

The impact of herbivores in a Mongolian forest steppe

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The impact of herbivores in a Mongolian forest steppe

De invloed van herbivoren op een Mongoolse bossteppe
(met een samenvatting in het Nederlands)

Proefschrift

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Maartje Adriana van Staalduinen
geboren op 10 februari 1956 te 's Gravenzande

Promotor: Prof. Dr. M.J.A. Werger
Plant Ecology Group, Department of Biology, Utrecht University

Ter herinnering aan mijn vader

To the memory of my father

Voor Peter

To Peter

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Chapter 1

General Introduction

The Mongolian steppe is one of the last relatively undisturbed areas of the steppe ecosystem that once covered a large part of the Eurasian continent (Hilbig 1995; Gunin et al. 1999; Wallis de Vries et al. 1996). It is a semi-open grassland ecosystem that comprises a large diversity of grasses, herbs and herbivores.

The Eurasian steppes are considered as climatogenic primary grasslands, occurring in a region where the climate is too arid for the development of forest, but with enough moisture to develop a semi-open vegetation consisting of grasses, sedges, and frequently dwarf shrubs. Generally the steppes occur on gentle slopes and plains with a deep loamy soil and good drainage.

Nowadays the steppe landscape has been highly affected by human activities. In large parts of the typical steppes the grasslands have been totally converted to agricultural land (Numata 1979). Only in Central Asia, especially Mongolia, one can still find relatively unspoiled steppes (Lavrenko and Karamysheva 1993).

However, due to enormous increases in the number of livestock in Mongolia, the grazing pressure has intensified. Together with a decline of sophisticated traditional grazing practices this has led to a situation of overgrazing. In many areas the overgrazing resulted in a serious decrease of the vegetation cover, productivity and plant species diversity, while in heavily degraded areas the grasses have disappeared and are replaced by *Artemisia* species (CBD-report 1996; Kharin et al. 1999). In some areas the vegetation cover has completely disappeared and the bare soil is left, susceptible for wind erosion, and leading to desertification.

In order to be able to come to a sustainable management of the pastures and to combat the degradation of the vegetation and desertification, a better understanding is needed of the role of herbivory in the sustainability of the ecosystem, and of the mechanisms underlying grazing effects on the vegetation.

Role of herbivory in the sustainability of the ecosystem

Herbivores play a key role in the sustainability of natural grasslands like steppes and savannas through their influence on the structural and functional properties of the ecosystem (Frank et al. 1998; Werger 1983; McNaughton 1985; Whicker and Detling 1988a). Large populations of herbivores are supported by natural grazing land and may locally consume more than 50% of the aboveground net primary production (ANPP) (Frank et al. 1998; Detling 1998). Compared to many other terrestrial ecosystems, that lose less than 10% of their ANPP, grasslands have a large proportion of ANPP going through consumers, and this affects the diversity of herbivores (Prins and Olff 1998) and numerous ecosystem processes.

Much research on plant herbivore interactions has been performed in natural grasslands as the African savanna and North-American prairie (Frank et al. 1998; Whicker

and Detling 1988a). However, little is known about the steppe ecosystem of the temperate regions in Eurasia.

Herbivores potentially alter plant species composition and abundance, plant biomass and productivity of a vegetation (Bakker et al. 1983; Bakker et al. 2003; Sala 1988; Werger et al. 2002; Willems 1983). They also affect plant nitrogen (N) content, and N-cycling processes (Detling 1998; McNaughton 1985; Frank and Groffman 1998). These herbivore induced alterations of the vegetation may feedback on herbivores of the same or other species (McNaughton et al. 1997).

Herbivore species interact with each other by competition and facilitation. When herbivore species forage on the same resource which is limiting population growth, competition occurs. Facilitation of feeding-site selection for other herbivores can occur by improving forage quality by grazing (Detling 1998; Coppock et al. 1983; McNaughton 1985; Jaramillo and Detling 1988; Frank et al. 1998) or by changing the sward structure so that it becomes suitable for other, often smaller grazers (Werger 1977; Prins and Olff 1998). Across the seasons the nitrogen content of forage can drop dramatically, while protein is one of the most important nutrients for herbivores. Forage quality can be improved by increasing N-concentration in grazed shoots (Frank et al. 1998; Holland and Detling 1990).

Rodents in arid regions are generally considered as keystone species because of the major effects of their burrowing activities on soil nutrient cycling, productivity and plant species diversity and succession (Brown 1990; Kinlaw 1999; Whicker and Detling 1988a). It is often observed that the digging activities of rodents cause a nutrient enrichment of their burrows compared to the surrounding environment, and form favourable plant growth microhabitats. Other herbivores often prefer these sites for foraging, because of the higher concentration of nutrients of that forage (Whicker and Detling 1988b). In Mongolia marmots are widespread on the steppes, deserts and mountain steppes (Gunin et al. 1999; Rogovin 1992), where they have a great impact on the landscape by creating mounds and altering the vegetation structure and composition.

The present study is aimed at the impact of large and small herbivores, the takh (Przewalski horse) and Siberian marmot, respectively, on the vegetation of a forest steppe in Mongolia. We investigate the effect of the type and intensity of grazing (takh or marmot) on plant species abundance, plant productivity and plant nutrient concentrations (chapter 3) and we study the effect of marmot disturbances on the vegetation (chapter 5).

Mechanisms underlying grazing effects on the vegetation

The effect of herbivores on plant species diversity appears to depend on the type and abundance of herbivore species and environmental factors like precipitation and soil fertility (Olff and Ritchie 1998; Proulx and Mazumder 1998). For example, natural populations of large grazers are reported to increase plant species diversity (McNaughton 1985), but domesticated grazers at high stocking rates can decrease diversity (Hobbs and Huenneke 1992).

A change in grazing intensity can also lead to a shift in dominance of plant species with a different growth form and different palatability (Bakker 1983; Willems 1983; Mitchley and Willems 1995; Werger and Leistner 1975; Werger 1977). In many semi-arid grassland areas, e.g. Inner Mongolia, Northern China and North American steppe (Mack and Thompson 1982; Milchunas et al. 1988; Xie and Wittig 2003) it is a common phenomenon that when grazing pressure by livestock increases the original dominating caespitose species are being replaced by rhizomatous species.

In studies on the vegetation of the *Stipa* steppe of Mongolia it is observed that under light or moderate grazing the caespitose *Stipa krylovii* is the dominant grass species, but under a higher grazing intensity *Stipa* decreases and the rhizomatous *Leymus chinensis* and *Carex duriuscula* become dominant (Hilbig 1995; Fernandez-Gimenez and Allen-Diaz 2001). This shift in dominance has been attributed to a higher grazing tolerance of the rhizomatous species, and the occurrence of compensatory growth, which might mitigate the potential negative effects of defoliation (Anten et al. 2003; Gold and Caldwell 1989; Oesterheld and McNaughton 1988). Rhizomatous species have large belowground storage organs and the reallocation of carbohydrates is probably an important mechanism contributing to the stronger compensatory growth in these species (Chapin et al. 1990; Kobe 1997; McPherson and Williams 1998; Wang et al. 2004). To further pursue this question we tested the capacity for compensatory growth of *Stipa krylovii* and *Leymus chinensis* in a greenhouse experiment (chapter 4).

Mongolia, study area and funding of the research project

The field research was conducted in central Mongolia in the forest steppe region, on a research site in Hustain National Park. This is a national park located at about 100 km from Ulaan Baatar. In chapter 2, a description is given of the history of Hustain National Park and the objectives and institutional setting of the Hustain Nuruu Steppe Reserve project (HN-project).

The present research project started with a first contact with Inge Bouman, chairman of the Foundation Reserves Przewalski Horses (FRPH). The FRPH was, together with the Mongolian Association for the Conservation of Nature & Environment (MACNE), responsible for the execution of the Reintroduction Project for the takh in Hustai National Park. For the reintroduction of the takh, knowledge about the vegetation and the carrying capacity of the area was needed, and therefore the foundation was interested to support research on this subject.

Together with professor Marinus Werger, who had much experience with research in arid grasslands and had visited Mongolia before, I worked out a proposal for a PhD-study in the Mongolian forest steppe. We submitted the proposal to the Stichting Technische Wetenschappen (STW) in order to get a grant for the whole period of the PhD-study. Unfortunately, after I had already started the research, the grant was not assigned. However, the exclosures for the grazing experiment having been build already in Hustai, and since I had obtained some financial support from FRPH and the Hugo de

Vries Fonds, I decided to go on with the research project. In order to further finance the project, I applied for smaller grants on a yearly basis to cover the basic costs.

This study was thus supported by the Hugo de Vries Fonds (2000), the FRPH (2000 through 2003) and the Schure-Beijerinck-Popping Fonds (2001 through 2003). In Mongolia, MACNE gave me permission to perform experiments in Hustain National Park, and the HN-project supported the research project by the supply of transport and the use of an office in the well equipped research centre of the park. Above all, essential support to the project was given through the assistance by the biologist of the research centre with the field work. Their results of a monitoring programme regarding the vegetation and fauna of the park were of great use. In 2002 four Mongolian biologist of Hustai National Park were invited to come to Utrecht University for a three months special fellowship program funded by Nuffic. The exchange of researchers further intensified the cooperation.

Thesis outline and objectives

In chapter 2, a short description is given of the characteristics of the zonal semi-arid grassland areas of the world, the evolution and origin of steppes, and, in more detail, the climate and zonal vegetation types of Mongolia. Also the relation between biomass production and annual precipitation of steppe areas was surveyed. In that chapter, the importance of Hustai National Park for the conservation of species diversity of the steppe ecosystem is discussed. A description is given of the vegetation and wildlife of the park, the human impact and conservation of biological diversity in Mongolia, and the conservation in Hustai National Park.

