mean Mg^{2+} concentrations in soil solution from 15 and 30 cm depth of our grasslands increased from 2002 to 2003 significantly from 2.3 to 4.6 mg Mg^{2+} l^{-1} (Appendix, Table XVI-XVII).

In 2003, the mean concentrations in soil solution of our grassland stands (Table 39) ranged from 2.4 up to 5.2 mg Mg^{2+} l^{-1}. Significant differences were found between treatments (*Ref* / stand I-V) and between treatments at particular depths (Appendix, Table XVII). Only slight differences due to stand composition were found in concern of Mg^{2+} concentrations in 2003.

Table 39 Mean Mg^{2+} concentration in soil solution from 15, 30 and 90 cm depth of *Ref* and experimental grassland stands I-V in 2003

Depth [cm]	***Ref***	**I**	**II**	**III**	**IV**	**V**	Tukey HSD	F	*P*
	----------[mg Mg^{2+} l^{-1}]----------								
15	4.7	4.8	4.3	4.1	3.9	5.9	ns	0.84	0.536
30	6.8	3.9	5.2	3.3	5.0	5.2	ns	1.74	0.167
90	8.1 ^{a}	3.2 ^{b}	3.1 ^{b}	2.4 ^{b}	2.7 ^{b}	2.7 ^{b}	*	7. 26	0.000

Significant distinctions between stands are indicated by different letters (one way-ANOVA: dF = 5; Tukey HSD-Test; *Ref* n = 3, stand I-V n = 5).

Stand III (*P. lanceolata*) showed tendentiously lower Mg^{2+} concentrations than the other grassland stands. The grassland stands showed significantly lower Mg^{2+} concentrations than *Ref* in soil solution from 90 cm depth.

Ca^{2+} Concentrations

In 2002, the mean Ca^{2+} concentrations in soil solution of our grassland stands (Table 40) ranged from 7.1 to 14.5 mg Ca^{2+} l^{-1} and in seepage solution from 44.7 to 52.4 mg Ca^{2+} l^{-1}. Significant differences were found between treatments (*Ref* / stand I-V), between soil solution from 15 and 30 cm and between soil solution and seepage (Appendix, Table XVI). No differences between grassland stands could be found in concern of Ca^{2+} concentrations.

Table 40 Mean Ca^{2+} concentration in soil solution from 15 and 30 cm depth of *Ref* and experimental grassland stands I-V in 2002

Depth [cm]	***Ref***	**I**	**II**	**III**	**IV**	**V**	Tukey HSD	F	*P*
	----------[mg Ca^{2+} l^{-1}]----------								
15	15.5	13.3	14.5	18.1	14.0	15.0	ns	0.81	0.554
30	18.6 ^{a}	8.5 ^{ab}	9.4 ^{ab}	7.1 ^{b}	8.7 ^{ab}	9.0 ^{ab}	*	2.73	0.046

Significant distinctions between stands are indicated by different letters (one way-ANOVA: dF = 5; Tukey HSD-Test; *Ref* n = 3, stand I-V n = 5)

Stand III (*H. lanatus* + *P. lanceolata*) showed tendentiously lower Ca^{2+} concentrations than the other grassland stands. Grassland stands showed lower Ca^{2+} concentrations than *Ref* in soil solution from 30 cm depth and in seepage.

From 2002 to 2003, the mean Ca^{2+} concentrations in soil solution from 15 and 30 cm depths of our grassland stands increased significantly from 11.8 to 25.2 mg Ca^{2+} l^{-1} (Appendix, Table XVII). Ca^{2+} in soil solution of the grassland stands (Table 41) ranged from 8.2 to 39.9 mg Ca^{2+} l^{-1}.

Table 41 Mean Ca^{2+} concentration in soil solution from 15, 30 and 90 cm depth of *Ref* and experimental grassland stands I-V in 2003

Depth [cm]	***Ref***	**I**	**II**	**III**	**IV**	**V**	Tukey HSD	F	*P*
	----------[mg Ca^{2+} l^{-1}]----------								
15	36.1	34.5	33.2	28.6	28.2	39.9	Ns	0.81	0.553
30	31.5 ^{a}	16.7 ^{ab}	21.1 ^{ab}	13.2 ^{b}	19.4 ^{ab}	21.3 ^{ab}	*	2.78	0.043
90	27.1 ^{a}	10.6 ^{b}	10.4 ^{b}	8.2 ^{b}	9.7 ^{b}	9.3 ^{b}	***	29.16	0.000

Significant distinctions between stands are indicated by different letters (one way-ANOVA: dF = 5; Tukey HSD-Test; *Ref* n = 3, stand I-V n = 5)

Implications of functional diversity were not found. Since stand III was almost a *P. lanceolata* monoculture, lower Ca^{2+} concentrations in 30 and 90 cm depth were due to species traits. A significant decline in Ca^{2+} concentration with depth and significant differences between treatments (*Ref* / stand I-V) was found (Appendix, Table XVII).

b Base Cation Fluxes with Seepage in 2003

In 2002, base cation fluxes were biased by concrete dissolution products. Since no reasonable interpretation is possible, base cation fluxes are not shown.

In 2003, the mean K^+ fluxes under our grassland stands (Figure 34) ranged from 2.1 to 2.3 g K^+ m^{-2} yr^{-1}. Almost no differences in K^+ fluxes between grassland stands were found in 2003. K^+ fluxes under grassland stands were significantly lower than under *Ref* (34 % at maximum).

The mean Mg^{2+} fluxes under our grassland stands (Figure 35) ranged slightly from 0.6 to 1.0 g Mg^{2+} m^{-2} yr^{-1}. Higher Mg^{2+} fluxes may be attributed to dominant functional group (grasses) in stand I and similarity in root system in stand I and II (*A. elatius* + *H. lanatus*; *H. lanatus* + *G. pratense*) showed tendentiously higher Mg^{2+} fluxes than any other grassland stand. Fluxes under grassland stands were significantly lower than under *Ref*. Fluxes under grassland stands accounted for 25% of fluxes under *Ref* at maximum.

The mean Ca^{2+} fluxes under our grassland (Figure 36) stands ranged slightly from 2.0 to 3.2 g Ca^{2+} m^{-2} yr^{-1}. Stand I showed tendentiously higher and stand II significantly higher Ca^{2+} fluxes than any other grassland stand. Higher Ca^{2+} fluxes were due to grass dominance in stand I. High grass contribution to stand and higher water fluxes led to highest Ca fluxes under stand II. Fluxes under grassland stands were significantly lower than under *Ref*. At maximum, fluxes under grassland stands accounted for 23 % of fluxes under *Ref*.

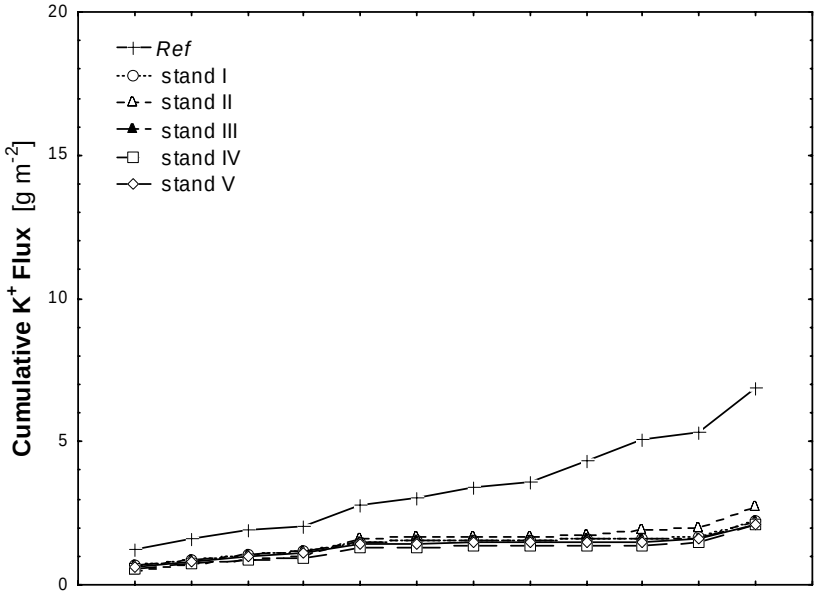


Figure 34 Mean cumulative K^+ flux under *Ref* and experimental grassland stands I-V in 2003

Significant distinctions between stands are indicated by different letters (one way-ANOVA: dF = 5, F: 34.81, $p < 0.001$; Tukey HSD ***; *Ref* n = 3, stand I-V n = 5).

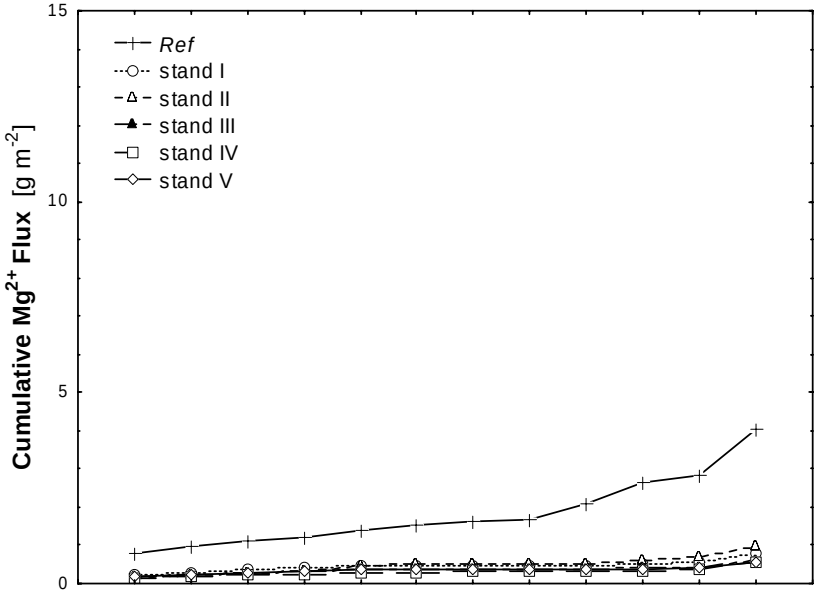


Figure 35 Mean cumulative Mg^{2+} flux under *Ref* and experimental grassland stands I-V in 2003

Significant distinctions between stands are indicated by different letters (one way-ANOVA: dF = 5, F: 18.99, $p < 0.001$; Tukey HSD *; *Ref* n = 3, stand I-V n = 5).

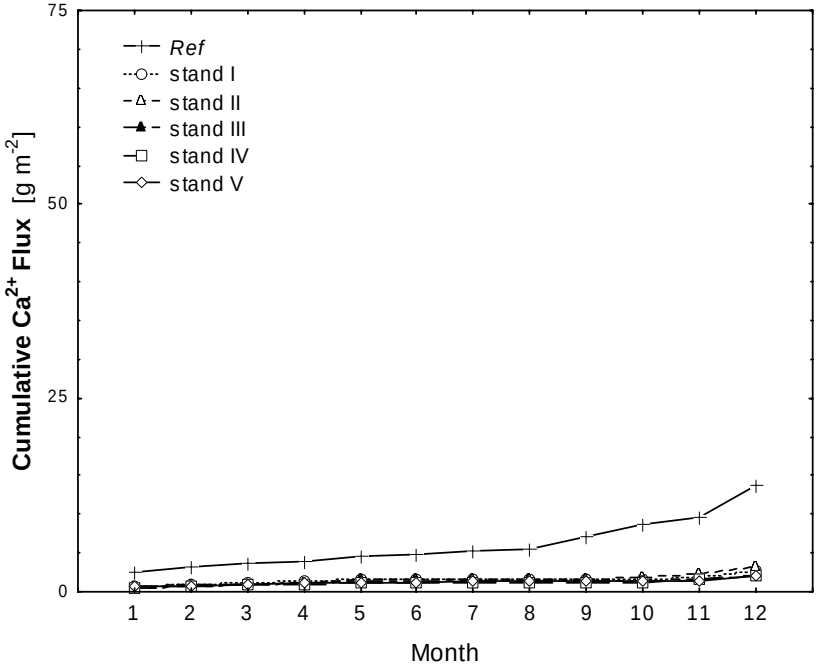


Figure 36 Mean cumulative Ca^{2+} flux under *Ref* and experimental grassland stands I-V in 2003

Significant distinctions between stands are indicated by different letters (one way-ANOVA: dF = 5, F: 54.57, $p < 0.001$; Tukey HSD *; *Ref* n = 3, stand I-V n = 5).

c Grassland Stand Implication on Base Cation Use 2002 / 2003

In both years the Mg^{2+} and Ca^{2+} concentrations in soil solution were regarded as very low. SCHEFFER (2002) stated that adequate concentrations in soil solution should not remain below 5 mg Mg^{2+} l^{-1} or 20 mg Ca^{2+} l^{-1}. Lower concentrations of Mg^{2+} and Ca^{2+} were predominantely due to low contents of NH_4Cl-extractable fractions of these nutrients (chapter 2.1.2.2).

Both, in 2002 and in 2003, stand III showed tendentiously lower base cation concentrations in soil solution. Significantly higher K_{stand}, Mg_{stand} and Ca_{stand} in 2002, indicate implications of species traits of *P. lanceolata.* These species traits are also reflected in higher contents of Mg and Ca in aboveground biomass compared to *H. lanatus* and *A. elatius* (Appendix, Table VI-VII). However, even in 2003, when stand III comprised a mere monoculture of *P. lanceolata,* no significant differences in base cation concentrations were found between stand III and the other grassland stands. This finding is explained by soil desorption processes, which buffer cation soil solution concentrations despite of enhanced acquisition by plants.

In 2003, Mg^{2+} and Ca^{2+} fluxes under stand I and II were slightly higher than under the other grassland stands. Higher base cation fluxes reflect lower Mg_{stand} and Ca_{stand} in these stands to some extent. No consistent correlations between stand biomass, base cation accumulation and base cation concentrations in seepage or fluxes could be found.

NAEEM ET AL. (1994) did not find implications of functional diversity on K^+ availability in a multi trophic experiment (ECOTRON). These results support our findings, that implications of functional diversity on K^+ availability are rather low.

Significant correlations between soil moisture parameters and base cation fluxes were found for 2003 (Table 42). In the absence of indicators for dilution processes these findings suggest a certain control of base cation fluxes by grassland stands through ET processes. Lower soil moisture may lower the mobility of nutrients and thus hinder leaching. Reduced microbial activity may also have led to reduced desorption of cations from exchanging sites.

Table 42 Correlation matrix for mean soil moisture parameters, mean base cation concentration in seepage and mean fluxes under grassland stands I-V in 2003

Parameter	K^+	Mg^{2+}	Ca^{2+}	K flux	Mg flux	Ca flux
	----------[mg l^{-1}]----------			----------[g m^{-2} yr^{-1}]----------		
Soil moisture 20 cm	0.12	-0.05	-0.08	0.44 *	0.18	0.28
Soil moisture 40 cm	0.26	0.09	0.20	0.65 *	0.29	0.48 *
Soil moisture 60 cm	0.09	0.06	0.02	0.65 *	0.35	0.52 *
Seepage rates	0.12	0.39	0.20			

* Significant correlations between parameters ($p < 0.05$)

3.1.4 DOC Characteristics

DOC concentrations in soil solution and seepage and DOC fluxes were used as indicators for release of recalcitrant carbon compounds in grassland stands by exudates or by exudate induced priming effects.

3.1.4.1 DOC Concentrations in Soil Solution and Seepage

In 2002, DOC concentrations in soil solution of our grassland stands ranged from 6.2 to 13.1 mg C l^{-1} (Table 43). A significant decline in DOC with depth was found (Appendix, Table XI). Stand I (*H. lanatus*) and III (*H. lanatus + P. lanceolata*) showed slightly higher DOC in solution from 30 cm depth than any other grassland stand. Grassland stands showed higher DOC concentrations than *Ref*.

Table 43 Mean DOC concentration in soil solution from 15 and 30 cm and from seepage of 100 cm depth of *Ref* and experimental grassland stands I-V in 2002

Depth [cm]	***Ref***	**I**	**II**	**III**	**IV**	**V**	Tukey HSD	F	*p*
	----------[mg C l^{-1}]----------								
15	10.5	13.1	11.6	13.5	11.2	13.3	ns	2.15	0.100
30	6.5 ^{b}	9.4 ^{ab}	8.4 ^{ab}	9.9 ^{a}	7.8 ^{ab}	8.1 ^{ab}	*	2.87	0.038
100	4.7	6.4	6.2	7.2	7.6	7.5	ns	1.85	0.144

Significant distinctions between stands are indicated by different letters (one way-ANOVA: dF = 5; Tukey HSD-Test; Ref n = 3, stand I-V n = 5)

The mean DOC in soil solution of our grassland in 2002 did not differ from samples taken in 2003 (Appendix, Table XVIII). The concentrations ranged from 5.6 to 14.5 mg DOC l^{-1} (Table 44). A significant decline in DOC concentrations with depth was found for all treatments (*Ref* / stand I-V).

Table 44 Mean DOC concentration in soil solution from 15, 30 and 90 cm depth of *Ref* and experimental grassland stands I-V in 2003

Depth [cm]	***Ref***	**I**	**II**	**III**	**IV**	**V**	Tukey HSD	F	*p*
	----------[mg C l^{-1}]----------								
15	9.2 ^{b}	14.5 ^{a}	13.5 ^{a}	12.0 ^{ab}	13.5 ^{a}	14.5 ^{a}	**	5.67	0.000
30	7.3	9.5	8.0	8.7	7.8	7.6	ns	2.56	0.028
90	4.5 ^{c}	6.3 ^{a}	5.3 ^{bc}	6.5 ^{a}	5.6 ^{b}	6.4 ^{a}	*	10.23	0.000

Significant distinctions between stands are indicated by different letters (one way-ANOVA: dF = 5; Tukey HSD-Test; *Ref* n = 3, stand I-V n = 5)

Significant differences were also found for treatments (*Ref* / stand I-V) and for treatments at particular depths (Appendix, Table XIX). DOC was significantly lower in soil solution of 90 cm depth under stand II (*H. lanatus + G. pratense*) and IV (*P. lanceolata + A. elatius + G. pratense*). Grassland stands showed significantly higher DOC concentrations than *Ref* solution from 15 and 90 cm depth.

3.1.4.2 DOC Fluxes with Seepage

In 2002, the mean DOC fluxes with seepage under our grassland stands (Figure 37) ranged from 2.1 to 3.1 g C m^{-2} yr^{-1}. Stand II (*H. lanatus*) showed tendentiously lower DOC fluxes. However, the difference was almost marginal. Despite lower DOC concentration in 90 cm soil solution, *Ref* accounted for slightly higher DOC fluxes with seepage as compared to grassland stands.

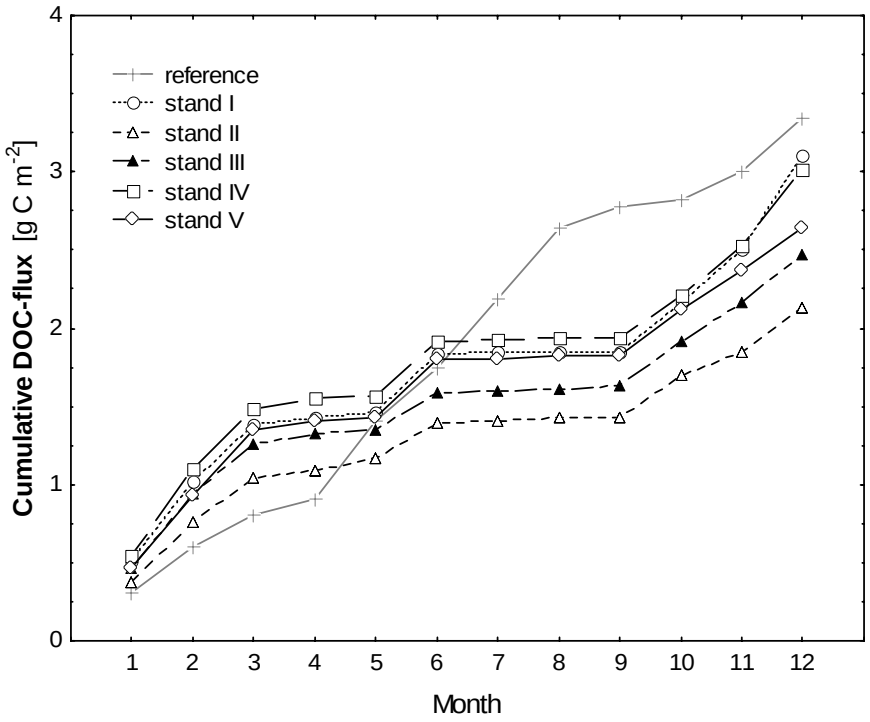


Figure 37 Mean cumulative DOC flux with seepage in 100 cm depth under *Ref* and experimental grassland stands I-V in 2002

Significant distinctions between stands are indicated by different letters (one way-ANOVA: dF: 5, F: 0.73, $p > 0.05$; *Ref* n = 3 stand I-V n = 5)

In 2003, the mean DOC flux ranged (Figure 38) from 1.5 to 1.8 g C g m^{-2} yr^{-1}. Differences between grass dominated stands and grass/herb mixtures were not found. Almost no differences occurred between grassland stands and *Ref.*

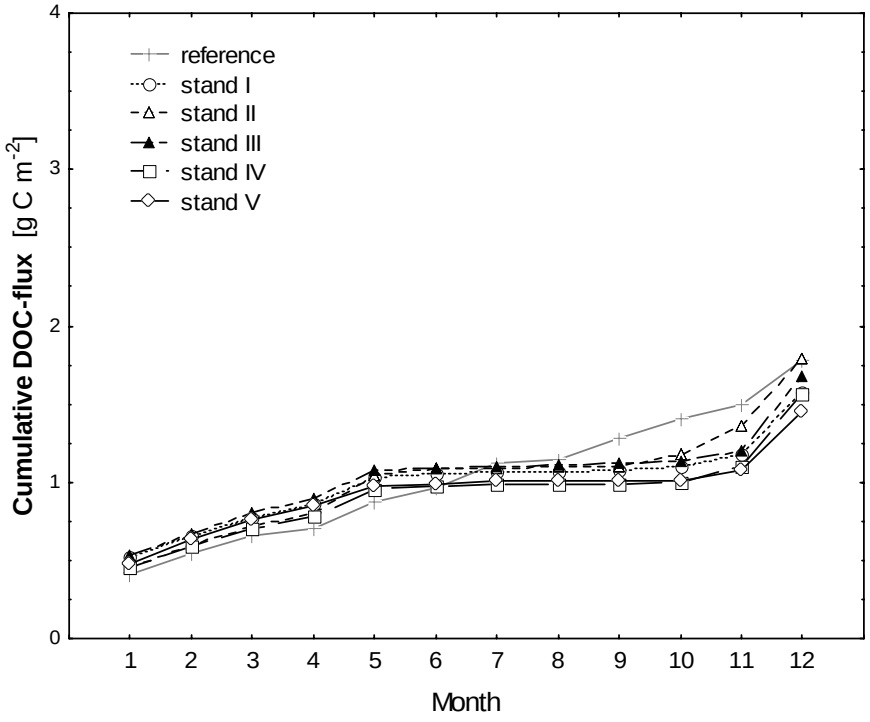


Figure 38 Mean cumulative DOC flux with seepage in 100 cm depth under *Ref* and experimental grassland stands I-V in 2003

Significant distinctions between stands are indicated by different letters (one way-ANOVA: dF: 5, F: 1.10, $p > 0.05$; *Ref* n = 3 stand I-V n = 5)

3.1.4.3 Grassland Stand Implication on DOC Dynamics

The DOC concentrations in soil solution under grasslands can range from 2 to 5 mg C l^{-1} (QUIDEAU & BOCKHEIM, 1996), or from 7 to 8 mg C l^{-1} under fallow grasslands (HAGEDORN ET AL., 2000; CHANTIGNY, 2003). MCTIERNAN ET AL. (2001) gave ranges from 10 to 35 mg C l^{-1} for *Trifolium repens* / *Lolium perenne* pastures at low fertilizer application (6.5 g N m^{-2} yr^{-1}).

Table 45 Correlation matrix for mean soil moisture parameters and mean DOC concentration in seepage and mean DOC fluxes for grassland stands I-V in 2003

Parameter	**DOC** [mg C l^{-1}]	**DOC flux** [g C m^{-2} yr^{-1}]
Soil moisture 20 cm	0.15	0.43 *
Soil moisture 40 cm	-0.16	0.59 *
Soil moisture 60 cm	-0.14	0.33
Seepage rates	-0.52 *	

* Significant correlations between parameters ($p < 0.05$)

Regarding these values, DOC concentrations in soil solution were rated medium to high. DOC concentrations were likely increased by lingering of initial mineralisation and repeatedly pertubation due to soil sampling. However, significant differences in DOC concentrations between grassland stands were not found. Carbon compounds that can be released by herb species (MARSCHNER, 2002) were likely rapidly mineralised by mircororganisms (MCTIERNAN ET AL., 2001). Some compounds released by grass species are also prone to rapid mineralisation. Higher root turnover-rates likely also affect DOC concentrations in soil solution.

CHANTIGNY (2003) gave ranges of DOC fluxes under grasslands from 0.5 to 8.4 g C m^{-2} yr^{-1}. MCTIERNAN ET AL. (2000) reported of DOC fluxes under *Trifolium repens* / *Lolium perenne* pastures of 4.2 g C m^{-2} yr^{-1}. The DOC fluxes under our grasslands were rated low. Besides microbial mineralisation, organic compounds may also be adsorbed to organic matter or mineral surfaces (KAISER & ZECH, 2000; KAISER & GUGGENBERGER, 2000).

No consistent correlations between biomass parameters and DOC concentrations or DOC fluxes were found. Negative correlation between seepage rates and DOC concentration (Table 45) suggest dilution through enhanced percolation of the soil profile. Positive correlations between soil moisture in 20 and 40 cm depth or seepage rates and DOC fluxes indicate major importance of ET for DOC leaching from grassland stands.

3.1.5 Budgets for Water, Nutrients and DOC in Solution

3.1.5.1 Water, Nutrient and Carbon Budgets

In 2002, seepage water loss (Table 46) accounted for 40 to 41 % of the water gain (precipitation, irrigation). Evaporation on *Ref* amounted only up to 12 % of water input. ET of grassland stands varied only slightly. Stand II (*H. lanatus*) showed tendentiously lower ET than other stands.

Table 46 Mean total water, N_{min} and carbon gains and losses with seepage in 100 cm depth for *Ref* and experimental grassland stands I-V in 2002

Parameter	**---gains---**	***Ref***	**I**	**II**	**III**	**IV**	**V**	Tukey HSD	F	*P*
		----------seepage losses----------								
		----------[l m^{-2} yr^{-1}]----------								
Water	**944**	835 [a]	556 [b]	572 [b]	552 [b]	558 [b]	555 [b]	***	86.44	0.000
		----------[g m^{-2} yr^{-1}]----------								
N_{min}	**12.5**	24.3 [a]	0.3 [b]	0.4 [b]	0.1 [b]	0.2 [b]	0.1 [b]	***	30.86	0.000
DOC	**2.5**	3.3 [a]	3.1 [a]	2.1 [a]	2.5 [a]	3.0 [a]	2.6 [a]	ns	0.73	0.606

Significant distinctions between stands are indicated by different letters (one way-ANOVA: dF = 5; Tukey HSD-Test; *Ref* n = 3, stand I-V n = 5)

A minor fraction of gains in N_{min} with precipitation, irrigation and fertilization was lost with seepage under grassland stands in 2002. However, *Ref* showed a two-fold loss compared to the input.

The mean losses of K^+, Mg^{2+} and Ca^{2+} are not shown because they were affected by concrete solution. Since N_{min} and DOC concentrations were only marginally affected by concrete dissolution, they were used for further interpretation.

The mean DOC losses matched the gains for both, grassland stands and *Ref*. Stand II, III and V showed almost tendentiously lower losses than stand I and IV.

