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der Christian-Albrechts-Universität zu Kiel

**Short-term effects of defoliation on herbage productivity and
herbage quality in a semi-arid grassland ecosystem of
Inner Mongolia, P.R. China**

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Chapter 1
Introduction

1. The Problem of Grassland Degradation in Inner Mongolia, P.R. China

In the People's Republic of China approx. 400 million ha of the total land area are grasslands, what corresponds to 35% of China's total land area and is equivalent to 12% of the world's grassland area. Inner Mongolia is the third largest out of 33 provinces in China (figure 1). It was founded in 1947 receiving the status of an autonomous region. Inner Mongolia is situated in the north-west of China, bordering to the north on the Republic of Mongolia and Russia and to the south on 8 Chinese provinces.



Figure 1: Map of the People's Republic of China

Inner Mongolia's main feature is its vast grassland area (79 million ha) covering about 70% of the total land area of Inner Mongolia and corresponding to 20% of China's total grassland area (FAO, 2001). The climate of Inner Mongolia is temperate and the continental influence entails long, cold winters and short, but hot summers. Mean annual precipitation is rather low and the inter-annual and intra-annual variation is high. The annual precipitation fluctuation rate ranges between 45-95%, correspondingly the fluctuation in aboveground biomass production ranges between 30-60% (Li and Vinczeffy, 1998). A precipitation gradient can be observed

from the north-east, which receives about 600 mm year⁻¹, to the west, which obtains only about 100 mm year⁻¹ or less (figure 2).

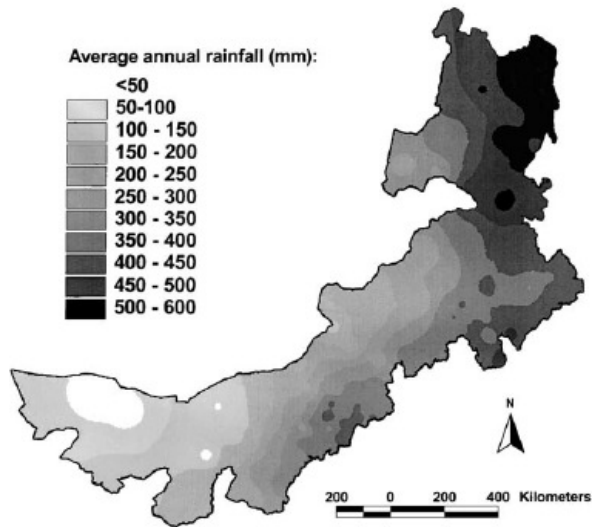


Figure 2: Spatially interpolated map of average rainfall (mm) in Inner Mongolia, 1982-1991 (Yu et al., 2004)

The traditional way of farming this huge grassland area is grazing. For centuries nomadism was the dominant life form utilising the grassland in a sustainable way. Since the 1950's nomad families were settled down in permanent farms and villages, simultaneously more Chinese from other parts of China moved to Inner Mongolia, as it was only sparsely populated. Today Inner Mongolia is inhabited by 24 million people, of which 80% belong to the group of Han-Chinese and only 17% descend from Mongols. The population density is 20 inhabitants per km², not much when compared to the 906 inhabitants per km² in Beijing, but ten times as much as in the Republic of Mongolia, where only 2 inhabitants per km² can be found. The increasing population demanded food and a source of income, what both is provided by agriculture in Inner Mongolia. But also the generally increasing population of China stimulated the demand for agricultural products like meat and milk. Consequently, the number of livestock units grazing on Inner Mongolia grasslands increased substantially. Between 1949 and 1985 the number of sheep units (ewe with nursing lamb) increased from 7.7 to 61.5 million sheep units and increased further to 70.3 million sheep units in 1998 (Jiang and Meurer, 2001). Livestock density exceeds the carrying capacity in large parts of Inner Mongolia (Jiang and Meurer, 2001; Yu et al., 2004). The carrying capacity is closely related to annual precipitation since precipitation is the crucial factor on which biomass production depends. In Figure 3 the correlation between the average rainfall-based carrying

capacity and the actual livestock density is presented, demonstrating that livestock density extensively exceeds the calculated carrying capacity in most rural counties in Inner Mongolia.

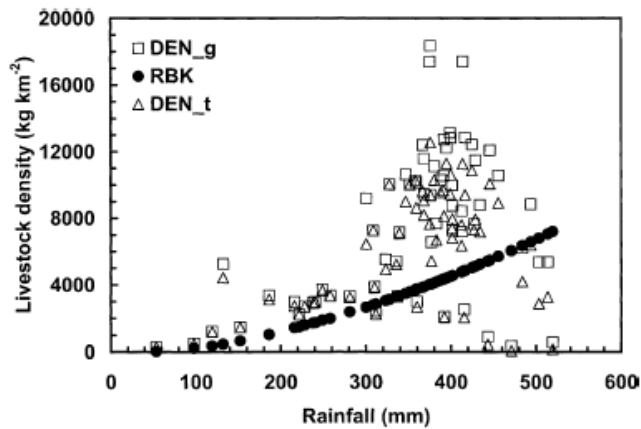


Figure 3: Average rainfall-based carrying capacity (RBK, kg km⁻²) and actual livestock density (kg km⁻²) for rural counties in the Inner Mongolia Autonomous Region, 1982-1991 (DEN_t = density based on total area; DEN_g = density based on grazing areas) (Yu et al., 2004)

The main result of high livestock density is persistent overgrazing of the grasslands and following grassland degradation is currently the most serious ecological and socio-economical problem in Inner Mongolia.

In general degradation is characterised by progressive loss of secondary productivity and diversity (Milton et al., 1994). Sneath (1998) summarised definitions of degradation in a similar way: “a more or less permanent decline in the rate at which land yields livestock products, although it is often impossible to determine whether declines in productivity are permanent and to what extent they result from of human activities or natural processes”. However, no common definition when grassland is considered as degraded is available for Inner Mongolia grasslands. Several authors report that about 30-50% of the Inner Mongolia grasslands are degraded (Ellis, 1992; Sneath, 1998; Li and Vinczeffy, 1998; FAO, 2001; Jiang and Meurer, 2001; Zhou et al., 2002).

Degradation of Inner Mongolia grasslands results in decreasing productivity and severe environmental damage. Reduced productivity of the grassland limits the economic turnout of the local farmers, jeopardising their existence and aggravating the ecological problems. Farmers in Inner Mongolia do not own the land they are farming and the right of use was usually limited to short periods. Therefore farmers only had limited interest in sustaining a sound grassland ecosystem and were striv-

ing for the highest short-term output from the area. In short-term high grazing intensities provide higher economical return (Wang et al., 1999a). This policy was changed in recent years and farmers can lease farm land for longer periods (~ 30 years, personal communication). This change is connected with the hope that the farmers take better care of their farm land, when they have a long-term perspective. However, overgrazing was common practice for decades resulting in severe ecological problems like wind and water erosion, which cause loss of high amounts of fertile soil material. Special attention has been driven to dust and sand storms, which are a natural phenomenon in this part of the world, however increasing in severity and number in recent years (Wang et al., 2004). In this context also the risk to turn the Inner Mongolia grasslands from a carbon sink into a carbon source need to be considered, especially against the background of global change. Carbon loss due to erosion and reduced carbon input resulting from decreasing below-ground biomass productivity could contribute to such changes in the carbon cycle of grasslands (Cui et al., 2005).

2. MAGIM-Project

This thesis is the result of research activities conducted in the framework of the MAGIM project. MAGIM is the abbreviation of **M**atter Fluxes in **G**rasslands of **I**nners **M**ongolia as influenced by Stocking Rate. MAGIM is a sino-german research group funded by the Deutsche Forschungsgemeinschaft (DFG 536) that especially emphasizes the scientific exchange between Chinese and German scientists. Against the background of the above described degradation problem in Inner Mongolia grasslands the complex plant-soil-animal interactions of this ecosystem are addressed by the MAGIM project. 9 sub-projects out of several scientific fields (soil science and geology, plant nutrition, grassland science, animal nutrition, meteorology and climatology, hydrology) are involved in the MAGIM project focusing on the evaluation and assessment of the impact of different land-use practices on above- and belowground biomass productivity and composition, local and regional water, carbon and nitrogen budgets, soil erosion, and animal productivity. The sub-project providing the basis for the present work is focusing on the influence of grazing management on grassland productivity, herbage quality and in the long-term on persistence of the steppe grasslands. Further details are given in section 3 of this chapter.

2.1 Study area

The present study was carried out in the experimental area of the Inner Mongolia Ecosystem Research Station (IMGERS). IMGERS is situated about 60 km south-east of Xilinhot, which is the regional capital of the Xilin Gol league. Xilinhot is about 500 km (in linear distance) north of Beijing (figure 1). IMGERS is located in the southern part of the Xilin River Basin, which was selected as the main research area of the whole MAGIM-project (figure 4).

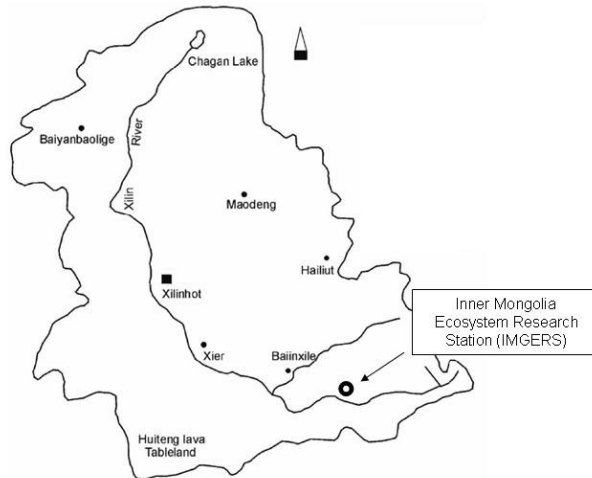


Figure 4: Map of the Xilin River Basin, Inner Mongolia (Tong et al., 2004)

The climate in the Xilin River Basin is typical for temperate steppe regions. The mean annual temperature is 0.7°C and the mean annual precipitation is 350 mm, of which 85% occur between May and September (figure 5). The vegetation period is about 150 days long, only 100-135 days are frost-free. A stable snow cover can be found from end of November until end of March.

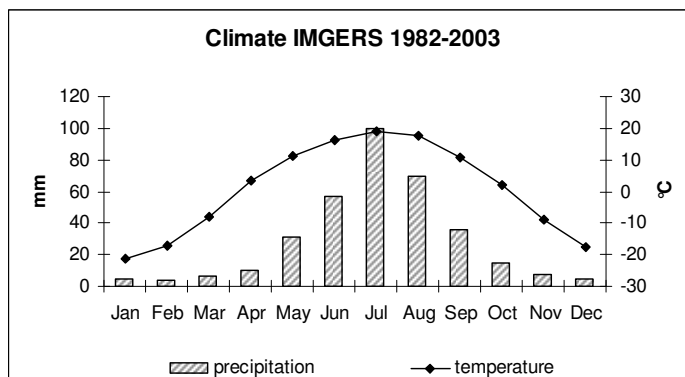


Figure 5: Mean monthly precipitation (mm) and temperature (°C) measured at IMGERS between 1982 and 2003

In the Xilin River Basin three types of steppe can be found. The dominant type is typical steppe (> 60%), whereas meadow steppe contributes about 6% and desert steppe about 20% (Li et al., 1988). The distribution of the different steppe types depends on the precipitation pattern and the steppe types are characterised by plant species more or less adapted to water stress (figure 6).

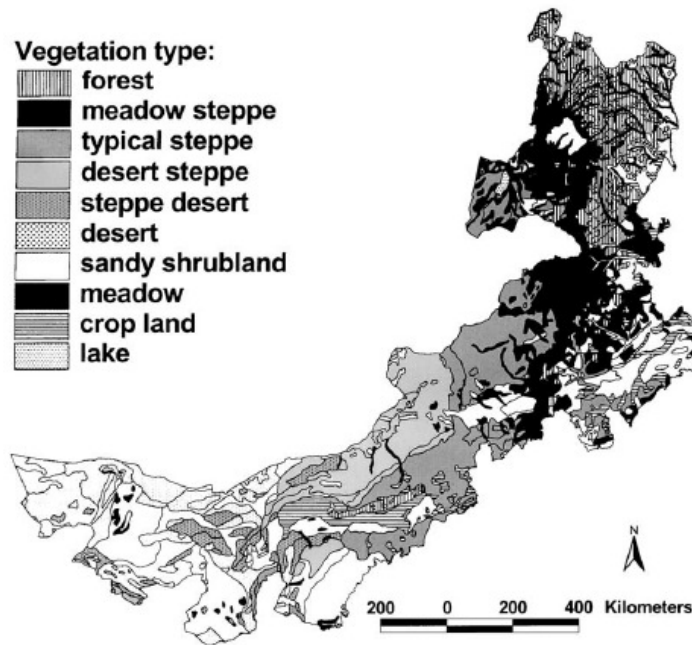


Figure 6: Vegetation map of Inner Mongolia (Yu et al., 2004)

The most prevalent communities of the typical steppe type found in the Xilin River Basin are *Stipa grandis*- and *Leymus chinensis*- communities. *Stipa grandis* P. Smirn is a bunchgrass belonging to the family of needlegrasses. *S. grandis* can be mainly found in dryer areas of the Xilin River Basin. *Leymus chinensis* (Trin.) Tsvetlev (syn. *Aneurolepidium chinense*) is a xeric rhizomatous grass dominating the vegetation in areas providing more plant available water, but usually the species co-exist in most areas. Next to the dominant grass species several other grasses can be found, but also some forbs and semi-shrubs.

A *L. chinensis*-community in the Xilin River Basin yielded on average 194 g DM m^{-2} (peak standing crop), ranging between 107 and 253 g DM m^{-2} over a 10-year period (Xiao et al., 1995). Peak standing crop of a *S. grandis*-community in the same study was on average 152 g DM m^{-2} , ranging between 93 and 206 g DM m^{-2} . The communities comprise of C3-grasses, except *Cleistogenes squarossa* which is the only C4-grass found in the Xilin River Basin (Tieszen and Song, 1990). In over-grazed areas of the Xilin River Basin especially the semi-shrub *Artemisia frigida*

and the forbs *Potentilla* spp., as well as primary shrubs like *Carragana microphylla*, emerge and grasses like *S. grandis* and *L. chinensis* decrease (Li, 1989; Christensen et al., 2003; Barger et al., 2004; Tong et al., 2004; Xie and Wittig, 2007). The soils in the study area are mostly Calcic Chernozems. The thickness of the Ah-horizon varies between 20 and 100 cm, depending on the topography (Zhao et al., 2007).

3. Objectives and Outline of the Thesis

The MAGIM sub-project 3 is the basis of this thesis and entitled as follows: “Impact of grazing management on yield performance, herbage quality and persistence of grassland ecosystems of Inner Mongolia”. The main objective of this sub-project is to provide a data base for scenario analysis, which may contribute to the development of sustainable management strategies for the Inner Mongolia grasslands. To achieve this objective the first approach is to study the formation process of degradation and the involved mechanisms.

3.1 Scientific background

Only few studies are available that have examined the degradation process in its formation. The majority of studies dealing with the degradation problem of Inner Mongolia grasslands are retrospective, examining grasslands of different degrees of already developed degradation in end-point evaluations. A commonly used method to investigate different states of degradation is the definition of grazing gradients in increasing distance from villages or watering points. Status of degradation and/or definition of the grazing intensity the grassland is subjected to are assessed by e.g. the proportion of biomass consumed by grazers (Wang, 2004), plant height (Wang et al., 2002), monitoring of existing data about livestock densities by interviewing officials and local farmers (Xie and Wittig, 2003, 2007) or plant biomass production and plant cover (Tong et al., 2004). Only a few studies were carried out under controlled conditions, like the grazing experiments described by Wang et al. (1999 a, b), Zhang et al. (2004) and Zhao et al. (2005).

The main result of the retrospective studies is that aboveground- and belowground biomass are much lower under moderate to heavy grazing intensities, whereas it is seldom defined what moderate or heavy grazing intensities are (Li, 1989; Wang and Ripley, 1997; Xie and Wittig, 2003, 2007; Wang, 2004; Yi et al., 2004).

Changes in species composition were judged as the most important indicators for the degree of degradation in typical steppe grasslands (Tong et al., 2004). Climax grassland communities are dominated by grasses, but when the grassland is subjected to high grazing intensity the palatable species (e.g. *S. grandis* and *L. chinensis*) are reduced and less valuable (e.g. *Artemisia frigida*) and unpalatable species (e.g. *Potentilla* spp. and *Carragana microphylla*) become dominant (Li, 1989; Wang and Ripley, 1997; Zhang, 1998; Wang et al., 2002; Barger et al., 2004; Zhao et al., 2005).

Declining productivity and changing species composition were used as diagnostic instruments to assess the degradation status of an already degraded grassland sward, but the actual degradation process was not yet directly documented, though the degradation process was simulated in a modelling approach (Christensen et al., 2003).

The assessment of the degradation status of a grassland area after degradation has become apparent does not allow counteracting this degradation, but restoration is then the only way to re-establish productive and diverse grassland swards. Management strategies that enable livestock farmers to subsist themselves and sustain the grasslands as a productive and ecologically sound environment are urgently needed and were demanded by several authors (Li and Vinczeffy, 1998; Tong et al., 2004; Yu et al., 2004; Nan, 2005). However, management strategies developed on the basis of scientific results are rare. Grazing studies (Wang et al., 1999a, b; Zhang et al. 2004; Zhao et al., 2005) provide suggestions for appropriate grazing intensities for the investigated grasslands, but alternative management systems were not proposed. Management strategies that would help to avoid grassland degradation were suggested by several authors (Li and Vinczeffy, 1998; Jiang et al., 2003; Yu et al., 2004; Yi et al., 2004; Tong et al., 2004), but commonly the proposed strategies were not tested.

3.2 Experiments

Cutting-frequency experiment

A cutting-frequency experiment, based on an orthogonal experimental design, was initiated in June 2004 that aimed at the description of short-term changes in a typical *Stipa grandis*/*Leymus chinensis* community subjected to different defoliation intensities, concentrating on the effects on the dominant species *S. grandis* and *L. chinensis*. Parameters of classical growth analysis (chapter 2) as well as herbage

quality parameters (chapter 3) were used to evaluate and assess short-term responses of the grassland sward and the dominant species to different defoliation intensities in the course of the vegetation periods of 2004 and 2005. Further details about the design and implementation of the cutting-frequency experiment are given in chapter 2 and 3.

Grazing experiment

The central experiment of sub-project 3 within the MAGIM project is a grazing experiment that will provide detailed information about the degradation process when the grassland is subjected to different grazing intensities. This experiment commenced in June 2005 and is carried out in close cooperation with the MAGIM sub-project 4, which is conducted by the Institute of Animal Nutrition and Physiology, University Kiel (Glindemann, 2007; Wang, 2007). Six grazing intensities (1.5, 3.0, 4.5, 6.0, 7.5 and 9.0 sheep ha⁻¹) and an ungrazed control are examined in 2 replications. Two management strategies are compared: one is the traditional management system that permanently uses grassland areas either only for grazing or only for hay making. Usually areas in the vicinity of farms and villages are grazed and more distant areas are used for hay making only. The alternative tested in this experiment is the so called mixed system, which means that the utilization of grassland areas is changed between grazing and hay making every year. The advantages and disadvantages of the two compared management strategies can be summarised as follows:

Traditional system:

- soil nutrients are depleted in haymaking areas by constant biomass removal
- the grazing pressure is high in grazing areas, especially on palatable species, so that
 - plant reserves can not be replenished
- plants are limited in seed production

Mixed System:

- in haymaking years plants are released from grazing stress and can seed and replenish their reserves
- in grazing years nutrients are recycled to the system via animal faeces

but,

- the infrastructure needed for this system, like fences in remote areas from where sheep can not return to the farm every evening, is yet not available.

The structure of the grazing experiment will be not further described as it is not the main subject of this thesis. The grazing experiment is a long-term experiment and has to be interpreted as such in the next years. Nevertheless, the data obtained from the grazing experiment in 2005 could be used to address an additional question. In Chapter 4 a comparison of in vivo and in vitro obtained digestibility of organic matter is presented. The in vivo digestibility was determined by the Institute of Animal Nutrition and Physiology (Glindemann, 2007; Wang, 2007) for all grazing intensities in the mixed system and is compared to the in vitro digestibility of the corresponding herbage samples. The aim of this comparison is to test to what extent the quality of herbage ingested corresponds to the quality of herbage on offer across the different grazing intensities and whether those differences can be used as an index for the selectivity of grazing sheep.

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Chapter 2

**Short-term responses to defoliation stress of a semi-arid grass-
land sward in Inner Mongolia, China.**

1. Plant growth analysis

Abstract

Grassland degradation due to overgrazing and the economical and ecological consequences are the major problems that have to be faced in the semi-arid grasslands of Inner Mongolia, P.R. China. For the development of sustainable management systems, a basal knowledge of the degradation process is required. Much information is available regarding the long-term effects of grazing stress in Inner Mongolia grasslands, but information about the short-term responses is rare. A cutting-frequency experiment was carried out in the typical steppe grassland of the Xilin River Basin, Inner Mongolia. The natural grassland was subjected to low, moderate and high defoliation stress and several plant related parameters were examined over the vegetation periods of 2004 and 2005, in order to identify the short-term responses to defoliation on plant and community level.

The cumulative dry matter yield increased with increasing defoliation frequency from 204 to 277 g DM m⁻² in 2004 and from 87 to 158 g DM m⁻² in 2005. The low biomass productivity in 2005 is based on the low precipitation rate in this year. The positive effect of defoliation on productivity was also confirmed by the nitrogen yield that increased from 2.9 g N m⁻² to 6 g N m⁻² in the more frequently defoliated treatments in 2004 and from 1.2 g N m⁻² to 2.8 g N m⁻² in 2005. Specific leaf area was determined for the dominant species *S. grandis* and *L. chinensis* in 2004 and increased from about 100 to 160 cm² g leaf DM in *S. grandis* and from 40 to 140 cm² g leaf DM in *L. chinensis* after frequent defoliation. The leaf area index of the two dominant species was low, but significantly influenced by defoliation, nonetheless the leaf area index never exceeding 0.6 in *S. grandis* and 0.4 in *L. chinensis*. The root mass ranged between 815 and 1006 g OM m⁻² (0-15 cm) and was not significantly affected by defoliation in both years. This is also true for the root carbohydrate reserves that ranged on a low level between 1.3 and 1.6% of root OM. Species composition and tiller density did as well not indicate significant short-term effects of frequent defoliation.

It can be concluded that in the short-term defoliation stress stimulates productivity and N uptake, whereas significantly negative effects were not observed. This implies that the steppe grassland is resistant to short-term defoliation stress and that degradation processes are the result of mid- and/or long-term dynamics of defoliation or grazing stress, respectively. Furthermore the key role of annual precipitation in this grassland ecosystem became apparent.

1. Introduction

In Inner Mongolia, P.R. China, about 70% of the country's total area is native grassland (FAO, 2001). One third (Sneath, 1998; Zhou et al., 2002) of this grassland has been degraded during the last century, mainly as a consequence of overgrazing as the number of animals was multiplied tenfold in Inner Mongolia in the last 60 years (Jiang and Meurer, 2001). Overgrazing has been identified as the main reason for the degradation of the steppe grasslands (Wang and Ripley, 1997; Liu et al., 1998; Verburg and Van Keulen, 1999).

Decreasing grassland productivity and ecological threats like wind and water erosion are the main attributes of grassland degradation. Management strategies that prevent the grazing areas from degradation and provide sustainable production systems that still enable the farmers to make their livings are urgently needed (Zhou et al., 2002, Tong et al., 2004). More research activity has been demanded by several authors to understand the different abiotic and biotic factors influencing the grassland ecosystem and therewith the degradation process, (e.g. Wang et al., 2002, Tong et al., 2004). Various ecological and phytological studies have been conducted in Inner Mongolia grassland steppes examining degradation in a retrospective way (e.g. Li, 1989; Xiao et al., 1996; Wang and Ripley, 1997; Wang et al., 2002; Yi et al., 2004; Bai et al., 2004). Only a few studies have investigated the degradation process in its formation under grazing stress to provide information that can be used to support management decisions (Wang et al., 1999; Zhang et al., 2004; Zhao et al., 2005). Christensen et al. (2003) have tested the applicability of the Savanna ecosystem model, originally developed for East-African savannas (Coughenour, 1993), to the situation in Inner Mongolia grasslands. The Savanna ecosystem model simulates ecosystem processes including vegetation and livestock production. Modelling was carried out on data from studies conducted in the Xilin River Basin, one of the most representative geographic areas in Inner Mongolia (Tong et al., 2004). They predict a steep decline in above and below ground biomass, as well as a shift from grass to shrub vegetation types, when the grassland is subjected to heavy grazing intensities (> 3 sheep ha^{-1} year $^{-1}$). Especially when heavy grazing coincides with low precipitation, dramatic changes in the steppe vegetation were expected, what was confirmed by the results of Yu et al. (2004), who analysed the relationship between rainfall and aboveground productivity in Inner Mongolia grasslands. Although these studies provide valuable informa-

tion about the grassland degradation process, they do not regard to short-term effects of grazing stress and their role in the formation process of degradation.

However, the development of management systems that prevent the grassland from degradation, require a broad knowledge about the degradation process as a whole. It has to be clarified what the major driving forces are, how they affect the grassland ecosystem and whether or not a threshold can be defined that indicate imminent degradation in an early, reversible state. To answer such questions experiments under controlled conditions are needed to separate the factors influencing the grassland ecosystem from each other and to assess their involvement in the degradation process.

The present study is a first approach in assessing the degradation process in its formation and development. The objective is to identify short-term effects of defoliation stress in a grassland sward in the typical steppe area of the Xilin River Basin, Inner Mongolia. Plant related parameters, known from the classical plant growth analysis (Hunt, 1978), are used to characterise short-term responses of the grassland sward to defoliation stress on plant and community level.

The results of a cutting-frequency experiment are presented, which was carried out in 2004 and 2005, comprising 3 different cutting frequencies to constitute low, moderate and high defoliation stress. The parameters dry matter- and nitrogen yield, root mass and root carbohydrate reserves are analysed mainly on community level, whereas the specific leaf area, leaf area index and leaf weight ratio are examined for the dominant species *Stipa grandis* and *Leymus chinensis*, which account together for approx. two thirds of the grassland sward. The species composition is also analysed, as it is the most frequently used parameter in the above cited studies to describe changes in grassland communities due to degradation. Additionally, the tiller density of *S. grandis* and *L. chinensis* is determined, as the two dominant species were classified as “decreaser”-species which are highly sensitive to grazing stress (Li, 1989; Wang and Ripley, 1997). However, short-term responses are not expected for species composition and tiller density, as changes in species composition usually take more than two experimental years (Jones et al., 1995).