In chapter 3, plant species abundance, plant biomass and plant N-concentration of the steppe vegetation after 3 years of exclusion of grazing by takh (*Przewalski* horse) and Siberian marmots is studied in an enclosure experiment. We address the question whether the abundance of rhizomatous species, and specifically *Leymus chinensis*, increases under a higher grazing intensity and whether the abundance of caespitose species, and specifically *Stipa krylovii*, decreases. We also investigate if there is an increased fragmentation of the bunches of *Stipa krylovii* under increased grazing and if there is an increased N-concentration in the shoots under a higher grazing pressure.

In chapter 4, the potential for compensatory growth of *Leymus chinensis* and *Stipa krylovii*, two co-occurring species, which differ in grazing tolerance, is studied in a greenhouse experiment. The plants are grown under dry and wet conditions and a clipping treatment is performed simultaneously. The study addresses the question what plant characteristics determine potential interspecific differences in compensatory growth and how this is affected by a reduction in water availability.

In chapter 5, we examine the relation between different types of marmot mounds

and the species composition, species cover, diversity, plant biomass and soil- and plant- N-concentrations of the local vegetation. The study is conducted on the *Stipa* steppe, and we address the question whether the species composition and species dominance on the different types of marmot mounds differ from the surrounding vegetation and whether the nutrient concentrations differ in the vegetation and in the soil of the different types of mounds.

In chapter 6, the main conclusions from the preceding four chapters are discussed and summarized.

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Chapter 2

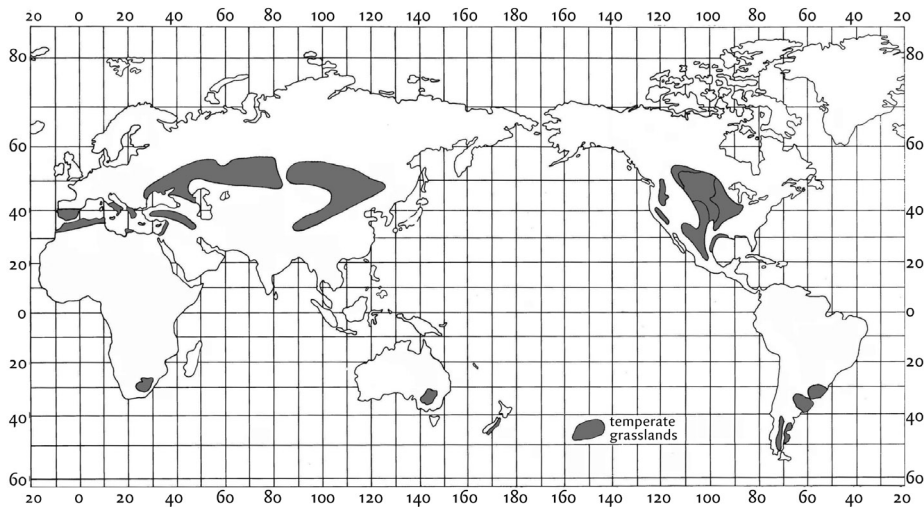
The steppes of Mongolia

M.A. van Staaldouin and M.J.A. Werger

Introduction

Natural grasslands occupy vast areas of land worldwide. They occur in semi-arid to sub-humid regions and carry an herbaceous plant cover that is the climax vegetation of those regions (Coupland 1992). In these regions the climate is too arid for the development of forest, but there is enough moisture to develop a closed perennial herb layer, which is lacking in the desert. The vegetation is primarily comprised of grasses and sedges (together called graminoids) and forbs (non-grass-like herbs), and frequently there are also dwarf shrubs. Generally they occur on gentle slopes with a deep loamy soil and good internal drainage. Various names as 'pampa', 'plain', 'poesta', 'prairie' and 'steppe' are used for these grasslands.

Fig. 1 Temperate grassland vegetation map of the world



In Figure 1 the distribution of temperate primary grassland worldwide is shown. Large areas of the northern hemisphere are occupied by temperate grasslands: in North America the prairies extend from the mid west of south Canada to the Gulf of Mexico, while on the Eurasian continent the steppe stretches out from the lowlands of Inner-Mongolia to the west coast of the Black Sea and into the poesta of Hungary (Numata 1979). Small patches of primary grassland occur in the most continental parts of Spain.

Compared to the extended prairies and steppes of the northern hemisphere the

grasslands of the southern hemisphere occupy a relatively small area. The largest area is the pampa in central-south and eastern Argentina, in the province of Buenos Aires and neighbouring provinces. Much smaller is the area of tussock grasslands in Otago in New Zealand. Other southern hemisphere grasslands are the Highveld in South Africa and the grasslands in southeastern Australia (Numata 1979). These grassland areas are primary climax biomes, determined by climatological conditions (Coupland 1992; Walter 1977). Apart from those there are extensive grassland areas in western and central Europe, China, North-America, New Zealand and Australia which result from forest clearing and subsequent grazing by livestock (Numata 1979; Ellenberg 1982; Whitford 1983; Looman 1983).

Climatic characteristics of grassland areas

The climate of natural grasslands exhibits a relatively great variation in precipitation, with annual droughts of several weeks to several months. In temperate grasslands the mean annual precipitation generally ranges from 250–750 mm, while in tropical and subtropical grasslands and savannas it ranges from 600 to 1500 mm according to Coupland (1979) and from 175 to 1400 mm according to Werger (1983). The Eurasian steppes are considered as climatogenic primary grasslands, associated with areas with an annual precipitation of 200–400 mm, which is intermediate between forest and true desert. In wintertime there are semi-permanent areas of high pressure (especially in Mongolia), leading to dry winters. Most of the precipitation falls in the summer when depression occurs, often with showers and thunderstorms. But also periods of drought occur during the growth season.

Next to rainfall, surface radiation exchange and continentality are the most important factors controlling the climatic patterns in the Eurasian grassland zone (Ripley 1992). Great contrasts between winter and summer occur, with mean monthly temperatures that can drop below -15°C in the winter and summer mean monthly temperatures that may exceed 32°C in the south.

Physiognomy

The steppes consist of an herbaceous climax vegetation of graminoids, herbs and shrubs. Trees are absent in the true steppe vegetation, which seems to be controlled by the climatic aridity and/or insufficient soil drainage (Coupland 1992; Walter 1977). However, towards the northern and western edges of the Eurasian steppe areas small clumps of trees and isolated forest patches occur, which are similar in species composition to the temperate forests further north and west. The occurrence of the woody patches can partly be explained by locally more favourable soil moisture conditions along these edges of the steppe biome, and partly as relicts reflecting dynamic shifts in climate over time (Walter 1977).

Nowadays the steppe landscape is highly affected by human activities. In large parts of the typical steppe, prairie, pampa and highveld zone, where rainfall is still sufficient for relatively tall stemmed annual crops, the grasslands have been totally converted to agricultural land: grains, soy beans and sunflowers are the main crops

there. This conversion is profitable because of the favourable rainfall conditions and the excellent soil conditions in these parts of the grassland zone (Numata 1979). Towards the dryer edges of the temperate grassland biome in the former Soviet Union considerable areas have been changed into irrigated croplands and still very much larger areas have been turned into desert-like ecosystems as a result of intense and prolonged overgrazing (Kharin 2002). Only in Central Asia, especially Mongolia, one can still find relatively unspoiled steppes (Lavrenko and Karamysheva 1993).

Evolutionary characteristics of Poaceae

The earliest records of Poaceae or related families were reported from the upper Cretaceous and the Paleocene and Eocene (Muller 1981; Linder 1986). Small amounts of grass pollen and fossils of grazing faunas were found in dry areas, which reveal that grasses established under arid conditions. The evolutionary adaptation of plants to aridity happened during large geological timescales. The shift to the herbaceous habit, and ultimately to an annual habit seem to be the most important adaptations. Crucial for the development of the modern grassy habit of grasses and sedges seems to be the achievement of a helophytic structure. In the Poacea helophytism as well as the tolerance to intense drought is common, and often occur among species from the same genus (*Bromus*, *Poa*, *Festuca* and *Calamagrostis*) (Bredenkamp et al. 2002). A characteristic trait for the Poacea is the intercalary meristem. The intercalary meristem is likely an adaptation to defoliation by herbivores and fires, as it allows a quick recovery of the loss of biomass.

Origin of Eurasian steppes

At the beginning of the Eocene period the world was almost completely forested and dominated by evergreen angiosperms with some gymnosperms at low and middle latitudes. At the end of the Eocene the conditions became dryer, and a grassy vegetation began to develop in the Eurasian landscapes. This gradually replaced the former forests. In the Oligocene the modern grassland vegetation types, as we know them today, appeared (Bredenkamp et al. 2002 and Numata 1979).