In 2003, the water gains in our grassland stands (Table 47) were 120 l m^{-2} yr^{-1} less than in 2002. Evaporation on *Ref* accounted for 49 % of water gains, whereas ET on grassland stands accounted for 61 % for stand II (*H. lanatus* + *G. pratense*) and up to 67 % for the other stands.

Under our grasslands stands, only minor amounts of N_{min} were lost with seepage; whereas *Ref* showed slightly higher N_{min} losses than gains. Stand II showed the highest (7 % gains) and stand III (*P. lanceolata*) showed lowest (0.4 % gains) N_{min} loss.

Table 47 Mean total water, nutrient and carbon gains and losses with seepage in 100 cm depth for *Ref* and experimental grassland stands I-V in 2003

Parameter	**---gains---**	***Ref***	**I**	**II**	**III**	**IV**	**V**	Tukey HSD	F	*p*
		----------seepage losses----------								
	----------[l m^{-2} yr^{-1}]----------									
	823	414 [a]	272 [c]	318 [b]	274 [c]	280 [c]	267 [c]	**	3.61	0.003
	----------[g m^{-2} yr^{-1}]----------									
N_{min}	**11.1**	13.8 [a]	0.2 [bc]	0.8 [b]	0.0 [d]	0.2 [c]	0.1 [cd]	**	79.63	0.000
K^+	**2.0**	6.8 [a]	2.2 [bc]	2.3 [b]	2.2 [b]	2.1 [b]	2.1 [b]	***	7.89	0.000
Mg^{2+}	**1.8**	4.0 [a]	0.8 [b]	1.0 [b]	0.6 [b]	0.6 [b]	0.6 [b]	*	14.34	0.000
Ca^{2+}	**2.9**	13.8 [a]	2.7 [bc]	3.2 [b]	2.2 [c]	2.2 [c]	2.0 [c]	*	13.68	0.000
DOC	**3.1**	1.8	1.6	1.8	1.7	1.6	1.5	ns	1.10	0.388

Significant distinctions between stands are indicated by different letters (one way-ANOVA: dF = 5; Tukey HSD-Test; *Ref* n = 3. stand I-V n = 5.

The mean K^+ losses under grassland stands matched the gains. K^+ losses in *Ref* were three-fold the gains. No considerable differences in K loss were found between grassland stands, despite significantly higher K accumulation in biomass of stand I-III (Table 47).

The mean Mg^{2+} and Ca^{2+} losses with seepage were considerably lower, compared to gains, of our grassland stands. Mg^{2+} losses of *Ref* were two-fold and Ca^{2+} losses to the four-fold higher than the gains. Slightly higher Mg losses were found for stand I and II compared to the other grassland stands. However, these stands did not show lower Mg accumulation in biomass (Table 47). Lower Ca accumulation in biomass of stand I (Table 47) was reflected in higher Ca losses.

The mean DOC losses were considerably lower than inputs. This was due to sorption, microbial fixation and mineralisation processes during soil passage. No significant differences occurred between the grassland stands.

3.1.5.2 Total Net Nutrient Losses from Grassland Stands

In 2002, total nitrogen loss with harvest and seepage from our grassland stands (Table 48) ranged from 13.3 to 15.4 g N m^{-2} yr^{-1}. The net N loss[6] ranged from 0.8 to 2.9 g N m^{-2} yr^{-1}. It was tendentiously lower in stand II (*H. lanatus*), whereas stand III and IV (*H. lanatus* + *P. lanceolata*) showed tendentiously higher net losses than the other grassland stands.

Table 48 Total nitrogen loss (seepage loss + aboveground biomass harvest ^) of experimental grassland stands I-V in 2002

Parameter	I	II	III	IV	V	Tukey HSD	F	*P*
	----------[g m^{-2} yr^{-1}]----------							
Total loss	14.0	13.3	15.4	15.3	13.5	ns	2.38	0.095
Total net loss [5]	1.5	0.8	2.9	2.8	1.0			

Significant distinctions between stands are indicated by different letters (one way-ANOVA: dF = 5; Tukey HSD-Test; stand I-V n = 5)
^ raw data: NEßHÖVER & BEIERKUHNLEIN, unpublished

This finding was due to tendentiously higher recover of N in belowground biomass in *H. lanatus* dominated stands II and stand V, featuring higher *H. lanatus* contribution compared to stand III and IV. Due to species implications of *A. elatius*, the contribution of accumulated aboveground N to N_{stand} in stand I did not differ from grass/mixture stands.

In 2003, total N loss with harvest and seepage from our grassland stands (Table 49) ranged from 7.7 to 12.6 g N m^{-2} yr^{-1}.

Table 49 Total nutrient loss (seepage loss + aboveground biomass harvest^) of experimental grassland stands I-V in 2003

Parameter	I	II	III	IV	V	Tukey HSD	F	*P*
Total loss	----------[g m^{-2} yr^{-1}]----------							
N	12.4 ^{a}	12.6 ^{a}	7.9 ^{b}	7.7 ^{b}	7.8 ^{b}	**	11.85	0.000
K	23.3 ^{a}	22.8 ^{a}	19.3 ^{ab}	16.8 ^{b}	17.7 ^{b}	*	7.08	0.001
Mg	2.0 ^{b}	2.7 ^{a}	1.9 ^{b}	1.6 ^{b}	1.7 ^{b}	*	7.62	0.001
Ca	5.7 ^{c}	9.3 ^{a}	8.7 ^{ab}	7.1 ^{b}	7.0 ^{b}	ns	10.78	0.000
Total net loss [5]	----------[g m^{-2} yr^{-1}]----------							
N	1.3	2.7	-3.2	-3.4	-3.3			
K	21.3	20.8	17.3	14.8	15.7			
Mg	0.2	0.9	0.1	-0.2	-0.1			
Ca	2.8	6.4	5.8	4.2	4.1			

^ raw data TÜNTE & BEIERKUHNLEIN, unpublished

Stand I (*A. elatius* + *H. lanatus*) and II (*H. lanatus* + *G. pratense*) had significantly higher N losses. Stand III-V showed a net accumulation of N amounting of 3.2 - 3.4 g N m^{-2} yr^{-1}.

[6] Net nutrient loss = *Total gains (fertilization + irrigation + precipitation)* – (*harvest loss*, Tab. 52 + *seepage loss*). No additional statistical procedure was applied

The net sequestration of N reflects mostly a considerable decrease in accumulation of N in aboveground biomass of stand III-V in 2003 by 13 – 17 % of N_{stand} in stand I and II and by 21 – 26 % N_{stand} in stand III-V. It clearly indicates a lower N supply for these grassland stands in 2003.

The total annual K losses of our grassland stands ranged from 16.8 to 23.3 g m^{-2} yr^{-1}. The present stock of NH_4Cl-extractable amounted 399 g K m^{-2}. These amounts could cover grasslands demands for 17 to 24 years at maximum. The K losses were lower for stand IV (*P. lanceolata + A. elatius + G. pratense*) and V (*P. lanceolata + A. elatius + T. officinale*) than for the other grassland stands.

The total annual Mg losses of our grassland stands varied from 1.6 to 2.7 g m^{-2} yr^{-1}. For the present stock of NH_4Cl-extractable Mg amounted 652 g Mg m^{-2}, which may cover grasslands demands for 326 to 407 years at maximum. Stand II showed significantly higher Mg losses than any other grassland stand. Stand IV and V showed a slight net accumulation of Mg.

The total annual losses of Ca from our grassland stands ranged from 5.7 to 9.3 g m^{-2} yr^{-1}. The present stock of NH_4Cl-extractable Ca amounted for 1218 g Ca m^{-2}. This stock could cover grasslands demands for 130 to 214 years at maximum. Stand II had a significantly higher Ca losses compared to stand I, IV-V. Stand I showed significantly lower net Ca losses than the other grassland stands.

3.1.5.3 Grassland Stand Implications on Nutrient Accumulation in Biomass and Nutrient Loss in 2002 / 2003

Tendentiously lower total net losses of N in grass dominated stands (I + II) in 2002 reflect mainly lower N yields (Table 52) in aboveground biomass which were mitigated by tendentiously higher N_{min} fluxes with seepage. Tendentiously higher N_{min} fluxes (Table 46) and significantly higher DOC fluxes hint at higher root-turnover in grass dominated stands.

Significantly higher seepage N_{min} fluxes and net total loss of stand I (*H. lanatus + A. elatius*) and II (*H. lanatus*) in 2003 are explained by higher *H. lanatus* detritus input for both stands. Tendentiously lower N yields (Table 53) and N_{min} fluxes (Table 47) reflect differences in physiological activity between stand I and II.

The net N sequestration amounting 3.2 to 3.4 g N m^{-2} yr^{-1} was found for stand III-V. This finding reflects lower accumulation of N (50 % of N_{stand}) in aboveground biomass in 2003 (Appendix, Table III/IV) than compared to stand I and II (58 % of N_{stand}). Since the differences in N accumulation in aboveground biomass did not account for the whole amount of sequestered N, considerable amounts N were immobilized by microorganisms. WEDIN & TILMAN (1996) reported of immobilization of N at a litter C/N wider than 32. The biomass C/N of all grassland species was significantly wider in 2002 (58 to 83) compared to 2003 (25 to 38, MANOVA: dF = F, F = 9.72, $p < 0.001$). No significant differences could be found for *H. lanatus* in different stands or for stands belowground biomass C/N. Hence C/N-ratios of plant litter were unlikely the driving factor for N sequestration in our grassland stands.

No differences in K^+ fluxes were found between our grassland stands in 2003. Higher net K losses of stand I and II were mainly due to higher K yields (Table 53). Higher net K losses indicate the importance of mineralizable *H. lanatus* detritus for biomass production and thus for nutrient yields.

In 2003, stand IV (*P. lanceolata + A. elatius + G. pratense*) and V (*P. lanceolata + A. elatius + T. officinale*) showed a slight net sequestration of Mg whereas slight losses occurred under stand I (*A. elatius + H. lanatus*) and III (*P. lanceolata*) and considerable losses under stand II (*H. lanatus + G. pratense*). Mg accumulation in aboveground biomass was only lower for stand IV and V compared to stand II. No indications for enhanced belowground storage were given. In comparison to stand I, higher net Mg losses in stand II were likely due to higher Mg^{2+} fluxes (Figure 3ä5) and higher contents of Mg for *G. pratense* (Appendix Table VI).

Despite of tendentiously higher Ca^{2+} fluxes, the net losses of Ca were lower in stand I (*A. elatius + H. lanatus*) compared to the other grassland stands in 2003. This was due to significantly lower Ca yields in biomass (Table 53). In general, grass species showed low Ca contents (Appendix, Table IV) with implications on Ca accumulation - yields and Ca^{2+} fluxes in grass dominated stands.

3.1.6 Assessment of Grassland Stands

Water- and nutrient use efficiencies were calculated as indicators of grassland stands that have advantages in concern of low water and fertilizer demands. Yields and loss/yield-ratios were used for assessing economical and ecological suitability of our grassland stands.

3.1.6.1 Water and Nutrient Use Efficiencies

In 2002, the slight differences in ET of our grassland stands (Table 50) were not reflected in mean water use efficiency based on accumulated biomass (WUE_{bm}). It ranged slightly from 2.4 to 2.6 g dm l $water_{transp}^{-1}$. No effects of functional diversity were found for WUE_{bm} of our grassland stands.

Table 50 Mean water- and nutrient use efficiencies for aboveground biomass in experimental grassland stands I-V in 2002

Parameter	I	II	III	IV	V	Tukey HSD	F	*P*
WUE_{bm}^ [g dm l $water_{transp}^{-1}$]	2.5	2.5	2.5	2.6	2.4	ns	1.54	0.229
NUE_{bm}^ [g dm g N_{accum}^{-1}]	72	71	66	67	70	ns	1.38	0.275
KUE_{bm}^ [g dm g K_{accum}^{-1}]	42 ^{a}	40 ^{a}	34 ^{b}	34 ^{b}	37 ^{a}	***	5.96	0.002
$MgUE_{bm}$^ [g dm g Mg_{accum}^{-1}]	790 ^{a}	770 ^{ab}	670 ^{b}	704 ^{ab}	741 ^{ab}	*	3.14	0.028
$CaUE_{bm}$^ [g dm g Ca_{accum}^{-1}]	335 ^{a}	327 ^{a}	154 ^{b}	173 ^{b}	184 ^{b}	***	115.05	0.000

Significant distinctions between stands are indicated by different letters (one way-ANOVA: dF = 5; Tukey HSD-Test; stand I-V n = 5)
^ raw data: NEßHÖVER & BEIERKUHNLEIN, unpublished

The mean nitrogen use efficiency based on accumulated aboveground biomass (NUE_{bm}) ranged slightly from 66 to 71 g dm g N_{accum}^{-1}. I (*H. lanatus* + *A. elatius*), II (*H. lanatus*) and V (*H. lanatus* + *P. lanceolata*) showed tendentiously higher NUE_{bm} than other stands. Stand III and IV (*H. lanatus* + *P. lanceolata*) showed lower grass contribution (Appendix, Table XIV). N contents in grass biomass (1.4 %) were significantly lower than in herb biomass (1.7 %; one way-ANOVA: dF = 1, F = 66.25, $p < 0.001$; Tukey HSD ***). Since the dominant herb species *P. lanceolata* only showed slightly higher N contents (1.5 %; one way-ANOVA: dF = 7; F = 19.36, $p < 0.001$, Tukey HSD ns), differences in NUE_{bm} between stands were only tendentious. Higher NUE_{bm} in grass dominated stands were reflected in tendentiously lower N_{stand}.

The mean K use efficiency (KUE_{bm}) ranged from 34 to 42 g dm g K_{accum}^{-1}. Stand I, II and V showed significantly higher KUE_{bm} than any other stand. This effect could not be attributed to functional diversity. Grasses showed significantly lower K contents (23.8 mg K g dm^{-1}) as herb species (34.9 mg K g dm^{-1}; one way-ANOVA: dF = 1, F = 82.14, $p < 0.001$; Tukey HSD ***). For *P. lanceolata*, K contents (32.5 mg g^{-1}) were significantly higher than for *H. lanatus* and *A. elatius* (25.1/22.6 mg K g^{-1}, one way-ANOVA: dF = 7, F = 40.30, $p < 0.001$; Tukey HSD ***).

The mean Mg use efficiency ($MgUE_{bm}$) of our grassland stands ranged from 670 to 790 g dm g Mg_{accum}^{-1}. Stand I showed a significantly higher and stand II and V tendentiously higher $MgUE_{bm}$ than any other stand. Stand III had a significantly lower $MgUE_{bm}$. Grasses showed significantly lower Mg contents (1.2 g Mg g dm^{-1}) than herbs 2.5 mg Mg g dm^{-1}; Appendix, Table XVI). For *H. lanatus* and *A. elatius* (1.2 / 1.1 mg Mg g dm^{-1}), the Mg contents were significantly lower than compared to *P. lanceolata*, Mg contents (1.7 mg Mg g dm^{-1}; one way-ANOVA: dF = 7, F = 65.16, $p < 0.001$; Tukey HSD ***).

The mean Ca use efficiency ($CaUE_{bm}$) of our grassland stands ranged from 154 to 192 g dm Ca_{accum}^{-1}. Grass dominated stands I and II showed significantly higher $CaUE_{bm}$ than any other stand. This finding was reflected in herb species showing significantly higher Ca contents (10.2 mg Ca g^{-1}) than grass species (2.9 mg Ca g dm^{-1}; Appendix, Table XVI). For *P. lanceolata*, Ca contents (9.1 mg Ca g dm^{-1}) were significantly higher than for any other species (one way-ANOVA: dF = 7, F = 65.16, $p < 0.001$; Tukey HSD ***).

Due to lower base cation contents in aboveground biomass, grass dominated stands had significantly higher base cation use efficiencies and K_{stand}, Mg_{stand} and Ca_{stand}. Hence, herb contribution to stand biomass was a factor determining KUE_{bm}, $MgUE_{bm}$ and $CaUE_{bm}$ of our grassland stands in 2002.

The mean WUE_{bm} of our grassland stands decreased significantly from 2002 to 2003 by 50% (Appendix, Table VIII). This finding is likely due to the hot and dry summer 2003. Luxury consumption of water due to irrigation, likely physiological mechanisms for enhanced WUE_{bm} made unnecessary grassland plants. No implications of functional diversity on mean WUE_{bm} (Table 51) could be found. Stand I (*A. elatius* + *H. lanatus*) and II (*H. lanatus* + *G. pratense*) had significantly higher WUE_{bm} than stand V (*P. lanceolata* + *A. elatius* + *T. officinale*).

Table 51 Mean water- and nutrient use efficiencies for aboveground biomass in experimental grassland stands I-V in 2003

Parameter	**I**	**II**	**III**	**IV**	**V**	Tukey HSD	F	*p*
WUE_{bm}^ [g dm l $water_{transp}^{-1}$]	1.7 a	1.5 a	1.1 b	1.0 b	1.0 b	***	28.44	0.000
NUE_{bm}^ [g dm l g N_{accum}^{-1}]	77	64	76	72	72	Ns	2.68	0.061
KUE_{bm}^ [g dm g K_{accum}^{-1}]	43 a	37 b	35 b	37 b	35 b	**	11.80	0.000
$MgUE_{bm}$^ [g dm g Mg_{accum}^{-1}]	769 a	464 b	468 b	504 b	488 b	***	48.55	0.000
$CaUE_{bm}$^ [g dm g Ca_{accum}^{-1}]	306 a	131 b	91 c	111 bc	110 bc	***	137.99	0.000

Significant distinctions between stands are indicated by different letters (one way-ANOVA: dF = 5; Tukey HSD^ Test; stand I-V n = 5)
raw data: TÜNTE & BEIERKUHNLEIN, unpublished

However, OPITZ VON BOBERFELD (1994) reported enhanced WUE_{bm} at higher levels of fertilization (10 g N m^{-2} yr^{-1}) for *A. elatius* stands. SCHINDLER ET AL. (2001) confirmed enhanced WUE_{bm} at lower N fertilisation (4-6 g N m^{-2} yr^{-1}) for *Hordeum vulgare* (Barley). In contrast to these findings, TSIALTAS ET AL. (2001) reported of decreased WUE for grass and herb species with increased N contents in leaf biomass.

LINDHAUER (1983) found higher water use efficiency of *Hordeum vulgare* seedlings due to higher K^+ supply. High availability of K^+ in soil solution may also have caused a higher WUE_{bm}. BERGMANN (1992) reported a higher capacity of grass species for K acquisition due to their homorhizal root system. No correlations were found between NUE_{bm}, KUE_{bm} and WUE_{bm}. Grass species might maintain enhanced WUE_{bm} at fairly increased K acquisition.

The mean NUE_{bm} increased tendentiously from 2002 to 2003 by 4 % (Appendix, Table VIII). Better supply with base cations might have affected NUE_{bm} to some extent. The mean NUE_{bm} in our grassland stands ranged from 64 to 77 g dm g N_{accum}^{-1}. In 2003 stand II showed tendentiously lower NUE_{bm} than any other grassland stand. This finding was well reflected in higher N_{stand}. Due to higher biomass yields, stand I had highest N_{stand}.

Herb species showed slightly higher N contents (1.6 %) than grass species (1.4 %; Appendix; Table XVI). General correlations between herb contribution and NUE_{bm} could not be found. The variability of N contents of *G. pratense* in different grassland stands was low. It showed only tendentiously higher contents in stand II than in stand IV and V (one way-ANOVA: dF = 1, F = 1.06, $p > 0.05$). *H. lanatus* only had tendentiously higher N contents in stand I (one way-ANOVA: dF = 1, F = 3.15, $p > 0.05$). Hence, lower NUE_{bm} of the species contributing to stand II seemed to be plant characteristics for both species and not strictly dependent on increased N availability of stand II.

The mean KUE_{bm} of our grassland stands ranged from 35 to 43 g dm g K_{accum}^{-1}. Stand I showed significantly higher KUE_{bm} than any other grassland stand. In 2003, grass species showed only tendentiously lower K contents than herb species (Appendix, Table XVI). However, Stand I dominating *A. elatius* showed significantly lower K contents (22.7 mg K g dm^{-1}) than *P. lanceolata* and *T. officinale* (27.6 / 50.6 mg K g^{-1}; one way-ANOVA: dF = 7, F = 83.05, $p < 0.001$; Tukey HSD ***). Due to higher biomass production, stand I showed similar K_{stand} than the other stands.

The mean $MgUE_{bm}$ of our grassland stands ranged considerably from 488 to 769 g dm g Mg_{accum}^{-1}. The range of $MgUE_{bm}$ was lower in 2002 than in 2003. Differences in $MgUE_{bm}$ likely occur more pronounced at higher Mg^{2+} concentrations in soil solution. (Appendix, Table XIII). In 2003, grass dominated stand I showed higher $MgUE_{bm.}$ Herbs had significantly higher Mg contents (2.6 mg Mg g dm^{-1}) than grass species (1.4 mg Mg g dm^{-1}; Appendix Table XVI).

The mean $CaUE_{bm}$ of our grassland stands ranged in 2003 from 40 to 138 g dm g Ca_{accum}^{-1}. It was considerably lower than in 2002. Analogous to K and Mg, higher soil solution concentrations of Ca in 2003 led to decreased use efficiencies of Ca.

Stand I showed a significantly higher $CaUE_{bm}$ for both years, whereas stand II showed a only tendentiously higher $CaUE_{bm}$ in 2003. In 2003, grass species showed significantly lower Ca contents (4.2 mg Ca g dm^{-1}) than herbs (12.0 mg Ca g dm^{-1}; Appendix, Table XIII).Hence, higher availability of Mg and Ca in soil solution reflected differences in physiological characteristics of plants more pronounced than other nutrients.

Water- and Nutrient Efficiencies in Grassland Stands 2002 / 2003

In 2003, WUE_{bm} was two times lower than in 2002 (Appendix, Table XIV). Due to the dry and hot summer in 2003, stands were irrigated, which in turn led to higher ET, because plants were not forced to save water. In temperate climate, WUE_{bm} for grasslands can range from 1.3 to 4.7 g dm l $water_{transp}^{-1}$ at high precipitation (FIELD ET AL., 1997; ARP ET AL., 1998; LUCERO ET AL., 2000). NELSON ET AL. (2004) reported of WUE_{bm} ranging from 2 to 7 g dm l $water_{transpir}^{-1}$ at low precipitation (320 l m^{-2} a^{-1}). WUE_{bm} of our grassland stands in was rated low for 2002 and 2003.

Higher WUE_{bm} in stand I (*A. elatius* + *H. lanatus*) and II (*H. lanatus* + *G. pratense*) between grassland stands could be explained by different factors. The contribution of *A. elatius* increased in stand I from 2002 to 2003 from 11 to 83 % of stand aboveground biomass (Appendix, Table X). Due to its enhanced resilience towards water stress (ELLENBERG, 1991) *A. elatius* might have enhanced WUE_{bm} to some extent.
TSIALTAS ET AL. (2001) found higher WUE_{bm} for grass species compared to herb species. They also underpinned the importance of the physiological traits in concern of species abundances in grasslands under water limitation. Significant negative correlations between herb biomass and WUE_{bm} were also found for 2003. Since correlation was based on the presence of stand I and II, mere coinciding of herb contribution and WUE_{bm} must be assumed.

EBDON ET AL. (1998) showed the importance of canopy temperature for transpiration and thus for WUE_{bm}. Since *H. lanatus* is adapted to better water supply (ELLENBERG, 1991), it may provide lower canopy temperatures for *A. elatius* by enhanced transpiration as suggested for *Trifolium repens* and *Lolium perenne* (HOGH-JENSEN & SCHJOERRING, 1997). Besides modification in canopy temperature and moisture, *H. lanatus* may have profited from shading provided by broad leaves of *G. pratense* in stand II.

Increased WUE_{bm} in stand I and II may have been due to slightly higher availability of N in these stands. SCHINDLER ET AL. (2001) reported of increased WUE_{bm} due to slightly higher N availability for *Hordeum vulgare*. In contrast to this, TSIALTAS ET AL. (2001) showed that WUE of grassland plants under water limitation is negatively correlated with N contents in aboveground biomass. The correlations between higher N availability and WUE_{bm} were dependent on the presence of stand I and II.

Since correlation between NUE_{bm} and WUE_{bm} were also not found, a mere coinciding between the high N availability in soil solution and WUE_{bm} in our grassland stands is likely. In agreement with TSIALTAS ET AL. (2001) WUE_{bm} was identified as important factor determining biomass production (Figure 39). The correlation was highly significant for both years, even when stand I and II were excluded from analysis.

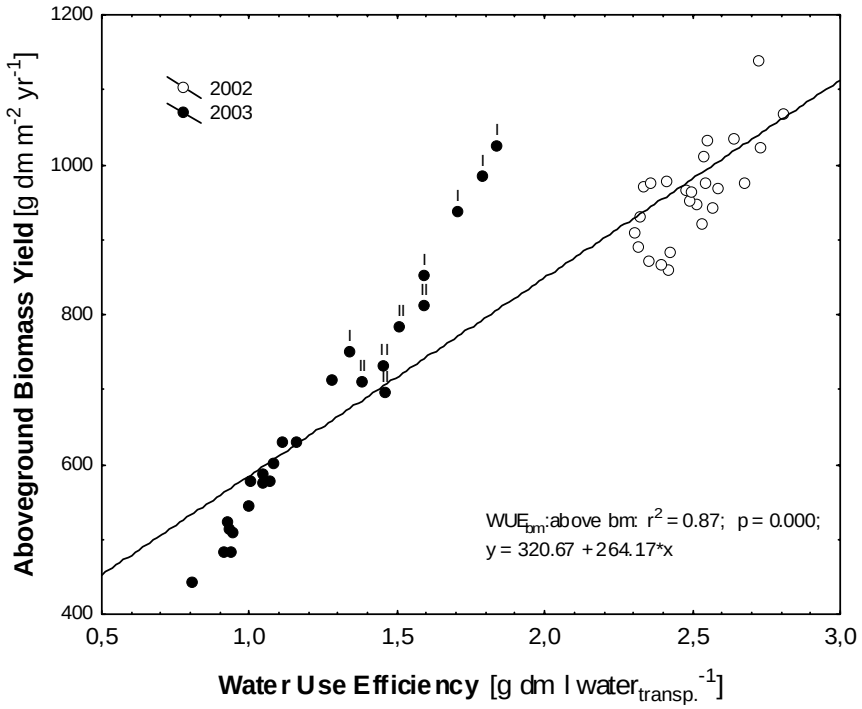


Figure 39 Correlation between water use efficiency and aboveground biomass yield of experimental grassland stands in 2002 / 2003

Negative correlations between herb contribution and WUE_{bm} were likely biased by higher *H. lanatus* detritus inputs in stand I (*A. elatius* + *H. lanatus*, ●I) and II (*H. lanatus* + *G, pratense*, ● II). Due to the lacking of permanent monocultures, single plant species or functional groups with higher WUE_{bm} could not be identified.

High K concentrations in soil solution likely enhance WUE_{bm} (BERGMANN, 1992). Significant correlation between soil solution concentration of K^+ or KUE_{bm} and WUE_{bm} could not be found for both years.

SCHILS ET AL. (1999) gave NUE_{bm} ranging from 37 to 49 g dm g N_{accum}^{-1}. *Hordeum vulgare* showed NUE_{bm} from 30 to 49 g dm g N_{accum}^{-1} (GORNY & SAKIEWICZ, 2001; DAEPP ET AL., 2001). Considering these values, NUE_{bm} for all stands were regarded as very high for both years.
Correlations between herb contribution and NUE_{bm} were not found. The biomass production seemed to be rather independent of NUE_{bm}.

KOUTROUBAS ET AL. (2000) reported of KUE_{bm} ranging from 66 to 180 g dm g K_{accum}^{-1} under laboratory conditions. In dependence on high or low availability, *P. lanceolata* showed a range of 69 to 153 g dm g K_{accum}^{-1}. MARSCHNER (2002) gave values of optimal nutrient contents for *Lolium perenne*. Deduced KUE_{bm} ranged from 29 to 40 g dm g K_{accum}^{-1}. Regarding these values, KUE_{bm} of our grassland stands were medium to high for both years.