2. Material and Methods

2.1 Study site

The presented study was carried out in the framework of the sino-german MAGIM-project (Matter fluxes of grasslands in Inner Mongolia as influenced by stocking rate). The cutting-frequency experiment was conducted near the Inner Mongolia Ecosystem Research Station (IMGERS) operated by the Institute of Botany, Chinese Academy of Sciences, Beijing. IMGERS is located in the Xilin River Basin, Inner Mongolia Autonomous Region, P.R. China (116°42' E, 43°38' N) at an altitude of approximately 1200 m. The climate is semi-arid, characterised by significant seasonal and inter-annual variability. The mean annual (1982-2003) temperature is 0.7°C and the mean annual precipitation 346 mm, of which 85% are occurring from May through September (figure 1). The vegetation period is about 150 days long, with only 100 to 135 frost-free days.

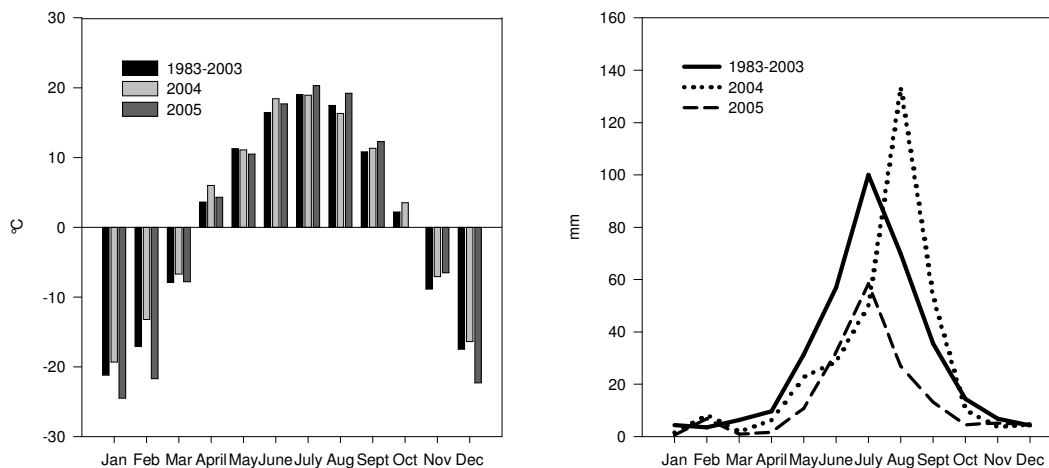


Figure 1: Mean temperature and mean precipitation per month averaged over 20 years (1983-2003) and for 2004 and 2005 measured at IMGERS, Inner Mongolia, China (yearly mean temperature 1983-2003, 2004, 2005: 0.7°C, 1.9°C, 0.1°C; yearly mean precipitation 1983-2003, 2004, 2005: 343 mm, 325 mm, 166 mm)

For the cutting-frequency experiment a 0.7 ha sized area was chosen, located on a uniform eastern exposure on a 4 % slope. The area was moderately grazed by sheep in the previous years and fenced from grazing by large herbivores in June 2004. The area can be classified as typical steppe (Yu et al., 2004). The vegetation is dominated by the perennial bunchgrass *Stipa grandis* P. Smirn. and the rhizoma-

tous *Leymus chinensis* (Trin.) Tsvelev, both grasses belong to the C3 photosynthesis type. This vegetation type can be considered as representative for large parts of the Xilin River Basin (Bai et al., 2004). Soils of the experimental area were classified as Calcic Chernozems (IUSS Working Group WRB, 2006) derived from aeolian sediments. Topsoils (0-15 cm) exhibited a loam to sandy loam texture, an organic carbon content of 21 mg g⁻¹ and a C/N-ratio of 10.

2.2 Experimental design and field measurements

Three treatments were tested in a randomised block-design with 4 replications. The treatments differed in cutting frequency: treatment I (T I) resembled the local practice of haymaking, which is cutting once a year between end of August and early September. The hay cut was performed by a bar mower used by local farmers, cutting height was approx. 8 cm above soil surface. Treatment II (T II) was cut every 6 weeks representing moderate defoliation intensity and treatment III (T III) was cut every 3 weeks representing high defoliation intensity. Cutting was carried out with a conventional lawn mower to 2.5 cm stubble height, to simulate intensive grazing by sheep. Each replication plot measured about 200 m² (~ 12 x 16 m).

The herbage sampling intervals partially differed from the cutting intervals. In 2004 T I and T II were sampled every 2 weeks, but T I was cut only once in September and T II was cut every 6 weeks, respectively. In T III cutting dates correspond to sampling dates, as T III was sampled every 3 weeks, right before each cut. In 2005 the herbage sampling interval of T I and T II was reduced to 6 weeks (adjusted to the cutting frequency of T II), T III was furthermore sampled every 3 weeks right before each cut. All herbage sampling and cutting dates are summarized in table 1. At the sampling dates herbage was clipped to 1cm stubble height in 4 randomly distributed 0.25-m² sampling quadrates within each plot. The clipping height of 1 cm represents the theoretically available biomass to sheep. The clipped herbage of the 4 quadrates was pooled and transferred to the laboratory in a cooling box. The pooled herbage sample was separated into 4 fractions: the dominant species *S. grandis* and *L. chinensis*, all remaining species combined and the standing necrotic material. Litter (necrotic material spread on the ground) was removed before clipping by gentle combing with a wool comb and not included into the herbage sample. The samples were dried at 60°C for 24 h in a forced-air drying-oven and weighted to derive the dry matter (DM)-yield of each fraction. The total DM-yield of the sward was determined by adding up the DM-yields of the 4 fractions.

Table 1: Herbage sampling and cutting dates 2004 and 2005

sampling	2004			2005		
	T I	T II	T III	T I	T II	T III
1	5 June	5 June	5 June	10 June	10 June	10 June
2	19 June	19 June	19 June			
3	3 July	3 July	3 July			30 June
4	22 July	22 July	27 July	22 July	22 July	22 July
5	4 Aug	4 Aug				
6	18 Aug	18 Aug	18 Aug			12 Aug
7	2 Sept	2 Sept	9 Sept	6 Sept	6 Sept	6 Sept
8	17 Sept	17 Sept				

(□ herbage sampling; ■ herbage sampling and cutting; ▣ species composition)

The cumulative DM-yield (cDMY) was calculated for T II and T III by summing up the total DM-yields of the sampling dates that were followed by cutting. The same was done for the DM-yields of each fraction. For T I the DM-yield of the 7th herbage sampling (out of 8 samplings) was considered as cDMY, because it was the maximum DM-yield in T I in both years.

The species composition was determined once a year in all treatments prior to the first cut in T II and T III in early July. Not only the 4 above mentioned fractions were separated, but the all species and their dry weight recorded.

The tiller density was determined for *S. grandis* and *L. chinensis* at each sampling date. A 10 x 10 cm frame was allocated at 3 random points inside each of the 4 sampling quadrates and the living tillers of *S. grandis* and *L. chinensis* were counted.

Leaf area measurements were conducted for *S. grandis* and *L. chinensis*. For this, separate samples of the two species were taken next to the sampling quadrates, wrapped into a wet towel and cooled directly in cooling boxes to prevent the leaves from convolving. In the laboratory the individual grass plants of *S. grandis* and *L. chinensis* were separated into leaf and stem, until 5 g of leaf fresh matter (FM) were available for the leaf area measurement. The leaf area was measured using a portable area meter (LI-3000A) connected to a transparent belt conveyer (LI-3050A, LI-COR Nebraska, USA). The leaves used for leaf-area measurement, and their corresponding stems were dried (60°C, 24 h) and weighted afterwards to calculate the specific leaf area (SLA), the leaf area index (LAI) and the leaf weight ratio

(LWR). The calculations for *S. grandis* took into account its needlegrass morphology and therefore doubled the measured leaf area for the calculation of SLA and LAI. In 2005 leaf area measurements were carried out only in T I.

After the last herbage sampling in mid September, root samples were taken with a cylindrical corer (15 cm depth, 10 cm diameter). On each plot 10 samples were taken randomly and soil was washed out right after sampling. Finally, root samples were drained using a conventional spin-drier and immediately frozen at -20°C. The samples were transported to Germany and meanwhile protected from thawing by using an insulated bag. Subsequently the samples were freeze-dried (Benchtop Series, VirTis, Gardiner, NY, USA) and weighted.

2.3 Laboratory measurements

The dried herbage and freeze-dried root samples were ground with a cyclotec mill (Tecator, Germany) to pass a 1 mm sieve. All samples were scanned with a NIR-Systems 5000 monochromator (Perstrop Analytical Inc., Silver Spring, MD, USA) with 2 replications over a wavelength range from 1100 to 2500 nm in 2 nm intervals. The software NIRS 2 by Infrasoft International® (ISI, Port Mathilda, PA, USA) was used for scanning, mathematical processing, calibration and statistical analysis of the spectra data. The laboratory analyses were carried out on calibration and validation sub-sets of herbage and root samples, which were chosen by the software NIRS 2.

The N-content of herbage sub-set samples and both C- and N-content of root sub-set samples were measured using a C/N-Analyzer (vario Max CN, Elementar Analysensysteme, Hanau, Germany) which is based upon the DUMAS combustion method.

The total non-structural carbohydrates (TNC) in roots were measured by high pressure anion exchange chromatography with pulsed amperometric detection (HPAEC-PAD) modified after Chatterton et al. (1989) and Shiomi et al. (1991). Prior to analysis the dried root samples were ground again with a ball mill to a particle size of 10 µm. To extract the TNC, 40 mg of the lyophilised and ground material were agitated with 2 ml deionised cold water for 60 minutes. After centrifugation (3600 rpm) the supernatant was purified with 67 µl Chloroform. The supernatant was separated from the pellet. The pellet was dried in a vacuum-dryer for 1 h at 55°C and stored at -20°C for starch analysis. The supernatant was diluted 1:5 in deionised water and 2 ml of the dilution were filtrated through a C18-cartridge

(Strata C18-E, Phenomenex Inc., Torrance, CA, USA). The filtrate was hydrolysed in 2N HCl for 2 h at 80°C to split fructans into glucose and fructose, but naturally also sucrose was split up. For starch analysis the frozen pellet was defrosted at room-temperature for 30 minutes. 2 ml enzyme solution, containing amyloglucosidase from *Aspergillus niger* (14U/mg, Roche Diagnostics) and Sodium-Acetate-Buffer (pH: 4.8) at a ratio of 1:13.6 were added and vortexed intensively for 20 seconds. The mixture was incubated over night (~ 14 h) at 37°C and afterwards extracted in the same way as described above. Because it was not always possible to measure the carbohydrates right after extraction, the extracts were stored at -20°C until analysis.

To quantify the carbohydrates in the extracts, glucose and fructose were separated on an Ion Chromatography system (DX-300, Dionex Corp., Sunnyvale, CA, USA) using a CarboPac PA 100 column (4 x 250 mm). The carbohydrates were eluted with NaOH (200 mmol l⁻¹) in deionised H₂O, with a NaOH gradient that increased from 28% at 0 minutes to 35% at 8 minutes and further to 50% at 9 minutes. To rinse the column, a further increase to 80% at 11 minutes was included, from which the gradient returned to 28% NaOH until the end of the program at 18.5 minutes. Flow rate through the system was 1.0 ml min⁻¹. A standard solution was prepared with equal proportions of chemically pure glucose, fructose and sucrose, with concentrations ranging from 10 mg l⁻¹ to 150 mg l⁻¹.

2.4 Statistical analysis

Data were subjected to analysis of variance separately for the two experimental years using the mixed procedure of the software package SAS[®]9 (SAS Institute Inc., Cary, NC, USA). Experimental factors were 'replication' and 'treatment', as well as 'sampling date' (mutual sampling dates 1, 4 and 7) for tiller density, SLA, LAI and LWR, which was considered as repeated measurement. Means with significant *F*-value were tested with Student's *t*-test and probabilities were corrected by the Bonferroni-Holm test (Horn and Vollandt, 1995). The level of significance of *P*<0.05 was chosen.

3. Results

3.1 Above- and belowground productivity

The cDMY increased significantly with increasing cutting frequency in both years (table 2), even though the cDMY was considerably reduced in 2005 in all treatments. Compared to 2004 the cDMY was reduced by 135% and 130% in T I and T II respectively, whereas in T III the cDMY was reduced by only 75%. The cutting frequency had no clear significant influence on the cDMY of all 4 herbage fractions in 2004 (table 2). In 2005 however, the cDMY of the *L. chinensis* and remaining species fractions increased significantly in T II and T III, whereas the necrotic material fraction significantly decreased. No significant effect of cutting treatment was found for the cDMY of the *S. grandis* fraction in 2005.

With increasing cutting frequency also the cumulative N-yield (cNY) was significantly increased in both experimental years (table 2). In 2004 the cNY increased significantly by 69% and 107% in T II and T III compared to T I. Although cNY was generally lower in 2005, a significant increase by 58% and 133% in T II and T III was observed. The mean N-content of herbage significantly increased in T II and T III in both years (table 2), but in 2005 the mean N-content was generally lower in all treatments compared to 2004.

Table 2: Cumulative DM-yield (cDMY) and N-yield (cNY), N-content of herbage in 2004 and 2005

	2004				2005			
	T I	T II	T III	SE	T I	T II	T III	SE
cDMY (g m⁻²)								
total	204.2 ^b	272.3 ^a	277.3 ^a	9.5	86.5 ^c	112.8 ^b	158.1 ^a	3.0
<i>Stipa grandis</i>	65.0 ^b	95.7 ^a	85.6 ^{ab}	6.1	34.7	33.4	40.6	3.7
<i>Leymus chinensis</i>	57.6	64.3	74.3	3.7	18.5 ^b	34.0 ^a	41.8 ^a	3.3
remaining species	56.4	83.6	93.0	9.2	24.3 ^c	44.4 ^b	75.8 ^a	2.5
necrotic material	25.2	28.6	24.4	5.1	8.9 ^a	0.7 ^b	-	1.1
cNY (g m⁻²)								
total	2.9 ^c	4.9 ^b	6.0 ^a	0.2	1.2 ^c	1.9 ^b	2.8 ^a	0.1
N-content (% DM)								
total	1.49 ^c	1.95 ^b	2.10 ^a	0.05	1.39 ^c	1.74 ^b	1.87 ^a	0.05

Values with different superscripts ^{a,b,c} are significantly different ($P < 0.05$) between treatments within years.

The root parameters (table 3) are expressed on organic matter (OM) basis to eliminate influences of high ash contents (Christiansen and Svejcar, 1988). The value "root mass" involves live and dead root material, as well as other fine particles of belowground biomass (e.g. not yet decomposed litter) from 0-15 cm. Differences in root mass between the treatments were not significant in 2004, but in 2005 a tendency ($P<0.1$) of decreasing root mass in T II and T III was observed. No significant differences were observed for the C- and N-content of root mass between the three treatments. The C-content was around 52 % of OM for all treatments in both years. The N-content did not differ significantly between treatments in 2004 and 2005, but was generally slightly higher in 2005 compared to 2004 in all treatments. Consequently the C/N-ratio was lower in 2005 compared to 2004. The TNC-content, ranging between 1.3 and 1.6 % of OM, was not significantly different between treatments in both years. In consequence of reduced root mass in T II and T III, the TNC-pool tended ($P<0.1$) to be reduced in these treatments in 2005.

Table 3: Root mass, C- and N-content and total non-structural carbohydrate (TNC)-content and TNC-pool in root OM in 2004 and 2005

	2004				2005			
	T I	T II	T III	SE	T I	T II	T III	SE
root mass (g OM m ⁻²)*	944	1005	838	163	1006 ^A	815 ^B	824 ^B	45
C-content (% OM)	52.0	51.7	51.9	0.17	52.3	52.3	52.3	0.31
N-content (% OM)	1.54	1.53	1.61	0.04	1.80	1.84	1.83	0.09
TNC content (% OM)	1.61	1.51	1.31	0.12	1.56	1.30	1.35	0.12
TNC pool (g m ⁻²)	15.7	15.0	11.3	3.16	15.8 ^A	10.7 ^B	11.1 ^B	1.21

* root mass from 0-15 cm

Values with different superscripts ^{a,b,c} are significantly different ($P<0.05$), values with different superscripts ^{A,B,C} tend to be different ($P<0.1$) between treatments within years.

3.2 Specific leaf area, leaf area index and leaf weight ratio

The development of the parameters over the growing season is presented in figure 2a-2f and the corresponding analysis of variance, regarding the experimental factors 'treatment' (T), 'sampling date' (S) and the interaction 'T x S', is given in table 4. The statistical analysis revealed that the interaction 'T x S' was highly significant ($P<0.01$) for SLA, LAI and LWR for both species in both experimental years, except for the LWR of *S. grandis* in 2005, where the interaction 'T x S' was only in tendency significant ($P<0.1$).

The SLA of *S. grandis* was constant in T I over the growing season of 2004, ranging around $100 \text{ cm}^2 \text{ g}^{-1}$ leaf DM (figure 2a). In T II and T III the SLA increased after the first cut to approx. $120 \text{ cm}^2 \text{ g}^{-1}$ leaf DM. In T II the SLA kept this level until the end of growing season, whereas in T III there was a further increase with the next cut and a decrease with the last cut. *L. chinensis* showed a steady increase in SLA over the growing season of 2004 in all treatments (figure 2b), but the increases in T II and T III exceeded the increase in T I. All treatments started with an SLA of $36 \text{ cm}^2 \text{ g}^{-1}$ leaf DM, which increased during the growing season to $92 \text{ cm}^2 \text{ g}^{-1}$ leaf DM in T I and 118 and $134 \text{ cm}^2 \text{ g}^{-1}$ leaf DM in T II and T III, respectively. In 2005 SLA was measured only in T I and almost no changes over the growing period were observed, neither in *S. grandis* nor in *L. chinensis*. Besides less dynamic development in 2005, the SLA of both species was much lower in 2005 compared to 2004. The LAI of *S. grandis* increased in T I from 0.2 to 0.6 (figure 2c) in the growing season of 2004. In T II the LAI decreased significantly after cutting, but increased again until the next cut. In T III the LAI indicated that the *S. grandis* plants had no time to recover from the cuts, because the LAI decreased steadily with each cut. In 2005 the LAI of *S. grandis* was reduced to 0.3 in T I as the highest value in mid July. In general *L. chinensis* had a lower LAI than *S. grandis* (figure 2d) between 0.1 and 0.4 in both years, but the development of the LAI after cutting was similar to the development of LAI in *S. grandis*. The available data for 2005 in T I displayed a vastly reduced LAI (< 0.1) compared to 2004.

The LWR of both species ranged between 0.60 and 0.85 over the vegetation period in 2004 (figure 2e and 2f). In *S. grandis* the LWR decreased after day 180 in all treatments. In T I the LWR increased again from day 220 on until the end of the season. In T II and T III the effect of cutting was demonstrated by a decrease in LWR after the cut and an increase until the next cut was carried out. The variation in LWR of *S. grandis* was high, thus no difference between the treatments was statistically significant. The LWR of *L. chinensis* was approx. 0.80 until day 180 followed by a decrease in all treatments. This decrease was more pronounced after the first cut in T II and T III than the decrease in T I. Afterwards the LWR of T II and T III were fairly similar, although the cutting frequency was different.

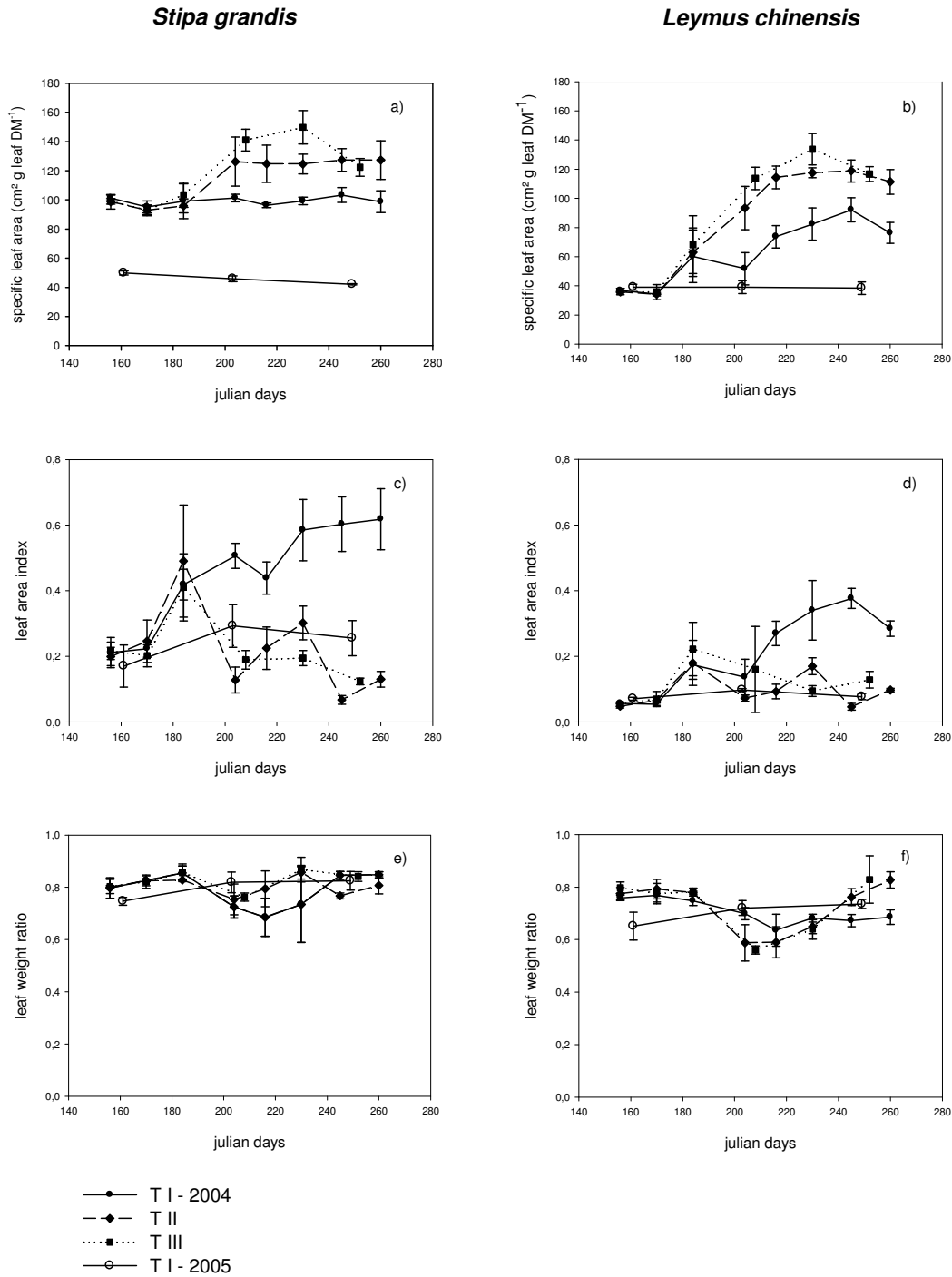


Figure 2: Specific leaf area (SLA), leaf area index (LAI) and leaf weight ratio (LWR) of *Stipa grandis* and *Leymus chinensis* in 2004 (closed symbols) and 2005 (open symbols) (Error bars indicating SD; Cutting dates (not indicated) in 2004: T I = day 260; T II = day 184, day 230, day 260; T III = day 184, day 203, day 230, day 245. Cutting dates in 2005: T I = day 249; T II = day 203, day 249; T III = day 181; day 203; day 224; day 249).

Table 4: Analysis of variance for specific leaf area (SLA), leaf area index (LAI) and leaf weight ratio (LWR) in 2004/2005 on the mutual sampling dates 1 (day 156/161), 4 (day 204/203) and 7 (day 245/249).

	<i>Stipa grandis</i>		<i>Leymus chinensis</i>	
	2004	2005	2004	2005
Specific leaf area				
treatment (T)	***	-	***	-
sampling date (S)	***	***	***	ns
T x S	***	-	***	-
Leaf area index				
treatment (T)	***	-	***	-
sampling date (S)	***	***	***	***
T x S	***	-	***	-
Leaf weight ratio				
treatment (T)	ns	-	ns	-
sampling date (S)	***	**	***	ns
T x S	*	-	***	-

(ns = non significant; * = $P < 0.1$; ** = $P < 0.05$; *** = $P < 0.01$);

Probabilities valid for species within years. Differences between sampling dates 1, 4, 7 were tested.

3.3 Species composition and tiller density

The species composition obtained in July did not differ significantly between the three treatments, in both experimental years (figure 3). This indicates that the species composition of the experimental area was homogeneous when the experiment started in 2004.

The tiller density of *S. grandis* was generally higher than the tiller density of *L. chinensis* in consequence of their different growth habits (table 5). Both species indicated a reduced tiller density in 2005 compared to 2004. No significant differences between cutting frequencies were observed in both years, neither for *S. grandis* nor for *L. chinensis*. Between the sampling dates however, significant differences were observed for both species.

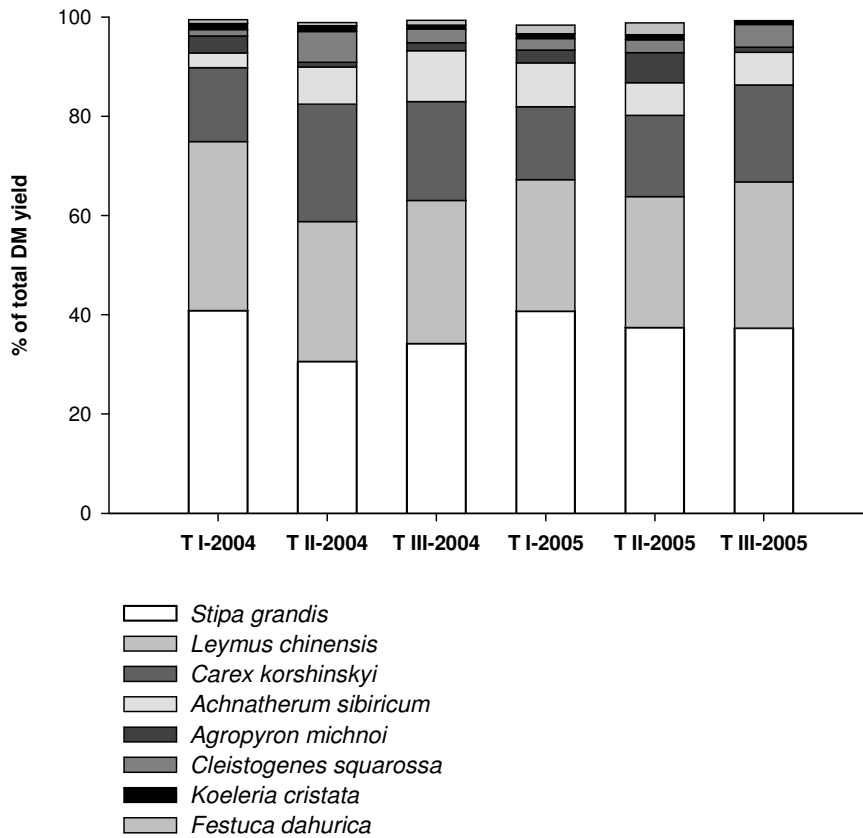


Figure 3: Species composition in July 2004 and 2005 (% of total DM yield; only species $\geq 1\%$ of total DM yield)

Table 5: Mean tiller density 2004 and 2005 (live tillers/m²)

	<i>Stipa grandis</i>		<i>Leymus chinensis</i>	
	2004	2005	2004	2005
sampling 1 [*]	2335 ^a	846 ^a	879 ^a	260 ^a
sampling 4	1012 ^b	947 ^a	334 ^b	257 ^a
sampling 7	870 ^b	553 ^b	230 ^b	134 ^b
SE	199.5	115.7	53.2	18.3

Means with different superscripts ^{a,b,c} are significantly different ($P < 0.05$) within species and year.