Since the Upper Eocene and during the Oligocene and Miocene, an intense process of co-evolution of grassland plants and animals occurred (Mack and Thomson 1982; Carroll 1988). General herbivore size increased due to the availability of large amounts of forage in the open grasslands and savannas, and many ungulates (hooved mammals) populated the grasslands. Ungulates evolved features that are adaptive for life on open grassland, in particular long legs to increase running speed. They also evolved large, complexly grooved molar teeth to grind their forage of grasses and other plants. The ruminants developed an improved fermentation system by elongation and sacculation of the stomach, which enabled them to digest the secondary compounds of the grasses. In this era the first horses, which belong to the Perissodactyla or odd-toed ungulates, appeared on the steppes (Carroll 1988). A diversification of the ungulates occurred together with a further expansion of the grasslands. Many of the familiar species of the Artiodactyla, or cloven-hooved ungu-

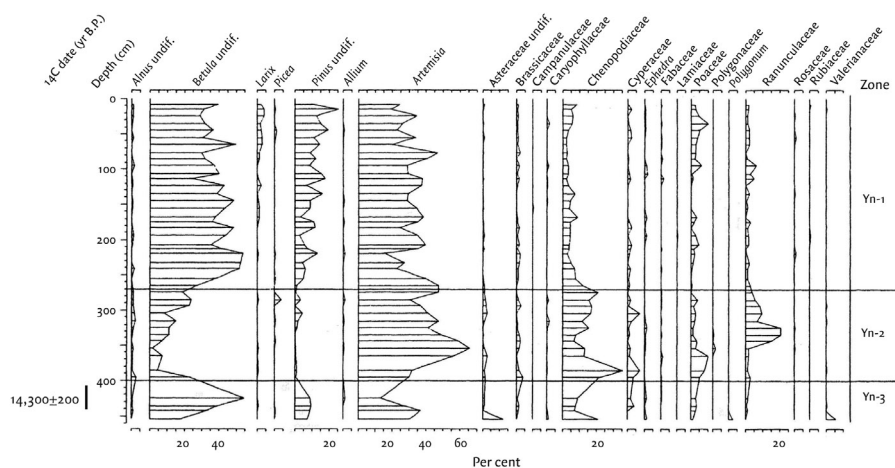
lates, as the sheep, goat, cows, camels, pigs, deer and antelopes appeared in the Oligocene and Miocene. During the Oligocene several families of rodents first appeared (Carroll 1988).

Recent history of steppe vegetation in Mongolia as shown by pollen records

Pollen records from western and northern Mongolia suggest that large areas of steppe and forest steppe already existed by 1,000,000 to 700,000 BP. Taxa which are widely distributed in Mongolia today, e.g., *Pinus*, *Betula*, *Artemisia* and *Chenopodiaceae* dominate pollen spectra of the Pleistocene, suggesting that the general composition of the Mongolian vegetation was similar to the present one (Gunin et al. 1999), although the vegetation boundaries might have shifted.

During late Glacial times and early Holocene (13,000-9,000 BP) the climate became dryer and colder and the steppe and desert extended north of their present position in Mongolia (Gunin et al. 1999; Liu et al. 1999). The pollen diagram from Yamant-Nur lake (Fig. 2) showed a shift to a dominance of herbaceous species, e.g. *Artemisia*

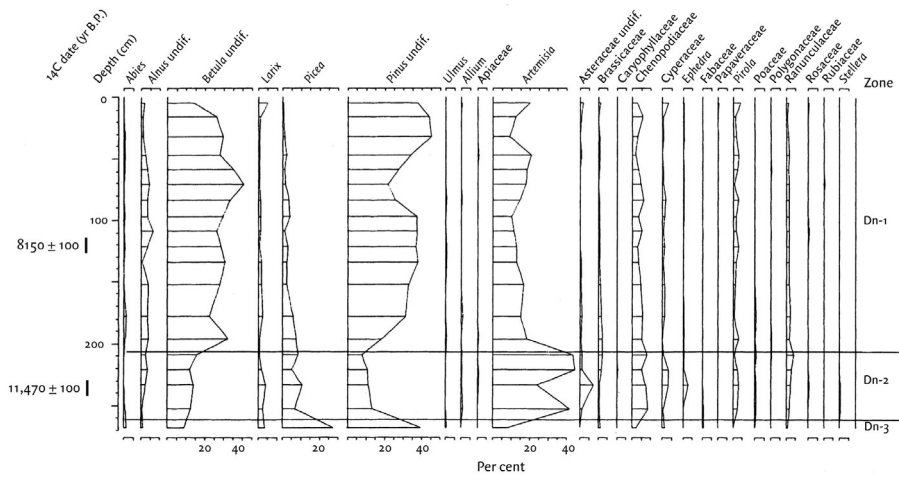
Fig. 2 Pollen diagram from Yamant Nur Lake (49°54'N, 102°36'E, 1000m a.s.l.)



30 – 70 % and *Chenopodiaceae* 10 – 40%, while woody species decreased to less than 5% in that period. During the period 12,500 – 12,100 BP the pollen diagram of Dood-Nur lake (Fig. 3) showed a substantial decrease in *Pinus* 10% and *Picea* 7 – 10% pollen, while *Betula* and *Larix* pollen percentages were unchanged. Herbaceous taxa e.g. *Artemisia*, *Chenopodiaceae*, *Ephedra*, *Asteraceae* and *Ranunculaceae* became more abundant (Gunin et al. 1999). Lakes in Mongolia were lower than today.

Since the early Holocene (8,000-4,000 BP) the climate became wetter, and humid forests spread in the former steppe area, creating a mosaic of *Betula* forest and steppe (Gunin et al. 1999; Liu 1998; Liu et al. 1999). In Yamant-Nur lake (Fig. 2) the pollen diagram showed an increase in *Betula* and *Pinus* pollen and a decrease in the herba

Fig. 3 Pollen diagram from Dood-Nur Lake (51°20'N, 99°23'E, 1538m a.s.l.)



ceous *Artemisia* and *Chenopodiaceae*. The pollen diagram of Dood-Nur lake (Fig. 3) is characterized by a co-dominance of *Betula* and *Pinus*. In the mountains of northern and western Mongolia there was an expansion of boreal coniferous trees (e.g. *Picea* and *Abies*) at sites where they do not occur today or are very much restricted.

In the middle Holocene (7500 - 5500 BP) the border of the forest steppe zone in Inner-Mongolia shifted north westward because of the warmer and wetter climate (Liu 1998). Temperate forest and forest steppe vegetation dominated in Inner-Mongolia north of 42° N latitude, replacing arid steppe (Gunin et al. 1999).

According to Liu (1998) agriculture developed in the forest steppe area at about 5900BP, but according to Von Wissmann et al. (1956) it started from 4500 BP. Since 4000 BP the climate tended to become colder and dryer and the moisture conditions became more or less similar as at present (Gunin et al. 1999). However, the process of desiccation was not gradual, but the climate fluctuated and dry-cool periods and warm-semi humid periods alternated (Fig. 4) (Gunin et al. 1999; Liu 1998). At about 2900-2800 BP the climate became definitely colder and dryer and agriculture was replaced by a nomadic cattle-breeding culture (Liu 1998; von Wissmann et al. 1956). As a result of dryer conditions and human impact the boreal conifers retreated, forest elements became more fragmented and the steppe area extended, leading to the present situation.

Climate in Mongolia

The continental position of Mongolia, far from the influences of oceans, together with its rather high altitude determines its climate. Great contrasts occur between winter and summer and also between day and night. Mongolia is an upland country with the greatest part lying at 1500 m or more above sea level (Gunin et al. 1999). Between important mountain ranges vast plateaus stretch between 1500 and 2000 m,

Fig. 4 Variation of mean annual temperatures in the north of China. Arrows show the periods of glacier activities in the northern hemisphere (Kharin et al. 1999)

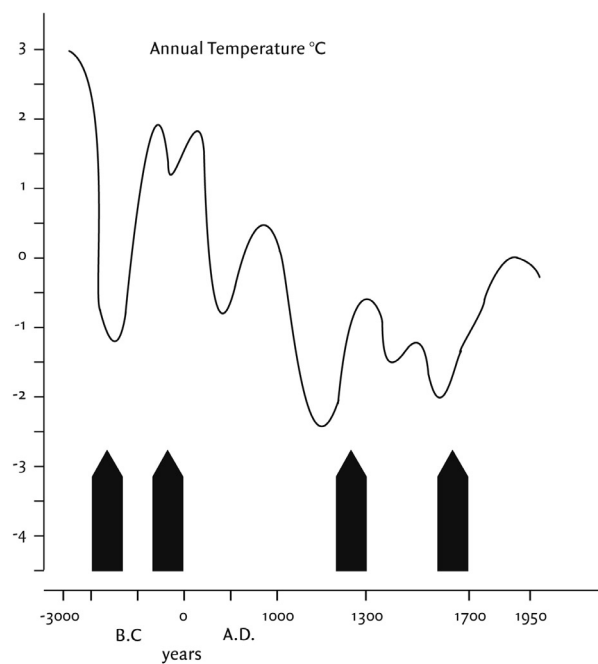
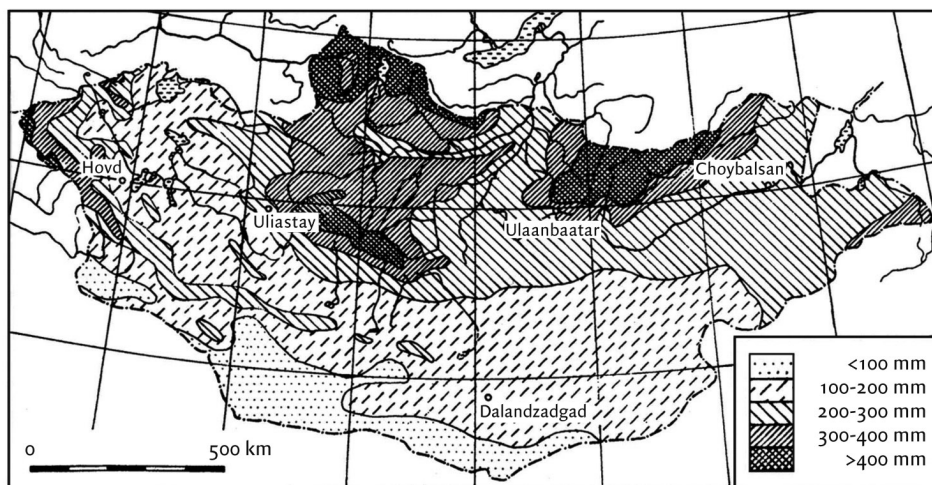