Deduced $MgUE_{bm}$ from values given by MARSCHNER (2002) ranged from 200 to 500 g dm g Mg_{accum}^{-1}. $CaUE_{bm}$ of *Lolium perenne* at optimal nutrition can range from 83 to 167 g dm g Ca_{accum}^{-1} (deduced after MARSCHNER, 2002). Regarding these values, $MgUE_{bm}$ and $CaUE_{bm}$ of our grassland stands were rated very high for both years.

KUE_{bm}, $MgUE_{bm}$ and $CaUE_{bm}$ decreased significantly with herb contribution in our grassland stands (Figure 40). This finding is likely explained by lower base cation demands of grass species (MARSCHNER, 2002). Significant correlations between soil solution concentrations and use efficiencies of Mg and Ca were identified as coinciding due to detritus inputs in stand I and II in 2003.

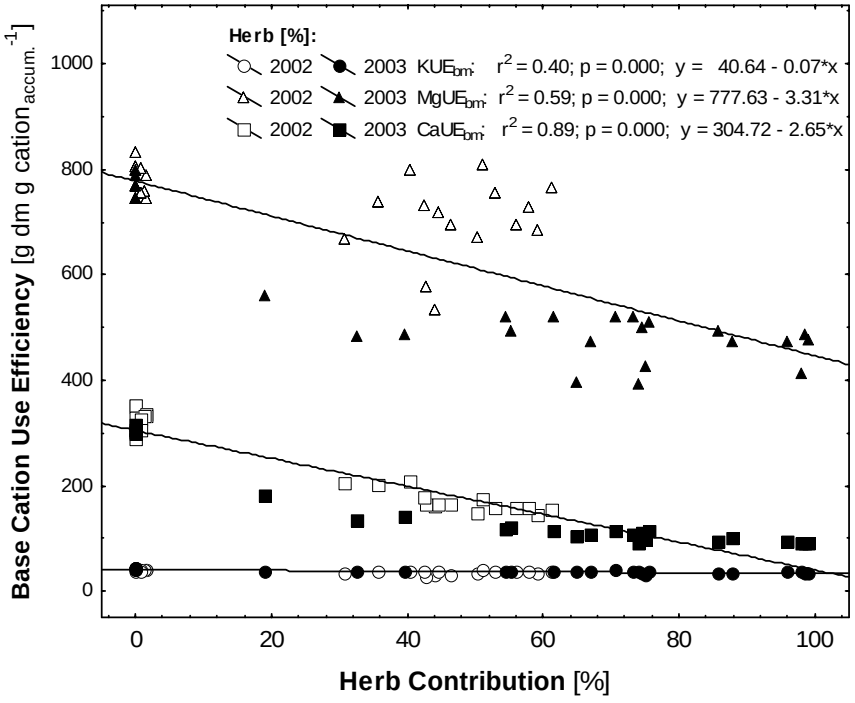


Figure 40 Correlation between herb contribution in above-ground biomass of experimental grassland stands and nutrient use efficiencies for K, Mg, Ca in 2002 / 2003

DACCORD ET AL. (2001) confirmed considerably lower K and Ca contents and tendentiously lower Mg contents of grass in comparison to herb species. Hence lower use efficiencies of K, Ca and for some extent of Mg for herb species compared to grass species are indicated for European grasslands. Deduced values gave for herbs mean use efficiencies for K 22, Mg 312 and for Ca of 73 g dm base cation accum^{-1}. In contrast to this, grass species showed for K 31, Mg 588 and for Ca 270 g dm g base cations$_{accum}^{-1}$. The findings in our grasslands highly agree with values given by DACCORD ET AL. (2001) for K and Ca, whereas the $MgUE_{bm}$ of the experimental grasslands was considerably higher. $MgUE_{bm}$ for herb species exceeded the given values by the two-fold and for grass species only slightly. These differences may be due to differences in species traits, but they also hint at low Mg supply in our grassland stands.

Neither KUE_{bm}, nor $MgUE_{bm}$ or $CaUE_{bm}$ showed significant correlation to aboveground biomass production. A dilution of base cation contents due to enhanced growth could not be found.

3.1.6.2 Nutrient Yield and Loss/Yield-Ratio

Nutrient yields and loss/yield-ratio were used as assessment of the grassland stands under economical and ecological vs. economical aspects.

In 2002, N aboveground yield of our grassland stands (Table 52) ranged from 12.9 to 15.2 g N m^{-2} yr^{-1}. It was tendentiously higher for stand III (*H. lanatus* + *P. lanceolata*) than for any other grassland stand.

Table 52 Nutrient removal with aboveground biomass (yield) and ratio of seepage loss to yield of experimental grassland stands I- V in 2002

Parameter	I	II	III	IV	V	Tukey HSD	F	*P*
Yield	----------[g m^{-2} yr^{-1}]----------							
N	13.6	12.9	15.2	14.9	13.4	ns	2.63	0.065
K	23.6 ^{b}	22.8 ^{b}	29.1 ^{a}	29.3 ^{a}	24.9 ^{b}	*	7.58	0.001
Mg	1.2 ^{b}	1.2 ^{b}	1.5 ^{a}	1.4 ^{ab}	1.3 ^{ab}	*	5.33	0.004
Ca	2.9 ^{c}	2.8 ^{c}	6.5 ^{a}	5.8 ^{ab}	5.1 ^{b}	*	50.14	0.000
Loss/yield-ratio	----------[g m^{-2} yr^{-1} / g m^{-2} yr^{-1}]----------							
N	0.03	0.03	0.01	0.03	0.01	ns	1.73	0.184

Significant distinctions between stands are indicated by different letters (one way-ANOVA: dF = 5; Tukey HSD-Test; stand I-V n = 5)
^ raw data: NEßHÖVER & BEIERKUHNLEIN, unpublished

In terms of N yield, *P. lanceolata* dominated stand III showed the best performance of our grassland stands in 2002. The loss/yield-ratio ranged from 0.01 to 0.03. It was lower for stand III. The stand showed the best performance in concern of N harvest and safety net function.

The mean K yield of our grassland stands ranged from 22.8 to 29.3 g K m^{-2} yr^{-1}. Stand III and IV (*H. lanatus* + *P. lanceolata*) showed significantly higher K removals than the other grassland stands. Stand III and IV showed best performance in concern of K harvest in 2002.

The mean yield in Mg ranged from 1.2 to 1.5 g Mg m^{-2} yr^{-1}. Stand I (*H. lanatus* + *A. elatius*) and II (*H. lanatus*) showed lower Mg removals than stand III-V. The differences were significant for stand III. Stand III-V showed best performance in concern of aboveground yield for Mg in 2002.

The mean yield in Ca of our grassland stands ranged from 2.8 to 6.5 g Ca m^{-2} yr^{-1}. Stand I and II had significantly lower Ca yields than stand III-V. Stand III appeared to be the grassland stand with the best performance in concern of N, K, Mg and Ca yield in 2002. In general, grass/herb mixtures showed better performance in nutrient yields.

In 2003, the mean N yield of our grassland stands (Table 53) ranged from 7.4 to 12.2 g N m^{-2} yr^{-1}. Stand I (*A. elatius + H. lanatus*) and II (*H. lanatus + G. pratense*) showed significantly higher N yields than stand III-V. The mean loss/yield-ratio ranged from 0.01 to 0.04. It was low for stand I. Stand I showed the best performance in concern of N yields and safety net function in 2003. Since loss/yield-ratio was significantly higher for stand II, the stand showed only good performance in concern of N yield.

Table 53 Nutrient removal with aboveground biomass (yield) and ratio of seepage loss to yield of experimental grassland stands I-V in 2003

Parameter	I	II	III	IV	V	Tukey HSD	F	*P*
Yield	----------[g m^{-2} yr^{-1}]----------							
N	12.2 ^{a}	11.7 ^{a}	7.8 ^{b}	7.4 ^{b}	7.6 ^{b}	**	10.75	0.000
K	21.1 ^{a}	20.1 ^{ab}	17.1 ^{abc}	14.6 ^{c}	15.6 ^{b}	*	6.51	0.002
Mg	1.2 ^{b}	1.6 ^{a}	1.3 ^{b}	1.1 ^{b}	1.1 ^{b}	*	8.24	0.000
Ca	3.0 ^{b}	6.0 ^{a}	6.5 ^{a}	4.9 ^{a}	4.9 ^{a}	*	9.65	0.000
Loss/yield-ratio	----------[g m^{-2} yr^{-1} / g m^{-2} yr^{-1}]----------							
N	0.02 ^{b}	0.08 ^{a}	0.01 ^{b}	0.04 ^{ab}	0.02 ^{b}	*	4.02	0.015
K	0.11	0.14	0.14	0.15	0.14	ns	1.62	0.207
Mg	0.68	0.65	0.50	0.53	0.55	ns	0.73	0.581
Ca	0.92 ^{a}	0.59 ^{b}	0.35 ^{b}	0.46 ^{b}	0.42 ^{b}	***	13.69	0.000

Significant distinctions between stands are indicated by different letters (one way-ANOVA: dF = 5; Tukey HSD-Test; stand I-V n = 5)
^ raw data: TÜNTE & BEIERKUHNLEIN, unpublished

The mean yield in K ranged from 14.6 to 21.1 g K m^{-2} yr^{-1}. Stand I showed significantly higher K yields than stand IV (*P. lanceolata + A. elatius + G. pratense*) and V (*P. lanceolata + A. elatius + T. officinale*). Stand II and III (*P. lanceolata*) had only tendentiously higher K yields than stand IV and V. The mean loss/yield ratio ranged from 0.11 to 0.15. Since stand I also showed tendentiously lower loss/harvest-ratios, it had the best performance in concern of K yield and safety net functions in 2003.

The mean Mg yield of our grassland stands ranged from 1.1 to 1.6 g Mg m^{-2} yr^{-1}. Stand II showed significantly higher Mg yields than the other stands. The mean loss/yield ratios ranged from 0.50 to 0.68. Due to tendentiously higher loss/yield-ratios, stand II only showed best performance in concern of Mg yield but not in concern of safety net functions for Mg in 2003. Stand III had lower yields, but also showed lower loss/harvest-ratios and thus, might be an alternative for stand II.

The mean yield in Ca ranged from 3.0 to 6.5 g Ca m^{-2} yr^{-1}. Stand I showed significantly lower Ca yields than stand II-V. Stand III showed the highest Ca yields with harvest. The mean loss/yield-ratio ranged from 0.35 to 0.92. It was tendentiously lower in stand III. Hence, stand III showed the best performance in concern of yield and safety net functions for Ca in 2002.

In 2003, the best performance in concern of yield and safety net function differed from 2002. In concern of N and K, highly productive grassland stand I took over best performance, whereas stand III appeared to be the stand with the best performance in concern of Mg and Ca yields as well as safety net function in 2003. In general, grass/herb mixtures showed better performance in nutrient yields and safety net functions for Mg and Ca.

DIERSCHKE & BRIEMLE (2002) gave average aboveground K yields of extensively used grasslands of 12 g K m^{-2} yr^{-1} for a two-cut regime at compensation fertilization. LFL (2003) gave aboveground yields of 9.5 to 11.5 g K m^{-2} yr^{-1}. Since 79 to 80 % of accumulated K was found in aboveground biomass (Appendix, Table III), K yields of our grassland stands were rated high for both years. Stand I (*H. lanatus* + *A. elatius*) and II (*H. lanatus*) showed tendentiously higher allocation of K to aboveground biomass than the other grassland stands in both years (83 to 84 %).
Lower K yields of stand I and II compared to stand III-V hint at implications of *P. lanceolata* species traits. Higher K yields of stand I (*A. elatius* + *H. lanatus*) in 2003 were due to *H. lanatus* detritus inputs.

The net K losses of stand III-V were lower than in stand I and II in 2003. This difference was mostly due to higher K yields for stand I and II despite higher KUE_{bm}. This finding clearly illustrates the limitation of biomass production and hence base cation yields by availability of N.

LFL (2003) gave 0.1 g Mg m^{-2} yr^{-1} as mean aboveground yields of extensive grasslands under a two- cut regime. Aboveground Mg accounted for 40 % of accumulated Mg in 2002 and decreased to 36 % in 2003 (Appendix, Table XIV). Mg accumulation in our grassland stands was rated very high. Analogous to N, and K accumulation, stand III and IV (*H. lanatus* + *P. lanceolata*) had higher Mg accumulation in biomass in 2002. This finding hints at functional complementary in concern of Mg accumulation between *H. lanatus* and P. *lanceolata* to some extent. In 2003, no differences between the grassland stands in concern of Mg accumulation were found. This was mostly due to a higher biomass production of stands with high $MgUE_{bm}$.

In 2003, stand IV (*P. lanceolata* + *A. elatius* + *G. pratense*) and V (*P. lanceolata* + *A. elatius* + *T. officinale*) showed slight sequestration of Mg and only slight losses under stand I (*A. elatius* + *H. lanatus*) and III (*P. lanceolata*) and considerable losses under stand II (*H. lanatus* + *G. pratense*). In comparison to stand I, higher Mg fluxes under stand II were likely due to higher seepage fluxes (Figure 26) and higher biomass contents of Mg^{2+} in *G. pratense* (Appendix Table XVI).

LFL (2003) gave 3.5 to 4.3 g Ca m^{-2} yr^{-1} as mean aboveground yield in extensive grasslands under two-cut regimes. Aboveground Ca accounted for 76 % of total Ca accumulation in 2002 and for 72 % in 2003 (Appendix, Table XIV). Ca accumulation in aboveground biomass of our grassland stands was rated very high. Stand II also had significantly higher Ca accumulation (80 % Ca_{stand}) than any other stand in 2003. In 2002, stands containing *H. lanatus* and *P. lanceolata* (III-V) showed higher Ca accumulation than stand I and II. This finding suggests belowground complementary in concern of Ca acquisition for both species analogous to N and K accumulation. In 2003, *P. lanceolata* monoculture (stand III) showed the highest Ca accumulation. Stand IV and V showed lower Ca accumulation in aboveground biomass, likely due to lower contribution of *P. lanceolata* to stand biomass. Whereas, stand I also showed low Ca accumulation in 2003, despite of change in dominance patterns, the upcoming of *G. pratense* in stand II (*H. lanatus* + *G. pratense*) and the dominance of *P. lanceolata* in stand III increased the Ca accumulation considerably.

Despite of tendentiously higher Ca fluxes with seepage, the net losses of Ca were lower in stand I (*A. elatius* + *H. lanatus*) in 2003. This was due to significantly lower Ca yields in biomass. In general, grass species showed low Ca contents with implications on Ca accumulation - yields and fluxes in stand grass dominated stands.

3.1.6.3 Assessment of Grassland Stands in Respect of Nutrient Yields and Safety Net Functions for 2002 / 2003

Higher WUE_{bm} in stand I and II in 2003 is assessed as a positive criterion for grassland stands, because global climatic change likely forces water saving management practices.

Stands with high NUE_{bm} may provide high productivity at low fertilizer inputs. In this concern, stand I (*H. lanatus* + *A. elatius*) showed slight advantages compared to *H. lanatus* monoculture and *H. lanatus* + *P. lanceolata* co dominated grassland stands in 2002. The N yields were tendentiously higher and loss/yields-ratios were lower in stands dominated by *P. lanceolata*.

In 2003, only stand II (H. *lanatus* + *G. pratense*) differed from the other stands with a lower NUE_{bm}. Low NUE_{bm} and high loss/yield-ratios classify stand II as a fertilizer consuming grassland stand with higher risk of N leaching compared to the other stands.
Our grasslands only received low compensation fertilization (10 to 11 g N m^{-2} yr^{-1}). Taking recommended fertilizer application for European meadow grasslands (30 to 70 g N m^{-2} yr^{-1}; WHITEHEAD, 1995) into consideration, stand II might have shown intolerable nitrogen concentrations (› 50 mg NO_3-N l^{-1}) and loss in seepage after such fertilizer applications.

Stand I (*A. elatius* + *H. lanatus*) had higher NUE_{bm}, high N yields and low loss/yield-ratios. Hence in concern of demand, yield and safety net functions for N grass dominated stand I was the grassland stand with the best performance in 2003.

P. lanceolata monocultures (stand III) showed higher N yields than grass/herb mixtures (stand IV/V). The effect of *P. lanceolata* contribution on N use parameters had decreased since N contents in 2003 were similar to grass species contents (Appendix, Table VI/VII).

In 2002, stands with a higher herb contribution (III-V) showed lower KUE_{bm}, $MgUE_{bm}$ and $CaUE_{bm}$. These findings were associated with higher yields in K, Mg and Ca. Thus in concern of safety net functions for K, grassland stands higher herb contribution were classified as more suitable. Since the main herb biomass was provided by *P. lanceolata*, the base cation use of stand III-V was due to species traits of *P. lanceolata* to a major extent.

In contrast to 2002, the grass dominated stand I had higher KUE_{bm} than the other grassland stands in 2003. Due to higher biomass production, stand I showed highest K yields and tendentiously lower loss/yield ratios than the other stands. In concern of K demand, grass dominated stands showed advantages.

In 2003, the highest $MgUE_{bm}$ indicated lower Mg demands for grass stand I. The Mg yields were low and the loss/yield-ratio was high. Therefore, high yields and low loss/yield-ratios classified stand III (*P. lanceolata*) as most suitable in concern of safety net functions for Mg in 2003.

Grass dominated stands I and II had higher $CaUE_{bm}$ in 2002. These stands showed considerably lower Ca yields and higher loss/yield-ratios. Stand III (*H. lanatus + P. lanceolata*) showed a lower $CaUE_{bm}$, higher Ca yields and lower loss/yield-ratios. Thus stand III was classified as most suitable in concern safety net functions for Ca in 2002.

Lower K, Mg and Ca use efficiencies were found in *H. lanatus + P. lanceolata* stands (III-V) in 2002 and in *P. lanceolata + A. elatius* in accessory of subordinates (IV-V). Since these features appeared to be most pronounced in monocultures, they are most likely due to species traits of *P. lanceolata*. At considerable contribution to stand biomass (› 50 %), the presence of *P. lanceolata* determined the base cation use of our grassland stands. Since *G. pratense* and *T. officinale* shared high base cation contents, they also contributed to base cation yield and safety net functions. However, their contribution was limited due to low biomass productivity.

In 2003, higher biomass production led to considerably higher K yields and lower loss/yield ratios despite of higher KUE_{bm} in stand I (*A. elatius + H. lanatus*). The grass species combination likely facilitated higher K acquisition compared to stand II by its homorhizal root system. BERGMANN (1992) confirmed higher K acquisition for grass species compared to herb species due to their homorhizal root systems. The presence of allorhizal belowground system of *G. pratense* in stand II obviously impaired K acquisition and led to higher loss/yield ratios than in stand I.

DAEPP ET AL. (2001) reported N aboveground yields to 10 g N m^{-2} yr^{-1} in a *Lolium perenne* two-cut regime. SCHILS ET AL. (1999) gave aboveground yields ranging from 9.1 to 13.6 g N m^{-2} yr^{-1} in a *Lolium perenne* two-cut regime with application of 8 g N m^{-2} yr^{-1}. DIERSCHKE & BRIEMLE (2002) gave aboveground yields of extensively used grasslands of 10 g N m^{-2} yr^{-1} for a two-cut regime at compensation fertilization. LFL (2003) confirmed aboveground yields ranging from 6.5 to 7.8 g N m^{-2} yr^{-1}. N aboveground yields of similar grassland stands of the former BIODEPTH-site ranged from 2 to 15 g N m^{-2} yr^{-1} (NEßHÖVER, 2005).

Nutrient accumulation of our grassland stands (Table 22, 23), included nutrients in above and belowground biomass. In 2002 aboveground accumulation accounted for 70-75 % of N_{stand} of the grassland stands, whereas the contribution of aboveground accumulation to N_{stand} decreased for all stands in 2003, ranging from 48 to 56 % (Appendix, Table III). Regarding this, the mean N accumulation in our grassland stands was rated medium to high for 2002 and 2003.

In 2002, stand III and IV (*H. lanatus* + *P. lanceolata*) showed somewhat higher N yields than stand I and II (*H. lanatus*). This finding reflects higher N accumulation to aboveground biomass due to *P. lanceolata* contribution. In 2003, higher N yields in biomass of stand I and II were very likely due to enhanced mineralisation (also 3.1.3.2) of *H. lanatus* detritus (Figure 22). However, in stand III-V detritus input was almost equal. Stand III (*P. lanceolata*) showed tendentiously higher N yields than stand IV - V. Hence, higher functional diversity in these stands did not lead to enhanced N accumulation. This finding hints at increased competition for nitrogen in comparison to stand III.

A decline in the contribution of aboveground N accumulation to N_{stand} likely indicated increasing belowground competition between plants in the grassland stands. Since this decline was found for all grassland stands in 2003, competitive rather than complementary relations between species were indicated, irrespective of functional group controlled N yields in our grassland stands.

In both years, grass dominated stands showed higher use efficiencies for K, Mg and Ca. Hence grass species showed lower demands in these base cations for biomass production. In concern of safety net functions, the performance of grass dominated stands was quite poor, due to higher demands grass/herb-mixtures showed lower loss/yield-ratios and thus higher safety net functions. In 2003, stand I showed despite of higher KUE_{bm} considerable K yields and low loss/yield-ratios. This finding was mainly attributed to a higher biomass production compared to the other grassland stands.

3.2 Rhizodeposit Experiment 2003

Implications of different Fe nutritional strategies on the release of rhizodeposits were investigated using four grassland species out of the pool of species used for the lysimeter experiments. The 1st biomass harvest of swards established in pots took place three and the 2nd harvest five months after establishment. Fe was re supplied three weeks after the 1st harvest.

3.2.1 Sward Composition / Biomass Characteristics

After three month growth (1st harvest), the median aboveground biomass in swards containing *H. lanatus* ranged from 1379 to 1520 g dm m^{-2} (Figure 41). *H. lanatus* dominated any diculture with at least 75 % of aboveground biomass.

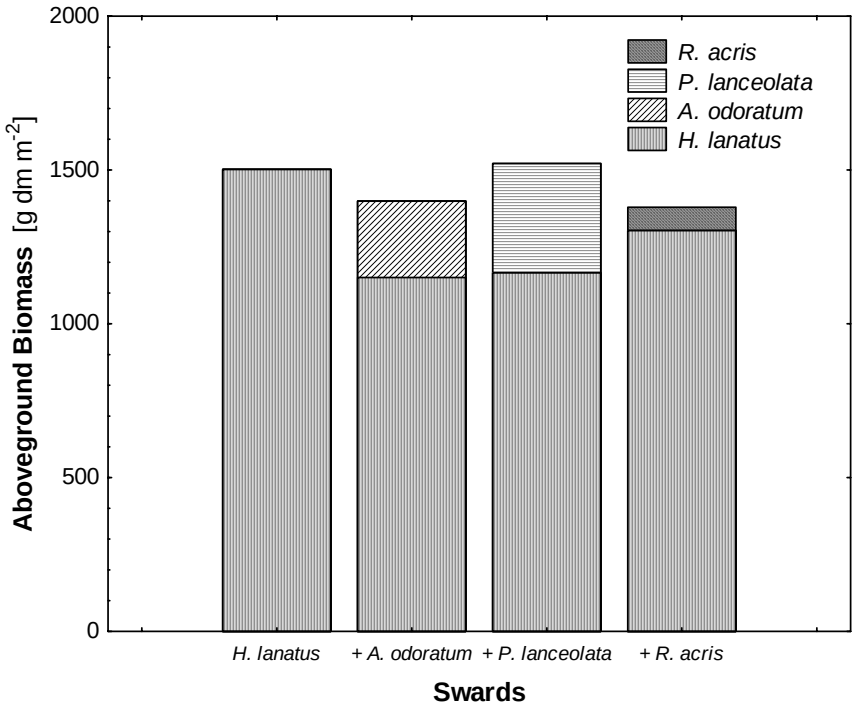


Figure 41 Median1st harvest aboveground biomass in swards containing *H. lanatus*

Total aboveground biomass Kruskal-Wallis-ANOVA: 1.21; p = 0.750; stand n = 4

The median individual aboveground 1st harvest biomass of *H. lanatus* (Table 54) ranged from 375 to 652 g dm m^{-2}. Individual *H. lanatus* biomass in monoculture was significantly lower than in diculture swards. It suggests high intra-specific competition in monocultures.

Table 54 Median (25th /75th Percentile) of individual aboveground biomass of *H. lanatus* per individual in mono- and diculture swards (1st harvest)

Parameter	***H. lanatus***	***+ A. odoratum***	***+ P. lanceolata***	***+ R. acris***	MW-U	KW-H	*p*
	----------[g dm m^{-2}]----------						
Aboveground dm (individual $^{-1}$)	375 ^{c} (345/401)	575 ^{b} (516/601)	583 ^{ab} (478/641)	652 ^{a} (636/691)	*	11.40	0.010

Significant distinctions between treatments are indicated by different letters (Kruskal-Wallis-ANOVA; Mann-Whitney U-Test; treatment n = 4)

At 1st harvest, the median aboveground biomass in swards containing *P. lanceolata* varied considerably from 953 to 1212 g m^{-2} (Figure 42). Significant distinctions between treatments (*Ref* / stand I-V) could not be found.

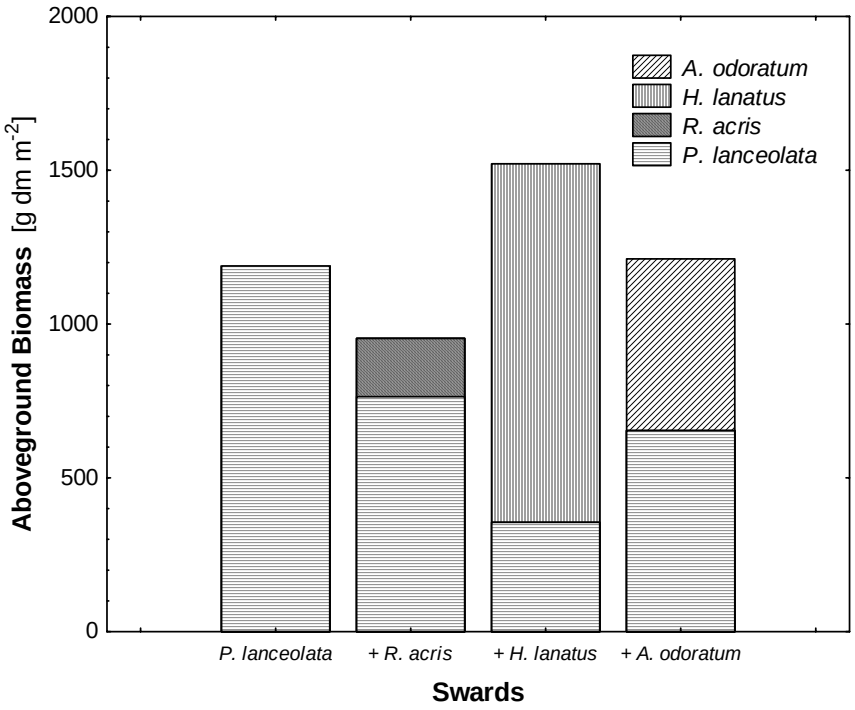


Figure 42 Median 1st harvest aboveground biomass of swards containing *P. lanceolata*

Total aboveground biomass Kruskal-Wallis-ANOVA: 7.70, $p = 0.053$

The aboveground biomass of swards containing *P. lanceolata* was considerably lower than in *H. lanatus* swards. *P. lanceolata* only dominated in dicultures with *R. acris*, whereas *A. odoratum* yielded 46% and *H. lanatus* yielded 75 % of the total aboveground biomass in dicultures. The mean individual 1st harvest aboveground biomass of *P. lanceolata* ranged from 178 to 382 g m^{-2} (Table 55).

In analogy to *H. lanatus*, individual aboveground biomass of monocultures was significantly lower than in dicultures with *R. acris* and *A. odoratum*. In dicultures with *H. lanatus*, individual *P. lanceolata* biomass was tendentiously lower than in monocultures.