^{*} for details see table 1.

4. Discussion

Effects of grazing on grasses or grass communities need to be examined in grazing trials. Grazing trials however, are very complex, expensive and difficult to manage, therefore a lot of studies analysing plant physiological processes resulting from grazing, have simulated grazing by defoliation through cutting (Brougham, 1956; Archer and Tieszen, 1983; Ruess, 1988; Hodgkinson et al., 1989; Turner et al., 1993; Leriche et al., 2003). Although cutting is inadequate to simulate a grazing system as a whole (Hart and Norton, 1988), cutting experiments provide the chance to study the effects of defoliation on grass physiology and morphology in detail with the knowledge about defoliation date and defoliation intensity. To get an overview of the short-term responses of the examined grassland sward to defoliation, this cutting-frequency experiment provides a reasonable basis.

4.1 Above- and belowground productivity

In agricultural terminology productivity of the aboveground herbaceous material is commonly referred to as DM-yield (DMY) (t Mannetje, 2000) or, when DM-increment was measured, the cumulative DM-yield (cDMY). The cDMY of T I was 204 and 86 g m⁻² in 2004 and 2005, respectively (table 2). These results fit well into the range of peak standing crop obtained by Xiao et al. (1995), who analysed the peak standing crop of a *S. grandis* and a *L. chinensis* dominated site (both fenced from grazing) over a 9-year period. The peak standing crop of the *S. grandis* site was on average 152 g m⁻² (93-206 g m⁻²) and of the *L. chinensis* site 194 g m⁻² (107-253 g m⁻²). Other studies conducted in the Xilin River Basin (Li, 1989; Bai et al., 2004) describe similar levels of biomass production for ungrazed or lightly grazed sites.

The frequently defoliated treatments (T II and T III) showed significantly increased cDMY in both experimental years, even though the production level differed markedly between the years. Increasing cDMY due to defoliation was not expected, as intensive defoliation has been always reported to have a negative effect on biomass productivity in the grassland of the Xilin River Basin (Li, 1989; Wang, 1992; Wang and Ripley, 1997; Christensen et al., 2003). Barger et al. (2004) report especially a reduction in perennial grasses, what was confirmed by Xie and Wittig (2003) for grassland in Ningxia, which is a neighbouring province of Inner Mongolia with similar environmental conditions. However, all these studies refer to long-term ex-

periments or examine grassland communities from a retrospective point of view, but do not account for short-term responses of biomass productivity to defoliation. Similarly, most of the studies examining defoliation effects on semi-arid grasslands report decreasing biomass production when defoliation intensity increased (Milchunas and Lauenroth, 1993; Fynn and O'Connor, 2000; Ferraro and Oesterheld, 2002). Nevertheless, some studies can be found reporting that defoliation stimulated aboveground biomass production and a compensation or even overcompensation in biomass production was observed (Georgiadis et al., 1989; Frank and McNaughton, 1993; Loeser et al., 2004). Several negative and positive effects of defoliation on plant growth have been identified (Noy-Meir, 1993). As negative effects the reduction in photosynthetic leaf area, removal of apical meristems and loss of stored nutrients have to be mentioned. Positive effects are increasing light intensity and improved water and nutrient supply to remaining leaves, reduced senescence of new leaves and increased allocation of stored and current photosynthates to new leaf area, and finally the activation of dormant meristems. The effect of defoliation on a grassland sward can not be generalised, not even for specific grassland types like steppes. Whether the effect of defoliation is negative or positive depends on the particular environmental conditions and on the defoliation management employed. Positive effects of frequent defoliation on productivity have especially been observed for low productive sites with a long history of moderate grazing (Milchunas and Lauenroth, 1993) and for plants suffering from drought stress (McNaughton, 1983; Coughenour et al., 1990). The positive response of drought stressed plants to defoliation was attributed to the removal of plant biomass and the subsequently reduced leaf area that results in reduced transpiration and therefore increased soil-water conservation and soil-water potential of the plant (Archer and Detling, 1986). Both suggested explanations apply to the situation in the semi-arid grasslands of the Xilin River Basin.

There are several approaches that can be consulted to explain the increase in cDMY after frequent defoliation, but from the obtained results it is not possible to exactly determine the responsible processes. The results indicate short-term effects that can not account for possible long-term effects, but the results demonstrate that in the short-term the examined grassland sward is resistant to defoliation-induced decreases in aboveground biomass productivity.

The increase in cDMY in T II and T III resulted from increasing cDMY of the dominant species, as well as of the remaining species fraction (table 2). In 2005 however, the increase in the remaining species fraction was more pronounced than in

2004 and increased significantly due to frequent defoliation. The increase in cDMY thus resulted to a great extent from the increase in cDMY of other species than *S. grandis* and *L. chinensis*. The remaining species fraction was not further analysed, but from observation it can be reported that prostrate species with planophile morphology like *Carex korshinskyi* and *Cleistogenes squarrosa* particularly increased after defoliation, what can be attributed to enhanced light, space and water availability after defoliation. Nevertheless, the overcompensation in T II and T III is not only a result of complementary effects through the advancement of growth conditions of certain species due to defoliation. Overcompensation due to defoliation was also demonstrated for *S. grandis* and *L. chinensis* in T II and T III in both years (table 2).

Stipa spp. are the predominant species in desert steppes (Xie and Wittig, 2003), while *L. chinensis* becomes predominant in regions that are more humid than the Xilin River Basin (Wang and Gao, 2003). It was therefore expected that the cDMY of the *L. chinensis* fraction would decrease more due to the drought in 2005 than the cDMY of the other fractions. This happened in T I, but not in T II and T III where the cDMY of the *L. chinensis* fraction increased like the fraction of the remaining species. This overcompensation of *L. chinensis* after frequent defoliation might be explained by the fact that in autumn of 2004 the precipitation rate was above-average and that the plants benefit from the wet autumn 2004 in spring 2005. When the drought became apparent in summer 2005 the frequently defoliated treatments benefited from defoliation, as the water loss due to transpiration was reduced by reducing the leaf area.

The considerable decrease in cDMY in 2005 compared to 2004 has to be discussed against the difference in precipitation rate between both years. Several studies point out the strong impact of precipitation on semi-arid grasslands (Noy-Meir, 1973; Le Houérou et al., 1988; Lauenroth and Sala, 1992; Xiao et al., 1995; Fynn and O'Connor, 2000; O'Connor et al., 2001; Knapp and Smith, 2001; Knapp et al., 2002; Christensen et al., 2003, Yu et al., 2004). Especially the variability in precipitation, both inter-annual and intra-annual, is a major influence on productivity in grasslands (Knapp and Smith, 2001). For Inner Mongolia grasslands Xiao et al. (1995) and Bai et al. (2004) explained approx. 40% of the variability in biomass production by variation in seasonal precipitation. This corresponds to results from the North American shortgrass steppe, where 39 to 45% of the variability in production was attributed to the relation between precipitation and biomass production (Lauenroth and Sala, 1992).

Rain-use-efficiency (RUE = biomass production per mm rainfall, $\text{g DM m}^{-2} \text{mm}^{-1}$) is a possibility to evaluate and compare the efficiency of precipitation use for biomass production on a mean annual or mean seasonal basis (Le Hou rou, 1984). For T I and T II the RUE was similar in both experimental years (table 6), evidencing that the differences in cDMY between years were mainly caused by the variability in precipitation rate. In T III however, the increase in cDMY in 2005 resulted in a, by approx. 20%, increased RUE. Mean RUE on a yearly basis, obtained at a similar, but not defoliated site was $0.57 \text{ g m}^{-2} \text{mm}^{-1}$ (Xiao et al., 1995) and $0.55 \text{ g m}^{-2} \text{mm}^{-1}$ (Yu et al., 2004) in model simulation, respectively. Our results indicate a similar RUE in T I, but as the cDMY increased significantly in T II and T III, also the RUE increased in these treatments.

Table 6: Rain-use-efficiency (RUE) for mean annual and mean seasonal precipitation in 2004 and 2005

	2004				2005			
($\text{g DM m}^{-2} \text{mm}^{-1}$)	T I	T II	T III	SE	T I	T II	T III	SE
annual mean	0.57 ^b	0.75 ^a	0.78 ^a	0.02	0.53 ^c	0.67 ^b	0.95 ^a	0.02
seasonal mean *	0.64 ^b	0.85 ^a	0.88 ^a	0.03	0.62 ^c	0.79 ^b	1.12 ^a	0.02

*mean seasonal precipitation = precipitation from May to September (mm).

Means with different superscripts ^{a,b,c} differ significantly ($P < 0.05$) between treatments within years and rows.

The cNY, the product of N-content of plant tissue and cDMY, increased in response to higher defoliation frequency in both years. Increasing N-yield due to increasing defoliation intensity has been observed in rangelands (Georgiadis et al., 1989; Coughenour et al., 1990; Green and Detling, 2000), as well as in temperate humid (Burton et al., 1963; Turner et al., 1996) and tropical grasslands (Van Man and Wiktorsson, 2003). Increasing N-yield after defoliation can be related to increasing N-content due to higher N uptake of roots and enhanced translocation of N to re-growing shoots, especially leaf blades. In 2005 cNY was generally lower in all treatments, what can be attributed to the lower cDMY, but also to the generally lower N-content of plant tissue (table 2). Both the lower cDMY and N-content result from water stress. Regarding the N-concentration of plant tissue, water stress or lack of plant available soil water constrains firstly the mineralization in the soil and secondly the ability of the plant to take up N (Hsiao, 1973). Nonetheless, increasing

cNY in T II and T III in 2005 indicated that defoliation stimulates the N-uptake by roots in the short-term, also under drought conditions.

Short-term effects observed for the root parameters were not significant. In 2004 no influence of defoliation frequency on root mass was observed, however in 2005 a tendency ($P < 0.1$) became apparent, indicating reduced root mass in the frequently defoliated treatments. The root masses obtained in the present study are comparable to data of other studies conducted in the same grassland type (Chen et al., 2006; Gao, 2007). The root mass is high in comparison to the aboveground biomass, but this has been widely observed in semi-arid grasslands (Werger, 1983).

Several studies have observed decreasing root mass caused by increasing defoliation intensity (Weaver, 1950; Lorenz and Rogler, 1967; Holland and Detling, 1990), also in semi-arid environments (Coughenour et al., 1985; Ruess, 1988; Turner et al., 1993; Chen et al., 2006). These studies attributed the reduction in root mass to a decrease in carbon allocation to the roots, caused by reduced photosynthesis and enhanced carbon demand for re-growth of aboveground biomass after intensive defoliation. Nevertheless, some studies from semi-arid environments did not find differences in root mass comparing different defoliation systems (Bartos and Sims, 1974; Coughenour et al., 1990; Milchunas and Lauenroth, 1993). However, these studies report observations from grazing systems with a long grazing history and it is argued that resident plants are well adapted to grazing, as the allocation of photosynthate is not completely shifted from root to shoot after defoliation, but a constant level of allocation to roots is maintained. As the root mass was not reduced in T I in 2005 compared to 2004, it seems likely that the reduction in T II and T III, although only in tendency significant, is not a result of drought, but can be ascribed to the defoliation frequency.

No differences have been observed in C- and N-content of root mass between treatments in both years (table 3). However, in 2005 the N-content was generally higher in all treatments compared to 2004, which can be attributed to the early senescence in 2005, resulting from drought. Re-translocation of N to the roots in the course of senescence is a widely accepted concept (Hayes, 1985).

Roots are considered to serve as storage organs for TNC (Weinmann, 1948; May, 1960; McIlroy, 1967; Pollock and Cairns, 1991), which play an important role in the energy status of grasses. Roots and rhizomes of temperate grasses store carbohydrates, especially at the end of the vegetation period and serve as energy reserves during winter (Steen and Larsson, 1986). Depletion of carbohydrate reserves by frequent defoliation during the vegetation period has been widely observed (Ward

and Blaser, 1961; White, 1973; Moritz, 1988; Fulkerson and Donaghy, 2001). The TNC-content of roots found in the present study is low compared to the TNC-contents found by other investigators working with grasses both in temperate-humid (Steen and Larsson, 1986; Christiansen and Svejcar, 1988; Moritz, 1988; Hume, 1991) and semi-arid environments (Buwai and Trlica, 1977; Menke and Trlica, 1983). In general a comparison of results is challenging, because methods and experimental designs are differing to a great extent, as do grass species and environmental conditions. However, the TNC-content of roots in the present study is particularly low. Gao (2007) investigated root mass dynamics in the same study area and found out that only about 30% of roots harvested by the soil corer method are living roots. Taking into account that dead roots are included in the OM, but do not contain soluble carbohydrates, the TNC-content obtained in the present study should be corrected for living root mass only.

A significant influence of defoliation on root TNC-content was not observed in the present study, neither in 2004 nor in 2005. This indicates that the induced defoliation stress was not as strong as to deplete the carbohydrate reserves, what emphasises the ability of the investigated grassland sward to resist defoliation stress in the short-term.

This result contradicts the above cited studies, but is supported by the results of Buwai and Trlica (1977) who observed, in one out of two rangeland grasses, that defoliation had no effect on the root TNC-content.

4.2 Specific leaf area, leaf area index and leaf weight ratio

The leaf area measurement of *S. grandis* and *L. chinensis* does confirm the results obtained for cDMY in 2004. Due to the loss of leaf area by defoliation, the production of new leaves with higher SLA was stimulated (figure 2a and 2b). Hence the photosynthesis rate must have been increased, what resulted in increased cDMY.

The development of SLA in T I reflects the different growth habits of *S. grandis* and *L. chinensis*. *S. grandis* shows a constant SLA over the growing season, what is, with regard to an increasing LAI, the result of an equal increase in leaf area and leaf thickness and/or density, which are the two main components of SLA (Garnier et al., 1997). In contrast, *L. chinensis* leaves increased the SLA over the growing season, what can be attributed to a stronger increase in leaf area in relation to the increase in leaf thickness and/or leaf density. In 2005 however, leaf area was only measured in T I due to methodological problems in measuring the leaf area.

Leaves were extremely small and convolved as a result of drought. SLA and LAI in T I indicate, that the climatic conditions have a strong impact on leaf area as well, as very low values were observed.

The LAI is closely related to cDMY in *S. grandis* and *L. chinensis*. The cDMY values of both years were plotted against the corresponding LAI values (figure 4) and resulted in high r -values, which confirm the close relationship between these two parameters. In comparison to temperate grasslands without water limitation (Brougham, 1956), cDMY and LAI are much lower in Inner Mongolia grasslands. The LAI of both dominant species does not even reach 1, what is mainly caused by the low plant density, which is characteristic for semi-arid grasslands (figure 2c and 2d). The relationship between cDMY and LAI does not vary among the different defoliation treatments.

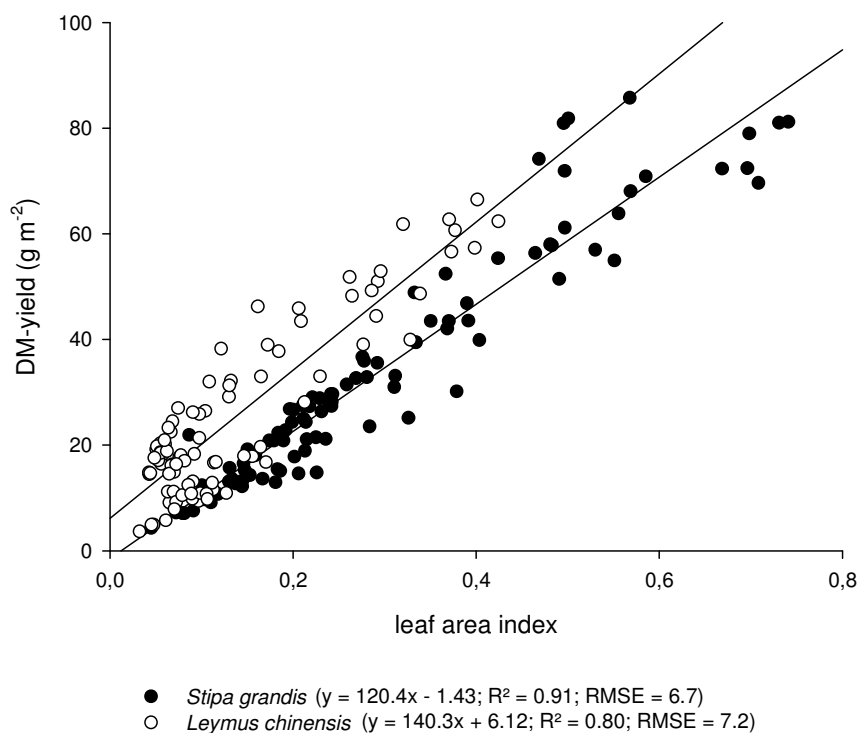


Figure 4: Relationship between DM-yield and leaf area index for *Stipa grandis* and *Leymus chinensis* in 2004 and 2005

The LWR of *S. grandis* and *L. chinensis* was mainly influenced by the sampling date (table 4), what can be expected since the LWR is mainly influenced by the

development of reproductive tillers in the course of the plant maturation process (Buxton, 1996). Reproductive tillers are characterised by pronounced stem development, what increases the stem proportion against the proportion of leaf (Minson, 1990). Defoliation retards the reproductive development of the grass plants; therefore the LWR should have been higher in the frequently defoliated treatments, but only small and non-significant differences in LWR between treatments were observed for both dominant species (figure 2e and 2 f). This observation implies that *S. grandis* and *L. chinensis* develop only few reproductive tillers, regardless of the defoliation frequency. The LWR remains therefore relatively constant over the growing period and short-term responses to defoliation are only marginal.

4.3 Species composition and tiller density

Species composition is a major tool to assess the condition of and the processes in a grassland ecosystem (Li, 1989; O'Connor et al., 2001; Xie and Wittig, 2003; Bai et al., 2004; Tong et al., 2004). Many studies conducted in Inner Mongolia grasslands indicate changes in species composition from perennial species communities to annual species communities to shrub communities (Li, 1989; Christensen et al., 2003; Bai et al., 2004; Barger et al., 2004) with increasing grazing intensity. Li (1989) classified the dominant species *S. grandis* and *L. chinensis* as “decreasers” when subjected to intensive grazing, what is supported by the results of Wang and Ripley (1997). Species composition, measured in all treatment plots prior to the first cut in T III, did not change significantly in the 2nd experimental year in consequence of defoliation in the first year (figure 3). A change in species composition was not expected, as such changes are not likely to occur after only 2 years (Jones et al., 1995); the results do therefore not contradict the studies mentioned above, because all studies were based on long-term observations.

The development of the tiller density (live tillers/m²) of *S. grandis* and *L. chinensis* also confirm the results obtained for the species composition; there was no significant change in tiller density between treatments. However, in the course of growing season especially in 2004, tiller density declined (table 5). This can be attributed to the commonly observed mortality of existing tillers and the reduced rate of new tiller recruitment after the peak in tiller population in early spring in cool-season grasses (Mitchell et al., 1998). In 2005 the development of tiller density was not as distinct, because of the limited water availability. A reduction in tiller numbers due to water stress has been often observed in grass swards (Busso and Richards, 1995; Par-

sons and Chapman, 2000). Examining *L. chinensis* tiller density against an aridity gradient in Inner Mongolia, Wang and Gao (2003) observed increasing tiller density with increasing annual precipitation. They derived a regression equation, which calculate a tiller density of 300 tillers m^{-2} for a precipitation amount of 340 mm year^{-1} , what corresponds to our results.

In summary, it can be stated that the aboveground herbage productivity was significantly stimulated by frequent defoliation in the short-term. The cDMY positively responded to defoliation, but was essentially depended on precipitation what was demonstrated by the concept of RUE. The cNY, as it depends on the cDMY, increased also significantly due to increased defoliation frequency. The SLA and LAI indicate significant short-term differences between the treatments as it was expected, especially the SLA was highly sensitive to defoliation and identified different levels defoliation induced plant stress. The root mass and root TNC reserves however, did not respond to defoliation in the short term, as well as the LWR, the species composition and the tiller density.

5. Conclusions

Short-term responses of the investigated semi-arid grassland sward to defoliation stress were positive with regard to increased aboveground biomass productivity and N uptake. Significantly negative short-term responses were not observed for any of the chosen parameters. This implies that the evaluated grassland ecosystem is resistant to defoliation or grazing stress respectively, in the short-term and that the process of grassland degradation therefore results from mid- and/or long-term grazing stress. Furthermore it became apparent that the mean annual precipitation and its intra-annual distribution have a substantial impact on this grassland ecosystem. The presented results underline the importance to refer to degradation dynamics on different time scales, that is to distinguish between short-, mid-, and long-term effects of defoliation stress.

6. References

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Chapter 3

**Short-term responses to defoliation stress of a semi-arid grass-
land sward in Inner Mongolia, China.**

2. Herbage quality

Abstract

Grassland degradation due to overgrazing is the major ecological and socio-economical problem in the Inner Mongolia steppes, P.R. China. Degradation and its consequences have often been described retrospective, but almost no information is available about short-term effects of intensive grazing. To completely understand the degradation process such information is crucial and the aim of the present study is to assess short-term responses of the steppe grassland through herbage quality parameters, when it is subjected to defoliation stress.

A cutting-frequency experiment, based on a randomized block design, was carried out in the natural grasslands of the Xilin River Basin, Inner Mongolia, comparing low (T I), moderate (T II) and high (T III) defoliation frequency. Over the vegetation periods of 2004 and 2005 herbage samples of the total green biomass and the two dominant species *Stipa grandis* and *Leymus chinensis* were consecutively taken and analysed by means of NIRS for crude protein (CP), cell wall content and composition, in vitro digestibility (IVDOM) and total non-structural carbohydrates (TNC). The CP content increased significantly due to frequent defoliation in T II and T III from on average 100 to 150 g kg⁻¹ DM in 2004 and 90 to 130 g kg⁻¹ DM in 2005. The cell wall content was generally high in the sampled herbage, reaching 700 g NDF kg⁻¹ DM already in the early growing season in all sward constituents. The cell wall content and its composition did not significantly respond to frequent defoliation, especially in 2005. The IVDOM of the herbage is generally low, ranging between 610 g kg⁻¹ OM in *L. chinensis* in 2004 and 514 g kg⁻¹ OM in *S. grandis* in 2005. Frequent defoliation caused an average increase in IVDOM of only 30 g kg⁻¹ OM in T II and T III in 2004, but in 2005 no responses of IVDOM were observed. The TNC content decreased after frequent defoliation in 2004 in all sward constituents, but in 2005 the differences were not significant. The results demonstrated that the herbage quality parameters were highly susceptible to differences in precipitation rate, as in 2005 none of the herbage quality parameters, except the CP content, responded significantly and consistently to frequent defoliation.

It can be concluded that short-term effects of frequent defoliation can be quantified by the CP content, while the cell wall content and IVDOM did not show distinct responses to defoliation. The TNC content showed significant short-term effects, but was highly susceptible to climatic and seasonal fluctuations which covered defoliation-induced effects. The influence of climatic fluctuations, especially precipitation

rate, plays a key role in the steppe ecosystem and does also substantially affect the herbage quality.

1. Introduction

Native grasslands cover about 70% of the territory of the Inner Mongolia autonomous region in P.R. China (FAO, 2001). About one third has been already heavily degraded (Sneath, 1998; Zhou et al., 2002). Livestock numbers increased tenfold in the last 60 years, what entailed overgrazing of the steppe grasslands (Jiang and Meurer, 2001). Attributes of steppe degradation are decreasing grassland productivity, resulting in reduced economical return from livestock husbandry and ecological consequences like wind and water erosion that cause substantial loss of soil and nutrients from the grassland ecosystem. Management strategies are urgently needed to avoid irreversible degradation of the steppe grassland and supply adequate amounts of good quality feed for the grazing animals, to enable local farmers to subsist themselves by livestock production (Zhou et al., 2002, Tong et al., 2004). Several studies have been conducted in the Inner Mongolia grassland, mainly concentrated on long-term ecological interrelations within the grassland ecosystem (Li, 1989; Xiao et al., 1996; Wang and Ripley, 1997; Bai et al., 2004; Yu et al., 2004). Only a few studies have examined the degradation process in its formation and development, rather than from a retrospective point of view (Wang et al., 1999; Zhang et al., 2004; Zhao et al., 2005). However, the comprehension of the degradation processes resulting from overgrazing is essential to develop adequate management strategies for sustainable agriculture in this grassland ecosystem, including information about short-term effects of defoliation stress. The aim of the present study is to evaluate such short-term responses to defoliation stress in a semi-arid grassland sward in Inner Mongolia. Parameters of classical growth analysis were used in chapter 2 to identify short-term effects of defoliation, which will be completed in the current chapter by evaluating herbage quality parameters for short-term responses to defoliation stress.

In the short term herbage quality is mainly influenced by the maturation process grass plants undergo during the vegetation period (Minson, 1990; Buxton, 1996). In the long term herbage quality may change when the species composition of a grassland sward is changing. The maturation process is directly influenced by the environmental factors light, temperature and precipitation. These environmental factors can vary from year to year (Buxton and Fales, 1994), however the mean

annual precipitation and its distribution is probably the most important one in semi-arid grassland ecosystems. Herbage utilisation by grazing or cutting retards the maturation process, so that the quality of the re-growth differs from the quality of mature grasses that undergo reproductive tillering. Hence, it can be expected that herbage quality parameters will respond directly to defoliation stress, in other words defoliation affects herbage quality in the short-term.

In literature, the quality of herbages is commonly described by crude protein (CP) content and *in vitro* digestibility (IVDOM). However other plant components like cell wall content and its composition, or the content of total non-structural carbohydrates (TNC) are also valuable parameters in describing herbage quality for grazing ruminants.

The objective of the present investigation is to describe short-term responses to different defoliation frequencies on community and plant level through the above mentioned herbage quality parameters. To achieve this objective a cutting-frequency experiment was carried out in 2004 and 2005 in the typical steppe area of the Xilin River Basin, Inner Mongolia. The natural grassland sward was subjected to 3 different cutting frequencies: low, moderate and high defoliation intensity. Herbage quality was determined over the vegetation periods for the total green biomass, and separately for the two dominant species *Stipa grandis* and *Leymus chinensis*, which account together for approx. two thirds of the total aboveground biomass in the present study.

2. Material and Methods

2.1 Study area, experimental design and herbage sampling

Detailed information about the field experiment has been reported in chapter 2 of this thesis. Briefly, the present study was carried out within the sino-german MAGIM-project (Matter fluxes of grasslands in Inner Mongolia as influenced by stocking rate). A cutting-frequency experiment was conducted near the Inner Mongolia Ecosystem Research Station (IMGERS), Chinese Academy of Sciences. The climate is semi-arid, characterised by significant seasonal and inter-annual variability (table 1). The vegetation is dominated by the perennial bunchgrass *Stipa grandis* P. Smirn. and the perennial rhizomatous *Leymus chinensis* (Trin.) Tsvetlev, both grasses belong to the C3 photosynthesis type. This vegetation type can be considered as representative for large parts of the Xilin River Basin (Bai et al., 2004).