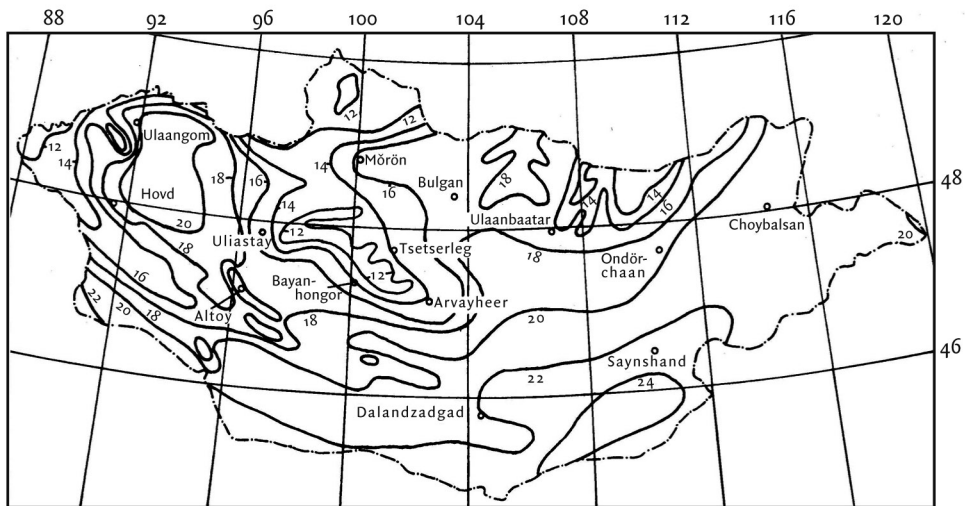
Fig. 5 Mean annual precipitation in Mongolia (Hilbig 1995)



and, more frequently, between altitudes of 2000 and 3000 m (Hilbig 1995). The highest mountain peaks of more than 4000 m are found in the Mongolian Altai. The lowest point (552 m) is the salt lake Höh-Nuur in the Uldz basin in the East (Hilbig 1995).

Going from north to south in Mongolia the aridity increases together with a steady decrease of the mean annual precipitation (Fig. 5). It decreases from 600 mm per year at the Hubsugul and Khentii Mountains to 25 mm per year or less in the Gobi desert (Gunin et al 1999). Isohyets run mainly east west, from west to the east some areas show comparatively low precipitation values because they are on the lee side of mountain chains. This effect is most pronounced in the Great Lakes Basin in north-western Mongolia.

Fig. 6 Mean July temperatures in Mongolia (Hilbig 1995)



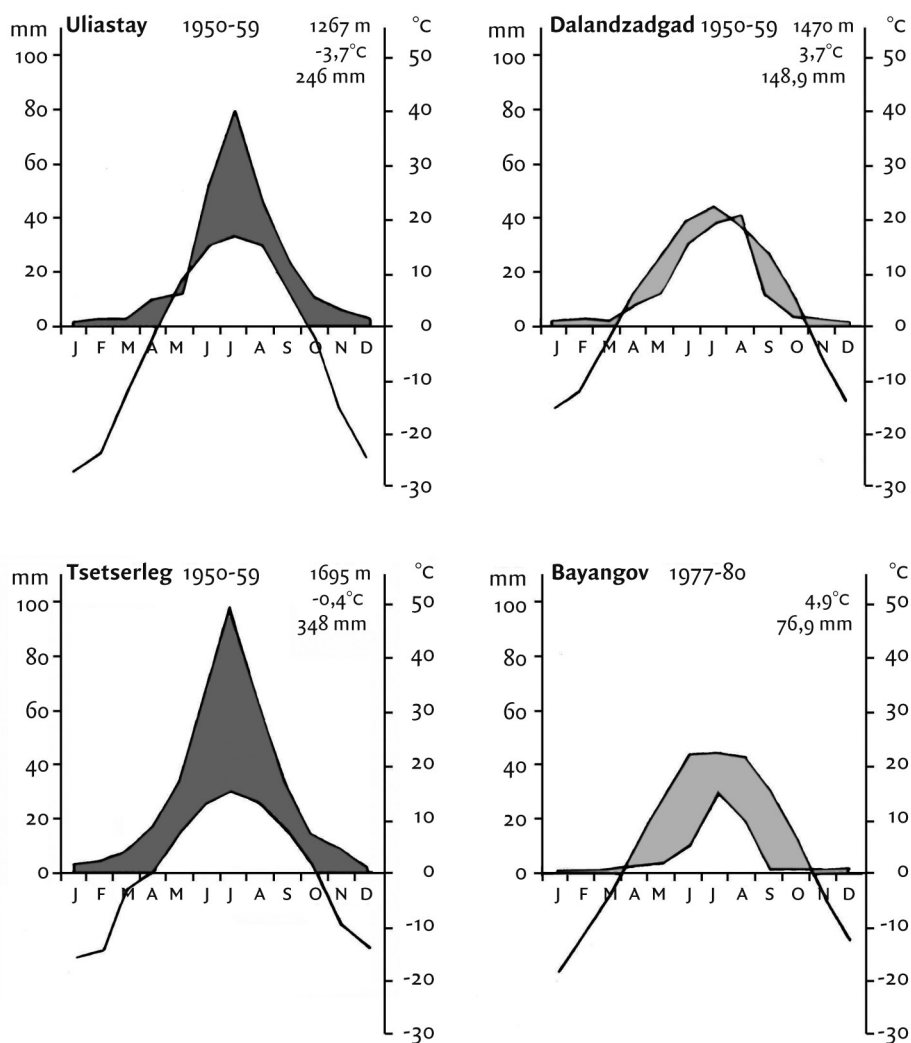
From north to south it gets warmer. The mean annual temperature is below zero in the north and above zero in the south. Figure 6 shows the mean July temperatures. July is the warmest month, with mean temperatures up to 15°C in the mountains and 20 to 30°C in the southern semi-deserts and deserts (Hilbig 1995).

In Mongolia the winters are very cold, with monthly averages below -15°C in January and minimum temperatures that can drop as low as -50°C , while the summers are warm, with monthly temperatures that may exceed 32°C in the south (Fig. 7). In wintertime there are semi-permanent cells of high pressure, leading to dry winters with less than 5 to 10% of the annual precipitation (Ripley 1992). Snow cover is not very common, and if present, it is usually thin.

In spring, when the temperature rises, there is still very little precipitation and strong winds are usual. Especially in areas with a sparse vegetation cover (degenerated steppe vegetation) fierce dust storms can develop, transporting dust deep into China.

Summer is the wettest season, with about 70% of the annual precipitation. Most of the precipitation falls when depression occurs, often in showers and thunderstorms. But also frequent periods of drought occur during the growth season. In fact, the

Fig. 7 Climate diagrams of Uliastay, Dalanzadgad, Tsetserleg & Bayangov (Hilbig 1995)



variation in summer rainfall between years increases as the total amount of summer rainfall decreases.

The autumn starts with a drastic decrease in precipitation and drop in temperature. On the steppe the plants desiccate and freeze while standing, leading to a freeze-dried vegetation, which can be grazed in winter.

Plant geographical setting of Mongolia

A brief history of the floristic exploration of Mongolia is given by Hilbig (Gubanov and Hilbig 1989; Hilbig 1995). Most plant exploration has been done by Russian botanists starting their research in the early 19th century.

Mongolia is part of the Holarctic floral Kingdom. Most of the country falls in the West and Central Asian Region, but the northern margin falls in the East Siberian Region, or the South Siberian-Daurian Subregion of the East Siberian Region, and the eastern corner in the Sino-Japanese Region (Meusel et al 1965; Walter & Straka 1970; Hilbig and Knapp 1983). Karamysheva and Khramtsov (1995) give a much more detailed account of the plant geographic classification of the Mongolian steppes and show the geographic distribution of the various units. Lavrenko (in Walter & Straka 1970) classifies the northern margin as the light needle-leaved part of the Eurasian taiga, and the rest of Mongolia as the Eurasiatic steppe region. Zohary (1973) discusses the various plantgeographic classifications of Central Asia, including Mongolia, in detail. He accepts Lavrenko's (1965) classification, with all of arid Mongolia as part of the Central Asian Subregion. Following Grubov (1959), Zohary (1973) lists the characteristic genera of this subregion. A more detailed account of the species of the different steppe types in Mongolia is given in Karamysheva and Khramtsov (1995).