Table 55 Median (25th /75th Percentile) of individual aboveground biomass of *P. lanceolata* in mono- and diculture swards (1st harvest).

Parameter	***P. lanceolata***	***+ R. acris***	***+ H. lanatus***	***+ A. odoratum***	MW-U	KW-H	*p*
	----------[g dm m^{-2}]----------						
Aboveground dm (individual^{-1})	297 ^{b} (270/317)	382 ^{a} (341/407)	178 ^{b} (170/186)	327 ^{a} (176/398)	*	8.03	0.045

Significant distinctions between treatments are indicated by different letters (Kruskal-Wallis-ANOVA; Mann-Whitney U-Test; treatment n = 4).

The median aboveground biomass at 2nd harvest (Table 56) differed distinctly from the 1st harvest (Figure 41). The median biomass of *H. lanatus* and *A. odoratum* was decreased and matched only 45 % (38 %) of the 1st harvest. Analogous to the 1st harvest, *H. lanatus* was dominant in all swards. The median individual *H. lanatus* biomass (not shown) was 117 to 131 g m^{-2} lower in monocultures than in dicultures similar to 1st harvest.

Table 56 Median (25th /75th Percentile) aboveground biomass of *H. lanatus* and an accompanying species in mono- and diculture swards (2nd harvest); swards n = 4

	H. lanatus	***+ A. odoratum***	***+ P. lanceolata***	***+ R. acris***
	[g dm m^{-2}]			
H. lanatus	636 (453/812)	552 (435/653)	541 (434/649)	580 (552/587)
accompanying species		87 (16/118)	82 (42/97)	66 (43/119)

Compared to 1st harvest (Figure 42), the median aboveground biomass of *P. lanceolata* (Table 57), was drastically lower at 2nd harvest (17 % of the 1st harvest biomass). Individual *P. lanceolata* biomass (not shown) accounted for ⅓ of monocultures in diculture with *A. odoratum*, whereas in diculture with *H. lanatus* it was two-fold and with *R. acris* it was four-fold the monoculture. Implications of Fe nutrition on biomass production can be assumed since uptake and reduction of NO_3^- and is closely related to Fe availability (AGNOLON ET AL., 2001; MARSCHNER, 2002).

Table 57 Median (25th /75th Percentile) aboveground biomass of *P. lanceolata* and an accompanying species in mono- and diculture swards (2nd harvest); swards n = 4

	P. lanceolata	***+ R. acris***	***+ H. lanatus***	***+ A. odoratum***
	[g dm m^{-2}]			
P. lanceolata	104 (88/253)	199 (176/238)	82 (44/118)	17 (13/36)
accompanying species		232 (192/288)	541 (433/649)	244 (191/375)

Lower biomass production of *P. lanceolata* in monoculture compared to dicultures with *R. acris,* suggests a certain importance of intraspecific competition for *P. lanceolata*.

ZHANG ET AL. (1999) found positive correlations between Fe nutrition and shoot biomass productions for *Glycine max* and *Cucumis sativus*. NIKOLIC & RÖMHELD (2002) confirmed higher fresh and dry matter of grapevine leafs as well as bigger leaf areas for green leaves compared to chlorotic leaves. Lower aboveground biomass is likely attributed to Fe deficiency.

The relative yield totals (RYT) for the 1st harvest indicate competition in concern of species biomass production for *H. lanatus* in diculture swards (Table 58). The competition ability (Cab) indicated higher competitive ability for *H. lanatus* in any diculture. Contrary to this finding, RYT of individual biomass indicated complementary which was accompanied by higher ability of *H. lanatus* to build up biomass. However, overyielding of *H. lanatus* led to high RYT. All accompanying species showed reduced competition ability in concern of biomass production.

Table 58 Relative Yield Total (RYT, DE WITT, 1960) and Competition Ability (Cab, WILSON, 1988) for species and individual biomass of *H. lanatus* swards

	+ ***A. odoratum***	+ ***P. lanceolata***	+ ***R. acris***	MW-U	KW-H	*p*
1st Harvest						
RYT [dm species^{-1}]	0.49 (0.48/0.51)	0.53 (0.47/0.58)	0.58 (0.55/0.61)	ns	4.77	0.092
Cab [dm species^{-1}]	1.27 (0.91/1.33)	0.97 (0.75/1.05)	1.15 (0.90/1.57)	ns	1.42	0.491
RYT [dm individual^{-1}]	0.98 (0.96/1.03)	1.09 (0.96/1.18)	1.15 (1.10/1.22)	ns	4.77	0.092
Cab [dm individual^{-1}]	1.27 (0.91/1.33)	0.97 (0.75/1.05)	1.15 (0.90/1.57)	ns	1.42	0.491
2nd Harvest						
RYT [dm species^{-1}]	0.56 (0.50/0.61)	0.81 (0.63/0.1.00)	0.61 (0.57/0.70)	ns	3.11	0.211
Cab [dm species^{-1}]	1.12 (0.74/1.94)	0.19 (-0.31/0.76)	0.96 (0.55/1.43)	ns	3.50	0.174
RYT [dm individual^{-1}]	1.13 (1.01/1.22)	1.61 (1.27/1.99)	1.25 (1.09/1.43)	ns	3.11	0.211
Cab [dm individual^{-1}]	1.12 (0.74/1.94)	0.19 (-0.31/0.76)	0.98 (0.60/1.38)	ns	3.50	0.174

RYT: 1 = complementary, ‹ 1 = competition
Cab: 0 = complementary, › 0 = key species (*H. lanatus, P. lanceolata*) with higher competitive ability, ‹ 0 accompanied species with higher competitive ability
Significant distinctions between treatments are indicated by different letters (Kruskal-Wallis-ANOVA; Mann-Whitney U-Test; treatment n = 4)

With an exception of swards containing *P. lanceolata*, all other *H. lanatus* swards showed similar biomass patterns at 2nd harvest. *H. lanatus* showed only slightly higher competition ability than *P. lanceolata* in concern of species biomass. Since overyielding was found for both species individual biomass, complementary relations with slight advantages for *H. lanatus* are assumed after re-supply of Fe. In general, *H. lanatus* appeared to be the species with tendentiously higher competition ability.

At 1st harvest, *P. lanceolata* swards were determined by competition in concern of species biomass (Table 59). *P. lanceolata* showed lower competitive ability than *H. lanatus* but almost equal competitive ability as *R. acris* and *A. odoratum.* For individual biomass, complementary was indicated by Cab. This was due to overyielding of both species with lower ability of *P. lanceolata* in comparison to *H. lanatus*. In swards accompanied with *A. odoratum,* both species showed almost equal individual biomass as compared to their monocultures.

Table 59 Relative Yield Total (RYT, DE WITT, 1960) and Competition Ability (Cab, WILSON, 1988) for species and individual biomass of *P. lanceolata* swards

	+ ***R. acris***	+ ***H. lanatus***	+ ***A. odoratum***	MW-U	KW-H	*P*
1st Harvest						
RYT [dm species^{-1}]	0.67 (0.57/0.80)	0.54 (0.46/0.58)	0.49 (0.41/0.59)	ns	3.58	0.167
Cab [dm species^{-1}]	-0.02 (-0.50/0.29)	-0.92 (-1.03/.-0.77)	0.25 (-0.74/0.40)	ns	3.50	0..174
RYT [dm individual^{-1}]	1.35 (1.14/1.60)	1.07 (0.94/1.15)	0.99 (0.82/1.18)	ns	3.58	0.167
Cab [dm individual^{-1}]	-0.02 (-0.50/0.29)	-0.97 (-1.05/-0.75)	0.25 (-0.74/0.40)	ns	3.50	0..174
2nd Harvest						
RYT [dm species^{-1}]	1.62 ^{a} (1.45/1.80	0.81 ^{b} (0.63./1.00	0.35 ^{b} (0.28/0.58)	*	8.77	0.012
Cab [dm species^{-1}]	0.34 ^{a} (0.14/0.77)	-0.19 ^{a} (-0.76/0.31)	-1.08 ^{b} (-1.26/-0.85)	*	7.23	0.026
RYT [dm individual^{-1}]	3.94 ^{a} (2.91/3.60)	1.61 ^{b} (1.27/1.99)	0.70 ^{b} (0.57/1.17)	*	8.77	0.012
Cab [dm individual^{-1}]	0.34 ^{a} (0.34/0.77)	-0.19 ^{a} (--0.76/0.31)	-1.08 ^{b} (-1.26/-0.85)	*	7.23	0.026

RYT: 1 = complementary, ‹ 1 = competition
Cab: 0 = complementary, › 0 = key species (*H. lanatus, P. lanceolata*) with higher competitive ability, ‹ 0 accompanied species with higher competitive ability
Significant distinctions between treatments are indicated by different letters (Kruskal-Wallis-ANOVA; Mann-Whitney U-Test; treatment n = 4)

At 2nd harvest, complementary was indicated by RYT for *P. lanceolata* species biomass when accompanied by *R. acris*. Competition was indicated for swards with *H. lanatus* and *A. odoratum*. In swards with *A. odoratum* competition is indicated with low competition ability for *P. lanceolata*. Individual biomass data suggest complementary for swards containing *R. acris* and *H. lanatus*. However, profit is less pronounced for *P. lanceolata* when accompanied by *H. lanatus*.

Since Fe was the only nutrient lacking in nutrient solution, it is assumed that competition for nutrients mainly focussed on Fe and thus Fe consumption determined biomass production.

The belowground biomass was determined at the end of the experiment, subsequent to 2nd harvest, three weeks after re-supply of Fe. The median belowground biomass in swards containing *H. lanatus* (Table 60) ranged from 106 to 131 g m^{-2}. The differences were almost marginal between the different stands. The median stand root/shoot-ratio varied only slightly from 0.18 to 0.20 g g^{-1}. It is in the range given for *herb species,* but lower than for *Triticum aestivum* on sand medium (0.35-0.38 g g^{-1}, ZHANG ET AL., 1999).

Table 60 Median (25th / 75th Percentile) belowground biomass and root/shoot-ratio for *H. lanatus* in mono- and diculture swards

Parameter	***H. lanatus***	***+ A. odoratum***	***+ P. lanceolata***	***+ R. acris***	MW-U	KW-H	*p*
	----------[g dm m^{-2}]----------						
Belowground dm	117 (84/160)	131 (86/206)	106 (97 /127)	120 (117/123)	ns	0.60	0.897
	----------[g g^{-1}]----------						
Root/Shoot-ratio	0.18 (0.18/0.20)	0.20 (0.19/0.28)	0.17 (0.17/0.0.20)	0.19 (0.17/0.20)	ns	1,21	0,750

Significant distinctions between swards are indicated by different letters (Kruskal-Wallis-ANOVA, Mann-Whitney U-Test, treatment n = 4)

The median belowground biomass (Table 61) in *P. lanceolata* swards ranged from 48 to 142 g m^{-2}. Compared to monocultures, dicultures with *R. acris* and *H. lanatus* showed significantly higher belowground biomass. The median root/shoot-ratios ranged from 0.17 to 0.46 g g^{-1}. Dicultures with *R. acris* and *H. lanatus* also showed significantly higher root/shoot-ratios, indicating enhanced competition in these swards. The ratios exceed values given for *P. lanceolata* exposed to 11 days of nil Fe supply (0.13 g g^{-1}, SCHMIDT & FÜHNER, 1998) by far.

Table 61 Median (25th / 75th Percentile) belowground biomass and root/shoot-ratio for *P. lanceolata* in mono- and diculture swards

Parameter	***P. lanceolata***	***+ R. acris***	***+ H. lanatus***	***+ A. odoratum***	MW-U	KW-H	*p*
	----------[g dm m^{-2}]----------						
Belowground dm	48 ^{b} (48/48)	142 ^{a} (103/158)	106 ^{a} (97/127)	61 ^{b} (43/87)	*	10.30	0.016
	----------[g g^{-1}]----------						
Root/Shoot-ratio	0. 46 ^{a} (0.20/0.49)	0.33 ^{b} (0.28/0.0.33)	0.17 ^{c} (0.17/0.20)	0.23 ^{c} (0.21/0.0.22)	*	11.00	0.012

Significant distinctions between swards are indicated by different letters (Kruskal-Wallis-ANOVA, Mann-Whitney U-Test, treatment n = 4)

CROWLEY ET AL. (2002) confirmed an increase in root/shoot-ratio with decreasing Fe supply for *Hordeum vulgare*. Lower root/shoot-ratios are due to the presence of grass species with higher aboveground productivity.

3.2.1.1 Chlorophyll Contents in Biomass

The median chlorophyll contents of *H. lanatus* (measured as chlorophyll-index; Figure 43) ranged from 360 to 430. *H. lanatus* in monoculture and in diculture with *P. lanceolata* showed a significantly higher chlorophyll-index than in other swards. It was lowest in dicultures with *A. odoratum.*

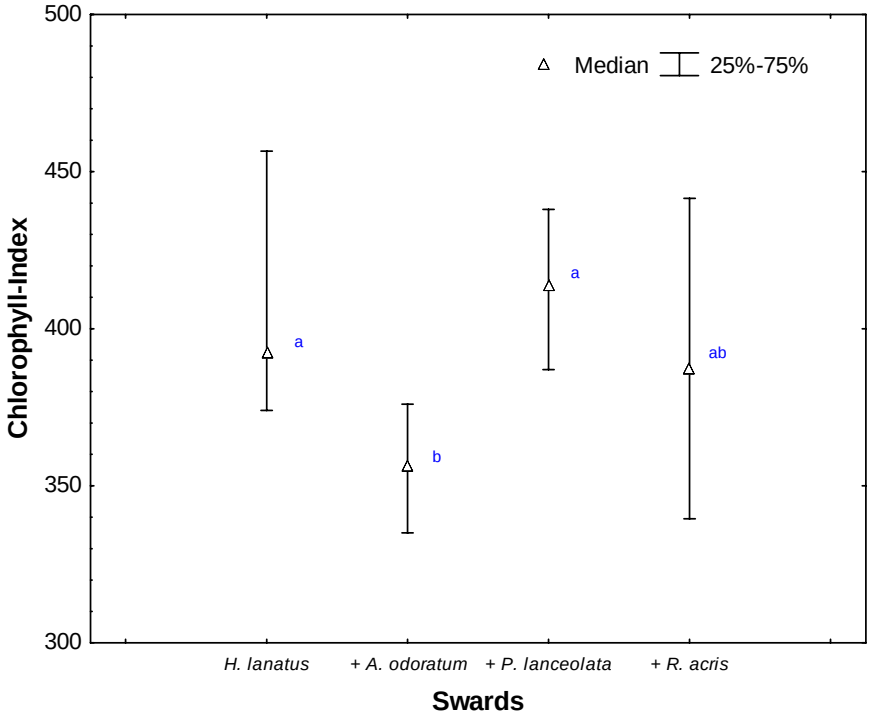


Figure 43 Median (25th /75th Percentile) Chlorophyll-Index of *H. lanatus* in mono- and diculture swards

Significant distinctions between treatments are indicated by different letters (Kruskal-Wallis-ANOVA: H = 8,85, p = 0.031; Mann-Whitney U-Test: ‹ 0.05; treatment n = 4

The median chlorophyll-index of *P. lanceolata* (Figure 44) ranged from 430 to 560. It was significantly lower when accompanied by *A. odoratum*. Lower chlorophyll-indices suggest higher competition for Fe in presence of *A. odoratum* for both central species.

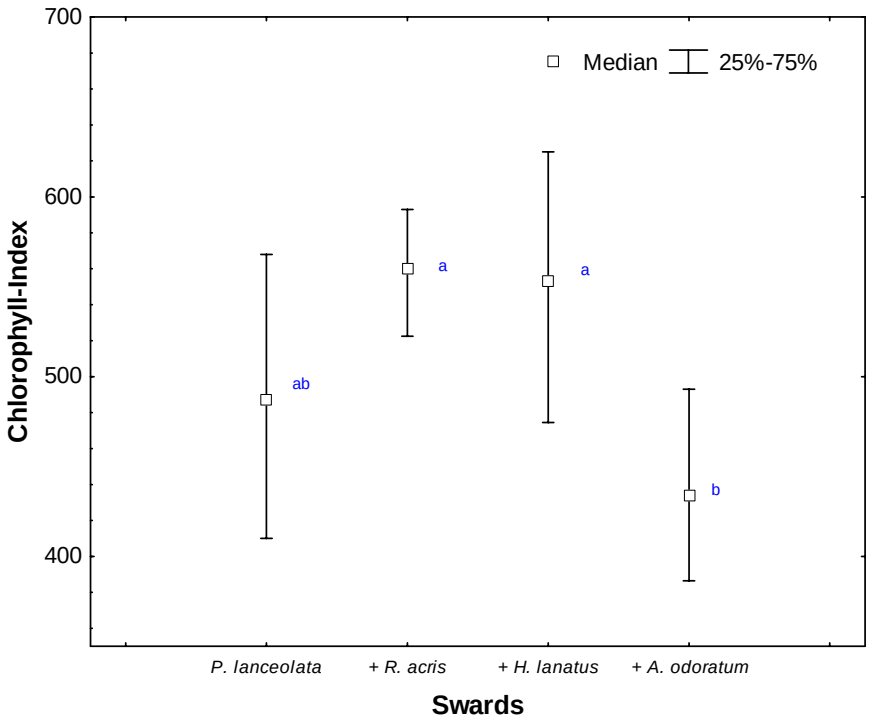


Figure 44 Median (25th /75th Percentile) Chlorophyll-Index of *P. lanceolata* in mono- and diculture swards

Significant distinctions between treatments are indicated by different letters. (Kruskal-Wallis-ANOVA: 9,57, p = 0,026; Mann-Whitney U-Test: ‹ 0.05; treatment n = 4

3.2.1.2 Fe Contents in Above- and Belowground Biomass

The median Fe contents in *H. lanatus* aboveground biomass (Table 62) ranged from 39 to 44 µg Fe g^1 dm^{-1} without Fe supply. It was slightly lower in monocultures, but increased after re-supply up to 54 to 62 µg Fe g dm^{-1}. After re-supply, *H. lanatus* monocultures showed tendentiously higher Fe contents in biomass than in diculture with the other species. MA & NOMOTO (1996) gave contents for sufficient *Triticum aestivum* of 234 and in deficient plants of 175 µg Fe g dm^{-1}.

Table 62 Median (25th /75th Percentile) Fe contents in aboveground biomass of *H. lanatus* prior to (--) and 3 weeks after Fe re-supply (+)

Fe-status	*H. lanatus*	+ *A. odoratum*	+ *P. lanceolata*	+ *R. acris*	MW-U	KW-H	*p*
	---------- Fe [µg dm g $^{-1}$]----------						
--	39 (39/49)	44 (40/60)	44 (40/47)	44 (40/43)	ns	0.82	0.846
+	62 (58/64)	54 (49/55)	59 (57/60)	56 (54/61)	ns	7.12	0.068

Significant distinctions between swards are indicated by different letters. (Kruskal-Wallis-ANOVA; Mann-Whitney U-Test; treatment n = 4

The median Fe contents in *P. lanceolata* aboveground biomass (Table 63) ranged from 42 to 53 µg Fe g dm^{-1} without Fe supply. *P. lanceolata* showed slightly higher Fe contents in dicultures with *R. acris*.

After re-supply, the Fe contents ranged from 60 to 132 µg Fe g dm^{-1}. They were tendentiously higher in monoculture biomass than from diculture swards. Swards with *A. odoratum* showed slightly higher Fe in aboveground biomass than the other dicultures.

Table 63 Median (25th /75th Percentile) Fe contents in aboveground biomass of *P. lanceolata prior to* (--) and 3 weeks after Fe re-supply (+)

Fe-status	*P. lanceolata*	+ *R. acris*	+ *H. lanatus*	+ *A. odoratum*	MW-U	KW-H	*p*
	---------- Fe [µg dm g $^{-1}$]----------						
--	42 (41/48)	53 (50/65)	47 (42/56)	42 (39/51)	ns	439	0.233
+	65 (57/118)	68 (61/99)	61 (53/70)	61 (49/71)	ns	6.02	0.115

Significant distinctions between swards are indicated by different letters. (Kruskal-Wallis-ANOVA; Mann-Whitney U-Test; treatment n = 4

NIKOLIC & RÖMHELD (2002) gave 134 µg Fe g dm^{-1} for green leaves and 77 µg Fe g dm^{-1} for chlorotic leaves of *Helianthus annuus*. MARSCHNER (2002) gave a critical deficiency content of 72 µg g dm^{-1} for C_3 plants. BERGMANN (1992) gave critical Fe contents of 50 µg g dm^{-1}. Low Fe contents in biomass indicate Fe deficiency for both central species even after re-supply of Fe.

At 1st harvest, RYT indicated competition in concern of Fe biomass contents for *H. lanatus* swards (Table 64). Cab indicated higher competitive ability for *H. lanatus* compared to *P. lanceolata* and *R. acris*. In concern of Fe contents per individual, RYT also indicated competition and higher competition ability for *H. lanatus* than for the other grassland species was indicated by Cab.

Table 64 Relative yield total (RYT, DE WITT, 1960) and Competition ability (Cab, WILSON, 1988) in concern of Fe contents and individual Fe stocks for *H. lanatus* in diculture swards

H. lanatus swards	**+ *A. odoratum***	**+ *P. lanceolata***	**+ *R. acris***	MW-U	KW-H	*P*
1st Harvest						
RYT [µg Fe g dm^{-1}]	0.58 (0.51/0.72)	0.53 (0.50/0.65)	0.70 (0.66/0.74)	ns	2.46	0.292
Cab [µg Fe g dm^{-1}]	0.02 (-0.06/0.18)	0.72 (0.36/0.88)	0.16 (-0.07/0.33)	ns	3.73	0.155
RYT [mg Fe individual $^{-1}$]	1.04 (1.04/1.04)	1.17 (0.98/1.38)	1.43 (1.22/1.53)	ns	1.68	0.437
Cab [mg Fe individual $^{-1}$]	1.32 (1.09/1.48)	1.02 (0.71/1.15)	1.00 (0.76/1.22)	ns	ns	2.00
2nd Harvest						
RYT [µg Fe g dm^{-1}]	0.46 (0.40//0.49)	0.36 (0.35/0.44)	0.42 (0.41/0.45)	ns	2.00	0.368
Cab [µg Fe g dm^{-1}]	-0.50 (-0.67/-0.21)	0.45 (0.01/0.72)	0.46 (0.43/0.55)	ns	6.58	0.037
RYT [mg Fe individual $^{-1}$]	1.15 (0.93/1.38)	1.17 (0.98/1.38)	1.23 (0.99/1.53)	ns	0.46	0.794
Cab [mg Fe individual $^{-1}$]	0.77 (0.54/1.72)	1.02 (0.71/1.15)	1.03 (0.52/1.44)	ns	0.34	0.981

RYT: 1 = complementary, ‹ 1 = competition
Cab: 0 = complementary, › 0 = key species (*H. lanatus, P. lanceolata*) with higher competitive ability, ‹ 0 accompanied species with higher competitive ability
Significant distinctions between swards are indicated by different letters (Kruskal-Wallis-ANOVA; Mann-Whitney U-Test; treatment n = 4)

The competition ability of *H. lanatus* was most pronounced in comparison to *P. lanceolata* for Fe contents and individual stocks of Fe.

At 2nd harvest, competition was indicated in concern of Fe contents between *H. lanatus* and all accompanying species. Cab indicated a considerably higher competition ability for *A. odoratum* in concern of Fe contents than for *H. lanatus*. *H. lanatus* had a higher competition ability compared to *P. lanceolata* and *R. acris.* In concern of individual Fe stock, *H. lanatus* showed higher competition ability than any other plant species. Competition ability of *H. lanatus* increased in the order *A. odoratum* › *P. lanceolata* › *R. acris*.

At 1st harvest, competition was indicated by RYT in concern of Fe-contents in any sward (Table 65). Besides lower competition ability of *P. lanceolata* compared to *H. lanatus*, equal abilities were found in swards with *R. acris* and slightly lower ability in swards with *A. odoratum*. In concern of individual Fe stocks, overyielding was indicated for the accompanying species *R. acris* and *H. lanatus.* Hereby, *P. lanceolata* showed slightly higher competition ability as *A. odoratum*.

Table 65 Relative Yield Total (RYT, DE WITT, 1960) and Competition Ability (Cab, WILSON, 1988) in concern of Fe contents and individual Fe stocks for *P. lanceolata* in diculture swards

P. lanceolata swards	**+ *R. acris***	**+ *H. lanatus***	**+ *A. odoratum***	MW-U	KW-H	*P*
1st Harvest						
RYT [µg Fe g dm^{-1}]	0.60 (0.51/0.62)	0.54 (0.50/0.65)	0.40 (0.34/0.44)/	ns	5.69	0.058
Cab [µg Fe g dm^{-1}]	0.03 (-0.14/0.09)	-0.77 (-0.88/-0.38)	-0.05 (-0.11/0.12)	ns	4.86	0.087
RYT [mg Fe individual $^{-1}$]	2.09 ^{a} (1.95/2.28)	1.17 ^{b} (0.98/1.38)	0.87 ^{b} (0.76/1.06)	*	8.77	0.012
Cab [mg Fe individual $^{-1}$]	-0.65 (-0.92/-0.06)	-1.01 (-1.15/-0.71)	0.22 (-0.52/-0.38)	ns	2.42	0.298
2nd Harvest						
RYT [µg Fe g dm^{-1}]	0.35 (0.29/0.44)	0.36 (0.35/0.44)	0.44 (0.39/0.54)	ns	1.88	0.387
Cab [µg Fe g dm^{-1}]	-0.71 (-0.95/-0.64)	-0.45 (-0.72/-0.01)	-0.19 (-0.61/0.21)	ns	4.19	0.123
RYT [mg Fe individual $^{-1}$]	2.02 ^{a} (1.87/2.21)	1.14 ^{b} (0.99/1.44)	0.63 ^{b} (0.51/1.13)	*	8.35	0.015
Cab [mg Fe individual $^{-1}$]	-0.55 ^{a} (-.0.75/-0.18)	-0.92 ^{a} (-1.21/-0.57)	-1.68 ^{b} (-1.99/-1.41)	*	7.27	0.026

RYT: 1 = complementary, ‹ 1 = competition
Cab: 0 = complementary, › 0 = key species (*H. lanatus, P. lanceolata*) with higher competitive ability, ‹ 0 accompanied species with higher competitive ability
Significant distinctions between swards are indicated by different letters (Kruskal-Wallis-ANOVA; Mann-Whitney U-Test; treatment n = 4)

Concerning Fe contents of the 2nd harvest, RYT indicated competition between *P. lanceolata* and any other species. Its competition ability decreased in the order *R. acris* ‹ *H. lanatus* ‹ *A. odoratum*. In concern of Fe stocks in individual biomass, overyielding was indicated for *R. acris* and *H. lanatus*. The competition ability of *P. lanceolata* decreased in the order *R. acris* › *H. lanatus* › *A. odoratum*.

Inverted competition ability in concern of Fe contents and individual Fe stocks is likely explained by Fe dilution. Biomass production may be facilitated by *P. lanceolata* at cost of Fe content (trade-off), thus by a physiological plasticity in Fe demand.

Significant correlations (Spearman $p < 0.05$) were found between individual biomass production and Fe content for *P. lanceolata* biomass from the 2nd harvest (Figure 45). *R. acris* (not shown) showed slight but not significant correlations between individual biomass production and Fe contents. No correlations between biomass production and Fe content could be found for *H. lanatus* and *A. odoratum*.