Table 1: Temperature (°C) and precipitation (mm) as mean of 20-years and during the growing seasons of 2004 and 2005

	Temperature (°C)			Precipitation (mm)		
	1983-2003	2004	2005	1983-2003	2004	2005
May	11.3	10.8	10.6	31	23	11
June	16.5	18.2	17.7	57	29	32
July	19.0	18.7	20.13	100	50	59
August	17.4	16.2	19.23	70	133	27
September	10.8	11.5	12.33	36	53	13
annual mean	0.7	1.9	0.1	343	325	166

Three treatments were tested in a randomised block-design with 4 replications. The treatments differed in cutting frequency: treatment I (T I) was cut once in mid September, resembling the local practice of haymaking. The hay cut was performed by a bar mower used by local farmers, cutting height was approx. 8 cm above soil surface. Treatment II (T II) was cut every 6 weeks as moderate intensity of defoliation, whereas treatment III (T III) was cut every 3 weeks to represent high defoliation intensity. Cutting was carried out with a conventional lawn mower to 2.5 cm stubble height, to simulate intensive grazing by sheep.

The herbage sampling intervals differed from the cutting intervals. In 2004 T I and T II were sampled every 2 weeks, T III was sampled every 3 weeks, directly before cutting. In 2005 the herbage sampling interval of T I and T II was reduced to 6 weeks (adjusted to cutting frequency of T II), T III was furthermore sampled every 3 weeks right before each cut. All herbage sampling and cutting dates are summarized in chapter 2 (table 1).

At sampling dates herbage was clipped to 1cm stubble height at four randomly distributed 0.25-m² quadrates within each plot. The herbage sampled in the 4 quadrates was pooled and afterwards separated into 4 fractions: the dominant species *S. grandis* and *L. chinensis*, all remaining species and the standing necrotic material. Litter (necrotic material spread on the ground) was removed before clipping by gentle combing with a wool comb. The samples were dried at 60°C for 24 h in a forced-air drying-oven, weighted and afterwards ground with a cyclotec mill (Tecator, Germany) to pass a 1 mm sieve.

2.2 Herbage quality analysis

The herbage quality parameters were predicted by Near-Infrared-Spectroscopy (NIRS) for all herbage samples. All dried and ground samples were scanned with a NIR-Systems 5000 monochromator (Perstrop Analytical Inc., Silver Spring, MD, USA) with 2 replications over a wavelength range from 1100 to 2500 nm in 2 nm intervals. The software NIRS 2 by Infrasoft International® (ISI, Port Mathilda, PA, USA) was used for scanning, mathematical processing, calibration and statistical analysis of the spectra data. The laboratory analyses were carried out on calibration ($n = 138$) and validation ($n = 25$) subsets of herbage samples, which were randomly chosen by the software NIRS 2. The accuracy of the NIRS-prediction for the quality parameters is given in table 2.

Table 2: Calibration and validation statistics of the NIRS-prediction of herbage quality parameters

	n ^a	mean ^b	min –max ^b	SD ^c	SEC ^d	R ^{2e}	SEP ^f
OM	132	935.9	881.7 – 965.4	20.45	3.36	0.973	6.58
CP	132	97.0	44.0 – 193.7	37.19	2.26	0.996	3.36
NDF	132	713.7	606.3 – 824.0	33.90	11.47	0.886	12.51
ADF	137	348.4	268.1 – 443.2	41.40	14.50	0.877	11.72
ADL	135	46.1	16.4 – 80.9	12.50	5.42	0.815	5.26
IVDOM	122	588.1	442.8 – 694.3	50.85	11.43	0.950	25.96
TNC	126	42.2	2.9 – 99.3	26.97	4.37	0.974	9.13

a: number of samples included into the calibration

b: mean in g kg⁻¹ DM, except IVDOM in g kg⁻¹ OM

c: standard deviation of the laboratory analysis values

d: standard error of calibration

e: coefficient of determination (relationship between NIRS predicted and laboratory determined values)

f: standard error of prediction

The laboratory analyses of samples from the calibration- and validation subset were carried out as follows. Dry matter (DM) content was determined by drying 1 g of the herbage samples at 105 °C until a constant dry weight was reached. Organic matter (OM) content was calculated as the difference between the dry sample and the residue (ash) after incineration of the dry sample at 550 °C over night. The crude protein (CP) content was calculated from the nitrogen (N) content (CP =

N x 6.25), which was analysed by a C/N-Analyser (vario Max CN, Elementar Analysensysteme, Hanau, Germany) which is based upon the DUMAS-combustion method. Neutral detergent fibre (NDF), acid detergent fibre (ADF) and acid detergent lignin (ADL) were determined sequentially using a semi-automated Ankom 200 Fiber Analyzer (Ankom Technology, Macedon, NY, USA) according to the procedures described by Van Soest et al. (1991). Hemicellulose and Cellulose were calculated as follows: Hemicellulose = NDF - ADF and Cellulose = ADF - ADL. NDF and ADF are expressed including residual ash.

The digestibility was estimated by an in vitro method. The Cellulase technique described by De Boever et al. (1986) was used, following the standardised procedure of Naumann and Bassler (1993). The in vitro cellulase digestible OM (IVDOM) was estimated by equation [1] developed by Weissbach et al. (1999).

$$\text{Eq. [1]: IVDOM}^a \text{ (\%)} = 100 \cdot (940 - \text{CA} - 0.62 \cdot \text{EULOS} - 0.000221 \cdot \text{EULOS}^2) / (1000 - \text{CA})$$

(^a CA = crude ash, EULOS = enzyme insoluble OM; CA and EULOS in g kg⁻¹ DM)

The total non-structural carbohydrates (TNC) were measured by high pressure anion exchange chromatography with pulsed amperometric detection (HPAEC-PAD) modified after Chatterton et al. (1989a) and Shiomi et al. (1991). Prior to analysis the herbage samples were ground again with a ball mill to a particle size of 10 µm. To extract the TNC, 40 mg of the ground material were agitated with 2 ml deionised cold water for 60 minutes. After centrifugation (3600 rpm) the supernatant was purified with 67 µl Chloroform. The supernatant was separated from the pellet. The pellet was dried in a vacuum-dryer for 1 h at 55°C and stored at -20°C for starch analysis. The supernatant was diluted 1:5 in deionised water and 2 ml of the dilution were filtrated through a C18-cartridge (Strata C18-E, Phenomenex Inc., Torrance, CA, USA). The filtrate was hydrolysed in 2N HCl for 2 h at 80°C to split fructans into glucose and fructose, but of course also sucrose was split up. For starch analysis 2 ml enzyme solution, containing amyloglucosidase from *Aspergillus niger* (14U/mg, Roche Diagnostics) and Sodium-Acetate-Buffer (pH: 4.8) at a ratio of 1:13.6, were added to the defrosted pellet and vortexed intensively for 20 seconds. The mixture was incubated over night (~ 14 h) at 37°C and afterwards extracted in the same way as described above. Because it was not always possible to measure the carbohydrates right after extraction, the extracts were stored at -20°C until analysis.

To quantify the carbohydrates in the extracts, glucose and fructose were separated on an Ion Chromatography system (DX-300, Dionex Corp., Sunnyvale, CA, USA) using a CarboPac PA 100 column (4 x 250 mm). The carbohydrates were eluted with NaOH (200 mmol l⁻¹) in deionised H₂O, with a NaOH gradient that increased from 28% at 0 minutes to 35% at 8 minutes and further to 50% at 9 minutes. To rinse the column, a further increase to 80% at 11 minutes was included, from which the gradient returned to 28% NaOH until the end of the program at 18.5 minutes. Flow rate through the system was 1.0 ml min⁻¹. A standard solution was prepared with equal proportions of chemically pure glucose, fructose and sucrose, with concentrations ranging from 10 mg l⁻¹ to 150 mg l⁻¹.

2.3 Statistical analysis

The quality parameters were determined for the 4 separated fractions *S. grandis*, *L. chinensis*, the remaining species and standing necrotic material. The quality of the green biomass was calculated by summarising the quality of *S. grandis*, *L. chinensis* and the remaining species according to their DM-yield. The yearly mean of the quality parameters is the arithmetic mean of the concentrations in DM at the sampling dates.

The statistical analysis was carried out separately for the two years, focusing on the differences between the 3 treatments. Data were subjected to an analysis of variance using the mixed procedure of the software package SAS[®]9 (SAS Institute Inc., Cary, NC, USA). Experimental factors were 'replication' and 'treatment'. Means with significant *F*-value were tested with Student's *t*-test and corrected by the Bonferroni-Holm test (Horn and Vollandt, 1995). The level of significance was *P*<0.05.

3. Results

In 2004 the experimental factor 'treatment' was significant for all quality parameters in the green biomass. In *S. grandis* 'treatment' was significant for all parameters, except for cellulose and in *L. chinensis* 'treatment' was significant for all parameters, except for hemicellulose. In 2005 the factor 'treatment' was only significant for OM, CP and hemicellulose in the green biomass. In *S. grandis* 'treatment' was significant for all quality parameters, except ADL and hemicellulose, whereas in *L. chinensis* 'treatment' was only significant for OM and CP. An interaction between 'treatment' and 'replication' was not observed, indicating that the block-design was

well defined. The quality of the green biomass and the species *S. grandis* and *L. chinensis* is described by mean values of the quality parameters for 2004 in table 3 and 2005 in table 4.

Table 3: Quality of the green biomass, *Stipa grandis* and *Leymus chinensis* in 2004

	green biomass				<i>Stipa grandis</i>				<i>Leymus chinensis</i>			
(g kg ⁻¹ DM)	T I	T II	T III	SE	T I	T II	T III	SE	T I	T II	T III	SE
OM	947.5 ^a	934.4 ^b	933.8 ^b	0.454	951.2 ^a	938.6 ^b	938.6 ^b	0.548	947.0 ^a	931.5 ^b	931.1 ^b	1.017
CP	101.9 ^c	135.6 ^b	143.8 ^a	2.094	98.92 ^b	146.0 ^a	145.9 ^a	2.082	104.3 ^b	155.0 ^a	155.8 ^a	2.415
TNC	56.23 ^a	46.71 ^b	48.12 ^b	1.204	58.88 ^a	46.10 ^b	47.55 ^b	1.250	43.40 ^a	36.38 ^b	37.93 ^{ab}	1.447
IVDOM*	558.8 ^b	580.3 ^{ab}	599.7 ^a	6.193	533.6 ^b	579.1 ^a	582.9 ^a	2.604	573.6 ^b	604.1 ^a	609.7 ^a	4.691
Cell wall components												
NDF	707.7 ^a	689.2 ^b	700.5 ^{ab}	3.299	728.8 ^a	704.7 ^c	710.3 ^b	1.194	703.3 ^a	683.7 ^b	684.5 ^b	3.277
ADF	328.7 ^a	320.0 ^b	318.1 ^b	1.367	321.0 ^a	307.0 ^b	307.4 ^b	1.172	339.8 ^a	318.1 ^b	314.2 ^b	1.575
ADL	41.86 ^a	37.60 ^b	36.51 ^b	0.479	44.00 ^a	32.43 ^b	33.32 ^b	0.416	36.30 ^a	29.98 ^b	30.08 ^b	0.659
Hemicellulose	379.0 ^{ab}	369.2 ^b	382.4 ^a	2.388	407.7 ^a	397.7 ^c	402.9 ^b	0.454	363.5	365.6	370.3	2.447
Cellulose	286.8 ^a	282.4 ^{ab}	281.6 ^b	1.126	277.0	274.6	274.1	1.049	303.5 ^a	288.1 ^b	284.2 ^b	1.530

* IVDOM is given in g kg⁻¹ OM

Values with different superscripts ^{a,b,c} are significantly different ($P < 0.05$) between treatments within sward constituents.

Table 4: Quality of the green biomass, *Stipa grandis* and *Leymus chinensis* in 2005

	green biomass				<i>Stipa grandis</i>				<i>Leymus chinensis</i>			
(g kg ⁻¹ DM)	T I	T II	T III	SE	T I	T II	T III	SE	T I	T II	T III	SE
OM	952.1 ^a	944.9 ^b	936.2 ^c	0.398	957.5 ^a	954.5 ^b	948.4 ^c	0.553	953.1 ^a	946.2 ^b	938.1 ^c	1.033
CP	96.94 ^b	111.7 ^a	115.9 ^a	2.900	86.63 ^b	107.3 ^a	106.1 ^a	1.733	109.4 ^b	122.0 ^{ab}	130.9 ^a	4.008
TNC	65.86	65.76	59.93	2.435	65.55 ^a	61.48 ^a	53.15 ^b	1.475	53.83	52.75	46.65	2.388
IVDOM*	566.5	571.2	567.7	6.294	531.2 ^a	526.9 ^a	514.2 ^b	2.546	575.3	575.6	567.5	8.230
Cell wall components												
NDF	712.5	702.7	706.2	3.509	738.2 ^b	738.5 ^b	752.3 ^a	1.414	706.8	703.0	708.1	5.363
ADF	332.8	337.1	341.1	2.557	327.2 ^b	330.2 ^b	340.1 ^a	2.070	340.1	339.4	337.2	4.003
ADL	47.21	46.31	47.92	0.504	49.90	49.70	50.73	0.382	44.68	41.83	42.50	0.656
Hemicellulose	379.8 ^a	365.5 ^b	365.1 ^b	1.985	411.0	408.4	412.2	1.801	366.7	363.6	370.9	2.418
Cellulose	285.6	290.8	293.2	2.125	277.3 ^b	280.4 ^b	289.4 ^a	2.123	295.4	297.5	294.7	3.341

* IVDOM is given in g kg⁻¹ OM

Values with different superscripts ^{a,b,c} are significantly different ($P < 0.05$) between treatments within sward constituents.

Figure 1 illustrates the development of the quality parameters CP, TNC and IVDOM in the green biomass for the two growing seasons. Figure 2 describes the development of the parameters NDF, hemicellulose, cellulose and ADL in the green biomass for the same periods. The quality development across the growing season for *S. grandis* and *L. chinensis* is not shown separately, because the quality development did not differ markedly between the three examined sward constituents.

The OM content was significantly reduced in T II and T III for the green biomass, *S. grandis* and *L. chinensis* in 2004. In 2005 the OM content was again significantly reduced and all three treatments were to separate statistically. In general the OM contents were higher in 2005.

In 2004 the CP content ranged between 99 g kg⁻¹ DM in T I of *S. grandis* and 156 g kg⁻¹ DM in T III of *L. chinensis*. In 2005 the CP content was generally lower and ranged between 87 g kg⁻¹ DM in T I of *S. grandis* and 131 g kg⁻¹ DM in T III of *L. chinensis*. The ranking between the sward constituents was consistent over the two years. Comparing between sward constituents, *L. chinensis* had the highest CP contents, while *S. grandis* had the lowest. The green biomass was ranked in between, indicating that other species besides *L. chinensis* and *S. grandis* had comparable CP contents. The CP content increased significantly when defoliation frequency increased (figures 1a and 1b), but the differences between T II and T III were not to separate statistically on a yearly mean basis for the green biomass.

The TNC content in the aboveground biomass ranged between 36 and 66 g kg⁻¹ DM, not differing much between the sward constituents, i.e. the green biomass, *S. grandis* and *L. chinensis*. The TNC content decreased significantly with increasing defoliation frequency in all three sward constituents in 2004, whereas in 2005 the TNC content only decreased significantly in T III of *S. grandis*. In 2005 the TNC content was generally higher than in 2004, and the differences between T I and the frequently defoliated treatments, as observed in 2004 were not significant, besides the above mentioned exception of *S. grandis*. The figures 1c and 1d demonstrate that the TNC content of the green biomass decreased in T II and T III after early defoliation, but the figures also reveal that by the end of the growing season TNC contents increased again. This development was also observed both in *S. grandis* and in *L. chinensis*.

Mean IVDOM values ranged between 533 g kg⁻¹ OM in T I of *S. grandis* and 610 g kg⁻¹ OM in T III of *L. chinensis* in 2004. In 2005 IVDOM generally decreased, with the lowest value in T III of *S. grandis* (514 g kg⁻¹ OM) and the highest in T I and T II of *L. chinensis* (575 g kg⁻¹ OM). In comparison to *L. chinensis*, the IVDOM values of

S. grandis were lower. *S. grandis* was about 4-6%-points less digestible in 2004 and about 10%-points in 2005. The IVDOM of the green biomass ranked between *S. grandis* and *L. chinensis*. In all sward constituents digestibility increased with defoliation frequency in 2004. In 2005 no significant differences were found between defoliation frequencies in the green biomass and *L. chinensis*, but *S. grandis* indicated slightly decreased IVDOM in T III.

The small differences in IVDOM are confirmed by the small differences observed for the cell wall content and its composition. The mean NDF content of the green biomass, averaged over all treatments, was 700 g kg⁻¹ DM in 2004 and 707 g kg⁻¹ DM in 2005. *S. grandis* and *L. chinensis* had comparable mean NDF contents of about 700 g kg⁻¹ DM. The NDF content of the green biomass, as well as of *S. grandis* and *L. chinensis* did not differ substantially between treatments. Although the NDF content decreased significantly in T II and T III in 2004, the mean decrease was only 3% for all sward constituents. In 2005 the decrease in NDF content was not significant in the green biomass and *L. chinensis*, whereas the NDF content in *S. grandis* increased in T III after frequent defoliation. The development of the NDF content (figures 2a and 2b) indicated that the dynamics in cell wall composition were not very pronounced. Although differences were partly statistically significant, no consistent differences in cell wall composition between treatments could be observed. The homogeneous development of the hemicellulose and cellulose content across treatments is documented in figures 2c to 2f. The ADL content however, decreased significantly in T II and T III in 2004 by 13%, 25% and 17% in the green biomass, *S. grandis* and *L. chinensis*, respectively. But in 2005 no significant differences in ADL content between treatments were found at all (figures 2g and 2 h).

In the appendix of this chapter the development of the quality parameters over the growing season is demonstrated for *S. grandis* (figure I-1a to 1f, figure I-2a to 2h) and for *L. chinensis* (figure II-1a to 1f and figure II-2a to 2h), like for the green biomass in figure 1a to 1f and figure 2a to 2h.

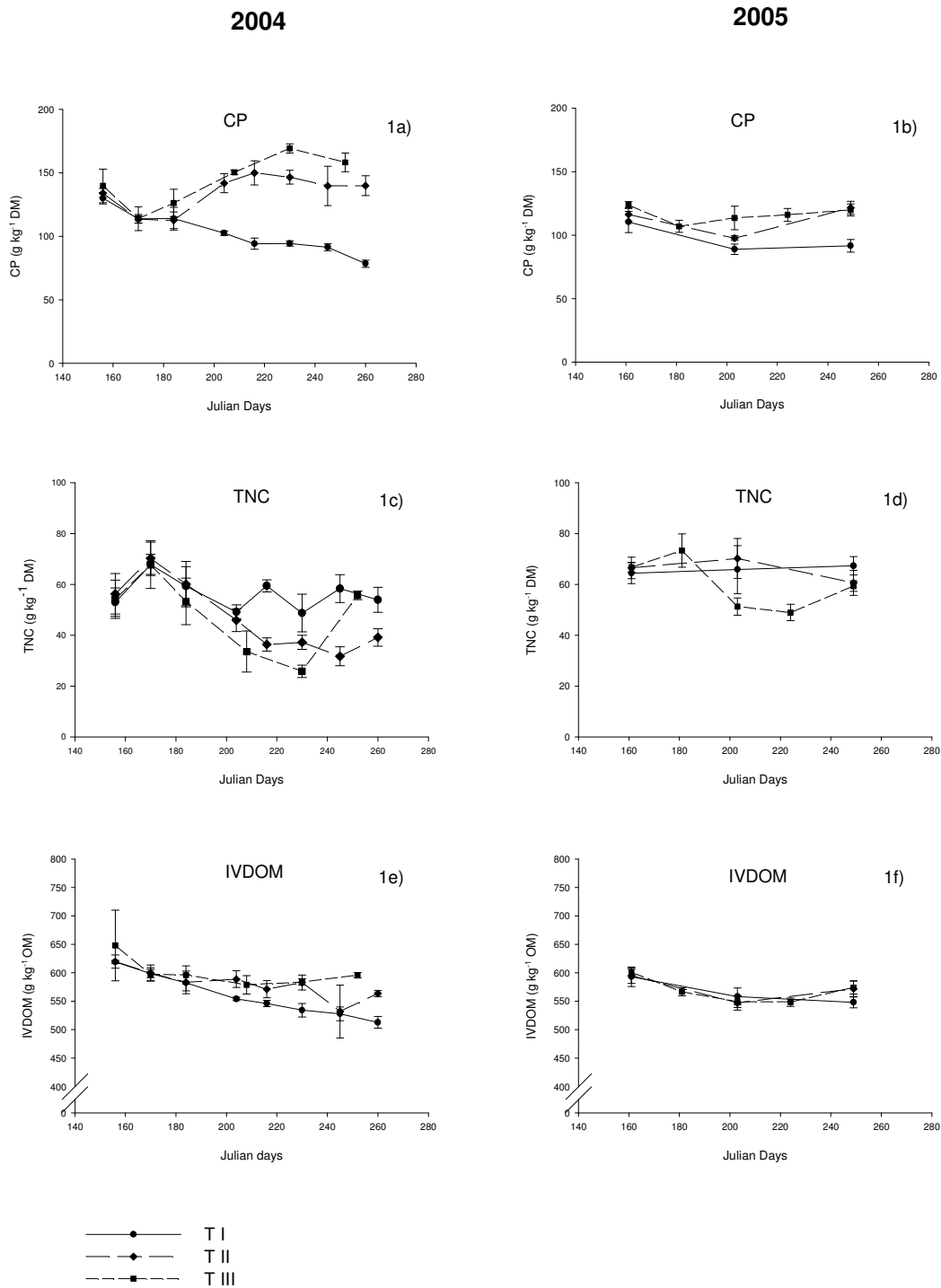


Figure 1: Development of crude protein (CP), total non-structural carbohydrates (TNC) and in vitro digestibility (IVDOM) of the green biomass across the growing seasons of 2004 and 2005 (Error bars indicating SD; cutting dates (not indicated) in 2004: T I = day 260; T II = day 185, day 231, day 260; T III = day 185, day 209, day 230, day 252; cutting dates in 2005: T I = day 250; T II = day 204, day 250; T III = day 182; day 204; day 225; day 250).

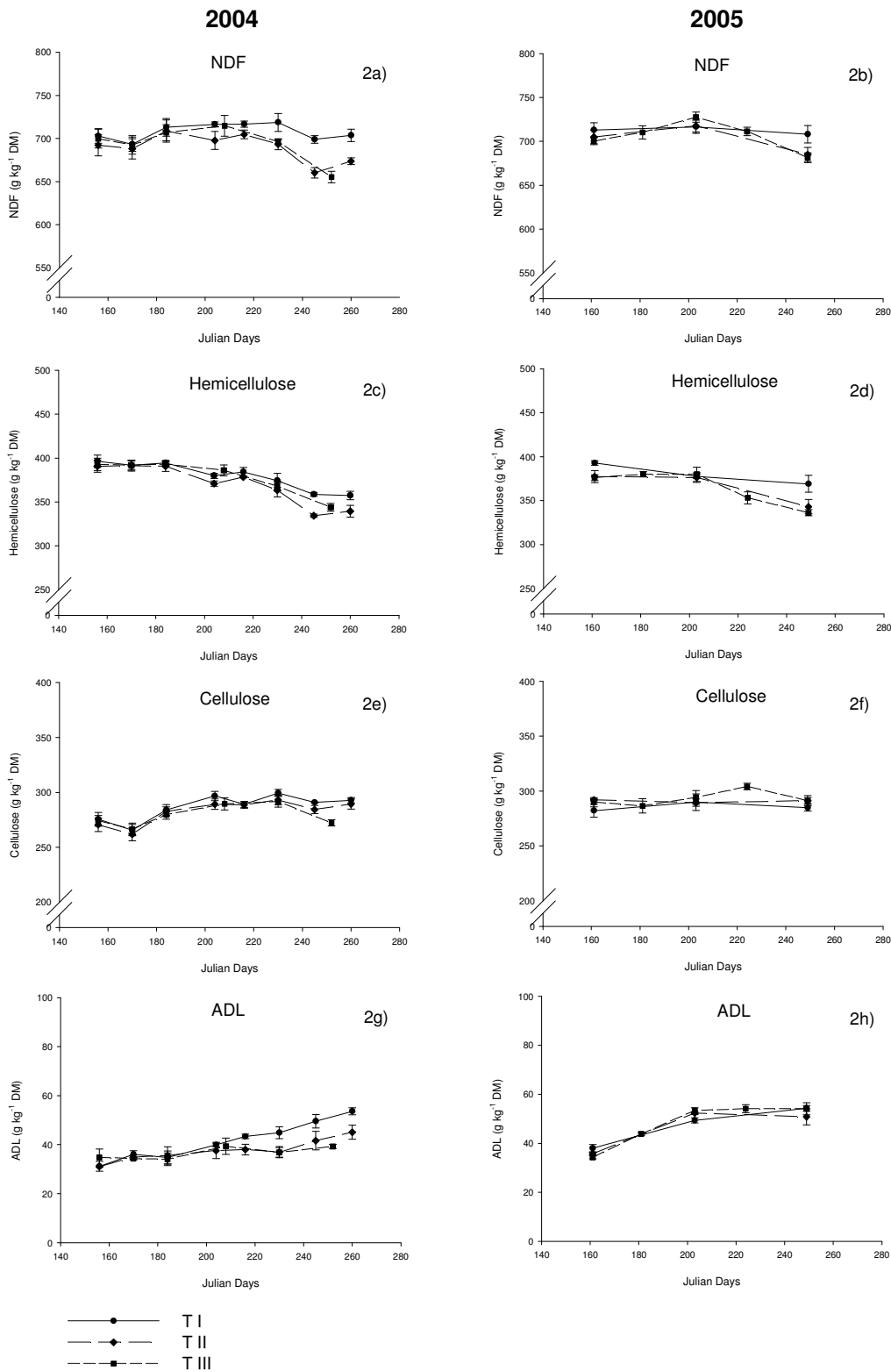


Figure 2: Development of neutral detergent fibre (NDF), hemicellulose, cellulose and acid detergent lignin (ADL) of the green biomass across the growing seasons of 2004 and 2005 (Error bars indicating SD; cutting dates are not indicated, see figure 1)

4. Discussion

In comparison to cool-season grasses investigated in humid temperate grasslands, much higher cell wall contents and lower CP and TNC contents were observed for grasses in the present study (Collins and Casler, 1990; Cherney et al., 1993; Turner et al., 1996; Ombabi et al., 2001). In contrast, compared to warm-season grasses the cell wall content was comparable (Hendrickson et al., 1997; Van Man and Wiktorsson, 2003), but the CP content tended to be higher (Mutz and Drawe, 1983; Minson, 1990; Madakadze et al., 1999). However, comparison with cool-season grasses growing in other semi-arid grassland ecosystems show similar quality, only the cell wall content tended to be higher in the present study (Pérez-Corona et al., 1994; Long et al., 1999; Vázquez-Aldana et al., 2000; Ganskopp and Bohnert, 2001).