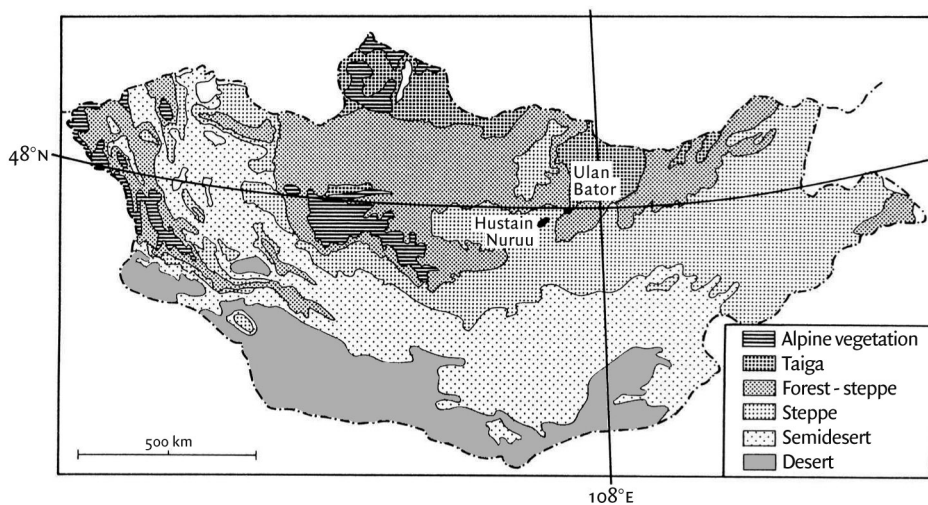
Zonal vegetation types and soils of Mongolia

The general zonation of the vegetation of Mongolia, based on floristical composition and physiognomy, is given by Walter (1974), based on the Russian authors Yunatov (1954) and Lavrenko et al. (1979), and by Hilbig (1995) who incorporates also his own research. Grubov (2001) made a more detailed classification by dividing the country into 16 plant and vegetation geographical regions. These classifications show that our study area at Hustai National Park is situated on the transition from the Mongolian-Daurian and the Central Chalcha subzones at the southern edge of the forest steppe zone, where it borders the true steppe zone.

In this chapter the nomenclature of plant species follows Grubov (2001).

In Mongolia the zoning of the vegetation corresponds rather well with the gradient of decreasing precipitation from the north to the south (Figs. 4 and 8). The zone

Fig. 8 Vegetation zones of Mongolia (after Wallis de Vries 1996) with the location of Hustai National Park and the capital Ulaan Baatar



with the highest precipitation (more than 400 mm per year) is in the north of the country where the needle-leaved forest, the so-called taiga, grows. Large parts of the mountains are covered with taiga, mostly dominated by *Larix sibirica* (72% of total forest area). These forests typically grow on parachernozem soils, and often have a species rich forb layer. Other needle leaved species are *Pinus sibirica* (12 %), *Pinus sylvestris* (7%) and *Picea obovata* (0.25%). *Betula platyphylla* (9%) often occurs in the forest canopy, and in clearings it becomes more important, even dominating in secondary woods (Hilbig 1995).

More southwards, in the zone with an annual precipitation between 300 and 400 mm with castanozem soils, lays the forest steppe zone, consisting of a mosaic of patches of forest and grassland. Due to differences in topography there is a differentiation of the vegetation in forest on the north-facing slopes and higher parts, and steppes on the south-slopes and in valleys.

Due to logging activities in this region, the forest has retreated and the steppes, especially meadow steppes, have been expanded. The very diverse flora of the *Thalictrum petaloidei*-*Helictotrichetum schelliani* meadow steppe (Hilbig 1995) reflects the forest-steppe transition. Diagnostic species of this vegetation are the herbaceous plants: *Artemisia laciniata*, *Artemisia sericea*, *Bromus pumpellianus*, *Dasiphora fruticosa*, *Pedicularis rubens*, *Sanguisorba officinalis*, *Scorzonera radiata*, *Senecio campester*, *Thalictrum petaloideum* and the graminoids *Helictotrichon schellianum* and *Trisetum sibiricum*. A meadow steppe type in which the dense herbaceous layer also includes several graminoids is the *Androsace ovczinnikovii*-*Helictotrichetum schelliani* steppe. Here the graminoids *Agrostis trinii*, *Bromus pumpellianus*, *Carex pediformis*, *Festuca lenensis*, *Helictotrichon schellianum*, *Koeleria macrantha*, *Poa attenuate* have intermediate cover values. In the flowering season numerous forbs create a sea of colors: *Adenophora lamarckii*, *Aster alpinus*, *Bupleurum multinerve*, *Campanula turczaninovi*, *Dianthus versicolor*, *Galium verum*, *Gentiana barbata*, *Gentiana macrophylla*, *Leontopodium ochroleucum*, *Papaver pseudocanescens*, *Pedicularis myriophylla*, *Polygonum ellipticum* and *Patrinia sibiric* (Hilbig 1995).

Stumps of larch trees, or a parachernozem soil in a meadow steppe, are indications of a former forest site, as parachernozem is typical for forest and castanozem is typical for steppe (Hilbig 1987; Hilbig 1995).

A clearly defined broad-leaved forest zone like in temperate Europe does not occur in Mongolia. In north Mongolia, the Mongolian Altai and in Hingan needle-leaved forest now directly border the steppe. However, the question arises whether there was a belt of continuous broad-leaved forest, since Knapp (1989) showed that this was the original vegetation in the Högnö Tarna uul. Also in our study area at Hustai National Park a broad-leaved forest of *Betula platyphylla* and *Populus tremula* is described as climax vegetation (Wallis de Vries et al. 1996). This may have been the case throughout north Mongolia.

In the zone where the precipitation drops below 300 mm per year (200-300 mm), trees don't survive anymore and grasses dominate the vegetation. This is the region

of the typical steppe, or grass steppe, with vast areas of grasslands. The *Stipa* steppe (*Cymbario-Stipetum krylovii*; Hilbig 1995) is a characteristic community of this region. It has also been referred to as dry steppe in contrast to the moister meadow steppe. The common soil type under the *Stipa* steppe is the typical castanozem, with a humus-rich horizon of 30-50 cm and organic contents of 2-3% in the upper part (Haase 1983).

The *Stipa* steppe comprises of tall and medium-sized grasses, particularly tussock grasses, together with forbs as *Cymbaria dahurica*, *Artemisia adamsii*, *Goniolimon speciosum*, *Kochia prostrata* and *Saussurea salicifolia* and the subshrub *Caragana pygmaea*. Several subassociations of the steppe community are distinguished, referring to one or more dominant species. These communities are mostly grazing facies of a specific association, because differences in grazing intensity lead to a shift in dominance of the species (Hilbig 1995).

Further southwards in the direction of the Gobi, it gets dryer again. In this desert steppe zone, where an annual precipitation of 100 - 200 mm occurs and various types of desert soils occur, the vegetation becomes sparser. Two main types of vegetation can be distinguished; the *Stipa-Allium* semi-desert and the shrub semi-desert (Yunatov 1950). They occupy rocky, stony-gritty and sandy sites. The *Stipa-Allium* vegetation, which occurs over enormous stretches of shrubless land is characterized by the presence of *Stipa glareosa*, onion related species (*Allium polyrrhizum*, *A. mongolicum*) and *Anabasis brevifolia*. The shrub semi-deserts consist of several communities of shrubs and subshrubs like *Amygdalus pedunculata*, *Caragana leucophloea*, and *Zygophyllum xanthoxylon*, grasses and *Allium* species.

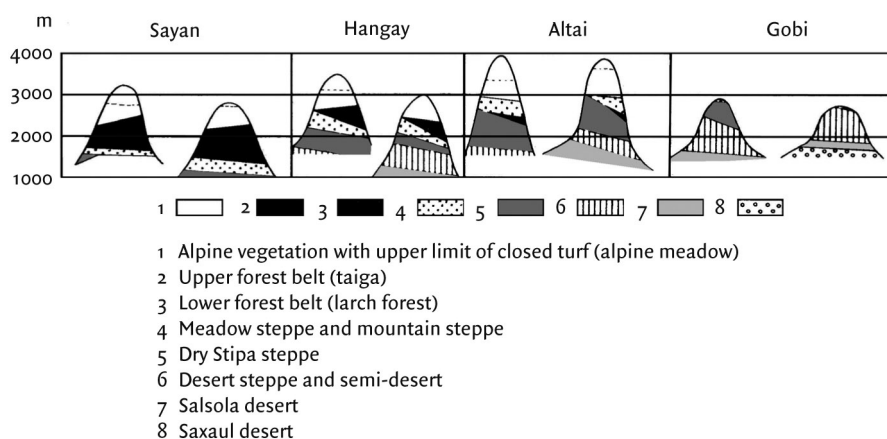
At some places the soil remains bare and drifting sand dunes develop. The dunes are often colonized by the *Nitraria* community, solely consisting of *Nitraria sibirica*. On saline solonchak soils succulent bushes of *Kalidium gracile* dominate the sparse vegetation (Hilbig 1995).

In the zone with a precipitation less than 100-150 mm lays the desert zone. Precipitation is almost exclusively in summer, but it can be that there is no precipitation for years. Grid and stone deserts cover vast areas, while sandy deserts are less widespread. The salt content of the soils may be rather high and solonchak deserts are widely distributed (Petrov 1966/67; Hilbig 1995).

The vegetation consists of shrubs and semishrubs, while grasses and *Allium* are almost absent. In extreme deserts there are hardly any plants over large areas. Several desert communities have been distinguished, of which the *Anabasis brevifolia* deserts and Saxaul deserts (*Haloxylon ammodendron*) are the most important and widely distributed.

Many desert species in the genera *Reaumuria*, *Kalidium*, *Nitraria*, *Zygopyllum*, *Anabasis* and *Haloxylon* have a high degree of succulence. In some species that grow on solonchak soils (*Reaumuria soongorica*, *Kalidium gracile*) a high water potential is reached through high salt contents in the cells (Hilbig 1995). Floristically the transition from

Fig. 9 Schematic profiles of different mountain regions in Mongolia with their altitudinal belts (Hilbig 1995)



steppe deserts to true deserts is gradual.