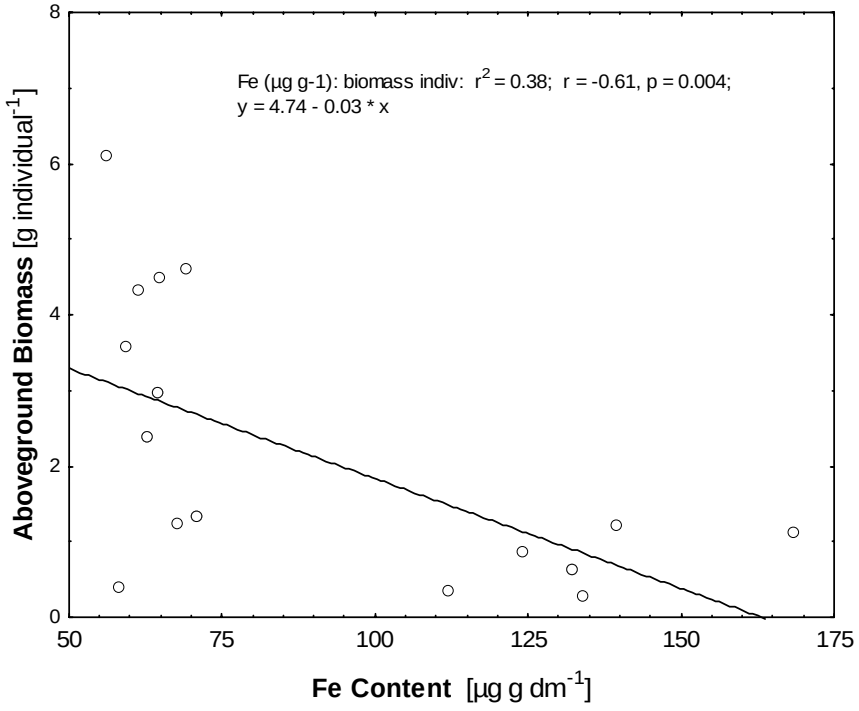


Figure 45 Fe contents vs. individual biomass production of *P. lanceolata* for 2nd harvest

However, negative correlations between Fe contents and biomass production suggest some increase in biomass production through plasticity in Fe demand for *P. lanceolata*. Interestingly, before Fe re-supply (1st harvest), the correlation between individual biomass production and Fe content were very weak for *P. lanceolata* (Spearman r = -0.16, $p > 0.05$) and analogous to 2nd harvest almost absent for the other species.

Three weeks after re-supply, the median Fe contents in belowground biomass (Table 66) from swards containing *H. lanatus* ranged from 57 to 101 µg g dm^{-1}. Belowground biomass from dicultures with *R. acris* showed tendentiously higher Fe contents. Higher contents were likely affected by high Fe contents in *R. acris* roots (102 µg g dm^{-1}). Low Fe contents in swards with *A. odoratum* are surprising, since *A. odoratum* had high contents in monoculture (102 µg g dm^{-1}). This finding may indicate enhanced competition for Fe between these species.

Table 66 Median (25th /75th Percentile) Fe contents in total belowground biomass of *H. lanatus* swards 3 weeks after Fe re-supply

Fe-status	***H. lanatus***	**+ *A. odoratum***	**+ *P. lanceolata***	**+ *R. acris***	MW-U	KW-H	*P*
	---------- Fe [µg g dm^{-1}]----------						
+	80 (58/107)	57 (51/61)	85 (71/108)	101 (52/195)	Ns	3.59	0.309

Significant distinctions between swards are indicated by different letters (Kruskal-Wallis-ANOVA; Mann-Whitney U-Test; treatment n = 4)

The median Fe contents in belowground biomass (Table 67) ranged from 85 to 158 µg g dm^{-1}. For swards containing *P. lanceolata*, they were significantly higher in monoculture and in diculture with *A. odoratum* than for other swards.

Interestingly, the combination with *A. odoratum* did not lead to considerable lower Fe contents in swards with *P. lanceolata*, whereas it decreased Fe contents in *H. lanatus* to a greater extent. This finding may suggest differences in competition for Fe between grass species and grass and herbs species. Lower Fe contents in swards with *R. acris* and *H. lanatus* suggest dominance in root biomass of the accompanying species, since they also feature lower Fe contents in monocultures.

Table 67 Median (25th /75th Percentile) Fe contents in total belowground biomass of *P. lanceolata* swards 3 weeks after Fe re-supply

Fe-status	***P. lanceolata***	**+ *R. acris***	**+ *H. lanatus***	**+ *A. odoratum***	MW-U	KW-H	*p*
	---------- Fe [µg g dm^{-1}]----------						
+	158 [a] 136/211)	99 [ab] (86/121)	85 [b] (71/107)	132 [a] (123/253)	*	8.21	0.042

Significant distinctions between swards are indicated by different letters (Kruskal-Wallis-ANOVA; Mann-Whitney U-Test; treatment n = 4)

MA & NOMOTO (1996) gave root Fe contents of 324 µg Fe g dm^{-1} for deficient and 1590 µg Fe g-1 dm^{-1} for sufficient *Triticum aestivum*. Though, VON WIREN ET AL. (1994) gave 33 to 37 µg Fe g dm^{-1} in roots of deficient and 83 to 88 µg Fe g dm^{-1} for roots of sufficient of *Zea mays* seedlings. Hence Fe contents in root biomass were an insecure indicator for Fe deficiency.

3.2.2 Rhizodeposit Solution Characteristics

pH in Rhizodeposit Solution

The median pH in rhizodeposit solution obtained from swards containing *H. lanatus* (not shown) ranged slightly from pH 7.1 to 7.3. Significant differences between stands were not found. The pH in rhizodeposit solution of swards containing *P. lanceolata* (not shown) ranged from pH 6.6 to 7.1. Dicultures with grass species *H. lanatus* and *A. odoratum* showed a significantly higher pH. The distinction between stands with grass species and pure herb cultures merely accounted for a total difference of 0.2 µM H^+ l^{-1}.

3.2.2.1 DOC Concentration

Prior to 1st harvest, the median DOC concentration in rhizodeposit solution of swards containing *H. lanatus* (Table 68) ranged from 15.2 to 29.7 mg C l^{-1}. The predominant amount of DOC was likely derived from degradation of the organic growth medium. No significant differences were found for *H. lanatus* swards.

Table 68 Median (25th/75th Percentile) DOC concentration in rhizodeposit solution of *H. lanatus* swards without Fe supply prior to and after 1st harvest

Sampling	*Ref*	*H. lanatus*	*+ A. odoratum*	*+ P. lanceolata*	*+ R. acris*	MW-U	KW-H	*P*
	----------[mg C l^{-1}]----------							
prior to 1st harvest	14.7 (13.2/18.5)	22.6 (16.1/26.8)	29.7 (24.9/33.8)	20.8 (19.1/24.3)	15.2 (12.5/19.7)	ns	8.93	0.063
after 1st harvest	10.4 [b] (9.7/11.7)	22.3 [a] (19.8/26.3)	22.2 [a] (20.6/23.9)	25.6 [a] (23.7/29.5)	21.1 [a] (20.7/22.3)	*	11.92	0.018

Significant distinctions between swards are indicated by different letters (Kruskal-Wallis-ANOVA; Mann-Whitney U-Test; stand treatment n = 4)

After 1st harvest, the DOC concentration in rhizodeposit solution of swards containing *H. lanatus* ranged from 21.1 to 25.6 mg C l^{-1}.

Compared to samples prior to 1st harvest, dicultures with *P. lanceolata* and *R. acris* showed distinctly higher DOC concentrations at after 1st harvest (Table 68). A comparison of purge solution obtained before collection of rhizodeposit (not shown) showed a significant decrease in DOC from 27.0 to 20.2 mg l^{-1} after 1st harvest for all swards of *H. lanatus* and *P. lanceolata* (Appendix, Table XXVII). Hence, increases in DOC concentrations are unlikely derived from degradation of root biomass repelled after harvest, but indicate enhanced rhizodeposition.

Prior to the 1st harvest, the median DOC concentration in rhizodeposit solution of swards containing *P. lanceolata* (Table 69) ranged from 20.8 to 30.0 mg C l^{-1}. *P. lanceolata* monocultures showed slightly higher DOC concentrations than diculture swards. However, the differences between mono and diculture swards were merely tendentious.

Table 69 Median (25th /75th Percentile) DOC concentration in rhizodeposit solution of *P. lanceolata* swards without Fe supply prior to and after 1st harvest

Sampling	***Ref***	***P. lanceolata***	***+ R. acris***	***+ H. lanatus***	***+ A. odoratum***	MW-U	KW-H	*p*
	----------[DOC mg l^{-1}]----------							
prior to 1st harvest	14.7 (13.2/18.5)	30.0 (25.7/32.9)	24.9 (17.2/33.5)	20.8 (19.1/24.3)	29.1 (25.2/32.6)	ns	9.24	0.056
after 1st harvest	10.4 ^{c} (9.7/11.7)	51.0 ^{a} (39.6/61.3)	23.3 ^{ab} (19.7/33.9)	25.6 ^{ab} (23.7/29.5)	31.8 ^{a} (27.2/55.3)	*	14.04	0.007

Significant distinctions between swards are indicated by different letters (Kruskal-Wallis-ANOVA; Mann-Whitney U-Test; stand treatment n = 4)

After 1st harvest, the DOC concentration in rhizodeposit solution ranged considerably from 23.8 to 51.0 mg C l^{-1}. Dicultures with *H. lanatus* showed significantly lower DOC concentrations than the other swards. For *P. lanceolata* monocultures increased DOC concentrations may indicate higher Fe stress compared to samples taken prior to 1st harvest.

Higher DOC concentrations in *H. lanatus* and *P. lanceolata* swards compared to Ref clearly indicate rhizodeposit release of soluble carbon compounds. Low rhizodeposition was observed for *H. lanatus* with *A. odoratum* prior to and with *P. lanceolata* after 1st harvest. In *P. lanceolata* swards monocultures and dicultures with *A. odoratum* showed higher rhizodeposition. However, rhizodeposition increased and differences were only significant after 1st harvest. *P. lanceolata* and *A. odoratum* showed enhanced rhizodeposition. Whereas *P. lanceolata* showed enhanced rhizodeposition under intra- as well as under interspecific competition, *A. odoratum* only showed 15.6 mg C l^{-1} prior to and 21.1 mg C l^{-1}after 1st harvest in monoculture.

3.2.2.2 Spectral Characteristics of DOC

Prior to1st harvest, the median intensity of specific UV-absorbance[7] (280 nm) in rhizodeposit solution (Table 70) of *H. lanatus* swards ranged from 0.09 to 0.14. After 1st harvest, the median intensity of UV-absorbance ranged from slightly from 0.13 to 0.14. The differences between *H. lanatus* swards were rather low prior to and after 1st harvest.

Table 70 Median (25th /75th Percentile) of specific UV absorbance (280 nm) of rhizodeposit solution from *H. lanatus* swards 3 weeks prior to and after 1st harvest

Sampling	*Ref*	*H. lanatus*	*+ A. odoratum*	*+ P. lanceolata*	*+ R. acris*	MW-U	KW-H	*p*
	----------specific UV-Absorbance 280 nm----------							
prior to 1st harvest	0.09 (0.08/0.10)	0.11 (0.10/0.15)	0.10 (0.07/0.12)	0.10 (0.08/0.12)	0.14 (0.14/0.16)	ns	8.84	0.065
after 1st harvest	0.08 (0.08/0.10)	0.13 (0.12/0.14)	0.13 (0.12/0.14)	0.14 (0.12/0.17)	0.13 (0.12/0.14)	ns	9.16	0.057

Significant distinctions between swards are indicated by different letters. (Kruskal-Wallis-ANOVA; Mann-Whitney U-Test; treatment n = 4)

The median intensity of emission spectra (435-480 / 300-345 nm) of *H. lanatus* swards (Table 71) ranged prior to 1st harvest from 2.3 to 5.6. Dicultures with *A. odoratum* and *P. lanceolata* showed tendentiously lower intensities than the other swards. After 1st harvest, intensities ranged from 4.9 to 6.7. Analogous to prior to 1st harvest, intensities were significantly lower in dicultures with *A. odoratum* and *P. lanceolata*.

Table 71 Median (25th /75th Percentile) of emission spectra (E2/E1) of rhizodeposit solution from *H. lanatus* swards 3 weeks prior to and after 1st harvest

Sampling	*Ref*	*H. lanatus*	*+ A. odoratum*	*+ P. lanceolata*	*+ R. acris*	MW-U	KW-H	*P*
	----------Emission 435-480 / 300-345 nm----------							
prior to 1st harvest	5.5 (3.6/6.6)	5.1 (4.7/5.9)	2.3 (1.5/3.8)	4.2 (3.3/5.2)	5.6 (5.0/8.2)	ns	7.39	0.117
after 1st harvest	14.4 ^{a} (14.3/14.7)	6.7 ^{bc} (6.1/7.4)	5.8 ^{c} (5.5/6.1)	4.9 ^{c} (4.3/5.5)	6.7 ^{b} (6.2/7.2)	*	15.71	0.003

Significant distinctions between swards are indicated by different letters. (Kruskal-Wallis-ANOVA; Mann-Whitney U-Test; treatment n = 4)

According to KALBITZ ET AL (2000; 2003), this finding indicates higher contribution of lower complexity compounds and thus hints at enhanced rhizodeposit release of aliphatic compounds.

[7] Spectral data had to be corrected by y = 1,304 +1,469(x), chapter 2.4.2

Prior to 1st harvest, the median intensity of specific UV absorbance of rhizodeposit solution (Table 72) from *P. lanceolata* swards ranged from 0.09 to 0.12. It was tendentiously higher in dicultures with *R. acris*. After 1st harvest, the absorbance ranged from 0.08 to 0.14. Analogous to *H. lanatus* swards, the differences in specific UV-absorbance between *P. lanceolata* swards were rather low prior to and after 1st harvest.

Table 72 Median (25th /75th Percentile) of specific UV absorbance (280 nm) of rhizodeposit solution from *P. lanceolata* swards prior to 1st harvest

Sampling	***Ref***	***P. lanceolata***	***+ R. acris***	***+ H. lanatus***	***+ A. odoratum***	MW-U	KW-H	*p*
	----------UV-Absorbance 280 nm----------							
prior to 1st harvest	0.09 (0.08/0.10)	0.09 (0.07/0.13)	0.12 (1.50/1.61)	0.10 (0.08/0.12)	0.11 (0.08/0.12)	ns	1.56	0.816
after 1st harvest	0.08 (0.08/0.10)	0.10 (0.09/0.12)	0.10 (0.07/0.11)	0.14 (0.12/0.17)	0.11 (0.09/0.12)	ns	8.33	0.080

Significant distinctions between swards are indicated by different letters (Kruskal-Wallis-ANOVA; Mann-Whitney U-Test; treatment n = 4)

The median intensities of emission spectra of rhizodeposit solution prior to 1st harvest (Table 73) ranged from 2.3 to 4.4. They were lower in monocultures and in dicultures with *A. odoratum* prior to and after 1st harvest. After 1st harvest, the intensities ranged from 4.9 to 7.1 This indicated higher contribution of low complexity compounds (KALBITZ ET AL., 2000; 2003), which may be released as rhizodeposits in these stands.

Table 73 Median (25th /75th Percentile) of emission spectra (E2/E1) of rhizodeposit solution from *P. lanceolata*. swards 3 weeks after 1st harvest

Sampling	***Ref***	***P. lanceolata***	***+ R. acris***	***+ H. lanatus***	***+ A. odoratum***	MW-U	KW-H	*p*
	----------Emission 435-480 / 300-345 nm----------							
prior to 1st harvest	5.5 (3.6/6.6)	3.2 (2.3/4.3)	4.4 (3.5/5.2)	4.2 (3.3/5.2)	2.3 (2.2/2.6)	ns	8.52	0.074
after 1st harvest	14.4 ^{a} (14.3/14.7)	3.6 ^{c} (3.1/4.5)	7.1 ^{b} (6.3/7.9)	4. 9 ^{bc} (4.3/5.5)	3.2 ^{c} (2.9/3.9)	*	15.24	0.004

Significant distinctions between swards are indicated by different letters (Kruskal-Wallis-ANOVA; Mann-Whitney U-Test; treatment n = 4)

Low intensities of emission spectra prior to (2.4) and after 1st harvest (3.1) for rhizodeposits from *A. odoratum* monocultures may suggest a considerable contribution of *A. odoratum* to the release of low complexity compounds in diculture with *P. lanceolata.*

3.2.3 Release of Carbon and Carboxylic Acids

Since plants photosynthetic area is of major importance for the production of organic compounds, aboveground biomass was used as basis for calculation of rhizodeposition. Prior to 1st harvest, the median DOC release of *H. lanatus* swards (Table 74) ranged from 0.26 to 0.31 mg C g dm^{-1}shoot biomass.

Table 74 Median (25th /75th Percentile) of DOC release per g total aboveground biomass (shoot) for *H. lanatus* swards 3 weeks prior to and after 1st harvest

Sampling	*H. lanatus*	*+ A. odoratum*	*+ P. lanceolata*	*+ R. acris*	MW-U	KW-H	*p*
	----------[mg C g shoot dm^{-1}]----------						
prior to 1st harvest	0.26 (0.23/0.30)	0.31 (0.27/0.38)	0.29 (0.25/0.36)	0.28 (0.25/0.37)	ns	1.61	0.657
after 1st harvest	0.66 (0.57/1.03)	0.63 (0.61/0.67)	0.96 (0.66/1.17)	0.64 (0.66/1.17)	ns	2.00	0,571

Significant distinctions between swards are indicated by different letters (Kruskal-Wallis-ANOVA; Mann-Whitney U-Test; treatment n = 4)

After 1st harvest, median DOC release ranged from 0.66 to 0.96 mg C g dm^{-1}. Enhanced rhizodeposition is likely due to higher Fe demands for plants' regrowth after the 1st harvest. Dicultures with *P. lanceolata* showed tendentiously higher DOC releases than other swards.

Prior to 1st harvest, median DOC release of *P. lanceolata* swards (Table 75) ranged from 0.29 to 0.52 mg C g dm^{-1}. Dicultures with *H. lanatus* showed a tendentiously lower DOC release compared to the other mono- and dicultures.

Table 75 Median (25th /75th Percentile) of DOC release per g total aboveground biomass (shoot) for *P. lanceolata* swards 3 weeks prior to and after 1st harvest

Sampling	*P. lanceolata*	*+ R. acris*	*+ H. lanatus*	*+ A. odoratum*	MW-U	KW-H	*p*
	----------[mg C g shoot dm^{-1}]----------						
prior to 1st harvest	0.48 (0.38/0.62)	0.52 (0.44/0.61)	0. 29 (0.25 /0.36)	0.46 (0.41/0.60)	ns	5.93	0.115
after 1st harvest	8.78 [a] (5.37/10.78)	0.93 [b] (0.83/1.25)	0.96 [b] (0.66/1.17)	2.65 [a] (2.17/3. 06)	*	11.97	0.007

Significant distinctions between swards are indicated by different letters (Kruskal-Wallis-ANOVA; Mann-Whitney U-Test; treatment n = 4)

After 1st harvest, the DOC release of *P. lanceolata* swards (Table 75) ranged from 0.93 to 8.78 mg C g dm^{-1}. Monocultures and dicultures with *A. odoratum* showed significantly higher releases. Low releases in *A. odoratum* monocultures (to 1.7 mg C g dm^{-1}) suggest competition effects on rhizodeposition.

3.2.4 Composition of Carboxylic Acids in Rhizodeposits

Prior to 1st harvest, the median carboxylic acid composition of swards containing *H. lanatus* (Figure 46) comprised succinic and malonic acids. The acid release amounted 0.001 to 0.2 µM g dm^{-1} shoot biomass. Maleic, fumaric and c-aconitic acid were found in traces (‹ 0.001 µM).

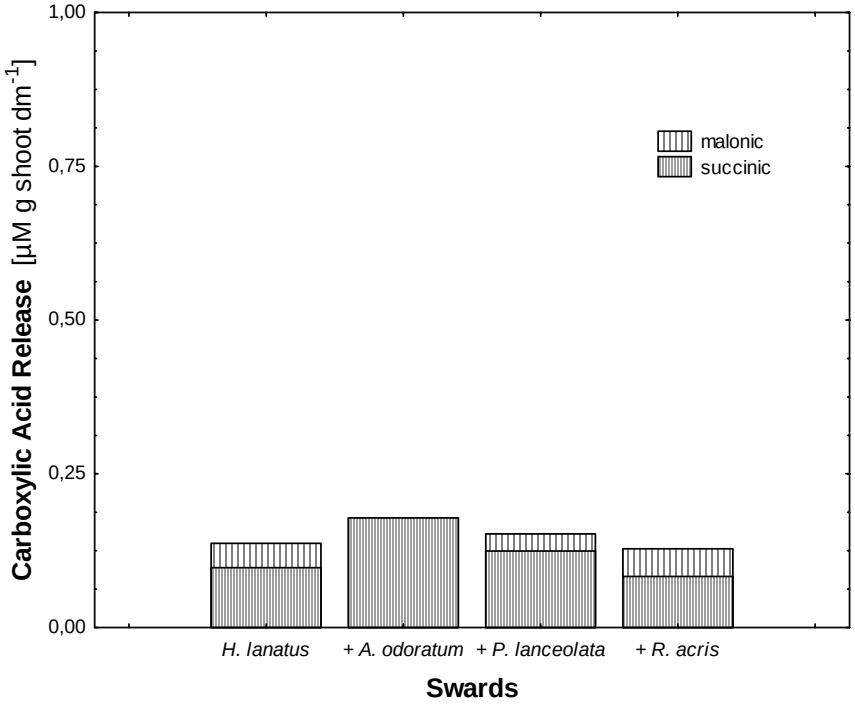


Figure 46 Median composition of carboxylic acids released per g total aboveground biomass (shoot) in swards containing *H. lanatus* 3 weeks prior to 1st harvest

After 1st harvest, the carboxylic acid release increased (Figure 45). The release amounted up to 2 µM g dm^{-1} of succinic acid in diculture with *P. lanceolata.* In monocultures and other dicultures succinic, malonic acid prevailed, but the release was also raised, compared to prior to 1st harvest.

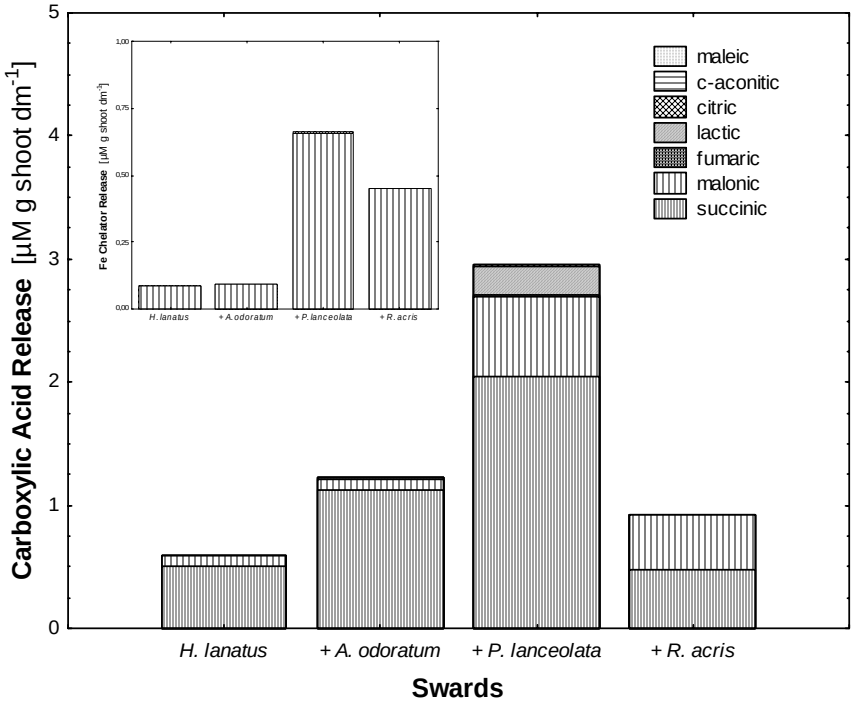


Figure 45 Median composition of carboxylic acids and potential carboxylic Fe-chelators (small graph) released per g total aboveground biomass (shoot) in swards containing *H. lanatus* 3 weeks after 1st harvest

Prior to 1st harvest, the median release of carboxylic acids in swards containing *P. lanceolata* (Figure 48) comprised of succinic, lactic, acetic and malic acid as major compounds. Fumaric, citric and malonic acid were found as accessory compounds. *P. lanceolata* monocultures showed the highest and dicultures with *H. lanatus* the least variety and amount of carboxylic acids.

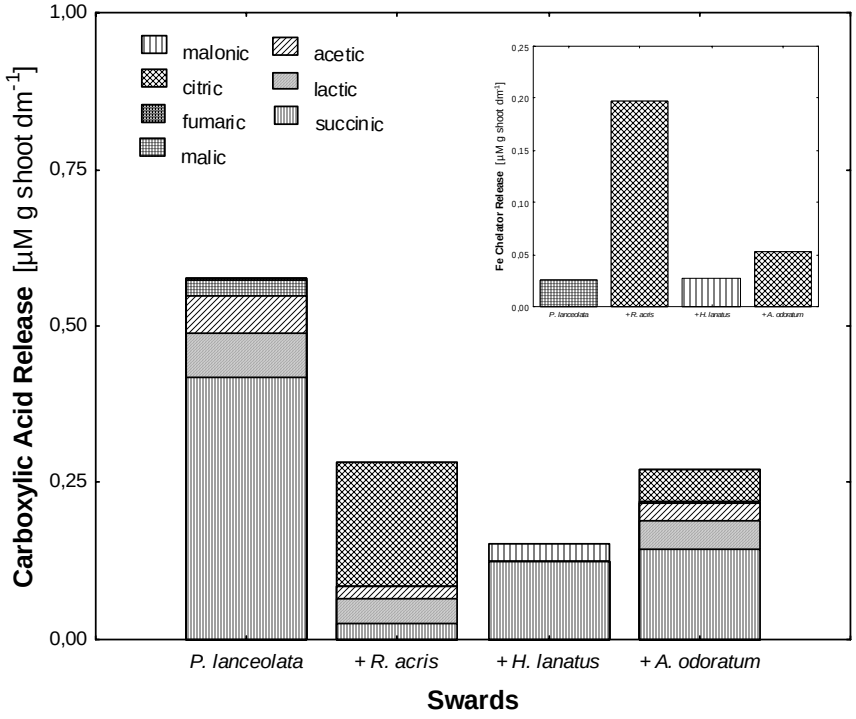


Figure 48 Median composition of carboxylic acids and potential carboxylic Fe-chelators (small graph) released per g total aboveground biomass (shoot) in swards containing *P. lanceolata* 3 weeks prior to 1st harvest

After 1st harvest, a distinct increase in carboxylic acid release was found (Figure 49). Monocultures of *P. lanceolata* had a higher release and variety of carboxylic acids compared to other swards. The diculture with *R. acris* had a very low carboxylic acid release.

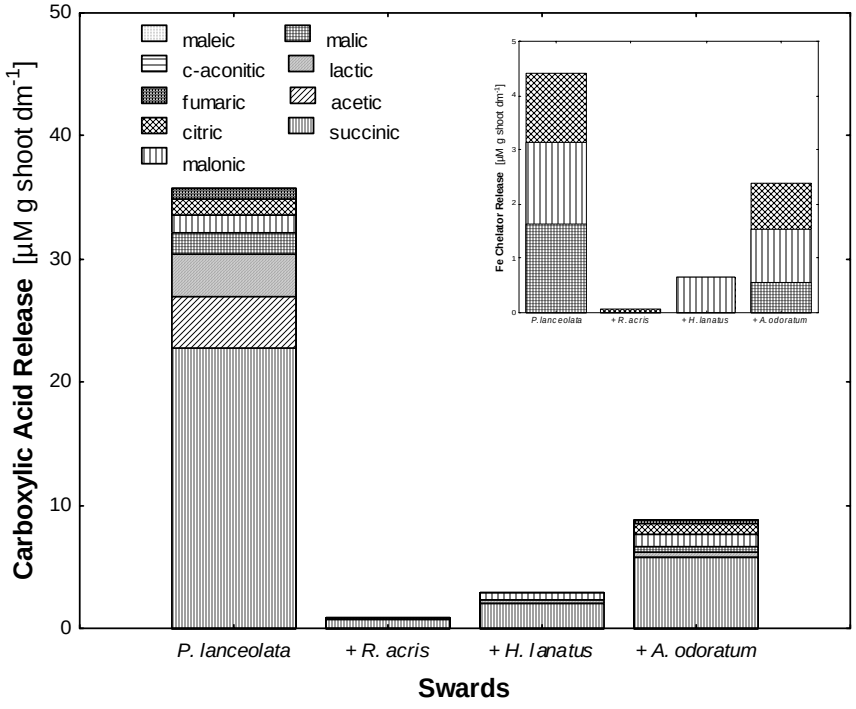


Figure 49 Median composition of carboxylic acids and potential carboxylic Fe-chelators (small graph) released per g total aboveground biomass (shoot) in swards containing *P. lanceolata* 3 weeks after 1st harvest

For *H. lanatus* swards, malonic acid was the only considerable potential carboxylic Fe-chelator released to rhizodeposit solution prior to and after 1st harvest (Figure 48). Malonic acid was released up to 0.05 µM g shoot dm^{-1} in *H. lanatus* monocultures and dicultures with *P. lanceolata* and *R. acris*. After the 1st harvest, the amounts of malonic acid were tendentiously higher for dicultures with *R. acris* and significantly higher for dicultures with *P. lanceolata* (0.5 to 0.75 µM g shoot dm^{-1}, Kruskal-Wallis 8.79, p = 0.0321, Mann-Whitney *). Traces of citric acid were detected in dicultures with *P. lanceolata*.