Improved quality of herbage re-growth after defoliation has been widely observed in cutting-frequency experiments (Binnie and Harrington, 1972; Mutz and Drawe, 1983; Willms and Beauchemin, 1991; Turner et al., 1996; Van Man and Wiktorsson, 2003) and grazing trials (Heitschmidt et al., 1989; Georgiadis and McNaughton, 1990; Wang and Wang, 1999; Schlegel et al., 2000; Garcia et al., 2003). Also in the present study increasing herbage quality was found after frequent defoliation, but not for all herbage quality parameters and not consistent for both experimental years (tables 3 and 4).

The OM content decreased significantly in T II and T III in 2004, in 2005 also differences between T II and T III were significant, compared to T I. This was observed for the green biomass and for *S. grandis* and *L. chinensis* as well (see appendix). The plant cover in the investigated semi-arid grassland is low, about 40% to 60% depending on the annual precipitation rate (M. Giese, personal communication). After removing the aboveground biomass by cutting the soil surface is directly subjected to rainfall. Rebounding raindrops transport soil particles and deposit them on the remaining grass stubbles. It has been demonstrated that sediment production from rainfall is negatively related to total aboveground biomass and coverage in Texas' rangelands (Thurow et al., 1986), as sufficient plant cover restricts sediment production through rainfall. In 2005 the OM content increased in all treatments and all sward constituents compared to 2004, what can be explained by less rainfall, and therefore less soil contamination of the stubbles in 2005. In addition, defoliation was carried out by a conventional lawn mower to 2.5 cm stubble height. Soil parti-

cles were dispersed by mowing and particle deposition may have contributed to the differences in OM content of the remaining grass stubbles.

The CP content increased significantly in the frequently defoliated treatments in both years, but the differences between the 3-week and the 6-week defoliation interval were not significant, except for the green biomass in 2004. This significant difference between T II and T III might be a result of short-term changes in species composition, as it was demonstrated for T II and T III in chapter 2 (table 2). The CP content was maintained on a higher level in the frequently defoliated treatments as it can be expected for juvenile re-growth. However, the increase in CP content in T II and T III was much lower in 2005 compared to 2004 in all sward constituents, what is probably a result of severe soil water deficit in the growing season of 2005. As water is the first limiting resource in semi-arid grassland steppes (Noy-Meir, 1973), after defoliation probably only low amounts of N were available for incorporation into the re-growing grass plants (Hsiao, 1973). The N content of the plants was therefore reduced in 2005.

In T I the CP content decreased during the vegetation period as the grass plants matured in both experimental years. Decreasing CP content has been attributed to decreasing leaf/stem ratio, as leaves contain more CP than stems (Terry and Tilley, 1964; Wilman and Rezvani Moghaddam, 1998). Minson (1990) reviewed several studies which examined temperate and tropical forages and provided information about the decline in CP content as plant maturation progressed. It was stated that the CP content on average decreases by $2.2 \text{ g kg}^{-1} \text{ DM day}^{-1}$ in maturing forages, with no significant differences between temperate and tropical forages. In the present study a much lower decline of only $0.5 \text{ g kg}^{-1} \text{ DM day}^{-1}$ and $0.2 \text{ g kg}^{-1} \text{ DM day}^{-1}$ was observed in T I in 2004 and 2005, respectively. This result suggests that plant maturation progresses very slowly in this dry environment and/or that the effect of maturation, namely the decrease in leaf/stem ratio, is less pronounced. Consequently, the decrease in CP content might be more a result of increasing senescence and connected to re-translocation of N, than of increasing amounts of stem. This assumption is supported by the results obtained for the cell wall content and its composition. It has been widely observed that the cell wall content increases when grass plants mature, mainly due to reproductive tillering (Bailey, 1973; Wilson, 1994). As frequent defoliation retards plant maturation and re-growth remains primarily vegetative thereafter (Allinson et al., 1969), it can be expected that the NDF content of re-growing grass plants is considerably lower. However, after the first cut almost no change in NDF content was observed for T II and T III. Only after the

following cut the NDF content of T II and T III decreased compared to T I in 2004 (figures 2a and 2b).

Like for the CP content, the main determinant of NDF content is the leaf/stem ratio (Nelson and Moser, 1994). The leaf weight ratio (leaf proportion of the whole tiller) is presented for *S. grandis* and *L. chinensis* in table 5, indicating only minor changes over the growing period in T I and also after frequent defoliation in T II and T III.

Table 5: Leaf weight ratio of *S. grandis* and *L. chinensis* in 2004 and 2005

date*	2004						2005		
	<i>S. grandis</i>			<i>L. chinensis</i>			<i>S. grandis</i>	<i>L. chinensis</i>	
	T I	T II	T III	T I	T II	T III	T I	T I	
1	0.80	0.80	0.80	0.76	0.77	0.80	1	0.75	0.65
2	0.83	0.82	0.82	0.77	0.79	0.78			
3	0.86	0.83	0.86	0.75	0.78	0.78			
4	0.72	0.75	0.76	0.70	0.59	0.56	4	0.82	0.72
5	0.69	0.79		0.64	0.59				
6	0.73	0.86	0.87	0.68	0.65	0.64			
7	0.85	0.77	0.84	0.67	0.76	0.84	7	0.83	0.74
8	0.85	0.81		0.69	0.83				

Analysis of variance

Treatment (T)	ns		ns	-	-
Date (D)	***		***	**	ns
T x D	*		***	-	-

*date = sampling date; sampling and cutting dates (grey shaded) in 2004 (julian days): T I = day 260; T II = day 184, day 230, day 260; T III = day 184, day 208, day 230, day 252; cutting dates in 2005: T I = day 249; (ns = non significant; * = P<0.1; ** = P<0.05; *** = P<0.01)

As explained above the leaf weight ratio is mainly influenced by the reproductive development of the grass plants. The small changes in leaf weight ratio in both dominant species can be explained by the fact that the proportion of reproductive tillers is low, both in *S. grandis* and *L. chinensis*. It has been reported that the leaf fraction yielded 47% in early growth stages of switchgrass, whereas in more mature growth stages the leaf fraction was reduced to only 26% (Twidwell et al., 1988). Looking at the leaf weight ratio of *S. grandis* and *L. chinensis* in T I over the vegetation period, the leaf fraction never fell below 69% and 64%, respectively. Wang et al.

(2001) reported that the reproductive shoot differentiation of *L. chinensis* was less than 5% under dry conditions and only about 17% when the soil water availability was sufficient. In the present study it was observed that 32% of *S. grandis*' DM-yield sampled in the end of the growing season in 2004, belonged to reproductive tillers. It can be further added that the leaf/stem ratio remains on a higher level under drought conditions, because the maturation process is slowed down due to water limitations (Albrecht et al., 1987). As spring was drier than average, both in 2004 and 2005, this may have contributed to the only minimal changes in leaf weight ratio in the present study.

Besides constant values over the vegetation period, the high NDF content ($> 700 \text{ g NDF kg}^{-1} \text{ DM}$) in early growing season is surprising. No comparable results were found in literature so far. Due to the unfavourable growth conditions, it seems possible that the native grasses protect themselves from environmental stresses like drought, by developing thick cell walls. Buxton and Casler (1993) stated that a common plant reaction to environmental stresses is cell wall thickening. Other authors reported thick, lignified cell walls to be characteristic for plants growing in dry habitats, attempting to enhance the resistance to water loss (Levitt, 1980; Melkonian, 1982; Frank et al., 1996; Frey and Löscher, 2004).

Like the NDF content, also the NDF composition was relatively constant over the growing season. Hemicellulose slightly decreased in the course of the growing season, whereas cellulose content remained unchanged in both years. Neither hemicellulose nor cellulose indicate relevant differences between defoliation treatments in 2004, whereas in 2005 hemicellulose decreased significantly in the green biomass and cellulose increased significantly in *S. grandis*. The ADL content decreased significantly due to defoliation in 2004, but differences between TII and TIII were not significant. In 2005 however, the ADL content also increased in the course of the growing season (figure 2g and 2h), but defoliation frequency did not alter the ADL content in T II and T III. Lignification of plant cell walls results from secondary wall thickening as it can be observed in ageing grass plants (Jung and Allen, 1995). Lignification is usually accelerated by high temperatures (Ford et al., 1979; Wilson et al., 1991; Van Soest, 1994). As temperatures were above average in July and August 2005 (table 1), this is probably the reason for slightly increased ADL contents in 2005. However, this does not explain why defoliation had no effect on ADL content in 2005. It can be assumed that constantly high ADL contents, like high NDF contents, contribute to the protection mechanism against drought.

From the animal nutrition point view, high lignin contents result in low digestibility, and constrict herbage quality. The strong negative correlation between lignin content and digestibility was frequently documented and lignin was used as indigestible marker for the estimation of herbage digestibility (Minson, 1982; Minson, 1990; Van Soest, 1994). Also in the present study the correlation between IVDOM and ADL content was negative and highly significant, regardless of the defoliation frequency (figure 3).

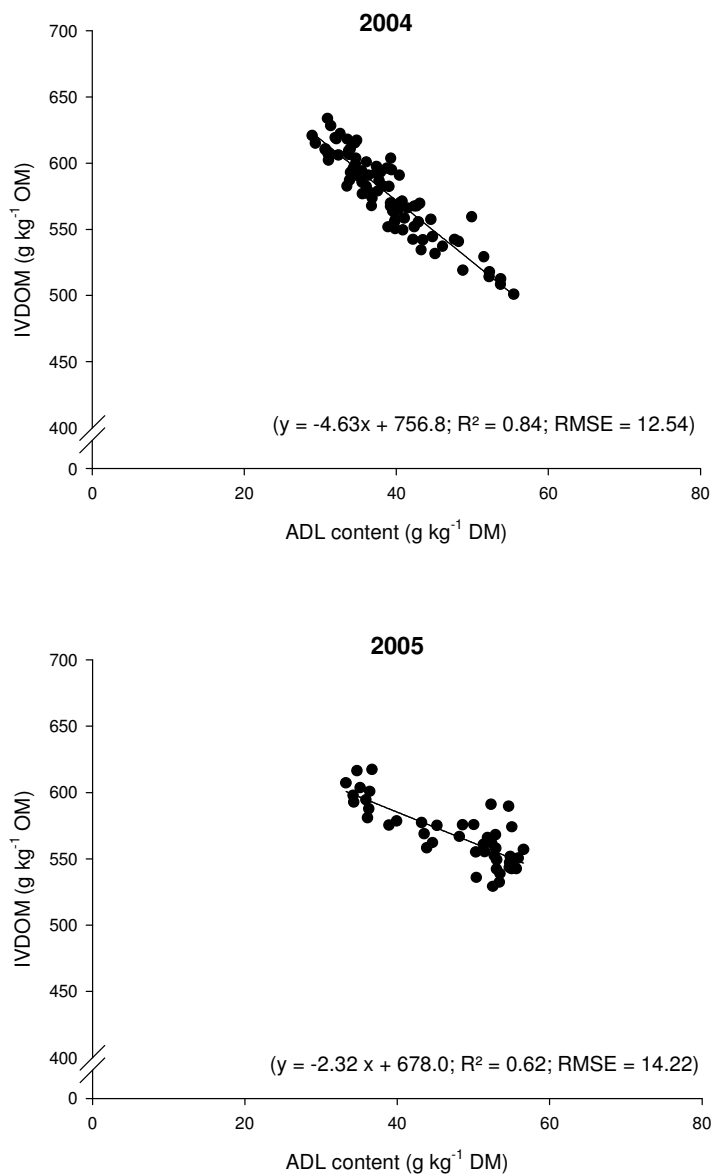


Figure 3: Relationship between IVDOM and ADL content in the green biomass in 2004 and 2005

It was expected that IVDOM increases after defoliation, because re-growing plants usually contain less cell wall, and especially have reduced ADL contents. In 2004 increasing IVDOM was observed in T II and T III, whereas in 2005 almost no differences were observed between treatments. Although significant, the magnitude of the decrease in IVDOM in 2004 was low, thus for grazing animals only minor improvements in feed conversion can be expected. This is confirmed by the small changes observed in cell wall content and its composition. The decrease in IVDOM after defoliation in 2004 can be almost completely explained by the decrease in ADL content ($R^2=0.84$, figure 3). In 2005 no changes in ADL content were observed and similarly the IVDOM did not change after defoliation, except for *S. grandis*. The IVDOM of *S. grandis* decreased in T III in 2005; this decrease can be probably attributed to the increase in NDF content, especially the proportion of cellulose, but the reasons for this higher NDF content remain unclear.

The TNC content of the investigated plant material is comparable to TNC contents obtained in experiments with other range grass species in semi-arid ecosystems (Trlica and Cook, 1972; White et al., 1972; Chatterton et al., 1989b; Forwood et al., 1992). In the present study the contents of TNC decreased significantly after defoliation in 2004 in the green biomass, as well as in *S. grandis* and *L. chinensis* (see appendix). Also in 2005 decreasing TNC contents were observed in all three sward constituents, but the decrease was only significant for *S. grandis* (table 3 and 4). Decreasing TNC content in defoliated grass plants has been widely observed (Brown and Blaser, 1965; McIlroy, 1967; White, 1973; Donaghy and Fulkerson, 1997). Defoliation reduces the leaf area and therefore the ability of the plant to photosynthesise. Stored carbohydrates are mobilised to re-establish enough leaf area for sufficient photosynthesis. This mobilisation of storage carbohydrates leads to depletion of the carbohydrate reserves, especially in the stem bases of grass plants. Usually only a few days after defoliation enough leaf area is re-grown and the plant does not depend on the stored carbohydrates anymore, and starts replenishment of the carbohydrate reserves (Davidson and Milthorpe, 1966; Prud'homme et al., 1992). If the plant is subjected to frequent defoliation it can be assumed that the reserves might not be replenished until the next defoliation is carried out and a permanent depletion follows. This was observed in the present study, as T I differed from T II and T III, but the differences in mean TNC content between 3-week and 6-week defoliation interval were not statistically significant. Since the moderate defoliation frequency (T II) did not differ from the intensive defoliation frequency (T III), the data suggest that the replenishment of carbohydrate reserves may have

taken more than 6 weeks in the described grass species. Looking at the TNC content in the course of the vegetation period, figure 1c and 1d demonstrate that the TNC content is not only influenced by defoliation frequency, but also by seasonal fluctuations. A similar level of TNC was observed in the end of the vegetation period across the three defoliation frequencies in both years. It seems that the TNC accumulate in the aboveground biomass around the end of the vegetation period, presumably induced by lower temperatures at this time of the year. Mean temperatures decreased gradually from late August on (table 1), what decreased respiration and slowed down plant growth. Photosynthesis was proved to be less sensitive to decreasing temperatures maintaining high activity, especially in the younger, defoliated plants (Caldwell et al., 1981). Reduced growth and maintained photosynthesis rates result in accumulation of TNC (Brown and Blaser, 1965; Chatterton et al., 1987). The TNC content increased in late growing season in the green biomass and in both dominant species, suggesting that the increase in TNC content is not species specific, but largely influenced by changing environmental conditions. The TNC content was generally higher in 2005 compared to 2004. Increasing TNC content has been often related to drought. Plant growth is substantially reduced by drought, but the photosynthetic activity is less sensible to environmental stresses like drought or low temperatures, as discussed above, and still active (Brown and Blaser, 1970; Hsiao, 1973; Busso et al., 1990). The result is accumulation of TNC in the plant tissue. The depletion due to defoliation was therefore less pronounced in 2005 and the effect of treatment was not significant.

Herbage quality differences between the total green biomass and the two dominant species *S. grandis* and *L. chinensis* were only small and consistent across the three sward constituents (see appendix). This is in accordance with the results of Ganskopp and Bohnert (2001) who analyzed herbage growth and quality of 7 native grasses from the semi-arid northern Great Basin (USA), and could explain only 10% of the variation in herbage quality by species effects, but 80% of the variation by seasonal effects. *L. chinensis* tended to be higher in herbage quality than *S. grandis* and the green biomass. After defoliation the development of herbage quality parameters was consistent across the three sward constituents, not indicating fundamental differences in their responses to frequent defoliation.

In accordance with the objective of the present study, which aimed at the identification of short-term responses of herbage quality parameters to different defoliation intensities, it can be stated that herbage quality is significantly influenced by frequent defoliation, although not all investigated quality parameters. However, it was

demonstrated that the climatic fluctuations between years substantially influenced the herbage quality as well, probably covering consistent short-term responses of herbage quality parameters to defoliation frequency.

Nevertheless, the CP content showed the most consistent response to different defoliation intensities, even in the dry year 2005. The OM content also showed significant differences between treatments, but these differences can be mainly attributed to the harvesting technique; therefore is the informational value of OM content obtained in the present study not transferable to grazing experiments. IVDOM responded only slightly and inconsistently. The steady digestibility is the result of the consistent cell wall content and its composition that showed only minor changes between defoliation frequencies. IVDOM and cell wall content are not suitable to identify short-term effects of defoliation stress. The TNC content has to be assessed in the same way; although significant short-term differences in TNC content were observed between defoliation frequencies, the TNC content was highly susceptible to climatic effects in both experimental years.

5. Conclusions

The CP-content is a reliable indicator for short-term effects of defoliation stress. For other herbage quality parameters the strong influence of climatic fluctuations and seasonal dynamics was demonstrated, which interfere to a great extent with short-term effects of defoliation. However, in the long-term herbage quality parameters might be useful indicators for changes caused by defoliation stress, as it is likely that herbage quality is influenced by substantial changes in the plant community, e.g. a shift from grass to shrub vegetation. From the animal nutrition point of view the quality of the investigated herbage is low and only suffices minimal nutritional requirements (Leng, 1990; Van Soest, 1994).

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Appendix

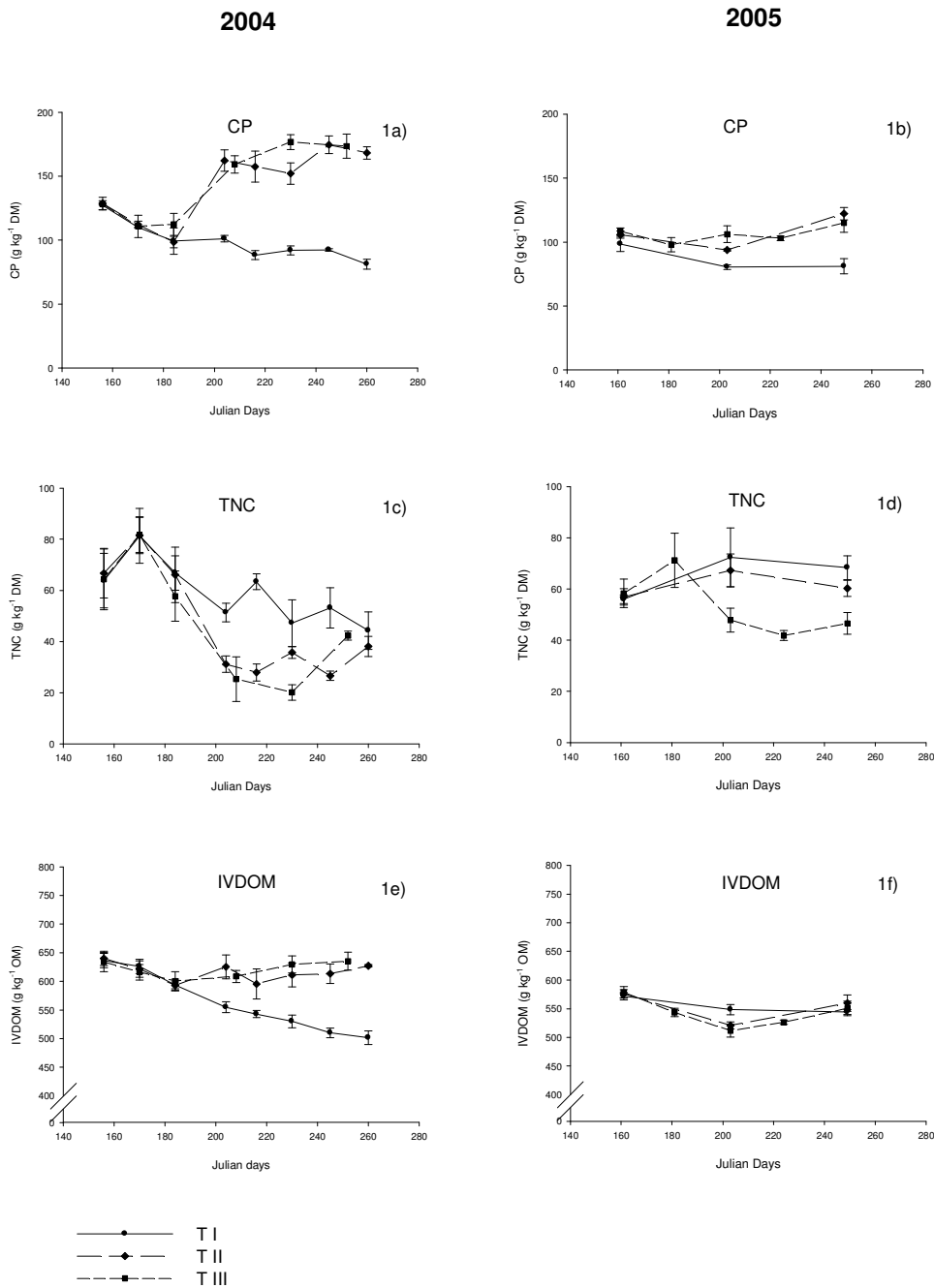


Figure I-1: Development of crude protein (CP), total non-structural carbohydrates (TNC) and in vitro digestibility (IVDOM) of *Stipa grandis* across the growing seasons of 2004 and 2005 (Error bars indicating SD; cutting dates (not indicated) in 2004: T I = day 260; T II = day 185, day 231, day 260; T III = day 185, day 209, day 230, day 252; cutting dates in 2005: T I = day 250; T II = day 204, day 250; T III = day 182; day 204; day 225; day 250)

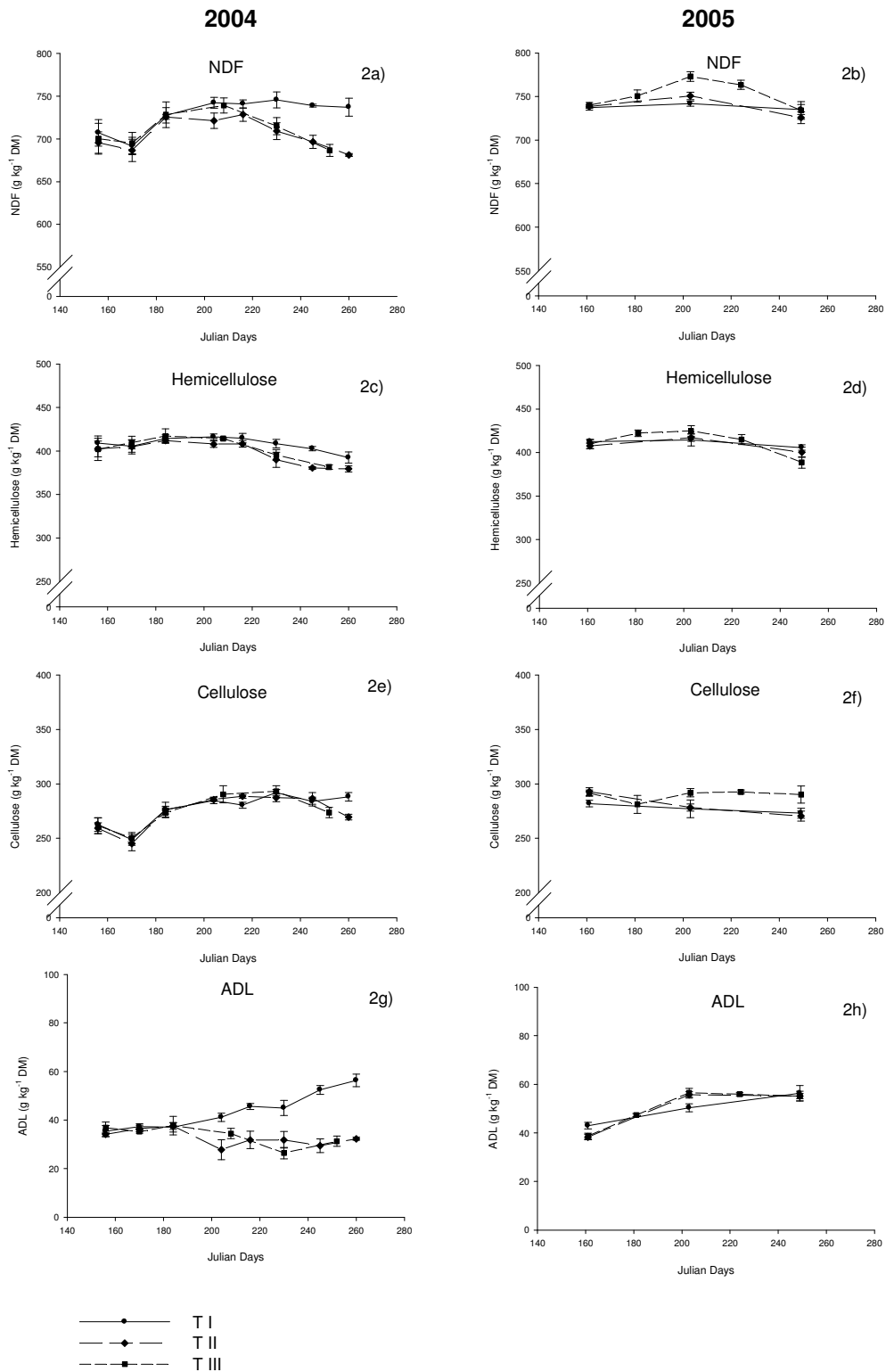


Figure I-2: Development of neutral detergent fibre (NDF), hemicellulose, cellulose and acid detergent lignin (ADL) of *Stipa grandis* across the growing seasons of 2004 and 2005 (Error bars indicating SD; cutting dates are not indicated, see figure I-1)

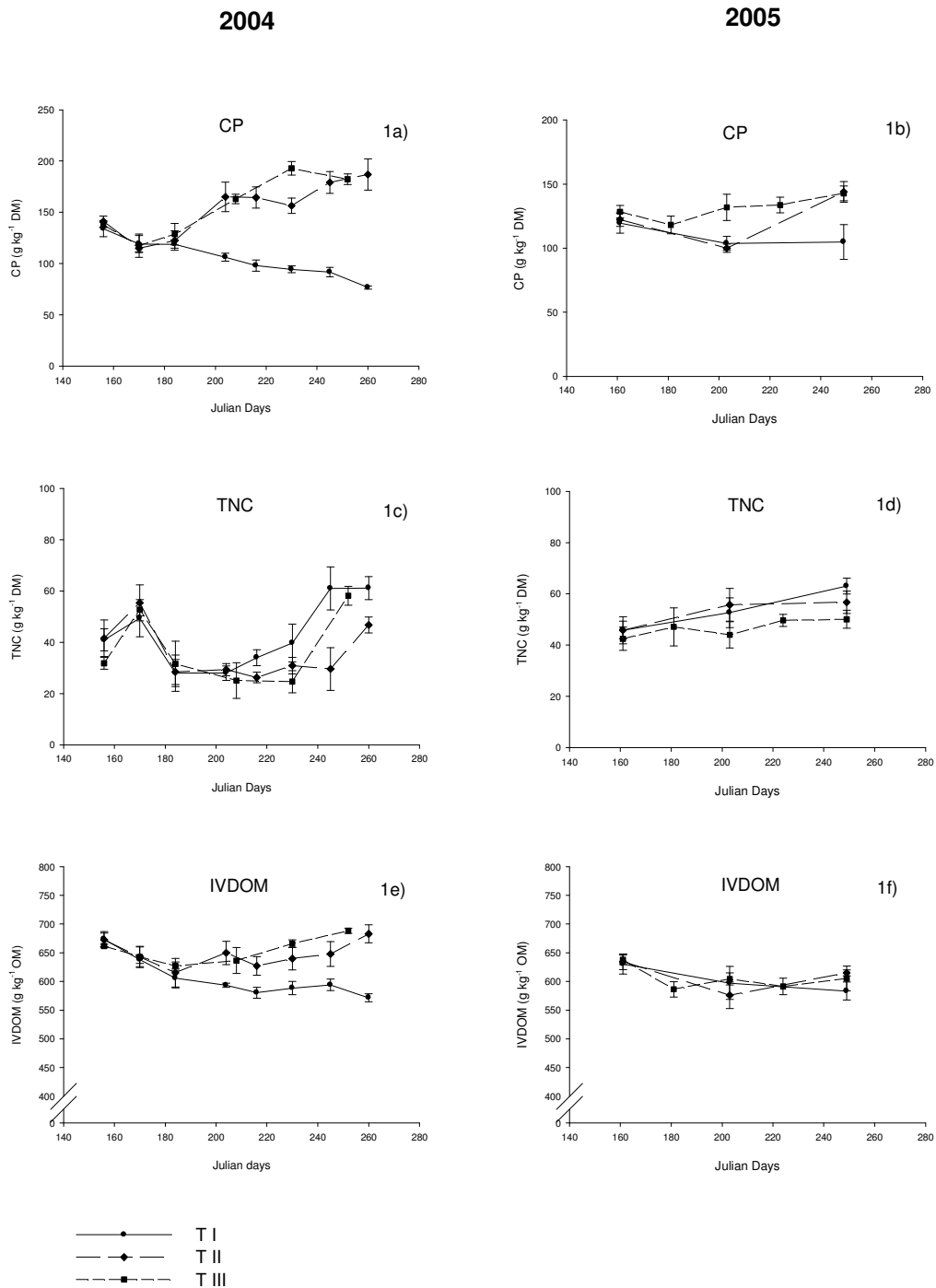


Figure II-1: Development of crude protein (CP), total non-structural carbohydrates (TNC) and in vitro digestibility (IVDOM) of *Leymus chinensis* across the growing seasons of 2004 and 2005 (Error bars indicating SD; cutting dates (not indicated) in 2004: T I = day 260; T II = day 185, day 231, day 260; T III = day 185, day 209, day 230, day 252; cutting dates in 2005: T I = day 250; T II = day 204, day 250; T III = day 182; day 204; day 225; day 250).