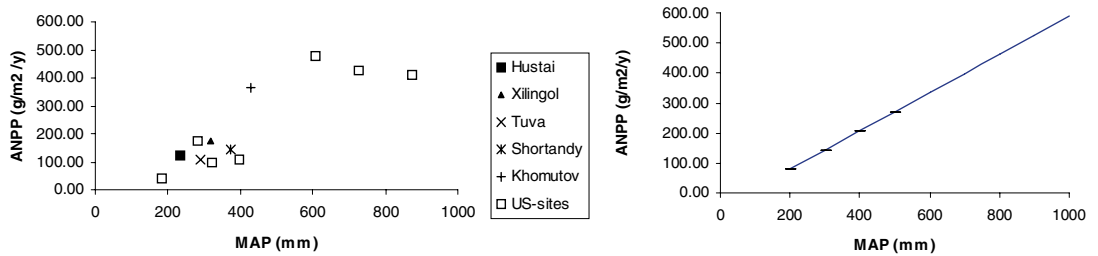
Besides the general north to south distribution of vegetation zones, there also is an altitudinal zonation on the mountains. This altitudinal distribution depends both on the exposition of a mountain slope and on latitude.

The altitudinal zonation of the Mongolian mountains is briefly as follows (Fig. 9). The hill belt in North Mongolia is covered by grass steppes; the mountains around the Great Lakes Basin carry grass steppes and semi-deserts; South Mongolia has semi-deserts; and the Transaltay-Gobi and Dzungarian Gobi both support semi-desert and deserts (Hilbig 1995). In the lower mountain belt of North Mongolia we find forests and meadow steppes. The lower montane forests consist mostly of Siberian larch (*Larix sibirica*) and the upper montane forests of Siberian pine (*Pinus sibirica*). In the South the mountain belt is characterized by mountain steppes, stands of *Juniperus Sabina* and *Juniperus pseudosabina*, and in the northern parts real forest remnants (Hilbig 1995). Shrubs and dwarf shrubs (*Betula rotundifolia*, *Rhododendron adamsii*, *Pinus pumila*, *Salix spp.*) occur in the subalpine belt. In the alpine belt a lower section with *Kobresia* meadows, and an upper section with alpine cushion plants on rocks and debris can be distinguished (Hilbig 1995). A much more detailed account can be found in Karamysheva and Khramtsov (1995).

Biomass production in relation to annual precipitation

In most of the forest steppe and steppe regions of the world plant growth seems to be limited mostly by water availability, resulting from the frequent droughts and low precipitation level. A classical positive relationship between biomass production and precipitation has been observed for many areas (Walter 1964; Lieth 1976; Rutherford 1980; Lauenroth and Sala 1992; Milchunas and Lauenroth 1993; Paruelo et al. 1999). It is remarkable that regression models fitted for different areas over the world are

Fig. 10 Relationship between aboveground net primary production (ANPP) and mean annual precipitation (MAP). The line corresponds to the regression model based on precipitation and production data of the sites.



almost similar.

Figure 10 shows the relationship between aboveground net primary production (ANPP) and mean annual precipitation (MAP) of sites in Xilingol (Inner-Mongolia, China), Tuva (Russia), Shortandy (Kazakhstan), Khomutov (Ukraine), the USA (Paruelo et al. 1999) and Hustai National Park (Mongolia).

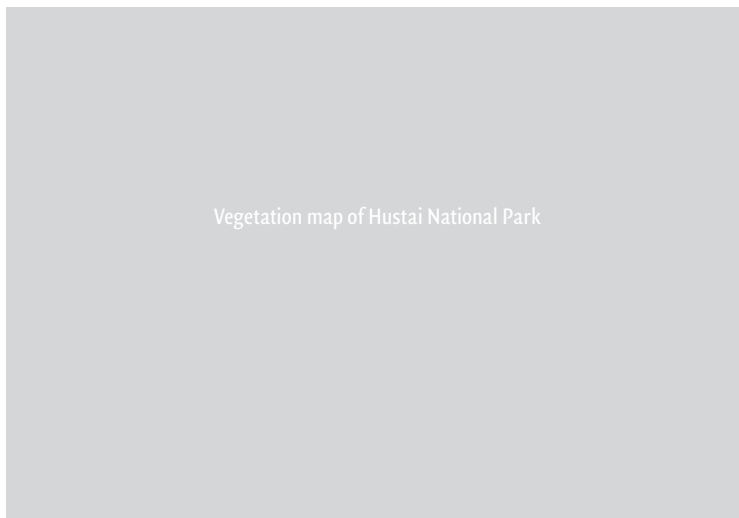
The line corresponds to the regression model based on precipitation and production data of the four Eurasian (excluding Hustai National Park) and seven US temperate grassland sites:

$$ANPP = -49.4 + 0.64 \times MAP$$

$$F = 24, r^2 = 0.73, n = 11, P < 0.001$$

Paruelo et al. (1999) have averaged ANPP and precipitation (see appendix) over a number of years for different sites in Eurasia and the USA and fitted a linear model

Fig. 11 Vegetation map of Hustai National Park



of these data (Fig. 10). For Hustai National Park, we averaged ANPP and MAP (see appendix) over the years 2000 to 2003 (Fig. 10).

The average productivity of Hustai National Park for its mean precipitation corresponds very well with the productivity of other sites at their typical rainfalls in the arid region (200-400 mm) of Eurasia. A regression model which includes data of Hustai National Park is almost similar to the former model:

$$\text{ANPP} = -44.2 + 0.63 \times \text{MAP}$$

$$F = 28, r^2 = 0.74, n = 12, P < 0.001$$

Vegetation of Hustai National Park

Hustai National Park is situated at a 100 km south west of Ulaan Baatar, the capital city of Mongolia and occupies 60.000 ha at elevations ranging from 1100 to 1840 m above sea level. Because of the location of the national park at the southern edge of the forest steppe zone, and because mountains, plains, dunes and a river valley lay in its area, several vegetation types of the forest steppe and typical steppe zones are represented in the park (Fig.11). Wallis de Vries et al. (1996) distinguished 11 vegetation types in the national park, based on their botanical characteristics, physiognomy, situation in the landscape, altitude, exposition and soil.

The largest part of Hustai National Park is covered with steppe vegetation dominated by several grass species, a variety of herbs and legume dwarf-shrubs. The bunchgrass *Stipa krylovii* is the dominant species of the lowland steppe (*Artemisia adamsii*-*Stipa krylovii* community) and the upland steppe (*Thermopsis lanceolata*-*Stipa krylovii* community), with *Caragana pygmaea* and *C. microphylla*, *Artemisia frigida*, *Heteropappus altaicus*, *Chamaerhodos erecta*, *Cleistogenes squarrosa*, etc as typical species. The species compositions of the two communities show many similarities, but the upland steppe is differentiated from the lowland steppe by a species group with *Poa attenuate*, *Koeleria macrantha* and *Thermopsis lanceolata* among others. The lowland steppe is found on the dry foot slopes of mountains and on plains, while the upland steppe is situated on slopes at a higher elevation, where higher soil moisture occurs. The average vegetation cover on the upland steppe (70%) is 10% higher than in the lowland steppe (Wallis de Vries et al. 1996).

The *Festuca lenensis* mountain steppe can be recognized by the blue color of the short bunchgrass *Festuca lenensis*, which dominates the vegetation. Low growing cushion- and rosette-forming species as *Chamaerhodos altaica*, *Androsace incana*, and *Arenaria capillaris* are characteristic and differentiate this community from the moister *Festuca sibirica* mountain steppe. The *Festuca sibirica* mountain steppe is found at higher altitude, above 1400m, and mainly on the northern exposed slopes. The vegetation is rich in herbs and dominated by the tussock grass *Festuca sibirica*. Differential species are *Festuca sibirica*, *Carex pediformis*, *Stellera chamaejasme* and *Galium verum*. In both *Festuca* steppes the species of the lower *Stipa* steppe are generally absent (Wallis de Vries et al. 1996).

The *Achnatherum splendens* tussock grassland is found in valleys at places with a fluctuating ground water level and along streams and rivers at higher places. The big and coarse tussock grass *Achnatherum splendens* is the dominant and characteristic species. Many steppe species occur in this community.

In valleys at altitudes above 1300 m, and along stream sides the *Geranium pratense* meadow can be found at soils with a continuous water supply. The vegetation is dominated by tall herbs such as *Geranium pratense*, *Sanguisorba officinales*, *Thalictrum simplex*, *Medicago falcata*, and *Campanula glomerata* (Wallis de Vries et al. 1996).

Only 5% of the total area of Hustai National Park is covered by forest, the *Betula platyphylla* forest, which grows on the northern slopes of the mountains from 1400 m upwards to 1800 m above sea-level (highest top is 1840 m). These sites have a high soil moisture content resulting from the summer thawing of the permafrost layer that reaches close to the surface.

The canopy, dominated by *Betula platyphylla* and *Populus tremula*, is rather open and leaves enough light reaching through for the development of an extensive shrub layer and species rich herb layer. The shrub layer consists of *Cotoneaster melanocarpa*, *Spiraea media* and *Rosa acicularis*. The herb layer consist of *Lathyrus humilus*, *Chamaenerion angustifolium*, *Poa angustifolia* and frequently species from the *Geranium pratense* group (Wallis de Vries et al. 1996).

The *Betula* forest is considered to be the original vegetation, as there are no larch trees or stumps of larch or other needle-leaved trees found in the forest, and also because of the name of the area. The mountain range in the centre of the national park is named 'Hustai Nuruu' which comes from the birch trees growing in the mountain forest. In Mongolian *hustai* means "with birch" and *nuruu* means "mountain range".

The *Betula* forest of Hustai Nuruu (Hustai National Park) might be one of the last remnants of the temperate broad-leaved forest belt that once occurred in north Mongolia.