Prior to 1st harvest, malic acid was found (0.02 µM g shoot dm^{-1}) as the only carboxylic Fe-chelator in rhizodeposits of *P. lanceolata* (Figure 48). In diculture with *R. acris* and *A. odoratum* considerable amounts of citric acid (0.20 µM g shoot dm^{-1}) were released. In rhizodeposits of the diculture with *H. lanatus*, 0.03 µM of malonic acid were found prior to 1st harvest. To 0.05 µM g shoot dm^{-1} of citric acid were detected in dicultures with *A. odoratum*.
After the first harvest, considerable amounts of carboxylic Fe chelators were found in rhizodeposit solution of *P. lanceolata* swards (Figure 49). *P. lanceolata* monocultures showed malic, citric and malonic acid (1.8, 1.3 and 1.3 µM g shoot dm^{-1}) in rhizodeposit solution. In dicultures with *A. odoratum*, 0.5 µM of malic acid, 0.7 µM of citric acid and 1.3 of malonic acid g shoot dm^{-1} were found. Citric acid was the only chelator found in rhizodeposit solution of dicultures with *R. acris* (0.20 µM g shoot dm^{-1}). Dicultures with *H. lanatus* showed considerable amounts of malonic acid (0.50 µM g shoot dm^{-1}) in rhizodeposit solution. However, the differences were not significant between different *P. lanceolata* swards.

Tendentiously higher diversity and amounts of Fe chelators were found in the presence of herbal species. In rhizodeposition of grass species solely malonic acid was found featuring Fe chelating properties. Citric acid was found in monocultures of *A. odoratum* (0.22 µM g shoot dm^{-1}, not shown) and in dicultures with herbal species, but it was not detected in dicultures with *H. lanatus* in both samplings. Preferential uptake by *H. lanatus* or degradation of carboxylic acids by *H. lanatus* rhizosphere microflora may cause these differences between swards. The amounts of chelators in rhizodeposit solution were lower than in dicultures with herbal species. The amounts of Fe chelators were generally lower in monocultures than in dicultures. This may also suggest enhanced degradation activity of rhizosphere microflora in concern of carboxylic acids.

In contrast to this finding, rhizodeposits of herbal species showed higher amount of Fe chelators in monocultures than in dicultures. This hints at herbal species as the primary sources for Fe chelating carboxylic acids. Lower amounts of Fe chelating carboxylic acids are explained by lower contribution of herbal species in sward biomass.

3.2.5 Implications of Fe Acquisition Strategy on Competition and Rhizodeposition

As perceived in the lysimeter experiments, *H. lanatus* and *P. lanceolata* gained dominance over *A. odoratum* and *R. acris* in dicultures. *H. lanatus* achieved overyielding of individual biomass in any diculture compared to monocultures. *P. lanceolata* only overyielded in diculture with *R. acris*. Cab indicated higher competition ability in concern of biomass for *H. lanatus* in any diculture. *P. lanceolata's* competition ability was generally lower, it increased after 1st harvest in dicultures with *H. lanatus* and decreased severely in dicultures with *A. odoratum.*

Chlorophyll-indices suggested higher competition for Fe for both *H. lanatus* and *P. lanceolata* in dicultures with *A. odoratum*.
Fe contents in above- and belowground biomass indicated Fe deficiency for all grassland plants. The contents increased after re-supply slightly. Fe acquisition may have been impaired by precipitation of Fe with PO_4^{3-} or as hydroxyde due to unbuffered nutrient solution and Fe source ($FeCl_3$).

The competition ability of *H. lanatus* for Fe contents in aboveground biomass as indicated by Cab was slighty higher than for *A. odoratum* and *R. acris* and considerably higher than for *P. lanceolata*. At 2nd harvest, dicultures overyielded but *H. lanatus* showed considerably lower ability than *A. odoratum*. In concern of Fe per individual, dicultures with *A. odoratum* showed overyielding with higher ability for *H. lanatus* at 1st harvest. At 2nd harvest, both species also overyielded and *H. lanatus* showed higher ability.

At 2nd harvest, dicultures of *P. lanceolata* showed overyielding in concern of Fe contents. However , *P. lanceolata* had a lower competition ability. The ability of *P. lanceolata* increased in the order *R. acris* ‹ *H. lanatus* ‹ *A. odoratum* but remained low. At 1st harvest, *P. lanceolata* had lower competitition ability in concern of Fe per individual in dicultures with *A. odoratum*. At 2nd harvest, considerable overyielding was found in dicultures with *R. acris* and *H. lanatus* and underyielding with *A. odoratum*. The competition ability of *P. lanceolata* decreased in the order *R. acris* › *H. lanatus* › *A. odoratum*. Inverted patterns of competition ability for Fe contents and Fe per individual suggest high plasticity in Fe demand for *P. lanceolata* . This species likely shows trade-offs between biomass production and Fe contents when exposed to interspecific competition.

The higher DOC and carboxylic acid concentrations in rhizodeposit solution of *P. lanceolata* swards suggest implications of herbal species on DOC quality and dynamics. Rhizodeposition was considerably increased after the harvest. This finding hints at the high importance of regrowth on Fe demand of plants.

In solutions from *H. lanatus* swards only malonic acid occurred as a Fe chelating carboxylic acid in low amounts. In contrast to this finding, malic, citric and malonic acid were found in *P. lanceolata swards*. The total amounts of carboxylic acids in rhizodeposits of *P. lanceolata* monoculture accounted to the 6-fold prior to and to 70-fold after 1st harvest for amounts of *H. lanatus* monoculture.

Herbal species were identified as primary sources of carboxylic acids in rhizodeposition solution. Lower release of carboxylic acids in dicultures hint at a dilution effect due to lower biomass contribution of herbal species. It may also be affected by microbial degradation of carboxylic acids.

Highest DOC and carboxylic acid release were found in monoculture of *P. lanceolata* and in diculture with *A. odoratum.* This hints at high relevance of intraspecific Fe competition and the plant specific modification of nutritional strategies. *A. odoratum* is likely able to enhance Fe acquisition due to its adaptation to calcareous soils, whereas *H. lanatus* might lack these physiological skill. However, degradation procesess of carboxylic acid and DOC production, which are likely affected by microbial activities, have to be kept in mind. Tendentiously lower intensities of emmision spectra suggest higher contribution of more complex organic compounds to rhizodeposit solution. These compounds might indicate rhizodeposit induced priming effects.

3.3 Root Mineralisation Experiment 2003

Fresh root tissues of *H. lanatus* and *R. acris* and rhizosphere media were obtained after the final harvest and incubated within different rhizosphere sand from the rhizodeposit experiment. Fresh root tissues were applied to *H. lanatus* rhizosphere, *R. acris* rhizosphere, diculture rhizosphere and *Ref* sand. It was conceived to elucidate whether mineralisation of root tissues is affected by the identity of rhizosphere microflora.

Root Tissues and Carbon Respiration

Root tissue application to the different sand media increased the median respiration significantly (Table 76). *H. lanatus* tissues led to the highest median respiration. The respiration rates (% Σ rhizosphere C_{org} + root tissues) were also significantly higher in rhizosphere sand with *H. lanatus*. The respiration was also increased after application of *R. acris* root biomass, but the respiration rates remained on the level of basal respiration. Hence, respiration rates were dependent on plant species root characteristics.

Table 76 Median (25^{th}/75^{th} Percentile) of basal respiration and respiration of *Ref* and different rhizosphere sands after application of 2.5 g of fresh root tissues of *H. lanatus* and *R. acris* after an incubation period of 236 hrs.

Respiration	*No application*	*H. lanatus* + 3000 [µM C]	*R. acris* + 5300 [µM C]	MW-U	KW-H	*p*
CO_2-C [g dm^{-1}]	4.2 [c] (2.4/5.5)°	29.8 [a] (25.6/33.1)	14.6 [b] (12.1/17.1)	***	36.98	0.000
Min C_{org} [%]	0.6 [b] (0.5/0.9)°	1.9 [a] (1.6/2.0)	0.6 [b] (05/0.7)	***.	28.66	0.000

(Kruskal-Wallis-ANOVA, Mann-Whitney U-test, n = 4, ° n = 3)

Ref and diculture rhizosphere sand showed lower mineralisation than rhizosphere sands of the *H. lanatus* and *R. acris* monoculture swards (Figure 50). The main cumulative CO_2 evolution was limited to the first 80 to 120 hrs in case of *Ref* and diculture rhizosphere sand. The CO_2 evolution also flatened for *R. acris* rhizosphere sand after 200 hrs, whereas *H. lanatus* rhizosphere sand had carbon mineralisation until the end of the experiment.

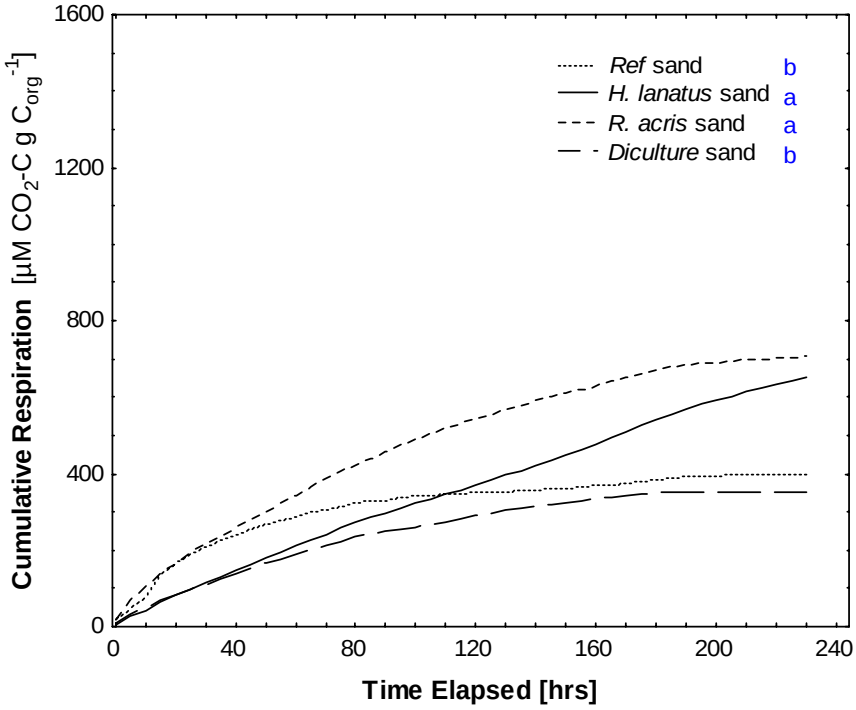


Figure 50 Median cumulative basal respiration of *Ref* and rhizosphere sand incubated over a period of 236 hrs at 20° C

(Kruskal-Wallis-ANOVA, H: 9.61, p ‹ 0.05; Mann-Whitney U: ‹ 0.05, n= 4, ° n= 3)

After application of 2.5 g *H. lanatus* root biomass to Ref and any rhizosphere sand, the CO_2 evolution was enhanced (Figure 51). After 200 hrs only a slight reduction in respiration was found.

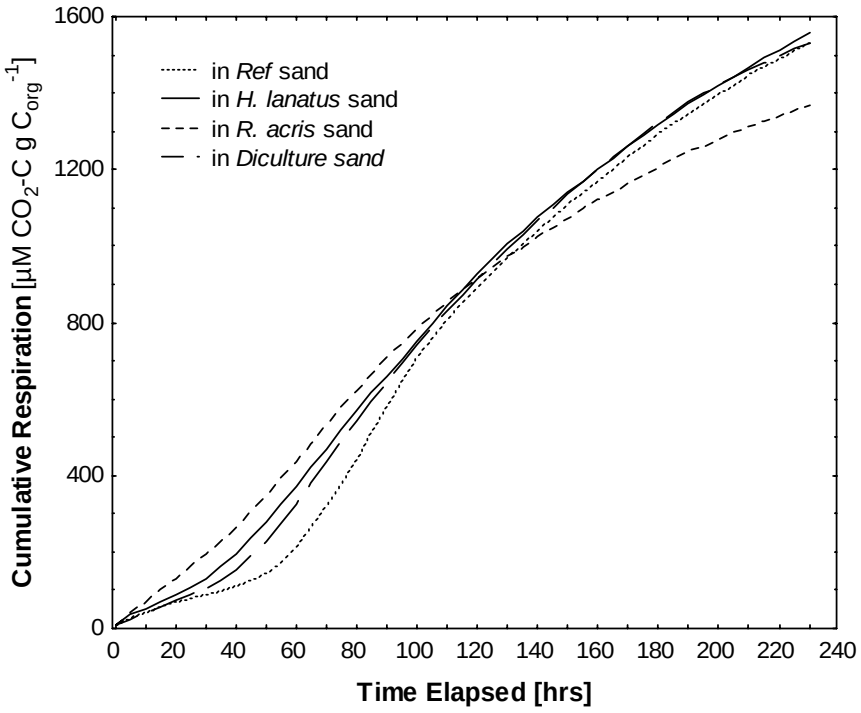


Figure 51 Median cumulative respiration of *Ref* and rhizosphere sand incubated over a period of 236 hrs at 20° C with application of 2.5 g *H. lanatus* root tissues

(Kruskal-Wallis-ANOVA, H: 2.01, p ‹ 0.05; Mann-Whitney U: ‹ 0.05, n= 4, ° n = 3)

The application of *H. lanatus* roots enhanced the mineralisation of C_{org}. This is likely due to low root diameter and high root surface rather than litter quality since C/N-ratio was tendentiously higher for *H. lanatus* roots compared to *R. acris* roots. No differences could be found in concern of rhizosphere sand identity and implications on mineralisation of root biomass.

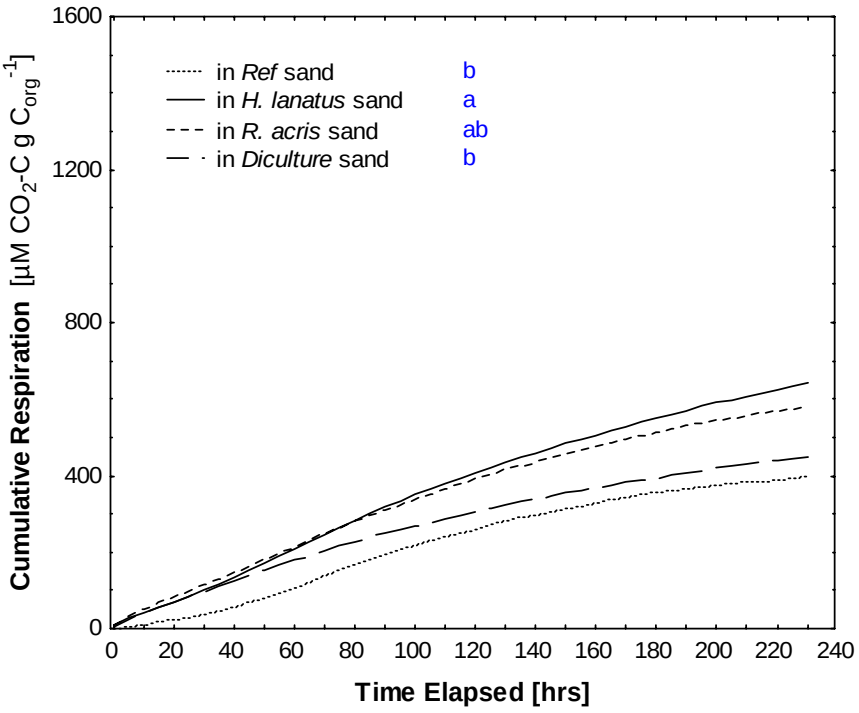


Figure 52 Median cumulative respiration of *Ref* and rhizosphere sand incubated over a period of 236 hrs at 20° C with application of 2.5 g *R. acris* root tissues

(Kruskal-Wallis-ANOVA, H: 4.01, $p < 0.05$; Mann-Whitney U: < 0.05, n= 4, ° n = 3)

Though more CO_2 was respired, the application of *R. acris* root biomass did not lead to higher mineralisation rates per unit C_{org} (Figure 52). *R. acris* root biomass seemed to feature similar quality for microbial degradation because C_{org} already accumulated during the rhizodeposition experiment. The higher performance in mineralisation of *H. lanatus* rhizosphere sand was also found after application of *R. acris* roots.

VAN DER KRIFT ET AL. (2001b) found lower degradation of *H. lanatus* compared to other grass species such as *A. odoratum* or *Festuca ovina*. The authors postulated lower degradation of this high fertility species due to higher N contents. But N contents in roots were lower than for low fertility species and thus likely affected degradation adversely. However, differences found between *H. lanatus* and *R. acris* in our experiment are predominately attributed to morphological features. Despite of tendentiously lower N contents, *H. lanatus* root biomass was rapidly mineralised, whereas *R. acris* root biomass very slowly. Due to low root diameter and higher root surface microorganisms likely have better access to easily degradable tissues. Hence, morphological root parameters rather than rhizosphere flora identity play an important role in initial mineralisation of root litter.

4 Summarizing Discussion

Experimental Grassland Stands on Lysimeter Facilities

Herb contribution to grassland stands rather than functional diversity showed implications on ecosystem functions such as nutrient use, use efficiencies, yields and loss with seepage. Table 77 gives an overview of the main results for the experimental grassland stands in 2002 and 2003.

Table 77 Assessment of biomass productivity, nutrient use and nutrient loss for main stand composition types in experimental grasslands compared within the year of appearance 2002 / 2003

	2002		2003		
Functional Groups	Grass	Grass/Herb	Grass	Grass/Herb	Herb/ Grass/Herb
Stand Composition	*H. lanatus* *H. lanatus* + *A. elatius*	*H. lanatus* + *P. lanceolata*	*A. elatius* + *H. lanatus*	*H. lanatus* + *G. pratense*	*P. lanceolata* *A. elatius* + *P. lanceolata*
Biomass Production					
aboveground yield	—	—	A[8]	B	C
belowground yield	—	—	A	B	B
Soil Resource Use					
Water	B	A	A	B	A
N	B	A	B	C	A
K	—	—	A	B	A
Mg	—	—	A	B	A
Ca	—	—	A	B	A
Use Efficiency					
WUE_{bm}	—	—	A	B	C
NUE_{bm}	A	B	A	B	A
KUE_{bm}	A	B	A	B	B
$MgUE_{bm}$	A	B	A	B	B
$CaUE_{bm}$	A	B	A	B	B
Nutrient Yield					
N	B	A	A	A	B
K	B	A	A	A	B
Mg	B	A	B	A	B
Ca	B	A	B	A	A
Loss/Yield-ratio					
N	A	B	B	A	B
K	nd	nd	B	A	A
Mg	nd	nd	A	A	B
Ca	nd	nd	A	B	B

A = high, B = medium , C = low — no differences, nd not determined

[8] *H. lanatus* detritus input stand I › stand II › stand III - V

No implications of functional diversity on ecosystem functions were found for the experimental grassland stands in 2002 and 2003. Differences in ecosystem performance were due to the identity of functional group of dominant and co dominant species (grass/herb). These findings support the mass-theory of GRIME (1998) which attributes dominant species having important implications on grassland ecosystem functions.

Table 78 Hypotheses for Experimental Grassland Stands on Lysimeter Facilities

	Functional group identity rather than functional diversity determines the use of soil borne resources in grassland stands	ok
	Stands with higher grass contribution feature:	
$\mathbf{I_a}$	Enhanced biomass production	no
$\mathbf{I_b}$	Lower evapotranspiration	no
$\mathbf{I_c}$	Lower sequestration of N, K, Mg and Ca in biomass	ok
$\mathbf{I_d}$	Increases in mineralisation of organic nitrogen	ok

Positive relations between higher nutrient availability and WUE_{bm} of both grass and herb species are indicated for stand I and II. TSIALTAS ET AL. (2001) identified grass species featuring higher WUE_{bm} compared to a variety of herb species. This finding could not be supported in this study. It was not possible to identify whether higher WUE_{bm} was caused by higher K supply or if N supply also played an important role. According to SCHINDLER ET AL. (2001) and BERGMANN (1992) positive effects of both nutrients on WUE_{bm} can be expected. In agreement to TSIALTAS ET AL. (2001), significant correlations between WUE_{bm} and aboveground biomass yields underpin the importance of WUE_{bm} for the performance of the experimental grassland stands in both years.

Grassland stands with higher herb contribution favoured higher nutrient sequestration in biomass and thus play an important role for safety net functions in experimental grassland ecosystems. The investigated grass species showed higher base cation use efficiency and hence provided considerably growth under low cation supply. DACCORD ET AL. (2001) report similar results with grass species featuring higher base cation use efficiencies compared to herb species. Grass dominated stands showed rather low performance in safety net functions for base cations. Lower base cation yields in biomass of grass dominated stands were not automatically reflected by higher cation concentrations in soil solution or losses with seepage. The cation exchange capacity of the soil led to an efficient buffering of cation concentrations in soil solution of the stands.

Slightly higher N_{min} concentrations in soil solution likely reflected higher root-turnover rates of grass dominated stands in 2002 (REUTER, 2006). This finding hints at an important phenological trait of grassland species, which might show important implications on ecosystem functions in grassland stands. As reported for rhizobial symbioses by SCHERER-LORENZEN ET AL. (2003), root-turnover-rates may have important implications on N dynamics in grassland stands.

According to the results summarized in Table 77, the general hypothesis I for the *Experimental Grassland Stands* is accepted. The hypothesis I_a and I_b have to be rejected and hypothesis I_c and I_d can be accepted (Table 78).

Rhizodeposit Experiment

P. lanceolata was identified as a species featuring lower competition ability (**Cab**, WILSON, 1988) in concern of building up of biomass and maintenance of Fe acquisition under Fe deficiency compared to *H. lanatus*. For swards containing *P. lanceolata* complementary was found in for individual biomass production and individual Fe stocks. *P. lanceolata* gained almost lower biomass than the accompanying species.

Table 79 Hypotheses for the Rhizodeposit Experiment

II	**Fe acquisition strategies of dominant plant species show implications on DOC quantity and quality in rhizosphere solution**	ok
	Grassland swards with herb dominance show:	
II_a	Higher concentrations of DOC in rhizosphere solution	ok
II_b	Differences in composition of organic compounds in rhizosphere solution compared to grass dominated swards	ok

Inverted patterns of Fe acquisition ability and the ability to build up individual biomass, hint at a trade-off between Fe demand and biomass build up for *P. lanceolata*. LAMBERS ET AL. (1998) report several physiological trade-offs between nutrient demands and biomass production for plants under competition.

The DOC release to rhizodeposit solution was enhanced after the 1st harvest. *P. lanceolata* showed a higher diversity of carboxylic acids and a considerable release of potential Fe chelators (malic, citric and malonic acid) to 1.3 to 1.7 µM g shoot dm^{-1}, while *H. lanatus* swards showed only a low release of carboxylic acids. These findings suggest dominant herb and grass species to agree with Fe strategies induced by MARSCHNER (2002).

Higher competition ability for species Fe contents after the 1st harvest indicated enhanced competition between *P. lanceolata* with *A. odoratum*. This finding was also reflected by higher DOC release and a release of potential Fe chelators amounting up to 2.3 µM g shoot dm^{-1} in swards of these swards. Due to physiological plasticity, even transient species in grassland stands may increase their competition ability under deficiency conditions.

The complementary in building up of individual biomass and individual Fe stocks also hints at a high importance of intraspecific competition under Fe deficiency driving the biomass production.

According to these results the hypotheses II, II_a and II_b (Table 79) for the *Rhizodeposit Experiment* can be accepted.

Root Mineralisation Experiment

The basal respiration of the rhizosphere sand obtained from the Rhizodeposit Experiment differed only tendentiously due to its origin (*H. lanatus*, *R. acris*, diculture rhizosphere or *Ref* sand). *H. lanatus* root tissues increased respiration rates significantly during a 236 hrs incubation period to a four-fold of basal respiration.

Table 80 Hypothesis for the Root Mineralisation Experiment

III	**The rhizosphere micro flora is adapted to "host" plant specific release of carbon compounds.**	
	The host plant's rhizosphere community performs:	
	Preferential mineralisation of litter derived from its "host" rather than litter derived from a different plant	no

The application of *R. acris* root tissues did not affect the respiration rates. Root tissue material was mineralised to the same extent as C_{org} material within the first 236 hrs. Higher respiration of *H. lanatus* roots was also reflected in higher mineralization in *Experimental Grasslands Stands* featuring high contribution of *H. lanatus* as reported by REUTER (2006).

No differences could be found caused by rhizosphere sand media. According to these findings the hypothesis III (Table 80) has to be rejected.

Outlook

Functional traits of dominant species rather than differences in phytodiversity had implications on ecosystem functions of our experimental grasslands. Higher base cation use efficiency (KUE_{bm}, $MgUE_{bm}$ and $CaUE_{bm}$) was identified for grass species. Higher root-turnover likely led to slightly higher N_{min} concentrations in soil solution of grass dominated stands in 2002. Theses findings underpin the importance of grasses and herbs in concern of feeding quality (DACCORD ET AL., 2001; JEANGROS ET AL., 2001ab) and N dynamics of grassland stands.

In comparison to grass species, herbs roots feature an enhanced release of carboxylic acids under Fe stress, which likely enhance SOM mineralisation through priming effects. The morphological quality of root detritus is of high importance for mineralisation performance of rhizosphere micro flora. Detritus of a grass species was mineralised more rapidly than detritus from a herb species likely due to lower root diameters and thus better access for microorganisms. The findings of both experiments (Rhizodeposit/Root Mineralization Experiment) show the need of further understanding of processes affecting C dynamics in grassland systems.

Further information about environmental and management implications on the performance of species traits such as base cation use efficiency, water use efficiency, root-turnover rates and rhizodeposition characteristics is needed for a close-up to agricultural practice. Furthermore, it is urgent to investigate effects of dominant species plant traits and the potential role of grassland ecosystems affecting the global climatic change.

5 Abstract

Within the framework of the **BMBF** funded project **BIOLOG-Bayreuth (01LC0014)** investigations on implications of functional groups on ecosystem functions related to water- nutrient- and carbon cycle were carried out. Three experiments were conceived to test for implications of dominant species traits and phytodiversity on ecosystem functions.

I Water, nutrient and DOC fluxes and losses from grasslands were investigated on *Experimental Grassland Stands on Lysimeter Facilities* situated in the Ecological Botanical Garden of the University of Bayreuth (ÖBG).

II Two dominant (*P. lanceolata / H. lanatus*) and two transient species (*R. acris / A. odoratum*), identified in Experimental Grassland Stands 2002 were used for the *Rhizodeposit Experiment*. The aim of the experiment was to investigate implications of different Fe acquisition strategies on rhizodeposition of organic compounds in nutrient solution cultures.

III The *Root Mineralisation Experiment* aimed at evaluating potential implications of the identity of rhizosphere microflora on mineralisation performance of root tissues from *H. lanatus* and *R. acris* derived from the Rhizodeposit Experiment.