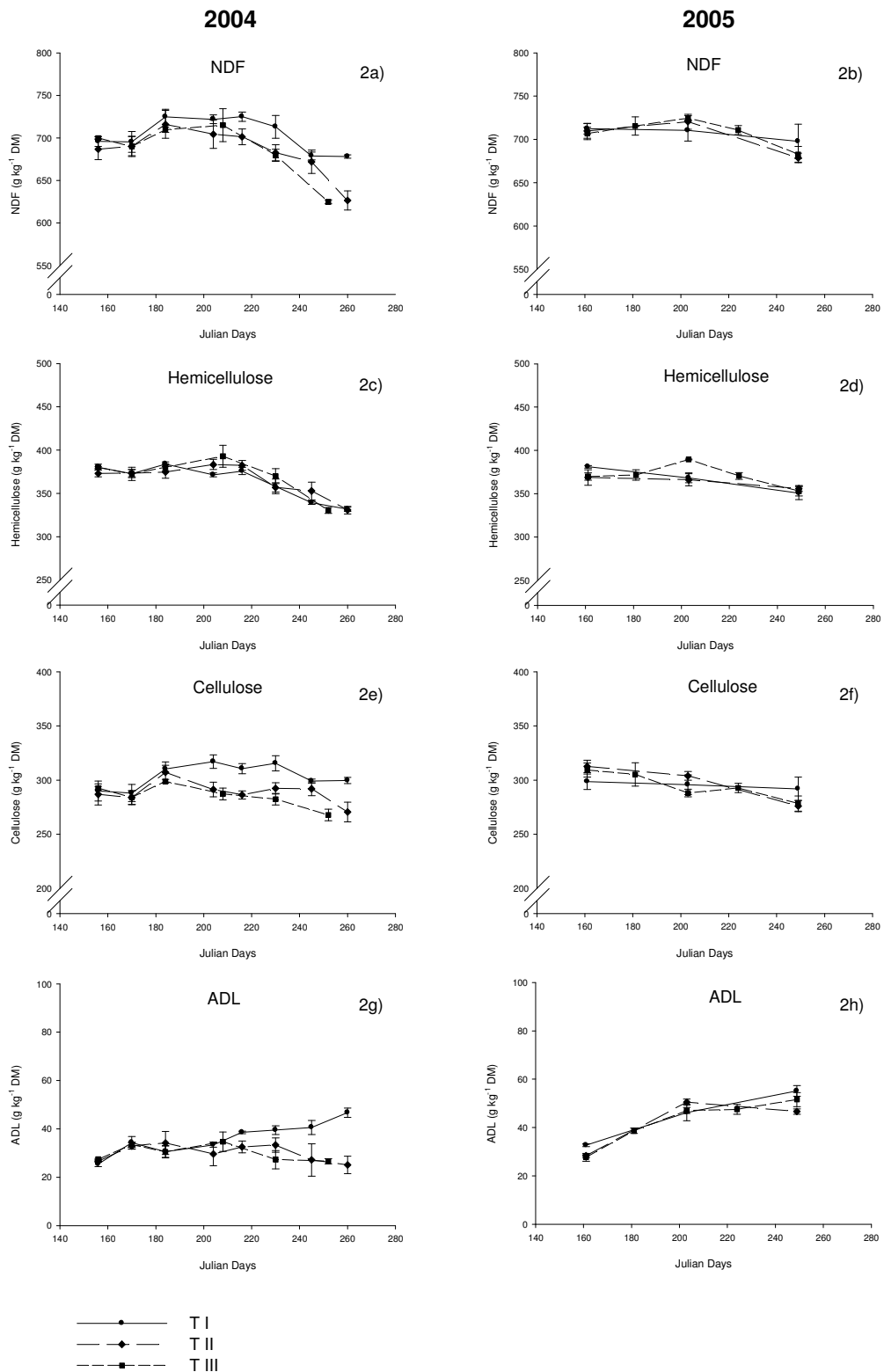


Figure II-2: Development of neutral detergent fibre (NDF), hemicellulose, cellulose and acid detergent lignin (ADL) of *Leymus chinensis* across the growing seasons of 2004 and 2005 (Error bars indicating SD; cutting dates are not indicated, see figure II-1)

Chapter 4

Comparing in vivo and in vitro determined organic matter digestibility in a grazing experiment conducted in the natural grasslands of Inner Mongolia, China

Abstract

Herbage ingested differs substantially from herbage on offer in composition and quality, when ruminants are grazing and selecting plants and plant parts of higher digestibility. Therefore it can be expected that the organic matter digestibility of herbage on offer is lower than the digestibility of the actually ingested herbage. However, when herbage on offer is limited grazing animals are not able to select their diet. The differences between herbage ingested and herbage on offer become increasingly smaller the more herbage offered is ingested, what was especially documented for temperate-humid and tropical grasslands but rarely for semi-arid grassland. The differences in digestibility of herbage ingested and herbage on offer can be used as criterion for dietary selection. If differences are large, animals have selected intensively, but if differences are small, only little dietary selection occurred.

A grazing experiment with 6 grazing intensities from light (1.5 sheep ha⁻¹) to very heavy grazing (9.0 sheep ha⁻¹) was conducted in the natural steppe grassland of Inner Mongolia, P.R. China. In July, August and September 2005 the digestibility of herbage ingested was determined by the faecal-nitrogen method (FDOM). Simultaneously the digestibility of herbage on offer was estimated using a Cellulase-technique (CDOM) and the Hohenheim gas test (GDOM). Additionally the amount of herbage on offer, the proportion of green (living) biomass, and further quality parameters of herbage on offer were determined.

Mean herbage mass on offer significantly decreased from 157 g DM m⁻² in the lowest to 60 g DM m⁻² in the highest grazing intensity. The quality of herbage on offer did not differ between grazing intensities, but decreased with proceeding vegetation period. Neither FDOM, nor CDOM or GDOM were influenced by grazing intensity, but decreased from July to September. CDOM constantly overestimated the FDOM by 3.9%-points. GDOM overestimated the FDOM in July, but in August and September GDOM and FDOM did not differ or differed only slightly by 1%-point.

GDOM corresponded well with FDOM in August and September in all grazing intensities, disproving the hypothesis that herbage on offer is less digestible than herbage ingested when herbage on offer is abundant. The correspondence between FDOM and GDOM demonstrated that herbage ingested and herbage on offer did not differ substantially from each other in the present study, suggesting that no or only little selection occurred. The applied estimation equation for CDOM

turned out to be unsuitable for the analysed herbage material, indicating a systematic prediction error.

1. Introduction

Organic matter digestibility (OMD) is the crucial quality parameter to characterise feeds and their value in animal nutrition. In vivo feeding trials are the ultimate method to measure the OMD, but in vivo methods are laborious and expensive. Therefore several in vitro methods, which are generally more efficient and reproducible than in vivo measurements, have been developed to estimate the OMD of feeds. The in vitro methods can be divided into methods still depending on the animal like gas production- (Menke et al., 1979; Pell and Schofield, 1993; Theodorou et al., 1994) and two-stage technique (Tilley and Terry, 1963), and enzymatic methods independent from the animal (Jones and Hayward, 1975; McLeod and Minson, 1978; De Boever et al., 1986). Nevertheless in vitro methods always depend on in vivo experiments to derive and validate equations for the estimation of OMD.

A particular challenge is the OMD determination in grazing experiments, because it is difficult to determine what free-ranging animals are actually ingesting, both quantitative and qualitative. To determine OMD of herbage ingested while grazing, indirect methods using indigestible markers such as acid-insoluble ash (Minson, 1990) or *n*-alkanes (Dove and Coombe, 1992) can be used. But methods based on indigestible markers rely on representative sampling of herbage and faeces, as do in vitro methods. Since ruminants are able to select their diet by preferring plants and plant parts of higher digestibility (Arnold, 1960; Lu, 1988; Jung and Sahlu, 1989), a discrepancy between herbage on offer and herbage ingested occurs. To get representative samples of herbage ingested many workers have used oesophageal fistulated animals, which is the only method to get samples of herbage actually ingested by an animal (Van Dyne and Torell, 1964; Schlecht et al., 1999; Coates and Penning, 2000). A less complex, but less accurate method is the hand-plucking method (Penning et al., 1991), where animals are observed in their grazing behaviour and samples of herbage are plucked from the sward in an attempt to mimic the ingestive behaviour of the animals. A further possibility to predict the OMD of herbage ingested is the use of faecal indices such as nitrogen (N) or chromogen (Rymer, 2000). In vivo determined digestibility is related to a faecal component and a regression can be established between in vivo digestibility and the component's con-

centration in the faeces. After establishing the regression herbage samples are not required anymore. The most common used component is N, which has been used successfully in several studies and is known as the faecal-N method (Lancaster, 1949; Corbett, 1960; Thomas and Campling, 1976; Schmidt and Jentsch, 1994; Lukas et al., 2005; Schlecht and Susenbeth, 2006).

From the grassland science point of view, a representative herbage sample represents the herbage on offer, which may also be defined as herbage yield. As explained above herbage on offer normally differs considerably from herbage ingested (Coates and Penning, 2000). If the OMD of herbage on offer is estimated to define herbage quality, it is obvious that this estimate does not represent the OMD of herbage ingested. However there is one constraint: two situations of herbage availability are conceivable, i.e. abundant herbage on offer and limited herbage on offer. When enough herbage is available, the animals will select their diet, but if herbage on offer is limited the animals need to ingest the herbage available in attempt to satisfy their nutritional requirements (Bryant et al., 1970). This relationship has been mainly investigated in temperate-humid (Hamilton et al., 1973; Jung et al., 1989) and tropical (Chacon and Stobbs, 1976) grasslands, but less information is available for semi-arid grasslands that produce only few herbage of poor quality. The hypothesis of the present study is that in semi-arid grasslands, because of the generally low herbage quality, the selectivity of the grazing animals is high and therefore the OMD of herbage ingested in grazing situations with abundant herbage on offer will be higher than the OMD of herbage on offer. However, if herbage on offer is limited, due to high grazing intensity for example, the OMD of herbage ingested and the OMD of herbage on offer will converge as it has been observed in indoor feeding trials (Cherney et al., 1990).

The discrepancy between OMD of herbage ingested and OMD of herbage on offer was additionally used as a criterion for dietary selection (Hamilton et al., 1973; Jung et al., 1989; Schmidt et al., 1999). This means that at large discrepancy the animals are selecting intensively, but at low or without discrepancy herbage on offer does not differ from herbage ingested and no selection occurs, or is not detectable.

A grazing experiment was initiated in 2005 in the semi-arid grasslands of Inner Mongolia, P.R. China. Six grazing intensities from light to very heavy grazing (1.5, 3.0, 4.5, 6.0, 7.5, 9.0 sheep ha⁻¹) and their impact on the grassland ecosystem were assessed, offering the opportunity to test the proposed hypothesis against a wide range of herbage availabilities. Results from the grazing period of 2005 are presented.

2. Material and Methods

2.1 Study site, experimental design and conditions

The described investigation is part of the Sino-German MAGIM-project (Matter fluxes in grasslands of Inner Mongolia as influenced by stocking rate). The experiment was carried out near the Inner Mongolia Ecosystem Research Station (IMGERS) operated by the Institute of Botany, Chinese Academy of Sciences, Beijing. IMGERS is located in the Xilin River Basin, Inner Mongolia Autonomous Region, P.R. China (116°42' E, 43°38' N) at an altitude of approximately 1200 m. The climate is semi-arid, characterised by significant seasonal and inter-annual variability (table 1).

Table 1: Mean temperature (°C) and mean precipitation (mm) on a yearly basis and for the growing season as 20-year mean, 2004 and 2005

	Temperature (°C)			Precipitation (mm)		
	1983-2003	2004	2005	1983-2003	2004	2005
May	11.3	10.8	10.6	31	23	11
June	16.5	18.2	17.7	57	29	32
July	19.0	18.7	20.13	100	50	59
August	17.4	16.2	19.23	70	133	27
September	10.8	11.5	12.33	36	53	13
annual mean	0.7	1.9	0.1	343	325	166

Mean annual temperature is 0.7°C and mean annual precipitation is 346 mm, of which 85% are occurring from May through September. The vegetation period is about 150 days long, only 100 to 135 days are frost-free. The area can be classified as typical steppe (Yu et al., 2004). The vegetation is dominated by grasses, which comprise more than 90% of the total biomass. Some forb species are also found, but no shrubs or trees. The perennial bunchgrass *Stipa grandis* P. Smirn. and the rhizomatous *Leymus chinensis* (Trin.) Tsvetlev are the dominant grass species, both belonging to the C3 photosynthesis type. Together these grasses account for approx. two-thirds of the dry-matter (DM)-yield of the experimental area. A grazing experiment was initiated in June 2005 on an area moderately grazed by sheep in the previous years. The experiment is a randomised block-design with two replicates. Six grazing intensities ranging from light to very heavy grazing (1.5, 3.0,

4.5, 6.0, 7.5 and 9.0 sheep ha⁻¹) are compared in terms of their impact on the steppe ecosystem. Wang et al. (1999) defined an optimal stocking rate of 3 sheep ha⁻¹ for a similar, but less productive herbage sward in the Xilin River Basin, using mature wethers. In the present study female sheep aged 15 month were used, which were smaller and lighter than mature wethers. Therefore the grazing intensities chosen can be classified as light (1.5 and 3.0 sheep ha⁻¹), moderate (4.5 and 6.0 sheep ha⁻¹) and heavy (7.5 and 9.0 sheep ha⁻¹) grazing intensities. Sheep were chosen, as they are the most frequent livestock in Inner Mongolia grazing the natural grassland. Groups of 6 to 18 sheep from a local fat-tailed breed grazed 12 paddocks (6 grazing intensities x 2 replicates) continuously from June through September. The female, non-lactating and non-pregnant sheep had an average body weight of 31.6 kg (SD \pm 4.8) in the beginning of the experiment. Sheep were not supplemented, had free access to water and minerals and were treated against endoparasites prior to the start of the experiment. Sampling periods were the 11th to the 15th July, 8th to 12th August and 12th to 16th September 2005.

2.2 Herbage sampling and analysis

Herbage on offer was defined as standing biomass cut to 1 cm stubble height, what was assumed to be the minimum bite height of a sheep under restricted but not starving conditions. Litter (dead biomass spread on the ground) was not included, but all standing dead biomass was sampled with the living biomass. The herbage on offer samples were taken only once during the sampling periods. In each paddock one sample was obtained from 3 sub-samples, taken from 0.5 m² (0.25 x 2 m) sized transects at previously defined representative areas. The 3 sub-samples were pooled and weighed. From the bulk sample an additional sample (ca. 40-50 g) was taken to separate green (living) herbage from dead herbage. Afterwards all samples were dried at 60°C for 24 h in a forced-air drying-oven and dry-weight was determined. The dried bulk samples were ground with a cyclotec mill (Tecator, Germany) to pass through a 1 mm screen. The quality of herbage samples was determined by means of Near-Infrared-Spectroscopy (NIRS). All samples were scanned twice with a NIR-Systems 5000 monochromator (Perstrop Analytical Inc., Silver Spring, MD, USA) over a wavelength range from 1100 to 2500 nm in 2 nm intervals. The software NIRS 2 by Infrasoft International[®] (ISI, Port Mathilda, PA, USA) was used for scanning, mathematical processing, calibration and statistical analysis of the spectra data. The laboratory analyses were carried out on calibra-

tion and validation sub-sets of herbage samples, which were randomly chosen by the software NIRS 2. Residual DM content was determined by drying at 105°C until a constant dry weight was reached. Organic matter (OM) content was calculated as the difference between the dry sample and the residue (ash) after incineration of the dry sample at 550°C over night. The crude protein (CP) content was calculated from the N content ($CP = N \times 6.25$), which was analysed by a C/N-Analyzer (vario Max CN, Elementar Analysensysteme, Hanau, Germany) which is based upon the DUMAS combustion method. Neutral detergent fibre (NDF), acid detergent fibre (ADF) and acid detergent lignin (ADL) were analysed sequentially by a semi-automated Ankom 200 Fiber Analyzer (Ankom Technology, Macedon, NY, USA) according to the procedures described by Van Soest et al. (1991).

2.3 Digestibility of herbage ingested

The OMD of herbage ingested was determined using a faecal-N-method and the equation of Wang et al. (2007). Six sheep per paddock were chosen and faeces samples were taken as grab samples from the rectum of these sheep on 5 consecutive days in each sampling period. The faeces samples of each sheep were pooled, frozen and homogenized to analyse the N content by the Micro-Kjeldahl procedure.

Equation 1 was used to estimate the OMD of herbage ingested from faecal-N (FDOM) (Wang et al., 2007).

$$\text{FDM} (\%) = 89.9 - 64.4 * \exp^{(-0.5774 * \text{faecal CP [g/kg OM]}/100)} \quad [1]$$

The non-linear mixed model procedure (SAS Institute Inc., Cary, NC, USA) was used to derive equation 1 from an extensive data set containing 721 values from in vivo experiments with mainly grass and legume silages, as well as data from difference trials with hay and soybean meal. The mean in vivo OMD of the tested feed-stuffs was 66.5%, ranging between 41% and 83%. The mean bias between predicted and in vivo measured OMD was -1.4%, with a standard error of 0.17.

2.4 Digestibility of herbage on offer

Two approved and standardised in vitro methods were chosen to estimate the digestibility of herbage on offer. One was the Cellulase-technique (CT) developed by De Boever et al. (1986) and the other one the Hohenheim gas test (HGT) working with rumen fluid (Menke et al., 1979).

The CT was carried out following the standardised procedure of Naumann and Bassler (1993). The cellulase digestible OM (CDOM) was estimated by equation 2 (Weissbach et al., 1999).

$$\text{CDOM}^a (\%) = 100 \cdot (940 - \text{CA} - 0.62 \cdot \text{EULOS} - 0.000221 \cdot \text{EULOS}^2) / (1000 - \text{CA}) \quad [2]$$

(^a CA = crude ash, EULOS = enzyme insoluble OM; CA and EULOS in g kg⁻¹ DM)

Equation 2 is based on the results of 125 in vivo digestibility trials with various grass products (fresh grass, grass silage, hay) of very different qualities and was independently validated on 160 further in vivo digestibility measurements. The mean OM digestibility ranged between 42% and 86%, the CP content between 5.4% and 23.3%. The relative standard error was 3.8% for the derivation of the equation and 4.2% for the validation.

The HGT was conducted according to the specifications of Menke and Steingass (1988), with the modification that rumen fluid was collected approx. 90 minutes after morning feeding. The wethers were fed twice daily at 0700 and 1700, getting 1.8 kg hay and 1.4 kg concentrate divided in 2 equal meals. The average weight of the wethers was 90 kg. The digestible OM from gas production (GDOM) was estimated by regression equation 3 (Menke and Steingass, 1988).

$$\text{GDOM}^b (\%) = 16.49 + 0.9042 \cdot \text{GP} + 0.0492 \cdot \text{CP} + 0.0387 \cdot \text{CA} \quad [3]$$

(^b GP: ml 200 mg⁻¹ DM in 24 h, CP and CA: g kg⁻¹ DM)

The equation was derived from a regression including data from 100 roughage feeds (50% hays, 25% straws, 25% grass cobs) tested in in vivo digestibility trials ranging from 30.4 to 75.9% in OMD. The relative standard error was 4.3% with $r^2 = 0.93$.

2.5 Statistical analysis

Digestibility values obtained from faecal-N, CT and HGT were subjected to an ANOVA using the mixed procedure of SAS[®]9 (SAS Institute Inc., Cary, NC, USA), including 'block', 'grazing intensity' (I), 'sampling period' (P) and the interaction 'I x P' as fixed factors. The three periods were considered as repeated measurements. With significant F-value ($P < 0.05$) means were tested with Student's t-Test and probabilities corrected by Bonferroni-Holm test (Horn and Vollandt, 1995).

The in vitro estimates (CDOM, GDOM) were tested against the FDOM estimates, which were taken as the reference values. The differences between FDOM and

CDOM, and the differences between FDOM and GDOM were also subjected to an ANOVA using the same model as before. By means of Student's t-test it was tested if the differences were to separate from zero. Furthermore it was investigated if the differences between FDOM and in vitro estimates were significantly different from zero as a mean of all intensities and periods.

3. Results

3.1 Herbage on offer

The factors 'grazing intensity' and 'sampling period' were significant for herbage on offer, but the interaction 'I x P' was not significant. Herbage on offer decreased with increasing grazing intensity (table 2). However, the differences between grazing intensities were only significant between 1.5 sheep ha⁻¹ and 7.5 sheep ha⁻¹. Mean herbage on offer in July and August was 104 g m⁻² and 100 g m⁻², respectively. In September herbage on offer decreased significantly to 71 g m⁻². The green herbage proportion of herbage on offer was not influenced by grazing intensity, but green herbage proportion decreased significantly from 95% in July to 82% and 79% in August and September, respectively.

Table 2: Herbage on offer and proportion of green herbage at sampling periods in July, August and September 2005

sheep ha ⁻¹	herbage on offer (g DM m ⁻²)					green herbage* (% of herbage on offer)				
	July	Aug.	Sept.	mean	SE	July	Aug.	Sept.	mean	SE
1.5	146	170	155	157 ^a		97	91	86	91 ^a	
3.0	121	126	107	118 ^{ab}		96	83	80	87 ^a	
4.5	100	72	50	74 ^{ab}	15	94	81	79	85 ^a	3
6.0	111	109	49	89 ^{ab}		96	81	75	82 ^a	
7.5	59	66	36	54 ^b		92	81	74	83 ^a	
9.0	89	61	30	60 ^{ab}		97	82	77	84 ^a	
mean	104 ^A	100 ^A	71 ^B			95 ^A	82 ^B	79 ^B		
SE		8					2			

* green herbage on offer = herbage on offer minus standing necrotic material

Superscripts ^{a,b,c} indicate significant ($P < 0.05$) differences between grazing intensities.

Superscripts ^{A,B,C} indicate significant ($P < 0.05$) differences between sampling periods.

The quality of herbage on offer was not significantly different between grazing intensities, but some quality parameters changed in the course of the growing season (table 3). The CP content decreased significantly from 98 to 88 and 77 g kg⁻¹ DM from July to September. ADF and ADL content increased significantly from July to September, whereas NDF did not change during this time.

Table 3: Quality of herbage on offer in July, August and September 2005*

(g kg ⁻¹ DM)	OM	CP	NDF	ADF	ADL
July	945 ^{ab}	98 ^a	730	340 ^b	41 ^c
August	944 ^b	88 ^b	726	348 ^{ab}	50 ^b
September	945 ^a	77 ^c	723	353 ^a	54 ^a
SE	1.4	2.8	3.2	2.7	0.7

* n = 12 for each quality parameter within sampling period

Superscripts ^{a,b,c} indicate significant ($P < 0.05$) differences between sampling periods.

3.2 Digestibility estimation

The experimental factor 'sampling period' was significant for FDOM, CDOM and GDOM, whereas the factor 'grazing intensity' and the interaction 'I x P' did not differ. Results of digestibility estimations are summarised in table 4. Grazing intensity did not significantly affect the digestibility of OM, neither in vivo (FDOM), nor in vitro (CDOM, GDOM). The sampling period however, had a significant influence on di-

gestibility, since the digestibility decreased as the vegetation period proceeded. The mean FDOM significantly decreased from 56.5% in July to 55.6% and 53.8% in August and September, respectively. The mean CDOM ranged between 60.3% and 57.8% and a significant decrease was observed only in September. The mean GDOM indicated the widest range of digestibility estimates of all methods, ranging from 60.5% to 52.9%, so that the differences in mean GDOM were significant between all sampling periods.