Shrublands are found in gullies (*Spiraea* shrubland), on topslopes (*Betula fusca*) and on south slopes on stony and rocky sites (*Amygdalus* shrublands). The *Spiraea aquilegifolia* shrubland occurs in erosion gullies and is dominated by *Spiraea aquilegifolia* and *Cotoneaster melanocarpa*, with *Geranium pseudosibiricum*, *Sedum aizoon* and *Allium leucocephalum* as characteristic species. Species from the mountain steppe (*Festuca sibirica* group) as well as species from the meadow steppe (*Geranium pratense* group) are present in this community. At some places *Ulmus pumila* trees occur together with the shrubs (Wallis de Vries et al. 1996)..

On higher slopes above 1400 m with a north exposition *Betula fusca* scrub can be found, with *Betula fusca*, *Cotoneaster melanocarpa* and *Saxifraga spinulosa* as typical species. Also species from the forest and mountain steppe (*Festuca lenensis* type) occur. The *Caryopteris mongholica*-*Amygdalus pedunculata* shrubland occurs on south slopes with stony and rocky soils. It consists of the shrubs *Amygdalus pedunculata* and *Spiraea*

aquilegifolia and the dwarf-shrubs *Caryopteris mongholica*, *Caragana pygmaea* and *C. microphylla*. Many lowland and upland steppe species occur, and at an altitude higher than 1450 m species from the mountain steppe (*Festuca sibirica*) occur (Wallis de Vries et al. 1996).

In the valley of the Tuul river meadows alternate with bushes of willows. The *Iris lactea* meadow found here has a high vegetation cover and is dominated by a mixture of grasses (*Poa pratensis* and *Agrostis mongholica*) and herbs (*Iris lactea*, *Potentilla anserina*, *Sanguisorba officinalis*) (Wallis de Vries et al. 1996).

Wildlife in Hustai National Park

Native ungulates are free-ranging within the park. The takh (*Equus przewalskii*), the last wild-living horse species of the steppe, has grown to a population of 158 individuals (01-01-2005), since it was successfully re-introduced in Hustai National Park as from 1992. The takh got extinct in the wild in the 1960s. The main habitats of the takh are the *Stipa* steppes, the mountain steppes and the birch forest.

A population of about 350 red deer (*Cervus elaphus*) inhabit the mountain steppes and birch forests of the park, together with a population of 10-20 roe deer (*Capreolus capreolus*) (Takhi reintroduction centre, 2001). An estimated number of 15-20 wild boar (*Sus scrofa*) lives in the birch forests and 100-500 Mongolian gazelles (*Procapra gutturosa*) graze in the Tuul valley, especially in wintertime (Takhi reintroduction centre, 2001). Occasionally some migrating Argali sheep (*Ovis ammon*) were observed in the mountains.

In addition there live several small rodent species on the steppes, such as the long tailed souslik (*Citellus undulates*), the grey - and the striped hamster (*Cricetulus migratorius* and *barabensis*), the Brandt's vole (*Lasiopodomys brandtii*) and the Siberian jerboa (*Allactaga sibirica*), together with the bigger Siberian marmot (*Marmota sibirica*) that live on foot slopes and slopes of mountains (Takhi reintroduction centre, 2001). In the central and best protected areas of the park the marmots reached a rather high density (3.85 marmots per ha) (Takhi reintroduction centre, 1998). For the population of about 60 grey wolves (*Canis lupus*) that live in the park, the marmots are an important prey. Other predators are the corsac fox (*Vulpes corsac*) and siberian lynx (*Lynx lynx*).

Supported by the large population of rodents, raptors including the Black Vulture (*Aegypius monochus*), Golden Eagle (*Aquila chrysaetos*) and Saker Falcon (*Falco cherrug*) are abundant in the park. During spring and autumn the wetland of the Tuul river is an important foraging stop for migratory birds. Most birds migrating through Mongolia breed at Lake Baikal, only 400 km to the north of Hustai National Park in Siberia, which is a significant centre for Asian and European waterbirds (www.owc.org.mn/macne/hustai/).

A great number of insect species, of which 289 species are registered, adds to the diversity in the park (Nansalma B 1999). Most of the insects are herbivorous, and the large herbivorous insects like grasshoppers, cicadas and locusts, can have a big

impact on the steppe vegetation. Especially in hot and dry summers locusts can become very abundant, and consume a large amount of the grasses and herbs.

Human impact

Overgrazing is a serious threat to the sustainability of the grasslands in Mongolia, of which a significant proportion already is degraded. Estimates of The Botanical institute of the Academy of Sciences state that one third (41.9 million ha) of grazing land has been degraded (CBD-report 1996).

The high pressure on the steppe ecosystem as we face today is ascribed to the enormous increase in the population and livestock during the 20th century. Even though Mongolia still looks a land of vast and open landscapes with lonely hills and mountains, the increase in numbers of people and livestock has been dramatic over the past century. From 1918-1990 the population of the country increased almost three-fold (Table 1) (Kharin et al. 1999; Kharin 2002). This was due to a good health care system and a relatively rapid economic development. In that period Mongolia was a satellite of the Soviet Union, and received much help from there.

Table 1 Population growth in Mongolia (Kharin et al. 1999)

Year	Population (*10 ³)	Population density (persons km ⁻²)
1918	647.5	0.41
1925	651.9	0.42
1936	738.2	0.47
1940	738.6	0.47
1944	759.2	0.48
1950	845.5	0.54
1956	758.7	0.48
1960	936.9	0.60
1963	1017.1	0.65
1969	1197.6	0.76
1970	1230.5	0.79
1979	1596.0	1.02
1980	1639.7	1.05
1988	2074.0	1.33

During the same period the number of livestock, consisting of sheep, horses, cows or yaks, goat and camels, increased 2.3 times (Table 2) (Kharin et al. 1992). These animals all had to live from the same plant resources as before, since the country did not, or hardly, import any fodder, while the biomass productivity of the steppe is very low (Fig. 10).

Table 2 Number of livestock in Mongolia (Kharin et al. 1999)

Year	Camels (*10 ³)	Horses (*10 ³)	Cows (*10 ³)	Sheep (*10 ³)	Goat (*10 ³)	Total (*10 ³)
1918	228.7	1160.5	1078.4	5700.1	148.9	9645.6
1924	275.0	1339.8	1512.1	8444.8	2204.4	13776.1
1961	751.7	2889.3	1637.4	10981.9	4732.6	20392.9
1970	638.5	2317.9	2107.8	13311.7	4204.0	22574.9
1980	591.5	1985.4	2397.1	14230.7	4568.7	23771.4
1985	559.0	1971.0	2408.1	14429.8	4298.6	22485.5

In 1995 the number of livestock was estimated at 28.5 million (CBD-report 1996), which is an increase of about 25% since 1985. When the communist regime fell in 1990 and Mongolia became independent of Soviet influence, this led to an economic crisis and the closing of factories. Many unemployed people and their families left the cities and returned to the nomadic life-style on the steppe.

Long and intensive grazing pressures by livestock, together with a decline of sophisticated traditional grazing practices lead to a situation of overgrazing. After the collapse of the communist system, the system of maintenance of the wells failed and many wells broke down. So, more herdsmen and their livestock stayed in the neighbourhood of the wells that still worked, causing local overgrazing. Also around soums (villages and administrative units) there was a concentration of herdsmen and their livestock. This occurred because the accessibility of education and health care for the nomadic people became worse after the political change. Many herdsmen and their families stayed close to the schools and health care facilities of the soums, which very often lead to a degradation of the vegetation in the surrounding area.

The overgrazing resulted in a decrease of the vegetation cover, productivity and plant species diversity in many degraded areas (CBD-report 1996; Kharin et al. 1999). The original dominant *Stipa* grasses were replaced by other grasses like *Leymus chinensis*, *Cleistogenes squarrosa* and ruderal plant species (Hilbig 1995), or by the sedge *Carex duriuscula*. In heavy degraded areas the grasses have disappeared altogether and are replaced by *Artemisia* species. Sometimes the vegetation cover has completely disappeared and the bare soil is left susceptible for wind erosion, leading to desertification.

In degraded areas small rodents, like Brandt voles (*Lasiopodomys brandtii*), can increase enormously in number and aggravate the situation of the degradation. Such high abundances of small rodents are considered as indicators of overgrazing, together with high numbers of their predator, the buzzard (*Buteo lagopus*). At such sites many buzzards can be seen.

Livestock is not allowed into Hustai National Park, except during extreme circumstances in harsh winters. So, in the park overgrazing is not a problem and there is enough forage for the wild horses, red deer and marmots. However, close to the park many herdsman and livestock are camping in the valley of the Tuul river, causing a severe diminishing of the vegetation cover and degradation. For the Mongolian gazelles who used to forage in big herds in this area this is a problem, because there is hardly any good pasture left for them.

Soil degradation and a degraded vegetation of abandoned croplands also are problems occurring in the steppe area. Since the 1960's increasing amounts of land were brought under cultivation for wheat and fodder, and in 1990 1.34 million hectares were cultivated. However, the ploughing of the land and the planting of cultivated plants caused great losses of soil by wind erosion. A survey of arable land (1990-1993) found that 46.5% of the land surveyed was affected by erosion (CBD-report 1996). However, since 1990 there was a steady decrease in the area of croplands (CBD-report 1996). The main reasons for this were that the crop yield per hectare was often too low and the harvest often failed. Croplands were taken out of cultivation and abandoned.

After the abandonment of the fields, the vegetation did not recover to the original steppe vegetation, but remained covered by weeds for years. In many places the vegetation did not recover even after a period of 15 to 20 years. In the buffer zone of Hustai National Park there is an area of abandoned crop fields and after 15 years the vegetation still consists of weeds. Livestock avoids the fields for grazing so they are unproductive, and the soil is susceptible for wind and water erosion, because of the low soil cover by the weeds.