In 2001, *Experimental Grassland Stands* were sown on lysimeter facilities (1.3×1.3×1.0 m). The facilities were filled with 70 cm of sub-) and 30 cm topsoil of tillered material derived from a Stagnic Cambisol. The different stands were sown with five replicates. Precipitation was collected and soil solution was obtained by using tension suction cups (300 hPa) at 15, 30 and 90 cm depth. Soil moisture was measured at 20, 40 and 60 cm depth using a TDR tube probe (trime RS 44) inserted in rhizotrons. Seepage was collected at a depth of 100 cm. KCl-extractable N_{min} was determined in June and September. NH_4, NO_3, DON, DOC, K, Mg and Ca were measured in solution and nutrients in above- and belowground biomass.

For the *Rhizodeposit Experiment*, sampling from rhizosphere quartz sand cultures was carried out once a month. Due to short half life of many rhizodeposit compounds (e.g. carboxylic acids, sugars), metabolites accumulated since the last sampling were purged out. The pots were logged with H_2O dem. for 20 min. The logging procedure was repeated and after 20 min the solution was repeatedly percolated and the pots were logged for further 5 min. The solution was sterilized by a Na Ag Cl salt (Micropur, 1 Tabl. = 0.1 g Ag l^{-1}). Analysis of organic acids was conducted by reversed phase HPLC as described by NEUMANN ET AL. (1999) at the Institute of Plant Nutrition of the University of Hohenheim. Chlorophyll contents of *H. lanatus* and *P. lanceolata* were measured colormetrically with a N Test (Hydro-Agri GmbH, Dühmen).

Root biomass for the *Root Mineralization Experiment* was obtained from plants of the *Rhizodeposit Experiment*. Root tissue C/N was determined at the *Chair of Plant Nutrition of the Alexander von Humboldt University* Berlin with aid of a C/N Elementanalyzer (varioMAX-CNS). The rhizosphere sand and root samples were transferred to a Respicond device at *Chair of Soil Science and Soil Ecology of the Ruhr University Bochum*. CO_2 evolution was measured continually once an hour (Respicond apparatus, Nordgren Innovations, Bygdea, Sweden). CO_2 was accumulated in 10 ml of a 0.6 M KOH and changes in electrical conductivity were used for calculating CO_2 evolution per hour.

In *Experimental Grassland Stands* on lysimeter facilities, herb contribution to grassland stands rather than functional diversity showed implications on ecosystem functions such as nutrient use, use efficiencies, yields and loss with seepage. Differences in ecosystem performance were due to the identity of functional group of dominant and co dominant species (grass/herb). Positive relations between higher nutrient availability and WUE_{bm} of both grass and herb species were indicated for experimental grassland stands. Grassland stands with higher herb contribution favoured a higher nutrient sequestration in biomass and thus played an important role for safety net functions in grassland ecosystems. Slightly higher N_{min} concentrations in soil solution likely reflected higher root-turnover rates of grass dominated stands in 2002. The investigated grass species showed higher base cation use efficiency and hence provided considerably growth under low cation supply. Grass dominated stands showed rather low performance in safety net functions for nutrients. Lower base cation yields in biomass of grass dominated stands were not automatically reflected by indicators for use of soil nutrients. In contrast to N_{min}, base cation concentrations and losses with seepage did not reflect differences in base cation use by the grassland stands.

In the *Rhizodeposit Experiment P. lanceolata* was identified as a species featuring lower competition ability in concern of biomass building up and Fe acquisition (**Cab**; WILSON, 1988) under Fe deficiency compared to *H. lanatus*. For swards containing *P. lanceolata* complementary was found in concern of individual biomass production and individual Fe stocks. *P. lanceolata* gained lower biomass than the accompanying species. Inverted patterns of Fe acquisition ability and the ability to build up individual biomass, hint at a trade-off between Fe demand and biomass build up for *P. lanceolata*. DOC release to rhizodeposit solution was enhanced after the 1st harvest. *P. lanceolata* showed the highest release of DOC, a higher diversity of carboxylic acids as well as a considerable release of potential Fe chelators (malic, citric and malonic acid) to 1.3 to 1.7 µM g shoot dm^{-1}, while *H. lanatus* swards released only small amounts of carboxylic acids. Higher competition ability for species Fe contents after the 1st harvest indicated enhanced competition between *P. lanceolata* with *A. odoratum*. This finding was also reflected by higher DOC release and a release of potential Fe chelators amounting up to 2.3 µM g shoot dm^{-1} in these swards. It was found that even transient grasslands species may show a high competition ability in concern of Fe-acquisition under Fe-deficiency.

During the *Root Mineralization Experiment*, the basal respiration of the rhizosphere sand obtained from Rhizodeposit Experiment differed only tendentiously due to its origin (*H. lanatus*, *R. acris*, diculture rhizosphere or *Ref* sand). *H. lanatus* root tissues were identified to increase respiration rates significantly during a 236 h incubation period to a four-fold of basal respiration. The application of *R. acris* root tissues did not affect the respiration rates. Root tissue material was mineralised to the same extent as C_{org} material within the first 236 hrs. Since no differences of chemical parameters (eg. C/N-ratio) were found for roots of the two species, enhanced mineralization of *H. lanatus roots* in the initial phase are likely due to lower root diameters and higher root surface areas.

Zusammenfassung

Im Rahmen des **BMBF** geförderten Projektes **BIOLOG-Bayreuth (01LC0014)** wurden Untersuchungen zum Einfluss pflanzlicher funktioneller Gruppen auf Ökosystemfunktionen wie den Wasser-, Nährstoff- und Kohlenstoffkreislauf vorgenommen. Drei Versuchsansätze sollten den Einfluß von dominanten Pflanzeneigenschaften und der Phytodiversität auf einzelne Ökosystemfunktionen belegen.

I *Experimentelle Grünlandbestände auf Lysimetern* im Ökologisch Botanischen Garten der Universität Bayreuth (ÖBG).

II Im *Rhizodeposit-Versuch* wurde anhand der, im Versuch I identifizierten dominanten Arten (*P. lanceolata / H. lanatus*) und wenig dominanten Arten (*R. acris* / *A. odoratum*), die Auswirkung verschiedener Fe-Nutzungsstrategien auf die organischen Komponenten der Wurzelexsudate in einem Nährlösungsexperiment untersucht.

III Im Wurzelmineralisierungsexperiment wurden Auswirkungen unterschiedlicher Rhizosphärenmikroflora auf die Mineralisation von *H. lanatus* und *R. acris* Wurzelstreu untersucht.

In Jahr 2001 wurden die Lysimeter (1,3×1,3×1,0m) mit 70 cm Unterboden und mit 30 cm Oberboden einer Pseudogley-Braunerde befüllt. Die *Experimentellen Grünlandbestände* wurden in 5-facher Wiederholungen angesät. Niederschläge und Lysimeterperkolat wurden aufgefangen und die Bodenlösung mit Saugkerzen (300 hPa) in 15, 30 und 90 cm Bodentiefe gewonnen. Die Bestimmung der Bodenfeuchte erfolgte in 20, 40 und 60 cm Tiefe mittels einer TDR Sonde (trime RS 44). KCl-extrahierbares N_{min} wurde im Juni und September bestimmt. NH_4, NO_3, DON, DOC, K, Mg und Ca wurden in der Bodenlösung, Nährstoffe in der unter- und oberirdischen Biomasse bestimmt.

Im *Rhizodeposit-Versuch* 2003 fanden monatlich Beprobungen der Rhizosphärenlösung aus Quarzsandkulturen statt. Aufgrund der geringen Halbwertzeit einiger Wurzelausscheidungsprodukte wie Carboxylsäuren und Zucker, wurden akkumulierte Metabolite vor der Beprobung aus dem Substrat mit H_2O dem. gespült. Die zu beprobende Lösung wurde nach 20 minütigen Überstau gewonnen und mit einem Na Ag Cl Salz (Micropur; 0,1 g Ag l^{-1})1 sterilisiert. Organische Säuren wurden mittels reversed phase HPLC (nach NEUMANN ET AL., 1999) am Institut für Pflanzenernährung der Universität Hohenheim analysiert. Die Chlorophyllgehalte von *H. lanatus* und *P. lanceolata* colorimetrisch mit einem N-Test (Hydro-Agri GmbH, Dühmen) bestimmt.

Im *Wurzelmineralisationsexperiment* wurde Wurzelbiomasse aus Versuch II verwendet. Das C/N Verhältnis des Wurzelgewebes wurde am Lehrstuhl für Pflanzenernährung der Alexander-von-Humboldt Universität in Berlin mittels eines C/N Elementanalyzer (varioMAX-CNS) bestimmt. Die Untersuchung und rechnerische Bestimmung der CO_2 Entwicklung der Wurzelproben fand mittels eines Respicond (Respicond apparatus, Nordgren Innovations, Bygdea, Sweden) am Lehrstuhl für Bodenkunde und Bodenökologie der Ruhr-Universität Bochum statt.

In *Experimentellen Grünlandbeständen* wirkten sich die Krautanteile an der Bestandesbiomasse stärker als die funktionelle Diversität auf Ökosystemfunktionen wie Nährstoffnutzung, -Nutzungseffizienzen, -erträge oder -verluste mit dem Sickerwasser aus. Unterschiede in der Ausprägung von Ökosystemfunktionen konnten teilweise auf die Zugehörigkeit der dominanten und co-dominanten Art(en) zu einer funktionellen Gruppe (Gräser oder Kräuter) zurückgeführt werden. Unterschiede in der Wassernutzung standen wahrscheinlich im Zusammenhang mit erhöhter N- und K-Verfügbarkeit in einzelnen Beständen. Die N-Mineralisation war unter grasdominierten Gründlandbeständen im Vergleich zu Gras/Krautmischbeständen erhöht. Dieser Befund lässt sich wahrscheinlich auf höhere Wurzelumsatzraten und eine bessere Mineralisierbarkeit der Wurzelstreu von *H. lanatus* zurückführen. In der Bodenlösung dieser Bestände traten nur tendentiell erhöhte N-Konzentrationen auf. Grünlandbestände mit höheren Krautanteilen wiesen eine höhere Nährstoffseqestrierung in der Biomasse als grasdominierte Bestände auf. Kräuter spielten damit eine wichtige Rolle für "safty net functions" in Grünlandbeständen. Die untersuchten Gräser wiesen höhere Nutzungseffizienzen für K, Mg und Ca auf. Trotz geringerer K, Mg oder Ca-Seqestrierung in der Biomasse konnten keine erhöhten Konzentrationen in der Bodenlösung oder höhere Sickerwasserverluste dieser Kationen nachgewiesen werden.

Im Rahmen des *Rhizodeposit Versuches* zeigte sich, das *P. lanceolata* im Vergleich zu *H. lanatus* eine geringere Konkurrenzkraft (**Cab**; WILSON, 1988) bezüglich des Biomasseaufbaus und der Fe-Nutzung bei Fe-Mangel aufweist. Komplementarität wurde für die individuelle Biomasseproduktion und Fe-Vorräte in Kulturen mit *P. lanceolata* nachgewiesen. Im Vergleich zu den Begleitarten baute *P. lanceolata* jedoch meist geringere Biomasse auf. Bei *P. lanceolata* wurde unter Konkurrenz Biomasse mit geringeren Fe-Gehalten aufgebaut. Dieses Ergebnis deutet auf einen „trade-off" (Ausgleich) zwischen Fe-Ansprüchen und dem Biomasseaufbau für diese Art. Die DOC Abgabe war nach der ersten Ernte bei allen Kulturen erhöht. *P. lanceolata* wies die höchste Abgabe von DOC und eine höhere Diversität an Carboxylsäuren und eine Abgabe von Fe-Chelatoren von 1,3 bis 1,7 µM g Wurzel dm^{-1} auf . Für *H. lanatus* hingegen konnten nur geringe Abgaben an Carboxylsäuren belegt werden. Höhere **Cab** im Bezug auf Fe-Gehalte einzelner Arten indizieren eine verstärkte Konkurrenz zwischen *P. lanceolata* und *A. odoratum*. Dieses Ergebnis spiegelt sich auch in einer höheren Abgabe von DOC von potentiellen Fe-Chelatoren bis zu 2,3µM g Spross TM^{-1} wider. Es wurde deutlich, dass unter Fe-Mangelbedingungen auch nicht dominante Grünlandarten bezüglich der Fe-Aneigung erhoehte Konkurrenzkraft aufweisen können.

Im Verlaufs des *Wurzelmineralisierungsexperimentes* variierte die Basalrespiration des Rhizosphärensandes einzelner Kulturen (*H. lanatus*, *R. acris*, Dikultur, *Ref* sand) nur leicht. Wurzelstreu von *H. lanatus* erhöhte die Respirationsraten während einer 236 Std. Inkubation bis auf das 4-fache der Basalrespiration. Die Wurzelstreu von *R. acris* wurde während der ersten 236 Std im gleichen Ausmaß mineralisiert wie C_{org}-Material der Sandkultur. Da keine Unterschiede in chemischen Parametern (z.B. CN) zwischen den Arten gefunden wurden, ist die höhere Mineralisation von *H. lanatus*-Streu wahrscheinlich auf morphologische Parameter (geringere Wurzeldurchmesser; hoehere Wurzeloberflächen) zurückzuführen.

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Appendix

Table I Results of a MANOVA on species contribution to aboveground biomass of experimental grassland stands I-V in 2002 / 2003[I] mean contribution of aboveground biomass in stand I-V[I]

Species	Predictor	SS	dF	MS	F	*p*	Tukey HSD	mean 2002^	mean 2003#
H. lanatus [I]	**year**	32564.39	1	32564.39	351.65	0.000	***	68	17
	stand	20436.04	4	5109.01	55.17	0.000			
	year×stand	1544.46	4	386.11	4.17	0.006			
A. elatius [II]	**year**	11145.77	1	11145.77	169.06	0.000	***	6	44
	stand	6666.46	2	3333.23	50.56	0.000			
	year×stand	4350.36	2	2175.18	32.99	0.000			
P. lanceolata [III]	**year**	3737.14	1	3737.14	49.57	0.000	***	47	69
	stand	4822.76	2	2411.40	31.99	0.000			
	year×stand	1556.25	2	778.13	10.32	0.001			
G. pratense [IV]	**year**	2515.56	1	2515.56	28.27	0.000	***	1	19
	stand	2891.23	2	1445.61	16.25	0.000			
	year×stand	2666.00	2	1333.00	14.98	0.000			

[I] in stand I, IV-V, [III] in stand III-V, [IV] in stand II, IV-V

^ raw data: NESSHÖVER & BEIERKUHNLEIN, unpublished
# raw data: TÜNTE & BEIERKUHNLEIN, unpublished

Table II Results of MANOVA on grass contribution to aboveground biomass of experimental grassland stands I-V in 2002 / 2003

Functional group	Predictor	SS	dF	MS	F	*p*	Tukey HSD	mean 2002^	mean 2003#
Grasses	**year**	9279.22	1	9279.22	97.30	0.000	***	71	44
	stand	36391.75	4	9097.94	95.40	0.000			
	year×stand	3158.71	4	789.68	8.28	0.000		[V]	[VI]

[V] mean grass contribution 2002: I, II › III-V

[VI] mean grass contribution 2003: I › II,V › IV › III

^ raw data: NESSHÖVER & BEIERKUHNLEIN, unpublished
# raw data: TÜNTE & BEIERKUHNLEIN, unpublished

Table III Results of MANOVA on nutrient accumulation in aboveground biomass in experimental grassland stands I-V ([%] of total biomass accumulation, $Nutrient_{stand}$)

Parameter	Predictor	SS	dF	MS	F	*p*	Tukey HSD	Year means	
								2002	2003
N	**year**	5101.40	1	5101.40	225.93	0.000	***	73	53
	stand	119.94	4	119.94	1.33	0.276			
	year×stand	323.62	4	323.62	3.58	0.014			
K	**year**	12.30	1	12.30	1.69	0.201	ns	80	79
	stand	674.75	4	674.75	23.24	0.000			
	year×stand	46.14	4	46.14	1.59	0.196		VII	VII
Mg	**year**	148.20	1	148.20	14.09	0.001	***	40	37
	stand	512.58	4	512.58	12.18	0.000			
	year×stand	351.76	4	351.76	8.36	0.000	***		VIII
Ca	**year**	223.50	1	223.50	16.77	0.000	***	76	72
	stand	268.33	4	268.33	5.03	0.002			
	year×stand	220.62	4	220.62	4.14	0.007	*		VIII

VII Stand I and II tendentiously higher in 2002 and 2003
VIII Stand II significantly higher in 2003

Table IV Results of a one way-ANOVA on nutrient accumulation in aboveground biomass of a grass dominated (II) and a grass/herb mixture (III) in 2002 and a grass dominated (I) and a herb dominated stand (III) in 2003 ([%] of total biomass accumulation, $Nutrient_{stand}$)

Parameter	SS	dF	MS	F	*p*	Tukey HSD	Stand IX means	
2002							**II**	**III**
N	42.80	1	42.80	3.84	0.086	ns	70	75
K	113.66	1	113.66	33.82	0.000	***	84	77
Mg	49.86	1	49.86	7.92	0.023	*	42	37
Ca	3.40	1	3.40	1.09	0.328	ns	76	77
2003							**I**	**III**
N	151.48	1	151.48	4.08	0.078	ns	56	48
K	314.73	1	314.73	47.32	0.000	***	84	73
Mg	22.56	1	22.56	1.43	0.265	ns	37	34
Ca	20.19	1	20.19	1.62	0.239	ns	69	72

IX In 2002 stand I (*H. lanatus* + *A. elatius*) was chosen as representative grass dominated and stand III (*H. lanatus* + *P. lanceolata*) as grass/herb mixture. In 2003 stand I (*A. elatius* + *H. lanatus*) was chosen as representative grass dominated and stand III (*P. lanceolata*) as herb monoculture

Table V Results of a MANOVA on nutrient contents in aboveground biomass of functional groups in experimental grassland stands I-V in 2002 / 2003

Parameter	Predictor	SS	dF	MS	F	*p*	Tukey HSD	grasses mean		herbs mean	
								2002	2003	2002	2003
N [%]	**year**	0.55	1	0.55	7.49	0.007					
	group	4.48	1	4.48	61.18	0.000	***	**1.4** ^{b}		**1.6** ^{a}	
	year×group	0.19	1	0.19	2.56	0.111	ns	1.4	1.4	1.7	1.6
K [mg g dm^{-1}]	**year**	60.10	1	60.10	0.98	0.323					
	group	3020.00	1	3020.00	49.32	0.000	***	**25.8** ^{b}		**32.2** ^{a}	
	year×group	1295.99	1	1295.99	21.16	0.000	*	24.2 ^{c}	27.4 ^{b}	34.7 ^{a}	29.6 ^{b}
Mg [mg g dm^{-1}]	**year**	5.18	1	5.18	15.98	0.000					
	group	109.60	1	109.60	338.45	0.000	***	**1.4** ^{b}		**2.6** ^{a}	
	year×group	0.95	1	0.95	2.94	0.087	ns	1.2	1.6	2.5	2.7
Ca [mg g dm^{-1}]	**year**	2077.75	1	2077.75	1174.73	0.000					
	group	1273.84	1	1273.84	720.21	0.000	***	**3.4** ^{b}		**7.5** ^{a}	
	year×group	1021.57	1	1021.57	577.58	0.000	***	2.6^{c}	4.2 ^{b}	3.1^{c}	12.0 ^{a}

Significant distinctions are indicated by different letters

Table VI Results of a MANOVA on nutrient contents of aboveground biomass for *H. lanatus* and *A. elatius*

Species / Parameter	Predictor	SS	dF	MS	F	*p*	Tukey HSD	year means	
								2002	2003
H. lanatus									
N [% dm]	**year**	0.03	1	0.03	0.41	0.521	ns	1.4	1.4
	stand	0.19	4	0.05	0.75	0.559			
	year×stand	0.20	4	0.05	0.82	0.513			
K [mg g dm $^{-1}$]	**year**	716.86	1	716.87	46.03	0.000	***	25.1	30.5
	stand	126.97	4	31.74	2.04	0.096			
	year×stand	56.77	4	14.19	0.91	0.461			
Mg [mg g dm^{-1}]	**year**	5.14	1	5.14	115.84	0.000	***	1.2	1.7
	stand	0.09	4	0.02	0.50	0.734			
	year×stand	0.17	4	0.05	1.10	0.360			
Ca [mg g dm^{-1}]	**year**	66.99	1	67.00	228.58	0.000	***	2.8	4.5
	stand	4.17	4	1.04	3.56	0.010	***		
	year×stand	3.29	4	0.82	2.80	0.030	***		
A. elatius									
N [% dm]	**year**	0.33	1	0.33	3.15	0.082	ns	1.4	1.3
	stand	0.02	2	0.01	0.10	0.905			
	year×stand	0.12	2	0.06	0.58	0.565			
K [mg g dm $^{-1}$]	**year**	0.09	1	0.09	0.01	0.935	ns	22.6	22.7
	stand	61.44	2	30.72	2.28	0.112			
	year×stand	26.64	2	13.32	0.99	0.379			
Mg [mg g dm^{-1}]	**year**	0.92	1	0.92	4.69	0.035	*	1.1	1.4
	stand	0.02	2	0.01	0.06	0.942			
	year×stand	0.49	2	0.24	1.24	0.298			
Ca [mg g dm^{-1}]	**year**	33.82	1	33.83	33.11	0.000	***	2.2	3.7
	stand	2.03	2	1.02	0.99	0.377			
	year×stand	1.17	2	0.59	0.57	0.567			

Table VII Results of MANOVA on nutrient contents of aboveground biomass for *P. lanceolata* and *G. pratense*

Species / Parameter	Predictor	SS	dF	MS	F	*P*	Tukey HSD	Year Means 2002	Year Means 2003
P. lanceolata									
N [% dm]	**year**	0.14	1	0.14	3.45	0.069	ns	1.5	1.4
	stand	0.02	2	0.01	0.24	0.790			
	year×stand	0.07	2	0.03	0.84	0.436			
K [mg g dm^{-1}]	**year**	355.61	1	355.61	7.71	0.008	**	32.5	27.6
	stand	23.00	2	11.50	0.25	0.780			
	year×stand	22.58	2	11.29	0.24	0.784			
Mg [mg g dm^{-1}]	**year**	2.48	1	2.48	14.28	0.000	***	1.8	2.2
	stand	0.02	2	0.01	0.05	0.956			
	year×stand	0.03	2	0.01	0.08	0.927			
Ca [mg g dm^{-1}]	**year**	1121.13	1	1121.13	1689.85	0.000	***	2.8	11.5
	stand	0.07	2	0.03	0.05	0.949			
	year×stand	0.09	2	0.05	0.07	0.934			
G. pratense									
N [% dm]	**year**	0.75	1	0.75	19.73	0.000	***	1.9	1.6
	stand	0.18	2	0.09	2.42	0.099			
	year×stand	0.03	2	0.02	0.41	0.666			
K [mg g dm^{-1}]	**year**	567.37	1	567.37	41.59	0.000	***	30.8	24.6
	stand	21.32	2	10.66	0.78	0.463			
	year×stand	30.32	2	15.16	1.11	0.337			
Mg [mg g dm^{-1}]	**year**	0.62	1	0.62	3.74	0.058	ns	3.0	2.8
	stand	0.61	2	0.31	1.84	0.168			
	year×stand	0.04	2	0.02	0.13	0.880			
Ca [mg g dm^{-1}]	**year**	1215.36	1	1215.36	206.98	0.000	***	3.3	12.3
	stand	11.71	2	5.86	1.00	0.376			
	year×stand	2.77	2	1.39	0.24	0.790			

Table VIII Results of MANOVA on water - and nutrient use efficiencies for aboveground biomass of experimental grassland stands I-V in 2002 / 2003

Parameter	Predictor	SS	dF	MS	F	*p*	Tukey HSD	year means	
								2002	2003
WUE_{bm} [g dm l $water_{transpir}^{-1}$]	**year**	199764.00	1	199764.00	1142695.00	0.000	***	2.5	1.2
	stand	10308.00	4	0.26	14741.00	0.000			
	year×stand	0.99	4	0.25	14229.00	0.000			
NUE_{bm} [g dm g N_{accum}^{-1}]	**year**	111.20	1	111.20	2932.00	0.095	ns	69	72
	stand	226.00	4	56.50	1490.00	0.223			
	year×stand	451.00	4	112.80	2973.00	0.031			
KUE_{bm} [g dm g K_{accum}^{-1}]	**year**	0.00	1	0.00	0.00	0.985	ns	37	37
	stand	377.91	4	94.48	13.86	0.000			
	year×stand	58.33	4	14.58	2.14	0.094			
$MgUE_{bm}$ [g dm g Mg_{accum}^{-1}]	**year**	481278.00	1	481278.00	183420.00	0.000	***	735	539
	stand	270196.00	4	67549.00	25744.00	0.000			
	year×stand	115017.00	4	28754.00	10959.00	0.000			
$CaUE_{bm}$ [g dm g Ca_{accum}^{-1}]	**year**	88820.00	1	88820.00	284111.00	0.000	***	234	150
	stand	272187.00	4	68047.00	217663.00	0.000			
	year×stand	41580.00	4	10395.00	33251.00	0.000			

Table IX Results of a MANOVA on volumetric soil moisture in 20, 40 and 60 cm depth of experimental grassland treatments (*Ref* / stand I-V) in 10, 2002

Predictor	SS	dF	MS	F	*p*	**Tukey HSD**	**20cm/40xm/60 cm**
depth	0.02	5	0.00	1.98	0.094	ns	38 / 38 / 39
treatment	0.01	2	0.00	1.73	0.186	ns	
depth×treatment	0.01	10	0.00	0.65	0.765	ns	

Table X Results of a MANOVA on volumetric soil moisture in 20, 40 and 60 cm depth of experimental grassland treatments (*Ref* / stand I-V) in 04-12, 2003

Predictor	SS	dF	MS	F	*p*	**Tukey HSD**	**20cm/40xm/60 cm**
depth	0.57	2	0.28	458.60	0.000	***	23 / 32 / 37
treatment	0.06	5	0.01	18.26	0.000	*	
depth×treatment	0.01	10	0.00	1.28	0.258	ns	

Table XI Results of a MANOVA on soil solution pH and eC in 15, 30 cm depth of experimental grassland treatments (*Ref* / stand I-V) in 2002 / 2003

Parameter / Predictor	SS	dF	MS	F	*p*	**Tukey HSD**	**2002 / 2003** **15 cm / 30 cm**	
Ph								
year	0.04	1	0.04	72.42	0.000	***	6.0	5.6
depth	0.06	1	0.06	118.73	0.000	***	6.1	5.5
treatment	0.01	5	0.00	4.07	0.002	*		
year×depth	0.00	1	0.00	0.90	0.346	ns		
year×treatment	0.00	5	0.00	1.15	0.339	ns		
depth×stand	0.00	5	0.00	0.72	0.611	ns		
year×depth×treatment	0.00	5	0.00	0.65	0.662	ns		
eC [µS cm^{-1}]								
year	2.41	1	2.41	123.80	0.000	***	131	261
depth	0.06	1	0.06	3.30	0.073	ns	196	175
treatment	0.41	5	0.08	4.24	0.002	*		
year×depth	0.01	1	0.01	0.35	0.557	ns		
year×treatment	0.02	5	0.00	0.20	0.962	ns		
depth×stand	0.18	5	0.04	1.88	0.107	ns		
year×depth×treatment	0.03	5	0.01	0.29	0.917	ns		

Table XII Results of a MANOVA on pH and eC in soil solution from 15, 30 and 90 cm depth of experimental grassland treatments (*Ref* / stand I-V) in 2003

Parameter / Predictor	SS	dF	MS	F	*p*	**Tukey HSD**	**group means**
pH							
depth	0.06	2	0.03	37.98	0.000	***	5.9^{a} / 5.2^{b} / 6.0^{a}
treatment	0.02	5	0.00	4.05	0.003	*	
depth×treatment	0.01	10	0.00	1.24	0.284	ns	
eC [µS cm^{-1}]							
depth	0.80	2	0.40	23.67	0.000	***	281^{a} / 242^{a} / 164^{b}
treatment	0.53	5	0.11	6.29	0.000	**	
depth×treatment	0.18	10	0.02	1.07	0.398	ns	