The differences between FDOM and CDOM, as well as the differences between FDOM and GDOM were tested against zero to determine if significant differences exist between the digestibility estimations. For each sampling period the gradients for the 3 digestibility estimations over the 6 grazing intensities are demonstrated in figure 1 and the statistical ratios are given in table 5. In July CDOM and GDOM overestimated FDOM on average by 3.8%- and 4.0%-points. The differences between FDOM and in vitro estimates were significantly different from zero, but the in vitro estimates did not differ among each other. In August CDOM still overestimated FDOM on average by 3.9%-points, but GDOM could not be separated statistically from FDOM. In September CDOM still overestimated FDOM rather constantly by approx. 4.0%-points over all grazing intensities, whereas GDOM slightly underestimated FDOM by 1.0%-point, especially in the lowest and the highest grazing intensity.

To evaluate if CDOM and GDOM differ significantly from FDOM irrespective of the sampling period, estimates were tested over all grazing intensities and all sampling periods.

Table 4: Digestibility estimated by faecal-N method (FDM), Cellulase-technique (CDM) and Hohenheim gas test (GDM) (%) in July, August and September 2005

	grazing intensity (sheep ha ⁻¹)						mean	SE
	1.5	3.0	4.5	6.0	7.5	9.0		
FDM (%)								
July	58.0	58.2	56.5	55.8	54.9	55.9	56.5 ^A	
Aug.	57.5	56.8	55.3	55.4	54.7	54.2	55.6 ^B	0.4
Sept.	56.4	54.6	54.0	53.1	53.0	51.9	53.8 ^C	
mean	57.3 ^a	56.5 ^a	55.2 ^a	54.7 ^a	54.2 ^a	54.0 ^a		
SE								0.8
CDM (%)								
July	60.0	60.1	61.3	61.5	60.4	58.5	60.3 ^A	
Aug.	59.7	60.8	59.8	59.9	58.4	58.8	59.6 ^A	0.5
Sept.	59.4	60.6	57.8	57.6	56.9	54.6	57.8 ^B	
mean	59.7 ^a	60.5 ^a	59.6 ^a	59.7 ^a	58.6 ^a	57.3 ^a		
SE								0.9
GDM (%)								
July	61.3	59.7	60.1	60.9	60.6	60.4	60.5 ^A	
Aug.	57.5	55.9	56.5	56.2	55.1	54.7	56.0 ^B	0.4
Sept.	53.7	54.6	53.3	53.4	51.7	50.5	52.9 ^C	
mean	57.5 ^a	56.7 ^a	56.6 ^a	56.9 ^a	55.8 ^a	55.2 ^a		
SE								0.8

Superscripts ^{a,b,c} indicate significant ($P < 0.05$) differences between grazing intensities within methods.

Superscripts ^{A,B,C} indicate significant ($P < 0.05$) differences between sampling periods within methods.

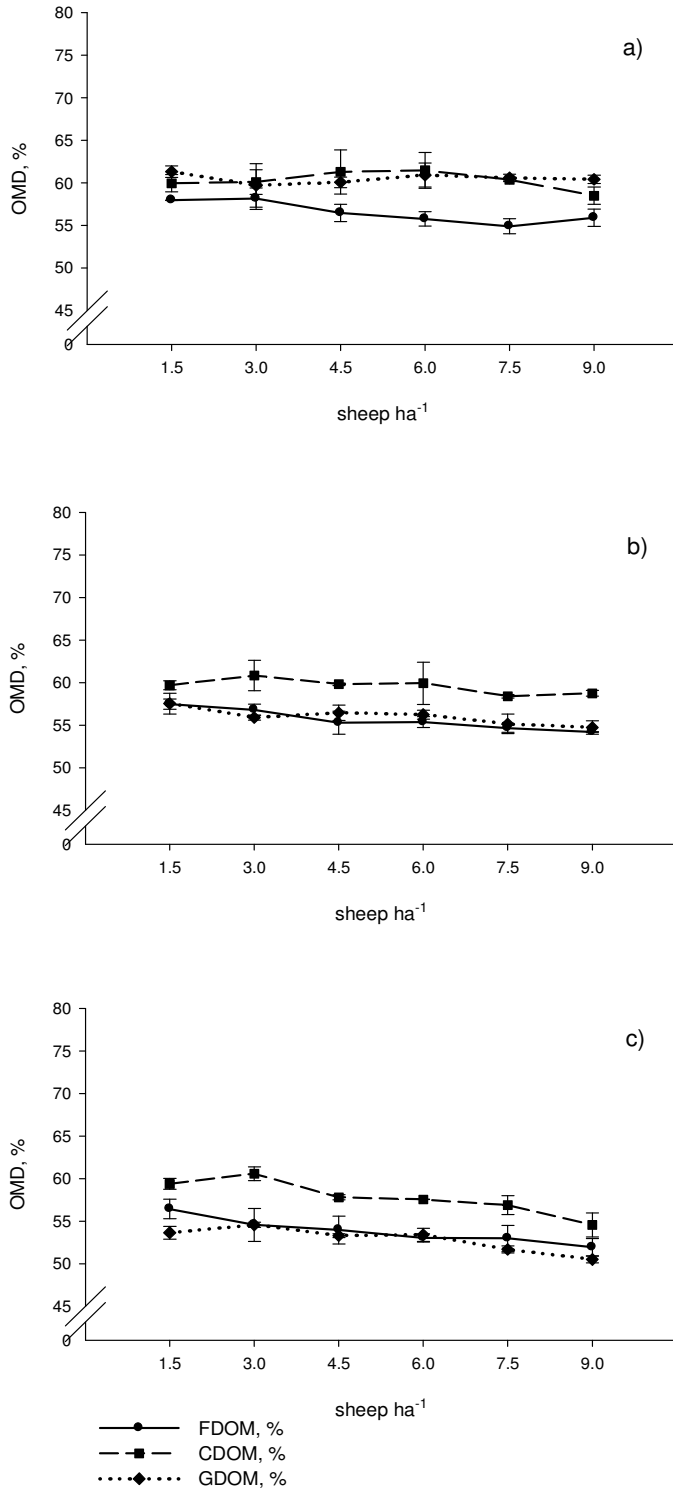


Figure 1: Digestibility estimated for the different grazing intensities by faecal-N (FDOM), Cellulase-technique (CDOM) and Hohenheim gas test (GDOM) at sampling periods in July (a), August (b) and September (c) 2005

The statistical analysis showed that CDOM in general significantly overestimated FDOM on average by 3.9%-points. GDOM overestimated FDOM significantly considering all sampling periods as well, but the average overestimation was only 1.1%-points (table 5).

Table 5: Statistical analysis of differences estimated by faecal-N method (FDOM), Cellulase-technique (CDOM) and Hohenheim gas test (GDOM) tested against zero

sampling period	FDOM	CDOM	FDOM - CDOM	GDOM	FDOM - GDOM
July	56.52	60.28	- 3.75***	60.50	- 3.98***
August	55.63	59.57	- 3.94***	56.00	- 0.37 ^{ns}
September	53.82	57.79	- 3.97***	52.86	0.96*
<i>SE</i>	<i>0.75</i>	<i>0.87</i>	<i>0.62</i>	<i>0.76</i>	<i>0.42</i>
mean	55.33	59.21	-3.89***	56.45	- 1.13**
<i>SE</i>			<i>0.07</i>		<i>0.05</i>

Differences are significantly different from zero: * ($P < 0.05$), ** ($P < 0.01$), *** ($P < 0.001$).

4. Discussion

In multi-species, low quality grassland swards pronounced herbage selection of grazing ruminants was often observed, in attempt to actively improve the diet with regard to nutritional requirements (Leigh and Mulham, 1967; Grant et al., 1982; Bartolomé et al., 1998). Especially sheep and goats show pronounced herbage selection (Jamieson and Hodgson, 1979; Lu, 1988). One premise for selectivity is that herbage is abundant. In high grazing intensities however, herbage on offer is reduced and selection becomes limited (Wilson and MacLeod, 1991). Grazing animals are forced to ingest more unpalatable, low quality sward components in attempt to meet their nutritional requirements (Cook et al., 1953; Milne et al., 1979; Senft, 1989; Animut et al., 2005). The digestibility of herbage ingested therefore decreases. This is especially expected in continuously grazed swards, particularly at the end of the grazing season when grazing pressure remains high, but herbage re-growth rate declines (Bryant et al., 1970).

In the present study six grazing intensities were examined, at least two can be classified as high grazing intensities (7.5 and 9.0 sheep ha⁻¹) for the examined natural semi-arid grassland. For FDOM however, no significant differences be-

tween grazing intensities were indicated, only between sampling periods (table 4). Herbage on offer decreased significantly with increasing grazing intensity, so this precondition for the expected decrease in digestibility of herbage ingested was met. Hamilton et al. (1973) have pointed out that the digestibility of herbage ingested is closely related to green herbage yield, which they found to be decreasing when herbage on offer was reduced. Jung and Sahlu (1989) have observed less green herbage on offer in a more intensively grazed sward compared to a lightly grazed one. Simultaneously these authors observed higher digestibility of herbage ingested for sheep grazing at light intensity, what they attribute to the superior chances to select high digestible green herbage. As demonstrated in table 2 the green herbage proportion of herbage on offer was not significantly influenced by grazing intensity, only the sampling date had a significant influence. This result underlines the observation made for the digestibility of herbage ingested. If the amount of green herbage on offer did not significantly change between grazing intensities, all sheep were offered the same proportion of green herbage mass in relation to mass of herbage on offer. This suggests that sheep did not, or only to a small extent, select between green and dead herbage on offer.

Although it was reported that sheep still select their diet when herbage on offer was limited, it seems that the sheep in the present study rather optimised their intake than the quality of their diet (Broom and Arnold, 1986; Garcia et al., 2003). Significant differences in herbage intake per sheep and day between grazing intensities were not observed in this experiment, what supports this assumption (Glindemann et al., 2007).

Digestibility of herbage ingested can also be influenced by herbage intake. Namely high intake rates are expected to result in faster ruminal passage rates, reducing the digestibility of herbage ingested (Van Soest, 1994). Since intake rate was not significantly altered between grazing intensities, it is unlikely that the digestibility of herbage ingested was affected by passage rate in this experiment.

The quality of herbage on offer was also not significantly influenced by grazing intensity (table 3). Herbage quality was characterised by high and constant cell wall contents (> 700 g NDF kg^{-1} DM) over the vegetation period. The CP content decreased significantly from July to September, but never fell below 70 g kg^{-1} DM, what has been defined as the minimum content for efficient ruminal fermentation (Van Soest, 1994). ADL increased significantly from July to September, as a result of plant maturing processes. Decreasing CP and increasing ADL account for the

decline in digestibility of herbage on offer as the vegetation period proceeded (Minson, 1990).

For light to moderate grazing intensities increasing quality of herbage on offer was observed (Arnold, 1960; Schlegel et al., 2000). Through grazing less grass plants become reproductive and therefore the proportion of the less digestible stem fraction is increasing to a lesser extent (Terry and Tilley, 1964; Laredo and Minson, 1975). For high grazing intensities (where feed intake exceeds re-growth potential) however, a reduction in green material was observed, which resulted in reduced quality of herbage on offer (Cook et al., 1953; Hamilton et al., 1973; Chacon and Stobbs, 1976; Animut et al., 2005). The reason for this reduction is that only lower, less digestible layers of the sward are left and still available to the grazing animals (Blaser et al., 1960). The major influence on the quality of herbage on offer is the proportion of green herbage. It was demonstrated that the green herbage proportion of herbage on offer was constant for all grazing intensities, what explains the small influence of grazing intensity on the quality of herbage on offer.

Selective behaviour was often observed in sheep, raising the question why selection could not be observed in the present study, although such a large gradient of grazing intensities was examined. Selectivity might be reduced, when the sward composition is rather homogenous (Arnold, 1981). This is unlikely to occur in multi-species grassland swards which are continuously grazed. It has been widely demonstrated that grazing results in patchy structures of grazed and ungrazed areas, resulting in areas of high and low herbage quality (Bakker et al., 1983; Willms et al., 1988). Particularly when herbage was abundant clear structures have been observed, whereas in more intensively grazed swards the structures were less significant. In the present study grazing started in mid-June 2005 and the sward conditions were the same for all grazing intensities as it was the first experimental year. On average 80 g DM m⁻² of herbage were offered in June. The horizontal structure was not examined, but from observation it can be reported that patchy structures occurred in the moderate and high grazing intensities, but were not very stable due to marginal re-growth of herbage as influenced by the persistent drought in 2005 (table 1). In the light grazing intensities clear patch structures were hardly observed, except close to the watering places.

Looking at the vertical quality structure of the two dominant species *S. grandis* and *L. chinensis* (table 6) in an additional experiment in July 2005, it is likely that due to a homogenous vertical quality structure the sheep were limited in their selection

possibilities. The additional experiment was carried out in the same location, as a cutting frequency experiment (Schiborra et al., 2006).

Table 6: Quality of *Stipa grandis*' and *Leymus chinensis*' vertical layers in July 2005

layer	<i>Stipa grandis</i>			<i>Leymus chinensis</i>		
	CP (g kg ⁻¹ DM)	NDF (g kg ⁻¹ DM)	CDOM (%)	CP (g kg ⁻¹ DM)	NDF (g kg ⁻¹ DM)	CDOM (%)
> 21 cm*	95.6 ^b	706.4 ^e	61.7 ^a	-	-	-
17-21 cm	102.5 ^a	720.2 ^d	60.5 ^a	109.2 ^b	722.5 ^a	58.3 ^b
12-16 cm	102.2 ^a	736.6 ^c	57.6 ^b	128.0 ^a	704.4 ^b	61.1 ^a
7-11 cm	100.4 ^a	749.2 ^b	55.4 ^c	124.3 ^a	710.2 ^a	61.3 ^a
1-6 cm	82.6 ^c	765.9 ^a	51.4 ^d	99.0 ^c	710.9 ^a	61.1 ^a
SE	0.9	2.4	0.5	2.2	3.0	0.2

* *Leymus chinensis* plants were smaller than 21 cm

Superscripts ^{a,b,c,d,e} indicate significant differences ($P < 0.05$) between layers within sampling period.

The two dominant species account together for about 65% of herbage on offer. The samples for the determination of the vertical quality structure were taken from plots cut only once in the end of the vegetation period (hay cut). The grass plants were divided into 5 cm layers, from 1 cm above ground level to the top. CP and NDF content, as well as CDOM were determined for each layer as described for herbage on offer. *L. chinensis* generally shows better quality than *S. grandis*. *S. grandis* increased significantly in quality from the bottom up, as it is expected for grasses and give the sheep the chance to select plant parts of higher quality (Wilkinson et al., 1970; Delagarde et al., 2000). *S. grandis* is a needlegrass and is characterised through very thin leaves, growing in crowded bunches, what constricts the sheep in selection between green and dead *S. grandis* shoots. *L. chinensis* however, the most abundant species, is a rhizomatous grass expanding single tillers, what facilitates selection. *L. chinensis* indicated only minor differences in its vertical quality structure (table 6). Particularly the CDOM did not vary significantly between the most productive layers. *L. chinensis* is highly palatable (Wang et al., 2001) and favoured by grazing animals, what is reflected in its common Chinese name "sheep grass" and probably further increases the proportion of *L. chinensis* ingested compared to the proportion of *S. grandis*. These findings further support the argument

that selective grazing was restricted and therefore no significant effect of grazing intensity on FDOM was observed.

As demonstrated not only grazing intensity, but the sampling period did significantly influence FDOM. From July to September the FDOM decreased significantly as the growing season proceeded, what has been widely observed in grazing experiments. Generally decreasing herbage quality is the result of plant maturation processes which have been examined extensively and reviewed by several workers (e.g. Nelson and Moser, 1994; Buxton et al., 1996). Furthermore the year 2005 was extremely dry. Normally mean yearly precipitation is about 350 mm, but in 2005 only 166 mm of rain were recorded in the region (table 1). The drought additionally accelerated the onset of plant senescence and therewith the decrease in quality of herbage on offer (table 3).

FDOM was estimated by the faecal-N method, which has been widely used to predict the digestibility of herbage ingested in grazing experiments (Corbett, 1960; Thomas and Campling, 1976; Schmidt et al., 1999; Boval et al., 2003; Lukas et al., 2005; Schlecht and Susenbeth, 2006). The majority of these studies have successfully used this method, but also indicated difficulties and restrictions, like the use of equations for selected feeds only (Greenhalgh and Corbett, 1960; Boval et al., 2003) or the influence of the vegetative stage of herbage (Minson and Kemp, 1961; Schmidt et al., 1999). The equation used here to estimate the digestibility of herbage ingested was derived from an extensive data pool ($n = 721$) including 33 results of digestibility trials with local hay from Inner Mongolia grasslands (Wang et al., 2007). The equation is of reasonable accuracy, but overestimates the digestibility of the hay from Inner Mongolia by 2.2%-points. As the digestibility estimates derived from this equation are closely related to the grazing sheep, they were taken as reference values in comparison with in vitro digestibility estimates.

It was hypothesised in the present study that the OMD of herbage on offer (CDOM, GDOM) will be lower than the OMD of herbage ingested (FDOM) in low grazing intensities, because the sheep can intensively select their diet from abundant herbage on offer. In the high grazing intensities however, selection becomes limited and therefore FDOM and the in vitro estimates should be similar. As demonstrated neither FDOM, nor CDOM or GDOM were influenced by grazing intensity, suggesting that herbage ingested and herbage on offer did not differ substantially from each other in all grazing intensities. As discussed for FDOM it seems sheep did not, or only to a very small extend, select their diet from herbage on offer. As argued above this is unlikely to occur, however all three used methods indicate no signifi-

cant differences between grazing intensities. Assuming that there are only minor differences between herbage on offer and herbage ingested for all grazing intensities, there should therefore be no differences between FDOM and the in vitro digestibility, neither estimated by CT nor by HGT.

CDOM was approx. 3.9%-points higher than FDOM in all three sampling periods. De Boever et al. (1986) observed an overestimation of in vivo digestibility by the CT for concentrates, but for grass silages and hays an underestimation was found, which increased with decreasing forage quality (De Boever et al., 1988; Andrighetto et al., 1992; Iantcheva et al., 1999). As the quality of herbage on offer is low compared to herbages grown in more humid environments, the overestimation in the present study is surprising. Taking into account that the used equation for CDOM, although derived from a wide range of herbage qualities, was developed from a data set of herbages grown in European pastures, it seems that this equation is not appropriate for the digestibility estimation of herbage from Inner Mongolia grasslands. Nevertheless the estimates for CDOM are still within the variation of 4.2%-points given for the used equation (Weissbach et al., 1999), and the fact that the overestimation by the CT was not significantly different between sampling periods is a strong argument for a systematic prediction error, resulting from inadequacy of the equation for the herbage tested.

The HGT did not provide as consistent results as the CT did. In July the GDOM was also 4.0%-points higher than the FDOM, whereas in August and September GDOM and FDOM corresponded very well in the digestibility estimations. In August the difference between GDOM and FDOM was not significant, whereas in September the difference, although less than 1%-point, was significant. The overestimation in July is difficult to reconcile with the findings in August and September. Either the sheep have selected their diet negatively in July, what is unlikely, or some methodological problems account for the overestimation. A possible influence of rumen fluid quality in the HGT method was avoided by taking the fluid from the same animals, which were fed and housed under standardised conditions. According to the instructions of Menke and Steingass (1988) two standard feedstuffs (hay, concentrate) were included to correct the gas production for possible quality differences. During analysis, the samples were randomly chosen and 6 times replicated on two different days, so that the influence of rumen fluid quality was the same for all sampling periods. Herbage on offer was sampled by cutting all standing biomass 1 cm above ground level, not including litter spread on the ground. If the sheep have ingested this very low quality material in July, the FDOM would have decreased,

whereas there was no effect on GDOM, because litter was not sampled. Considering the amount of herbage on offer in July and also the high proportion of green herbage on offer in this period, there was no need for the sheep to ingest litter. Using the differences between FDOM and in vitro digestibility CDOM and GDOM as criterion for dietary selection was a further concern of the present study. As argued above the CDOM seemed to be inapplicable to estimate the digestibility of herbage on offer. Therefore the differences between FDOM and CDOM can not be used as a criterion for selection. Despite the difficulties to explain the overestimation by GDOM in July, the results obtained in August and September are feasible to be used as selection criterion. The interpretation of the differences between FDOM and GDOM in August and September with regard to selection imply that no or only little selection occurred and that there were no differences between grazing intensities.

5. Conclusions

Although herbage on offer became limited in the high grazing intensities and thus dietary selection should have been limited, no significant differences in FDOM, CDOM or GDOM were observed between grazing intensities. Due to the uniform quality structure of herbage on offer, which was especially demonstrated for the vertical quality structure, it can be concluded that dietary selection, when it occurred, did not essentially improve the quality of herbage ingested. This argument is furthermore supported by the fact that the green herbage proportion of herbage on offer was constant between grazing intensities, implying that degree of selectivity did not differ between grazing intensities.

The applied equation to estimate OMD by CT seemed to be inadequate for the herbage from Inner Mongolia, as the constant overestimation of FDOM in all sampling periods is a strong indicator for a systematic prediction error. The GDOM did not or only marginally differ from FDOM in August and September, in July however also an overestimation of FDOM was observed. Despite the difficulty to interpret estimates from July, the results from August and September indicate that there were no significant differences between herbage on offer and herbage ingested. Thus, the conclusion that no dietary selection was detected in 2005 in the investigated natural semi-arid grassland was underlined once more.

6. References

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Chapter 5

General discussion

1. Introduction and summary of results

The degradation of grassland steppes due to overgrazing is the crucial ecological and socio-economical problem in Inner Mongolia. The degradation process is addressed by the MAGIM-project in a multidisciplinary approach on plot as well as on regional scale. The current thesis depicted the research results of sub-project 3, which were obtained in two experiments.

A cutting-frequency experiment was conducted successively in 2004 and 2005 to evaluate short-term responses to defoliation stress of a semi-arid grassland sward in the Xilin River Basin, Inner Mongolia (chapters 2 and 3). A grazing experiment was established in 2005 that is supposed to provide long-term information about the impact of grazing on the grassland sward and about the role grazing plays in the degradation process. One year data were available that provided the basis for a comparison of *in vivo* and *in vitro* determined organic matter digestibility, offering the possibility to assess differences in selective behaviour of the grazing animals in the 6 different grazing intensities (chapter 4). Both experiments are based on straight orthogonal experimental designs that build a strong basis for the statistical evaluation of the results and allow a reliable interpretation of the latter.

Cutting-frequency experiment

The aim of the cutting-frequency experiment was to evaluate short-term effects of defoliation stress on community and plant level, using plant-related parameters and herbage quality parameters. In the short-term defoliation stress had a positive influence on herbage aboveground productivity, nitrogen uptake and therewith the crude protein content. The positive effects on herbage productivity were confirmed by the evaluation of leaf area development under defoliation stress. Short-term effects on root mass and root carbohydrate reserves were not observed, as well as on species composition and tiller density. The herbage quality parameters cell wall content and its composition, the digestibility of organic matter and the non-structural carbohydrate content partly indicated short-term responses, but these responses were not consistent between treatments and years. This demonstrated that the herbage quality parameters were more susceptible to climatic fluctuations and seasonal dynamics than to defoliation stress. Also the evaluation of plant-related parameters revealed the strong impact of precipitation on the investigated grassland sward, as herbage productivity was in fact stimulated by frequent defolia-

tion in both experimental years, but simultaneously substantially reduced due to low precipitation rate in 2005.

The increase in herbage productivity and crude protein content in response to frequent defoliation in both experimental years shows that the steppe grassland is resistant to defoliation stress in the short term, even under drought conditions. Nevertheless, it has to be stressed again that these results are short-term results.

Grazing experiment

In this experiment it was hypothesised that when herbage on offer is abundant, i.e. in the low grazing intensities, the *in vitro* estimated organic matter digestibility (OMD) will underestimate the *in vivo* OMD, because herbage ingested by grazing sheep will differ from herbage on offer due to selective grazing. But when herbage on offer becomes limited, i.e. in the high grazing intensities, then herbage ingested and herbage on offer will not differ very much from each other anymore, because the grazing sheep are not able to select, but forced to ingest all herbage offered. Therefore the *in vivo* OMD and *in vitro* OMD will converge in the high grazing intensities. The differences between *in vivo* and *in vitro* OMD might be used as an index for the selectivity of the grazing sheep in the grazing experiment.

Herbage on offer significantly decreased with increasing grazing intensity, as it was expected. But the OMD was not significantly influenced by grazing intensity, neither the *in vivo* OMD, nor the *in vitro* OMD. Therefore the hypothesised convergence of *in vivo* and *in vitro* OMD in high grazing intensities was not observed. This result suggested that herbage ingested and herbage on offer were similar and that selectivity was not very pronounced in 2005. This argument is supported by the results that firstly, the quality structure of herbage on offer was rather homogenous, especially the vertical quality structure, and that secondly, the green herbage proportion of herbage on offer remained constant across the grazing intensities. A difference in selectivity between grazing intensities was therefore not observed in 2005.

It appears rather difficult to draw collective conclusions from the cutting-frequency experiment and the grazing experiment, as they are substantially different in design and objectives. Cutting- and grazing-induced defoliation stress differs markedly in the impact on the grassland ecosystem. These basic differences will be addressed in section 2 of the general discussion as well as the question, whether the short-term effects observed in the cutting-frequency experiment, namely the stimulatory

effect on herbage productivity, could also be observed in the grazing experiment in the first experimental year.

In all chapters however, one unifying conclusion was drawn: climatic fluctuations, especially in precipitation rate, had a fundamental influence on the grassland sward. Herbage productivity was substantially reduced (chapter 2) and short-term effects of defoliation stress, whether due to cutting or grazing, were likely to cover effects on herbage quality (chapters 3 and 4). These results are in line with results obtained in other semi-arid grasslands; therefore an overview of the influence of precipitation on semi-arid grassland ecosystems and its implications in connection with grazing stress are discussed in section 3 of the general discussion.

The present thesis was conducted in the framework of the MAGIM-project, so that section 4 will refer to the relationships of the current thesis to other sub-projects of MAGIM.

2. Cutting vs. grazing – is herbage productivity stimulated by grazing in the short-term?

Cutting and grazing are two substantially different ways of defoliation. Cutting implies an even defoliation of the whole grass sward to the same stubble height. Grass biomass is uniformly removed and only few nutrients are slowly recycled through senescent biomass (litter) which escaped harvesting. If the grass sward gets no supplementary nutrients through fertilization, the constant nutrient removal will deplete the soil nutrient pool and biomass production will decrease in the long-term.

In contrast, grazing is a dynamic process. Herbivores are known to select their diet from herbage on offer (Arnold, 1981; Milne, 1991). Palatable, highly digestible herbages are preferred to unpalatable, highly lignified or toxic plants, which are less severely or not grazed at all (Broom and Arnold, 1986). Because palatable herbages are grazed more frequently they suffer more from defoliation-induced stress than less grazed herbages. Li (1989), Wang et al. (2001) and Wang (2004) for example report that *L. chinensis* is highly palatable and that the preference of herbivores for *L. chinensis* resulted in reduction and finally disappearance of *L. chinensis* from intensively grazed grassland swards in Inner Mongolia.