Significant distinctions are indicated by different letters

Table XIII Results of a MANOVA on N_{min} concentrations in soil solution from 15 and 30 cm depth of experimental grassland treatments (*Ref* / stand I-V) in 2002 / 2003

Predictor	SS	dF	MS	F	*p*		**group means**
year	8.02	1	8.02	61.85	0.000	ns	0.6 / 2.0
depth	0.04	1	0.04	0.31	0.581	ns	1.0 / 1.1
treatment	22.40	5	4.48	34.54	0.000	*	
year×depth	0.01	1	0.01	0.11	0.736	ns	
year×treatment	0.67	5	0.13	1.03	0.403	ns	
depth×stand	0.23	5	0.05	0.36	0.877	ns	
year×depth×treatment	0.31	5	0.06	0.48	0.789	ns	

Table XIV Results of a MANOVA on N_{min} concentrations in soil solution from 15, 30 and 90 cm depth of experimental grassland treatments (*Ref* / stand I-V) in 2003

Predictor	SS	dF	MS	F	*p*		**group means**
depth	0.50	2	0.25	2.09	0.000	***	2.2^{a} / 1.9^{b} / 1.4^{c}
treatment	17.29	5	3.46	28.83	0.330	ns	
depth×treatment	1.17	10	0.12	0.98	0.096	ns	

Significant distinctions are indicated by different letters

Table XV Results of a MANOVA on contents of extractable N_{min} (ΣNH_4-N/NO_3-N) and potential mineralisation rates in soil samples from 0-15 and 15-30 cm depth of experimental grassland treatments (*Ref* / stand I-V) for 06/09, 2002 / 2003

Parameter / Predictor	SS	dF	MS	F	*p*		**group means**
Extractable N_{min}							
year	0.21	1	0.21	2.02	0.157	ns	1.2 / 1.4
date	2.80	1	2.80	26.73	0.000	***	1.7 / 1.0
depth	0.10	1	0.10	0.94	0.334	ns	1.3 / 1.4
treatment	14.40	5	2.88	27.47	0.000	*	
year×date	2.02	1	2.02	19.26	0.000	ns	
year×depth	0.02	1	0.02	0.15	0.703	ns	
date×depth	0.00	1	0.00	0.02	0.898	ns	
year×treatment	1.98	5	0.40	3.78	0.003	*	
date×treatment	0.68	5	0.14	1.30	0.266	ns	
depth×treatment	0.07	5	0.01	0.13	0.986	ns	
year×date×depth	0.01	1	0.01	0.06	0.802	ns	
year×date×treatment	4.95	5	0.99	9.44	0.000	*	
year×depth×treatment	0.55	5	0.11	1.04	0.396	ns	
date×depth×treatment	0.30	5	0.06	0.56	0.728	ns	
year×date×depth×treatment	0.37	5	0.07	0.71	0.617	ns	
Mineralisation Rate							
year	6.56	1	6.56	37.47	0.000	***	0.8 / 1.8
date	0.02	1	0.02	0.09	0.768	ns	1.2 / 1.2
depth	0.00	1	0.00	0.02	0.897	ns	1.2 / 1.2
treatment	1.20	5	0.24	1.38	0.236	ns	
year×date	2.25	1	2.25	12.87	0.000	**	
year×depth	0.50	1	0.50	2.83	0.094	ns	
date×depth	0.62	1	0.62	3.57	0.061	ns	
year×treatment	0.93	5	0.19	1.06	0.384	ns	
date×treatment	1.43	5	0.29	1.63	0.154	ns	
depth×treatment	1.23	5	0.25	1.40	0.226	ns	
year×date×depth	1.03	1	1.03	5.90	0.016	*	
year×date×treatment	1.89	5	0.38	2.16	0.061	ns	
year×depth×treatment	0.40	5	0.08	0.46	0.804	ns	
date×depth×treatment	0.36	5	0.07	0.41	0.842	ns	
year×date×depth×treatment	1.07	5	0.21	1.22	0.301	ns	

Table XVI Results of a MANOVA on contents of extractable N_{min} (ΣNH_4-N/NO_3-N) and potential mineralisation rates in soil samples from 0-15 and 15-30 cm depth of experimental grassland treatments (*Ref* / stand I-V) for 03, 06/09, 2003

Predictor / Parameter	SS	dF	MS	F	*p*		**group means**
Extractable N_{min}							
date	0.08	2	0.04	0.25	0.78	ns	1.5 / 14. / 1.3
depth	0.19	1	0.19	1.16	0.28	ns	1.3 / 1.5
treatment	11.12	5	2.22	13.85	0.00	*	
date×depth	0.15	2	0.07	0.47	0.63	ns	
date×treatment	6.33	10	0.63	3.94	0.00	*	
depth×treatment	0.35	5	0.07	0.44	0.82	ns	
date×depth×treatment	0.47	10	0.05	0.29	0.98	ns	
Mineralisation rate							
date	12.83	2	6.41	34.10	0.00	**	6.6 / 2.3 / 1.4
depth	0.08	1	0.08	0.44	0.51	ns	2.9 / 2.6
treatment	3.48	5	0.70	3.70	0.00	*	
date×depth	1.90	2	0.95	5.06	0.01	*	
date×treatment	11.00	10	1.10	5.85	0.00	*	
depth×treatment	0.55	5	0.11	0.59	0.71	ns	
date×depth×treatment	2.33	10	0.23	1.24	0.27	ns	

Table XVII Results of a MANOVA on concentrations of K^+, Mg^{2+} and Ca^{2+} in soil solution from 15, 30 cm depth of experimental grassland treatments (*Ref* / stand I-V) in 2002 / 2003

Parameter	SS	dF	MS	F	*p*
K^+					
year	0.58	1	0.58	21.09	0.000
depth	1.63	1	1.63	59.05	0.000
treatment	1.04	5	0.21	7.49	0.000
year×depth	0.07	1	0.07	2.68	0.105
year×treatment	0.16	5	0.03	1.15	0.338
depth×treatment	0.17	5	0.03	1.22	0.307
year×depth×treatment	0.21	5	0.04	1.49	0.203
Mg^+					
year	2.43	1	2.43	110.44	0.000
depth	0.00	1	0.00	0.00	1.000
treatment	0.28	5	0.06	2.58	0.032
year×depth	0.01	1	0.01	0.49	0.485
year×treatment	0.08	5	0.02	0.73	0.603
depth×treatment	0.31	5	0.06	2.81	0.021
year×depth×treatment	0.05	5	0.01	0.42	0.832
Ca^{2+}					
year	2.90	1	2.90	143.52	0.000
depth	1.15	1	1.15	56.85	0.000
treatment	0.38	5	0.08	3.76	0.004
year×depth	0.01	1	0.01	0.39	0.532
year×treatment	0.08	5	0.02	0.79	0.558
depth×treatment	0.29	5	0.06	2.87	0.019
year×depth×treatment	0.04	5	0.01	0.38	0.860

Table XVIII Results of a MANOVA on concentrations of K^+, Mg^{2+} and Ca^{2+} in soil solution from 15, 30 and 90 cm depth of experimental grassland treatments (*Ref* / stand I-V) in 2003

Parameter	SS	dF	MS	F	*p*
K^+					
depth	1.40	2	0.70	26.73	0.000 I
treatment	0.75	5	0.15	5.78	0.000
depth×treatment	0.37	10	0.04	1.41	0.197
Mg^{2+}					
depth	0.37	2	0.19	8.23	0.001 II
treatment	0.54	5	0.11	4.74	0.001
depth× treatment	0.42	10	0.04	1.83	0.072
Ca^{2+}					
depth	2.90	2	1.45	90.63	0.000 III
treatment	0.65	5	0.13	8.18	0.000
depth× treatment	0.32	10	0.03	1.98	0.050

I significantly higher in 30 and 90 cm depth
II significantly higher in topsoil solution
III significant decrease in concentrations from 33.2 to 11.4 mg Ca^{2+} l^{-1}

Table XIX Results of a MANOVA on DOC concentrations in soil solution from 15 and 30 cm and from seepage of 100 cm depth of experimental grassland treatments (*Ref* / stand I-V) in 2002

Parameter	SS	dF	MS	F	*p*
depth	13.73	2	6.86	132.02	0.000
treatment	1.56	5	0.31	5.99	0.000
depth×treatment	0.49	10	0.05	0.94	0.496

Table XX Results of a MANOVA on DOC concentrations in soil solution from 15, 30 and 90 cm depth of experimental grassland treatments (*Ref* / stand I-V) in 2003

Parameter	SS	dF	MS	F	*p*
depth	15.62	2	7.81	340.03	0.000
treatment	1.31	5	0.26	11.45	0.000
depth×treatment	0.61	10	0.06	2.66	0.003

Table XXI Comparison of DOC concentrations measured with LiquiTOC (I) and HighTOC (II) in rhizodeposit solution taken in 07/ 08, 2003

Date	column	I	II	date	column	I	II
7/19/03	A01	14.5	20.4	8/01/03	A01	15.5	24.6
7/19/03	A02	9.2	22.2	8/01/03	A02	6.5	nd.
7/19/03	A03	15.8	18.2	8/01/03	A03	14.2	22.0
7/19/03	A04	25.9	33.7	8/01/03	A04	33.9	61.7
7/19/03	A05	12.9	12.9	8/01/03	A05	13.3	nd.
7/19/03	A06	13.2	18.6	8/01/03	A06	15.5	17.5
7/19/03	A07	16.3	18.3	8/01/03	A07	16.9	26.9
7/19/03	A08	10.9	9.9	8/01/03	A08	13.5	21.5
7/19/03	A09	11.5	17.0	8/01/03	A09	12.4	18.5
7/19/03	A10	7.0	11.4	8/01/03	A10	9.0	nd
7/19/03	A11	17.8	26.0	8/01/03	A11	40.6	74.5
7/19/03	B01	12.9	20.0	8/01/03	B01	27.3	33.2
7/19/03	B02	10.7	15.3	8/01/03	B02	18.3	31.1
7/19/03	B03	11.6	13.5	8/01/03	B03	15.0	22.5
7/19/03	B04	10.0	16.0	8/01/03	B04	16.8	22.7
7/19/03	B05	20.9	24.3	8/01/03	B05	28.4	36.1
7/19/03	B06	6.9	10.0	8/01/03	B06	9.0	nd
7/19/03	B07	17.2	17.3	8/01/03	B07	22.7	42.1
7/19/03	B08	23.0	28.0	8/01/03	B08	28.6	38.1
7/19/03	B09	12.9	37.4	8/01/03	B09	14.5	23.1
7/19/03	B10	8.0	11.9	8/01/03	B10	5.9	nd
7/19/03	B11	21.4	21.9	8/01/03	B11	13.3	20.6
7/19/03	C01	19.7	32.0	8/01/03	C01	41.8	60.9
7/19/03	C02	14.2	19.5	8/01/03	C02	14.7	32.4
7/19/03	C03	11.3	14.8	8/01/03	C03	5.6	nd
7/19/03	C04	12.3	15.5	8/01/03	C04	8.1	nd
7/19/03	C05	13.8	21.2	8/01/03	C05	13.5	27.5
7/19/03	C06	26.2	33.1	8/01/03	C06	14.8	27.4
7/19/03	C07	20.1	32.6	8/01/03	C07	11.4	20.9
7/19/03	C08	14.0	17.4	8/01/03	C08	13.6	21.4
7/19/03	C09	14.3	27.1	8/01/03	C09	12.9	25.3
7/19/03	C10	20.4	30.1	8/01/03	C10	11.4	21.2
7/19/03	C11	16.6	26.6	8/01/03	C11	16.3	30.0
7/19/03	D01	11.2	15.3	8/01/03	D01	8.9	nd
7/19/03	D02	10.5	12.1	8/01/03	D02	11.9	23.1
7/19/03	D03	19.7	34.3	8/01/03	D03	12.1	25.6
7/19/03	D04	12.6	23.3	8/01/03	D04	23.3	41.1
7/19/03	D05	12.6	26.9	8/01/03	D05	13.1	22.1
7/19/03	D06	17.5	21.5	8/01/03	D06	18.6	25.8
7/19/03	D07	8.6	14.5	8/01/03	D07	7.7	nd
7/19/03	D08	15.9	29.3	8/01/03	D08	11.1	19.9
7/19/03	D09	15.0	19.0	8/01/03	D09	13.7	28.2
7/19/03	D10	15.3	32.2	8/01/03	D10	18.8	27.0
7/19/03	D11	8.4	15.2	8/01/03	D11	18.6	32.2

Table XXII Comparison of LiquiTOC (I) and HighTOC (II) measurements of rhizodeposit solution from *H. lanatus* swards taken in 07/ 08, 2003

	Ref	***H. lanatus***	***+ A. odoratum***	***+ P. lanceolata***	***+ R. acris***	**MW-U**	**KW-H**	*p*
	----------[mg C l^{-1}]----------							
I								
prior to 1st harvest	8.9 ^{b} (8.3/10.2)	12.9 ^{a} (12.1/14.9)	15.2 ^{a} (13.7/18.7)	15.0 ^{a} (13.6/16.6)	13.4 ^{a} (11.7/17.7)	*	10.00	0.040
after 1st harvest	7.8 ^{b} (6.2/8.9)	14.1 ^{a} (12.8/15.9)	14.5 ^{a} (12.1/15.7)	15.0 ^{a} (13.5/18.0)	13.3 ^{a} (12.4/13.8)	*	19.98	0.005
II								
prior to 1st harvest	14.7 (13.2/18.5)	22.6 (16.1/26.8)	29.7 (24.9/33.8)	20.8 (19.1/24.3)	15.2 (12.5/19.7)	ns	8.93	0.063
after 1st harvest	10.4 ^{b} (9.7/11.7)	22.3 ^{a} (19.8/26.3)	22.2 ^{a} (20.6/23.9)	25.6 ^{a} (23.7/29.5)	21.1 ^{a} (20.7/22.3)	*	11.92	0.018

Significant distinctions between swards are indicated by different letters. (Kruskal-Wallis-ANOVA; Mann-Whitney U-Test; stand treatment n = 4)

Table XXIII Comparison of LiquiTOC (I) and HighTOC (II) measurements of rhizodeposit solution from *P. lanceolata* swards taken in 07/ 08, 2003

	Ref	***P. lanceolata***	***+ R. acris***	***+ H. lanatus***	***+ A. odoratum***	**MW-U**	**KW-H**	***p***
	----------[mg C l^{-1}]----------							
I								
prior to 1st harvest	8.9 ^{b} (8.3/10.2)	21.3 ^{a} (16.1/24.4)	18.7 ^{a} (14.3/19.9)	15.0 ^{a} (13.6/16.6)	19.5 ^{a} (16.5/23.5)	*s	11.42	0.022
after 1st harvest	7.8 ^{d} (6.2/8.9)	24.6 ^{a} (21.3/15.9)	19.8 ^{bc} (11.8/19.9)	15.0 ^{c} (13.5/18.0)	19.8 ^{b} (16.5/27.3)	*	25.26	0.000
II								
prior to 1st harvest	14.7 (13.2/18.5)	30.0 (25.7/32.9)	24.9 (17.2/33.5)	20.8 (19.1/24.3)	29.1 (25.2/32.6)	*	9.24	0.056
after 1st harvest	10.4 ^{c} (9.7/11.7)	51.0 ^{a} (39.6/61.3)	23.3 ^{ab} (19.7/33.9)	25.6 ^{ab} (23.7/29.5)	31.8 ^{a} (27.2/55.3)	*	14.04	0.007

Significant distinctions between swards are indicated by different letters. (Kruskal-Wallis-ANOVA; Mann-Whitney U-Test; stand treatment n = 4)

Table XXIV Comparison of original (I) and conversed intensity data (II) of spectral parameter of rhizodeposit solution from *H. lanatus* swards taken in 07/08, 2003

	Ref	*H. lanatus*	*+ A. odoratum*	*+ P. lanceolata*	*+ R. acris*	MW-U	KW-H	*p*
	----------[Specific Absorbance 280 nm]----------							
I								
prior to 1st harvest	0.15 (0.13./0.19)	0.18 (0.17/0.19)	0.17 (0.15/0.21)	0.14 (0.13/0.15)	0.16 (0.14/0.19)	ns	5.34	0.254
after 1st harvest	0.14. (0.13/0.16)	0.21 (0.17/0.24)	0.23 (0.21/0.24)	0.22 (0.20/0.23)	0.22 (0.20/0.24)	ns	8.50	0.075
II								
prior to 1st harvest	0.09 (0.08/0.10)	0.11 (0.10/0.15)	0.10 (0.07/0.12)	0.10 (0.08/0.12)	0.14 (0.14/0.16)	ns	8.84	0.065
after 1st harvest	0.08 (0.08/0.10)	0.13 (0.12/0.14)	0.13 (0.12/0.14)	0.14 (0.12/0.17)	0.13 (0.12/0.14)	ns	1.21	0.876
	----------[Emission 435-480 / 300-345 nm]----------							
I								
prior to 1st harvest	5.5 (3. 7./6.6)	5.1 (4.7/5.9)	2.4 (2.1/5.2)	4.2 (3.3/5.2)	5.6 (5.0/8.3)	ns	5.68	0.224
after 1st harvest	14.5. [a] (14.4/14.8)	6.7 [b] (3.2/7.4)	5.8 [c] (5.5/6.2)	4.9 [c] (4.3/5.5)	6.7 [b] (6.2/7.5)	*	15.71	0.034
II								
prior to 1st harvest	5.5 (3. 6/6.6)	5.1 (4.7/5.9)	2.3 (1.5/3.8)	4.2 (3.3/5.2)	5.6 (5.0/8.2)	ns	7.39	0.117
after 1st harvest	14.4 [a] (14.3/14.7)	6.7 [bc] (6.1/7.4)	5.8 [c] (5.5/6.1)	4. 9 [c] (4.3/5.5)	6.7 [b] (6.2/7.2)	*	15.71	0.003

Significant distinctions between swards are indicated by different letters. (Kruskal-Wallis-ANOVA; Mann-Whitney U-Test; stand treatment n = 4)

Table XXV Comparison of original (I) and conversed intensity data (II) of spectral parameter of rhizodeposit solution for *P. lanceolata* swards taken in 07/08, 2003

	Ref	*P. lanceolata*	*+ R. acris*	*+ H. lanatus*	*+ A. odoratum*	MW-U	KW-H	*p*
	----------[Specific Absorbance 280 nm]----------							
I								
prior to 1st harvest	0.15 (0.13./0.19)	0.14 (0.10/0.19)	0.17 (0.13/0.21)	0.14 (0.13/0.15)	0.15 (0.13/0.15)	Ns	0.59	0.965
after 1st harvest	0.14. (0.13/0.16)	0.16 (0.14/0.20)	0.17 (0.14/0.19)	0.22 (0.20/0.23)	0.17 (0.16/0.18)	Ns	9.16	0.057
II								
prior to 1st harvest	0.09 (0.08/0.10)	0. 09 (0.07/0.0.13)	0.12 (0.10/0.14)	0.10 (0.08/0.12)	0.11 (0.08/0.12)	ns	0.587	0.965
after 1st harvest	0.08 (0.08/0.10)	0.10 (0.09/0.12)	0.10 (0.07/0.11)	0.14 (0.12/0.17)	0.11 (0.09/0.12)	ns	9.16	0.057
	----------[Emission 435-480 / 300-345 nm]----------							
I								
prior to 1st harvest	5.5 (3. 7./6.6)	3.2 (2.3/4.3)	4.4 (3.5/5.2)	4.2 (3.3/5.2)	2.3 (2.2/2.3)	ns	8.23	0.074
after 1st harvest	14.5. [a] (14.4/14.8)	3.6 [b] (3.1/4.5)	7.6 [a] (6.3/7.9)	4.9 [ab] (4.3/5.5)	3.4 [b] (2.9/3.9)	*	15.24	0.042
II								
prior to 1st harvest	5.5 (3. 6/6.6)	3.2 (2.3/4.3)	4.4 (3.5/5.2)	4.2 (3.3/5.2)	2.3 (2.2/2.6)	ns	8.52	0.074
after 1st harvest	14.4 [a] (14.3/14.7)	3.6 [c] (3.1/4.5)	7.6 [b] (6.3/7.9)	4. 9 [bc] (4.3/5.5)	3.2 [c] (2.9/3.9)	*	15.24	0.004

Significant distinctions between swards are indicated by different letters. (Kruskal-Wallis-ANOVA; Mann-Whitney U-Test; stand treatment n = 4)

Table XXVI Comparison of DOC release original (I) and conversed data (II) for *H. lanatus* swards in 07/08, 2003

	H. lanatus	***+ A. odoratum***	***+ P. lanceolata***	***+ R. acris***	**MW-U**	**KW-H**	***p***
	----------[mg DOC g shoot dm^{-1}]----------						
I							
prior to 1st harvest	0.16. (0.14/0.19)	0.18 (0.08/0.24)	0.18 (0.16/0.23)	0.17 (0.15/0.24)	ns	0.150	0.985
after 1st harvest	0.42 (0.36/0.65)	0.39 (0.39/0.41)	0.62 (0.42/0.76)	0.40 (0.36/0.44)	ns	2.00	0.571
II							
prior to 1st harvest	0.26 (0.23/0.30)	0.31 (0.27/0.38)	0.29 (0.25/0.36)	0.28 (0.25/0.37)	ns	1.61	0.657
after 1st harvest	0.66 (0.57/1.03)	0.63 (0.61/0.67)	0.96 (0.66/1.17)	0.64 (0.66/1.17)	ns	2.00	0,571

Significant distinctions between swards are indicated by different letters. (Kruskal-Wallis-ANOVA; Mann-Whitney U-Test; stand treatment n = 4)

Table XXVII Comparison of DOC release original (I) and conversed data (II) for *P. lanceolata* swards in 07/08, 2003

	P. lanceolata	***+ R. acris***	***+ H. lanatus***	***+ A. odoratum***	**MW-U**	**KW-H**	***p***
	----------[mg DOC g shoot dm^{-1}]----------						
I							
prior to 1st harvest	0.31 (0.24/0.40)	0.33 (0.28/0.39)	0.18 (0.16/0.23)	0.29 (0.27/0.39)	ns	5.93	0.115
after 1st harvest	5.76 [a] (3.50/7.15)	0.58 [b] (0.52/0.80)	0.62 [b] (0.42/0.76)	1.75 [a] (1.42/1.99)	*	11.94	0.008
II							
prior to 1st harvest	0.48 (0.38/0.62)	0.52 (0.44/0.61)	0. 29 (0.25 /0.36)	0.46 (0.41/0.60)	ns	5.93	0.115
after 1st harvest	8.78 [a] (5.37/10.78)	0.93 [b] (0.83/1.25)	0.96 [b] (0.66/1.17)	2.65 [a] (2.17/3. 06)	*	11.97	0.007

Significant distinctions between swards are indicated by different letters. (Kruskal-Wallis-ANOVA; Mann-Whitney U-Test; stand treatment n = 4)

Table XXVIII Comparison of DOC concentrations in purge solution prior to and after 1st harvest for *H. lanatus* and *P. lanceolata* swards

Central Species	**Prior to**	**After**	**MW-U**	**KW-H**	**p**
	----------DOC [mg C l^{-1}]----------				
H. lanatus	27.6 (23.5/29.9)	22.5 (18.4/27.0)	*	6.47	0.011
P. lanceolata	30.4 (27.8/36.0)	21.1 (19.4/24.1)	***	15.80	0.000

Significant distinctions between swards are indicated by different letters. (Kruskal-Wallis-ANOVA; Mann-Whitney U-Test; stand treatment n = 4)

Table XXIX Evaluation of outliers for the Root Mineralisation Experiment

Id	Replicate	x_i	25th Perc.	Median	75th Perc.	25th Perc. / x_i	x_i / 75th Perc.
di	I	354	**340**	**412**	**799**	1.04	0.44
di	II	300				0.88	0.38
di	III	470				1.38	0.59
di	IV	*1788*				5.25	~~***2.24***~~
Hol	I	534	**518**	**659**	**803**	1.03	0.66
Hol	II	471				0.91	0.59
hol	III	858				1.66	1.07
hol	IV	785				1.52	0.98
Ran	I	724	**679**	**706**	**739**	1.07	0.98
Ran	II	653				0.96	0.88
Ran	III	781				1.15	1.06
Ran	IV	687				1.01	0.93
Ref	I	399	**306**	**408**	**1370**	1.30	0.29
Ref	II	*30*				~~***0.10***~~	0.02
Ref	III	*4229*				13.80	~~***3.09***~~
Ref	IV	418				1.36	0.30
holcus di	I	1859	**1279**	**1542**	**1810**	1.45	1.03
holcus di	II	1291				1.01	0.71
holcus di	III	1246				0.97	0.69
holcus di	IV	1793				1.40	0.99
holcus hol	I	1676	**1540**	**1571**	**1614**	1.09	1.04
holcus hol	II	1550				1.01	0.96
holcus hol	III	1512				0.98	0.94
holcus hol	IV	1593				1.03	0.99
holcus ran	I	1131	**1303**	**1377**	**1439**	0.87	0.79
holcus ran	II	1394				1.07	0.97
holcus ran	III	1360				1.04	0.95
holcus ran	IV	1574				1.21	1.09
holcus ref	I	603	**1137**	**1429**	**1671**	0.53	0.36
holcus ref	II	1315				1.16	0.79
holcus ref	III	1543				1.36	0.92
holcus ref	IV	2054				1.81	1.23
ranunculus di	I	581	**419**	**450**	**501**	1.39	1.16
ranunculus di	II	402				0.96	0.80
ranunculus di	III	474				1.13	0.95
ranunculus di	IV	425				1.01	0.85
ranunculus hol	I	878	**479**	**627**	**703**	1.83	1.25
ranunculus hol	II	610				1.27	0.87
ranunculus hol	III	645				1.35	0.92
ranunculus hol	IV	*86*				~~***0.18***~~	0.12
ranunculus ran	I	638	**523**	**585**	**621**	1.22	1.03
ranunculus ran	II	615				1.18	0.99
ranunculus ran	III	555				1.06	0.89
ranunculus ran	IV	426				0.82	0.69
ranunculus ref	I	434	**306**	**373**	**407**	1.42	1.07
ranunculus ref	II	397				1.30	0.98
ranunculus ref	III	348				1.14	0.86
ranunculus ref	IV	180				0.59	0.44

Table XXX Comparison of respiration rates prior to and after the exchange of outliers by group medians for rhizosphere sand and rhizosphere

Rhizosphere Sand	***Ref***	***H. lanatus***	***R. acris***	***Diculture***	**MW-U**	**KW-H**	***p***
	----------[µM CO_2-C g C_{org}^{-1}]----------						
I	**408** (214/2323)	659 (502/822)	706 (670/753)	**412** (327/1129)	ns.	2.82	0.420
II	408 [b] (403/413)	659 [a] (502/822)	706 [a] (670/753)	354 [b] (327/412)	*	11.68	0.009
+ *R. acris* root dm							
I	373 (264/416)	**627** (348/762)	585 (491/627)	450 (413/528)	ns.	5.49	0.139
II	373 [c] (264/416)	645 [a] (627/762)	585 [ab] (491/627)	450 [b] (413/528)	*	11.16	0.011

sand with application of *R. acris* root biomass

Significant distinctions between swards are indicated by different letters. (Kruskal-Wallis-ANOVA; Mann-Whitney U-Test; stand treatment n = 4)

Erklärung

Die vorliegende Arbeit wurde von mir selbstständig verfasst und ich habe dabei keine anderen als die angegebenen Hilfsmittel und Quellen benutzt.

Ferner habe ich nicht versucht, anderweitig mit oder ohne Erfolg eine Dissertation einzureichen oder mich der Doktorprüfung zu unterziehen.

Bayreuth, den 15. November 2005

Guido Kossmann