Grazing also involves the development of vertical and horizontal structures within a sward. It was demonstrated that animals graze the upper strata of a sward first, as more leaves, that are higher digestible, can be found in the upper strata (Chacon

and Stobbs, 1976). In the horizontal direction grazing animals re-graze areas that have been grazed previously, because the re-growing juvenile herbage is of higher nutritional value; this results eventually in a mosaic of more or less intensively grazed and ungrazed patches (Bakker et al., 1983; Willms et al., 1988; O'Reagain and Schwartz, 1995; Laca and Lemaire, 2000). Especially continuously grazed swards show patchy structures, other grazing management strategies like strip grazing or rotational grazing impose a high, but short-term grazing pressure on herbage swards, similar to cutting systems. Selective grazing becomes limited due to restricted amounts of herbage on offer and the sward is more evenly defoliated (Black and Kenney, 1984), what was extensively discussed in chapter 4.

Besides the influence of selection another very important difference to cutting is the recycling of nutrients. Grazing animals recycle approx. 70-85% of the ingested herbage mass to the grazing area by faeces and urine (Russelle, 1992; Tamminga, 1996). The nutrients in faeces and urine are more readily available to soil microbes, providing rapidly available nutrients to plants. But grazing does not only influence the nutrient status of the soil, it also influences the soil bulk density. Through animal trampling considerable compaction of the soil can be observed in intensively grazed areas; this was also confirmed for Inner Mongolia grasslands by Krümmelbein (2007) within the MAGIM-project. Besides soil compaction trampling does also exert additional destructive stress to the herbage plants.

Taking all these differences between defoliation through cutting or grazing respectively, into account it must be concluded that cutting and grazing experiments are hardly comparable. However, cutting experiments as a model for grazing-induced effects have and will keep their eligibility, as they are less laborious and expensive and offer the possibility to distinguish between the different components of grazing that influence a grassland sward. Therefore comparisons between cutting and grazing treatments have been conducted to investigate, if relationships can be found that are generally valid and allow the extrapolation of results from cutting experiments to grazing situations. The comparisons of herbage productivity in cut and grazed swards of Frame and Hunt (1971) and Binnie and Chestnutt (1991) are considered exemplarily, although obtained in temperate-humid grasslands. Studies addressing this question in semi-arid grasslands were not found in literature so far. The results are contradicting, whilst Frame and Hunt (1971) observed 14-16% more OM-yield in grazed swards, did Binnie and Chestnutt (1991) obtain an 11% increase in DM production in the cutting treatments. Besides these two studies,

several others were conducted on the matter, but no general relationship between grazing and cutting could be confirmed (Wolton, 1963; Aldrich and Elliot, 1974).

In chapter 2 the short-term differences in DM productivity under cutting were presented and discussed. In both experimental years the more frequently defoliated treatments outyielded the treatment cut only once. The higher productivity resulted from over-compensatory growth of the frequently cut swards, the mechanisms and controversies on this topic were also discussed in chapter 2. However, the question arises if the stimulatory effect of defoliation on herbage productivity observed in the cutting-frequency experiment can be also detected in the grazing experiment in 2005. This question will be discussed in the following.

It was briefly explained in chapter 1 that 6 grazing intensities and two grazing systems are compared in the grazing experiment. Per grazing intensity one plot consists of two paddocks, one is exclusively grazed and the other one exclusively used for hay making (one cut per year) in the traditional system, while in the mixed systems the two paddocks are grazed in one year and used for hay making in the other year. The whole experiment was divided in 2 blocks, whereas one block is located in the flat part of the experimental area and the other block in slope part; therefore both systems are replicated two times. The cutting-frequency experiment was as well situated in the slope part of the experimental area, so that the results obtained in this experiment can be compared to the results obtained in the slope block of the grazing experiment. As 2005 was the first experimental year, no differences existed between the two systems, i.e. traditional and mixed system, so that the different systems could be used as replicates of the grazing intensities for the calculation of cumulative dry matter yield (cDMY) in 2005. The cDMY was measured by means of moveable enclosure cages in the grazing experiment (McNaughton et al., 1996). All paddocks were sampled in the beginning of June, July, August and September 2005 and the enclosure cages were moved after each sampling. Per paddock three cages were used, sampling 0.5 m² per cage by clipping all standing herbage (inclusive standing dead herbage) to 1 cm stubble height.

The cumulative herbage production was calculated as follows:

$$\text{cDMY}^a = \text{DMY July (inside)} + (\text{DMY August (inside)} - \text{DMY July (outside)}) \\ + (\text{DMY September (inside)} - \text{DMY August (outside)})$$

(^a: DMY = DM yield; inside = DMY sampled inside the cage; outside = DMY sampled outside the cage; grazing started middle of June 2005, so that DMY July (inside) contains the herbage that grew undisturbed until July)

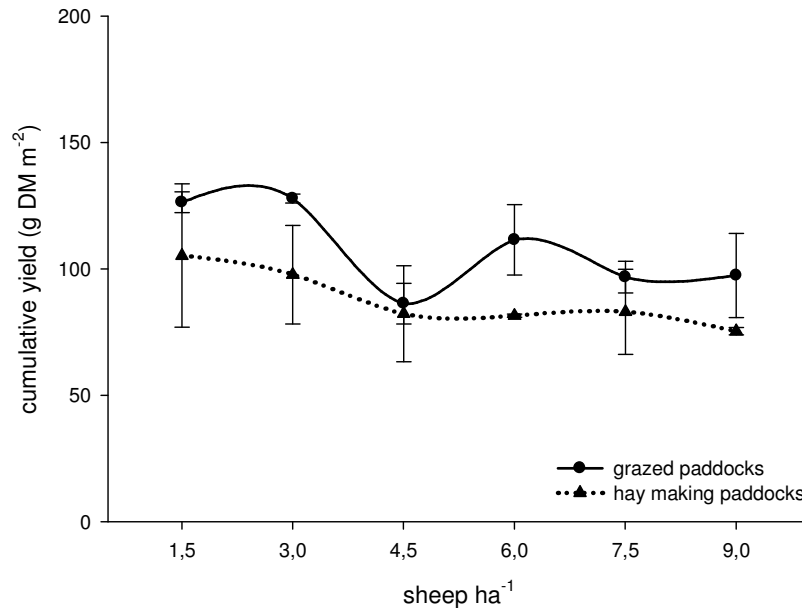


Figure 1: Cumulative DM-yield (cDMY) of grazing and hay making paddocks in the slope block of the grazing experiment in 2005

(Error bars indicate standard deviation; an ANOVA was carried out by means of SAS mixed model analysis, including grazing intensity (G) and method (M - grazing or hay making) and the interaction G x M as experimental factors: only M was significant (P=0.03), mean cDMY of grazed plots was 107 g DM m⁻² and 87 g DM m⁻² in hay making plots, SE = 5.84)

The question, whether also grazing stimulates herbage productivity in the short-term, as observed in the frequently defoliated treatments in the cutting-frequency experiment, can be positively answered. In the grazed paddocks on average 20 g DM m⁻² more herbage were produced compared to the hay making paddocks; this increase was statistically significant. Differences in herbage productivity between grazing intensities were not significant.

The results confirm that defoliation, whether it is conducted by grazing or cutting, stimulates the productivity of this *Stipa grandis*/*Leymus chinensis* community in the

short-term. This conclusion provides an interesting objective for the long-term research activities in the grazing experiment: for how long can the stimulatory effect on cDMY be maintained and which of the 6 grazing intensities facilitates the stimulatory responses in the long-term?

3. The influence of precipitation on semi-arid grasslands

Water is the primarily limiting resource in semi-arid grassland ecosystems (Lieth and Wittaker, 1975; Huxman et al., 2004). The amount and the distribution of yearly precipitation play a key role in semi-arid ecosystem functioning (Oesterheld et al., 1999, Knapp et al., 2002). The relationship between water availability and plant productivity was proved to be of fundamental nature (Noy-Meir, 1973). The concept of rain-use-efficiency that is based on the ratio of plant production to annual rainfall eliminates the factor precipitation rate and provides the possibility to evaluate the productivity of semi-arid ecosystems (chapter 2). The rain-use efficiency was proposed as a unifying concept in ecology of semi-arid and arid environments (Le Hou  rou, 1984).

The influence of precipitation rate on the productivity of aboveground biomass in Inner Mongolia grasslands has been documented by several authors as discussed in chapter 2 (Xiao et al., 1995, 1996; Bai et al., 2004; Yu et al., 2004; Ni, 2004). The importance of annual precipitation rate in this semi-arid ecosystem could also be demonstrated in the present thesis, as all three chapters document the influence of precipitation on plant productivity (chapter 2), herbage quality (chapter 3) and the ingestive behaviour of grazing ruminants (chapter 4). It was suggested that the drought in 2005 covered defoliation effects on herbage quality that were expected due to the results obtained in 2004 (chapter 3), as well as the expected differences in digestibility between grazing intensities caused by selective grazing in the grazing experiment (chapter 4).

However, the major focus of the MAGIM-project is the influence of grazing intensity on the semi-arid grassland, as overgrazing was identified to be the most important factor in the degradation process (Wang and Ripley, 1997; Liu et al., 1998; Verburg and Van Keulen, 1999). Nonetheless the question should be addressed how and to what extent grazing and precipitation contribute to the degradation of Inner Mongolia steppe grasslands. This aspect will be very important in comprehending the degradation processes in this grassland ecosystem.

Oosterheld et al. (1999) reviewed the three main influences on semi-arid and arid grassland ecosystems: grazing, fire and climatic fluctuations. These authors point out that the influence of climatic fluctuations, especially precipitation, on herbage productivity is much stronger than the influence of grazing. Figure 2 illustrates the outcome of the cited review.

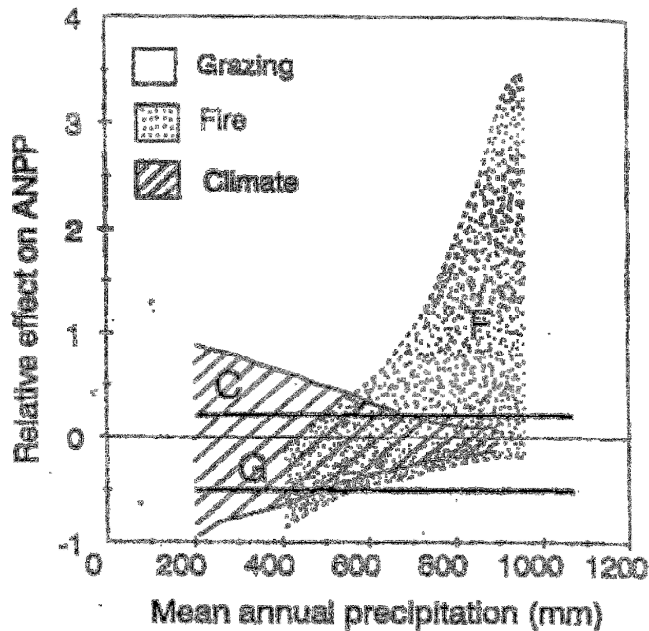


Figure 2: A conceptual model of the relative effects of grazing, fire and climate on above-ground net primary productivity along a gradient of precipitation (grazing effects are bounded by thick lines) (Oosterheld et al., 1999)

The effect of grazing remains unchanged over the investigated precipitation gradient of 200-1200 mm mean annual precipitation. The influence of climatic fluctuations however, was shown to be very high for environments receiving only 200-500 mm of rain per year. Disturbance due to fire does not need to be discussed as it is not a feature of the investigated grassland type.

Biondini et al. (1998) reported on results of a grazing experiment conducted in the semi-arid mixed-grass prairie, USA. Three grazing intensities were compared: no grazing, moderate and heavy grazing (50% and 90% removal of aboveground biomass) over an 8-year period. Plant productivity aboveground was significantly correlated to annual precipitation, whereas grazing did not have a significant and consistent effect on aboveground biomass. Changes in plant cover and species composition were primarily correlated to precipitation and it was concluded that the in-

investigated grassland has a high degree of resistance against drought and grazing effects. Substantial changes in productivity or species composition are only expected when drought events coincide with prolonged periods of overgrazing. A similar conclusion was drawn by Christensen et al. (2003) after the simulation of degradation processes for the Xilin River Basin using the Savanna ecosystem model (Coughenour, 1993; see chapter 2). Model simulations suggested that when intensive heavy grazing and drought events overlap the grassland ecosystem is vulnerable to loss of productivity and species diversity. The predominance of environmental variables, i.e. precipitation, rather than grazing was also emphasized in other studies conducted in semi-arid grassland ecosystems (Milchunas et al., 1989; Milchunas and Lauenroth, 1993; Biondini and Manske, 1996; Fynn and O'Connor, 2000). Fynn and O'Connor (2000) stated that the variance in aboveground biomass due to rainfall variability was almost twice as large as the variance accounted for by grazing in a semi-arid savanna in South Africa, but they also point out that if the condition of a grassland sward is already poor, due to persistent drought and overgrazing, the impact of grazing is much more pronounced than in grassland swards of good condition.

In contrast, Zhou et al. (2002) could not find a relationship between aboveground biomass and precipitation in grazed grassland sites of the North-East China Transect (NECT), but in ungrazed and mown sites. These findings implicate that the influence of precipitation is substituted by an increasing influence of grazing intensity. However, this conclusion has to be discussed with caution, as this study is based on one year data and failed to define what the experimental treatments, grazing, mowing and non-grazing, actually were and in what condition these sites have been during and before measurements were made.

The major impact of precipitation on the grassland ecosystem of the Xilin River Basin was clearly demonstrated in the current thesis, as for example the cumulative DM-yield which was reduced by more than 50% in 2005 compared to 2004 (chapter 2) or the retarded herbage quality development (chapter 3 and 4).

The grazing experiment offers the opportunity to investigate the interrelations of precipitation and grazing intensity more closely in the future, but this can only be achieved over a long time period, as the inter-annual variability in precipitation is high and extreme precipitation years influence the ecosystem function not only in the current year, but also in the following years (Frank and McNaughton, 1993; Fynn and O'Connor, 2000).

4. Relationships to other MAGIM sub-projects

As already described in chapter 1, the MAGIM-project follows a multidisciplinary approach to which 9 sub-projects contribute with their results obtained in different research fields. The results will be added up to a broad perspective of the grassland ecosystem in the Xilin River Basin and the influence of grazing on this ecosystem and its role in the degradation process. The main focus of the research group is the evaluation of matter fluxes, including water cycle, carbon and nitrogen cycling in the plant-soil-animal system, but also the atmospheric gas exchange. Further, a basic assessment of the ecosystem processes was intended, e.g. description of grassland vegetation and growth rate, assessment of the stability of soil organic matter, or the dimension of wind and water erosion. Eventually the data obtained by the 9 sub-project will be combined and used in biogeochemical, hydrological and erosion models, but as well in scenario analysis of grazing management systems.

Most sub-projects investigate the grassland ecosystem in end-point evaluations, comparing areas that had been classified to represent different levels of utilisation intensity (ungrazed since 1979 or 1999, moderate grazing during the vegetation period or during winter, overgrazing). The end-point evaluations provide valuable information about the current status of the grassland and the effects of different utilization intensities in the long-term. What can not be assessed in these studies is the process of degradation. It remains unclear what the determinants of degradation actually are, and how they interact. In contrast, the aim of our sub-project is the evaluation of the degradation process in its formation and development, distinguishing short-, mid- and long-term effects. This process-oriented evaluation will provide a better understanding of the degradation process and the involvement and interactions of different environmental influences and management factors.

In this we are closely connected to sub-project 4 (Institute of Animal Nutrition and Physiology, University of Kiel), as we have together established the grazing experiment and use the results obtained in this experiment mutually, like in chapter 4 or in the theses of Glindemann (2007) and Wang (2007).

The principle objective of sub-project 4 is examining the impact of grazing intensity on biomass availability, feed intake and feed quality, as well as on animal productivity. The definition of an "optimal stocking rate" that facilitates high animal productivity due to high herbage productivity and high herbage quality in a long-term sustainable grazing system is the unifying intention of the two sub-projects. The basic comprehension of the degradation process is essential to define such a long-term

sustainable management system. Management tools that can be used by local authorities or even farmers to assess the current carrying capacity of the grassland, with regard to environmental influences, are urgently needed to actively prevent the semi-arid grasslands from degradation. The results that will be obtained in the grazing experiment in the next years will provide basic data to design the needed management tools.

The identification of short-term responses of the steppe grassland to defoliation stress was the main objective of the chapters 2 and 3, as a first step in the assessment of the degradation process. It was shown that defoliation had a stimulatory effect on herbage productivity, what was also demonstrated for the grazing experiment. Sub-project 2 (Institute of Soil Science and Plant Nutrition, University of Kiel) as well determined above- and belowground productivity in order to evaluate ecological and physiological mechanisms of varying productivity under different utilization intensities. Gao (2007) showed in an end-point evaluation (as described above) that aboveground- and belowground productivity were significantly reduced in areas subjected to high grazing intensity compared to moderately or ungrazed areas, what is in line with many other studies conducted in semi-arid grasslands (see discussion chapter 2). One of the conclusions of Gao (2007) is that neither compensatory nor overcompensatory plant growth of aboveground biomass occurs in more intensively used areas compared to ungrazed areas. This conclusion however, has to be limited to long-term observations, as we have found overcompensatory plant growth in the short-term. Both Gao (2007) and the present study agree on the fundamental influence of precipitation on this grassland ecosystem, especially on the aboveground productivity.

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Chapter 6

Summary

6.1 Summary

The degradation of grassland steppes due to overgrazing is the crucial ecological and socio-economical problem in Inner Mongolia. The degradation of grasslands is addressed by the MAGIM-project (**M**atter fluxes in **G**rasslands of **I**nnner **M**ongolia as influenced by stocking rate) in a multidisciplinary approach, in close collaboration with Chinese Scientists. The degradation of Inner Mongolia grasslands was mainly described retrospectively by ecological studies, but the formation and development of degradation were only rarely examined. The present thesis was prepared within MAGIM sub-project 3, whose main focus is evaluating the degradation process in Inner Mongolia steppe grasslands with regard to short-, mid- and long-term effects of increasing grazing intensity. The objectives of the present thesis were to describe short-term effects of defoliation stress (i) by plant-related parameters known from classical growth analysis, as well as (ii) by herbage quality parameters, both obtained in a cutting-frequency experiment. A further objective was the comparison of the digestibility of herbage ingested and herbage on offer in a grazing experiment, comprising a gradient of 6 grazing intensities, in order to assess the selectivity of grazing sheep.

The cutting-frequency experiment was conducted in 2004 and 2005 in a semi-arid grassland sward of the Xilin River Basin, Inner Mongolia. The sward was subjected to three different cutting-frequencies to compare the effects of increasing defoliation stress.

Defoliation stress positively influenced the herbage aboveground productivity, the nitrogen uptake and therewith the crude protein content in both years. The positive effects on herbage productivity were confirmed by increased specific leaf area and increased leaf area index under defoliation stress. Short-term effects on root mass and root carbohydrate reserves were not observed, as well as on species composition and tiller density, what confirmed the expectation that species composition and tiller density are not changing in the short-term. The herbage quality parameters cell wall content and its composition, the digestibility of organic matter and the non-structural carbohydrate content partly indicated short-term responses, but these responses were not consistent between treatments and years. This demonstrated that the herbage quality parameters were more susceptible to climatic fluctuations and seasonal dynamics than to defoliation stress.

The strong impact of precipitation on the investigated grassland sward became also apparent in the evaluation of plant-related parameters, as herbage productivity was in fact stimulated by frequent defoliation, but simultaneously substantially reduced due to low precipitation rate. The increase in herbage productivity and crude protein content in response to frequent defoliation in both experimental years shows that the steppe grassland is resistant to defoliation stress in the short term, even under drought conditions.

The grazing experiment was started in June 2005 in the same study area as the cutting-frequency experiment. Besides the future objectives of this experiment regarding the assessment of the degradation process, it was tested on the basis of one-year data from 2005, whether the *in vitro* estimated organic matter digestibility (OMD) of herbage on offer differs from the *in vivo* determined OMD of herbage ingested, as it can be expected due to selective grazing. As six grazing intensities were compared it was hypothesised that the differences between herbage on offer and herbage ingested were high in low grazing intensities, because grazing animals were able to select and low in high grazing intensities, as selectivity was limited due to reduced herbage on offer. The differences between *in vivo* and *in vitro* OMD might be used as an index for the selectivity of the grazing sheep in the grazing experiment in 2005.

Herbage on offer significantly decreased with increasing grazing intensity, as it was expected. But the OMD was not significantly influenced by grazing intensity, neither the *in vivo* OMD, nor the *in vitro* OMD. Therefore the hypothesised convergence of *in vivo* and *in vitro* OMD in high grazing intensities was not observed. This result suggests that herbage ingested and herbage on offer were similar and that selectivity was not very pronounced in 2005. This argument is supported by the results that firstly, the quality structure of herbage on offer was rather homogenous, especially the vertical quality structure, and that secondly, the green herbage proportion of herbage on offer remained constant across the grazing intensities. A difference in selectivity between grazing intensities was therefore not observed in 2005.

It can be concluded that defoliation stress has a positive effect on productivity, and partly on herbage quality, in the short-term. Furthermore, the fundamental impact of climatic fluctuations, especially precipitation rate and distribution, on the investigated grassland ecosystem was revealed.

6.2 Zusammenfassung

Überbeweidung führte in letzten Jahrzehnten zu starker Degradation der Grasland-Steppen der Inneren Mongolei, so dass heute die Degradation das vordringlichste ökologische und sozio-ökonomische Problem in dieser Region ist. Die Forschergruppe MAGIM (**M**atter fluxes in **G**raslands of **I**nnner **M**ongolia as influenced by stocking rate) befasst sich mit diesem Problem in einem multi-disziplinären Ansatz in enger Kooperation mit chinesischen Wissenschaftlern. Bisher wurde die Degradation der Grasland-Steppen in ökologischen Studien zumeist rückblickend beschrieben, wohingegen die Entstehung und der Entwicklungsprozess nur selten beschrieben wurden. Die vorliegende Arbeit entstand innerhalb des MAGIM-Teilprojekts 3, dessen Hauptziel die Evaluierung des Degradierungsprozesses insgesamt und der kurz-, mittel- und langfristigen Effekte von zunehmender Beweidungsintensität ist. Das Ziel dieser Arbeit war es, kurzfristige Effekte von Beweidungsstress durch (i) pflanzenbaulich relevante Parameter, sowie (ii) Futterqualitätsparameter zu beschreiben. Diese Untersuchungen wurden in einem Schnittversuch durchgeführt, in dem Beweidungsstress durch verschiedene Schnittintensitäten simuliert wurde. Des Weiteren wurde in einem Beweidungsexperiment, das insgesamt 6 Beweidungsintensitäten umfasste, die Verdaulichkeit des aufgenommenen und des angebotenen Futters verglichen, um die erwarteten Unterschiede im Hinblick auf selektive Futteraufnahme zu interpretieren.

Der Schnittversuch wurde in den Jahren 2004 und 2005 im semi-ariden Grasland des Xilin-Flussbeckens in der Inneren Mongolei durchgeführt. Der Graslandbestand wurde drei verschiedenen Schnittintensitäten ausgesetzt, um den Einfluss zunehmender Schnittintensität zu prüfen.

Die Produktion oberirdischer Biomasse, sowie die Stickstoffaufnahme und damit der Rohproteingehalt, wurden durch zunehmende Schnittintensität in beiden Versuchsjahren signifikant gesteigert. Die positiven Effekte auf die Produktivität wurden auch durch die gesteigerte spezifische Blattfläche und den Blattflächenindex bestätigt. Kurzfristige Veränderungen der Wurzelmasse und der Kohlenhydratreserven in der Wurzel wurden nicht beobachtet, ebenso wie Veränderungen der Artzusammensetzung und der Triebdichte, was der Erwartung entsprach, dass Artzusammensetzung und Triebdichten sich kurzfristig nicht verändern würden. Die Futterqualitätsparameter Zellwandgehalt und -zusammensetzung, sowie die Verdaulichkeit der Organischen Masse (OMD) und die Gehalte an Nicht-

Strukturkohlenhydraten zeigten zum Teil kurzfristige Veränderungen, allerdings waren diese weder zwischen den Behandlungen, noch zwischen den Jahren konstant. Dies zeigte deutlich, dass die Futterqualitätsparameter mehr durch witterungsbedingte Schwankungen und Saisoneinflüsse beeinflusst wurden, als durch unterschiedliche Schnittintensitäten. Der starke Einfluss der Niederschläge auf das untersuchte Grasland zeigte sich ebenfalls deutlich in den pflanzenbaulich relevanten Parametern, z.B. in der Tatsache dass die Biomasseproduktivität 2005 zwar durch häufigere Schnittnutzung gesteigert wurde, aber gleichzeitig um mehr als 50%, im Vergleich zu 2004, reduziert wurde. Der Anstieg des Biomasseertrags und des Rohproteingehalts durch intensivere Schnittnutzung zeigte, dass die Grasland-Steppe kurzfristig einer intensiven Nutzung widerstehen kann, sogar unter Trockenstress wie im Jahr 2005.

Das Beweidungsexperiment startete im Juni 2005 im gleichen Untersuchungsgebiet wie der Schnittversuch. Neben den in Zukunft zu prüfenden Fragestellungen hinsichtlich des Degradierungsprozesses, war die Hypothese, die anhand einjähriger Daten geprüft wurde, dass die OMD des tatsächlich aufgenommenen Futters durch die in-vitro ermittelte OMD des angebotenen Futters unterschätzt wird, wenn das Futterangebot ausreichend ist, da den Weidetieren die Möglichkeit zur selektiven Futteraufnahme gegeben wird. Wenn das Futterangebot sinkt, z.B. durch höheren Beweidungsdruck, dann sollte die OMD des angebotenen Futters ungefähr dem des aufgenommenen Futters entsprechen, da den Weidetieren kaum Möglichkeit zur Selektion bleibt. Diese Differenzen zwischen der OMD des aufgenommenen und des angebotenen Futters können als Maß für die Selektivität der Weidetiere in den verschiedenen Beweidungsintensitäten genutzt werden.

Das Futterangebot war, wie erwartet, in den hohen Beweidungsintensitäten signifikant geringer. Die OMD war zwischen den Beweidungsintensitäten allerdings nicht signifikant verschieden, weder die in vivo OMD noch in-vitro OMD. Die erwartete Annäherung der beiden OMD-Werte wurde daher nicht beobachtet. Das Ergebnis, dass das aufgenommene Futter sich kaum vom angebotenen Futter unterschied, wurde durch zwei weitere Ergebnisse gestützt. Erstens, die Qualitätsstruktur des angebotenen Futters war in sich sehr homogen, besonders die vertikale Struktur, und zweitens war der Anteil an nekrotischer Biomasse im angebotenen Futter über alle Beweidungsintensitäten hinweg relativ konstant. So kann für das Jahr 2005 festgehalten werden, dass die Weidetiere kaum selektiert haben, bzw. selektieren konnten.

Höhere Nutzungsintensitäten haben kurzfristig einen positiven Effekt auf die Produktivität, und z.T. auch auf die Futterqualität der natürlichen Graslandvegetation der Inneren Mongolei. Es zeigte sich, dass witterungsbedingte Schwankungen, insbesondere die Menge und die Verteilung der Niederschläge, einen sehr großen Einfluss auf das gesamte Grasland-Ökosystem haben.

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