Long recovery times for old fields after abandonment are also known from the North American prairies, where it can take more than 20-40 years to reach the climax grassland vegetation (Lauenroth and Milchunas 1992).

Due to the increase in overgrazing and the abandonment of former cropland, desertification is increasing in Mongolia, as shown by the growing frequency of dust storms. There were an average of sixteen days with dust storms per year from 1960-1969, twenty-three per year in 1970-1979 and forty-one per year between 1980-1989. Land covered with sand increased by 38000 hectares between 1941 and 1990 (CBD-report 1996).

Recent change in climate and future developments

Climate change has potentially serious consequences for Mongolia's ecosystems. Studies (National Agency for Meteorology, Hydrology and Environment Monitoring, 2000) show that during the period 1940-2000 there has been a significant rise in annual mean air temperature of 1.56°C. The winter temperature has increased 3.61°C and the spring-autumn temperature 1.4-1.5°C. Particularly in March, May, September and November, the temperature has increased rapidly. The summer temperature, in

Fig. 12 Dead trees in the *Betula platyphylla* and *Populus tremula* forest of Hustai National Park (Arda Nederveen, August 2005)



contrast, has decreased 0.3°C . Summer cooling occurred mainly in June and July. During these 60 years, there was a slight increase in precipitation of 6%. However, although the summer precipitation increased by 11%, the spring precipitation decreased by 17%, causing a dryness in spring, which occurred mainly in May. It is probable that the rapid increase in temperature and considerable decrease in precipitation at the start of the growing season in May, had a significant negative impact on the growth of the vegetation during the past decades.

In Hustai National Park, which lies on the southern border of the forest steppe zone, a deterioration of the condition of the forest is observed from 2000 to 2004. In 2004 the forest almost completely died off (fig. 12; personal communication). The birch forests, which lay on the northern slopes of the mountains and consists of *Betula platyphylla* and *Populus tremula*, suffered in 2001 from insect attacks and since then the vitality of the forest decreased rapidly.

From 2000 to 2003 it was a dry period (of 2004 no data available) with a mean annual precipitation in Hustai National Park of 234 mm (Table 3). This is 20% below the long term annual precipitation of 296 mm (Hustai National Park 2000-2002, 2003). Especially 2000 and 2002 were extremely dry and several streams and gullies in the park dried up completely.

Table 3 Total precipitation in Hustai per year and per summer period (May, June, July, August, September) during 2000 – 2003.

	2000	2001	2002	2003
Yearly precipitation (mm)	186.6	249.1	166.9	334.9
Summer precipitation (mm)	149.4	207.9	111	309.9

It is likely that a lack of water is the main cause for the death of the trees. Insect plagues probably just played a secondary role.

This drying trend seems to be not just a local phenomenon in Hustai National Park, but part of a more regional pattern, as it was also observed in Bogd Uul, a protected forest near Ulaan Baatar at about 100 km from the park. In this forest also many trees (*Picea obovata*, *Larix sibirica*) died during the last years (personal communications).

Our results of a vegetation study on the *Stipa* steppe in Hustai National Park (chapter 2) are also in compliance with the trend of drying up. The results showed a shift to steppe species more adapted to dry conditions for the years 2000 to 2003 (chapter 2). Although there is only about 5% of forest in Hustai National Park on the northern slopes of the mountains, the forest is very important for the hydrology of the park. The forest catches water, which is held in the forest soil, and many streams originate from this forest area. For wildlife and horses it is essential to have surface water in their home-ranges, otherwise they can not use the pasture, even though it has a good quality of forage.

An assessment of potential impacts of climate change in Mongolia (National Agency for Meteorology, Hydrology and Environment Monitoring, 2000) predicted that sustained trends in warming will increase the area of arid lands and lead to a shift of the desert-steppe zone and steppe zone northwards. Scenario studies calculated that climate change in the 21st century will lead to a decrease of the forest-steppe and steppe area by 3-7%, while the desert will expand its area by 13%. The permafrost area can be reduced to 24-28% in 2040 and reduced even further to 16-25% in 2070. It is expected that water resources will increase until 2040 and then decrease until 2070.

Conservation of biological diversity

The large and relatively intact ecosystems in Mongolia, which have disappeared in adjacent countries, are of great global importance. The extended areas of steppes, although overgrazed at many places, still exhibit much of the original steppe vegetation and support large populations of wild ungulates. The characteristic saxaul forests (*Haloxylon ammodendron*) of the Gobi desert are also of great conservation value.

Mongolia now has several special protected areas with restrictions on economic activities. These reserves and national parks are of great importance for the protection of plant cover, botanical diversity and also for endangered animal species.

The takh (*Equus przewalskii*) was successfully reintroduced in Mongolia in Hustai National Park and grown to a population of 158 horses (01-01-2005). Other populations of takh had been reintroduced in reserves in the Gobi and in Western Mongolia.

Rare species, such as the Bactrian camel (*Camelus bactrianus*) and snow leopard (*Uncia uncia*) have important populations in Mongolia and are protected. The eastern steppe ecosystem is still the home to hundreds of thousands of migratory Mongolian gazelles and the mass migration of these gazelles is a spectacle as we only know from the Serengeti wildebeest migrations (CBD-report 1996).

Notable, from a zoogeographical point of view and for their conservation value, are the endemic fish species of the area. They are very different and live in various river systems of Mongolia, that flow to the Arctic or Pacific Oceans or endorheic in Central Asia (CBD-report 1996).

Conservation in Hustai National Park

Hustai National Park, the site where our research was carried out, is a national park in the forest steppe region of Mongolia. At the turn of the 19th century the area of the park was used as a hunting ground for the Bogd Khaan, the last ruling Khaan of Mongolia, and afterwards by Mongolian political officials (Bouman 1998). While nomads have also used the park as a pasture reserve for their livestock, the park never had a permanent settlement nor was it ever used for agriculture. This limited use allowed the preservation of one of the world's most threatened ecosystems: the steppe.

The park is covered by the larger 'Hustain Nuruu Steppe Reserve project' (HN-project), which is a long lasting Dutch Mongolian co-operation project. The HN-project is aimed at the re-introduction of the takh, financed by the Foundation Reserves Przewalski Horses (FRPH), and aimed at the restoration and conservation of the biodiversity in Hustai National Park (Bouman 1998). It is financed by the Dutch Ministry of Foreign Affairs, the Directorate General of International Co-operation. The Mongolian Association for the Conservation of Nature & Environment (MACNE) is responsible for the management of the park and its wildlife. FRPH and MACNE were jointly responsible for the execution of the Reintroduction Project for the Takh, which lasted ten consecutive years (1990 - 2000).

The takh (*Equus przewalskii*) is the last surviving ancestor of the modern domestic horse. The species once roamed the steppes of Central Asia and Europe, but since 1968 has got extinct in the wild. The Reintroduction Project for the Takh was set-up to return the most endangered species to its Mongolian homeland (Bouman 1998). Only about 150 takh lived in zoos and animal parks at the time of their extinction in the wild. These takh all originated from just 13 individual animals who were taken from the wild and bred in captivity.

In 1977 the Foundation for the Preservation and Protection of the Przewalski's Horse (FPPH) was established in the Netherlands by Jan and Inge Bouman and Annette Groeneveld. The foundation studied the genetic history of each takh and stimulated international cooperation between takh breeders. Because the takh had been in captivity for so long and began to show signs of domestication, a plan was formulated to increase genetic fitness. The takh were brought to semi-reserves where they could become adapted to more natural conditions before their release.

The Foundation Reserves for the Przewalski Horse (FRPH) was formed in 1980 by the Dutch World Wide Fund for Nature (WWF) and FPPH. Several semi-reserves were established in Germany and the Netherlands where genetically diverse takh from all over the world were able to adapt to living in large open territories. Here the animals

had to search for their own food and raise offspring in a more natural social context. The best adapted second-generation takh from these semi-reserves were chosen to be the first takh released back into the wild.

In Mongolia, a cooperation was started between Jan and Inge Bouman and Annette Groeneveld of the FRPH and Dr. Jachin Tserendeleg, vice-president of MACNE (Mongolian Association for Conservation of Nature and Environment). They searched for a good site for the re-establishment of the takh in Mongolia, and in the undisturbed forest steppe area of Hustai Nuruu they found the most suitable (Bouman 1998).

On 5 July 1992 the first transport of 16 takh arrived at Ulaanbaatar Airport and was welcomed by hundreds of enthusiastic people. For the old herdsmen the takh was an important symbol of the past, while for the younger generation, it was known as the mythical horse from their folklore. For conservationists, it was a keystone species whose re-introduction would help to protect the ecosystem at Hustai National Park and raise general awareness of environmental issues in Mongolia. In Mongolian 'takh' means god or spirit. It was like Mongolia got back its spirit, since it regained its independence from Soviet influence less than two years before.

The newly arrived takh were first released into acclimatisation areas to allow them to adapt to their new environment. After two years of acclimatisation, the harems were allowed to leave their enclosures and become free to range on the steppe. Now 84 takh have been re-introduced to the park, and they adjusted well to the harsh climate and to threats from predators. Each year, new foals add to the population and in 2005 a number of 158 horses was reached.

The general objective of Hustai National Park is to maintain, restore and preserve the biological diversity, the ecosystems and the cultural values of the Hustai National Park (www.owc.org.mn/macne/hustai/). It is tried to achieve this by means of:

- a) conservation of the ecosystems of Hustai National Park,
- b) development of a research and training centre
- c) development of eco-tourism
- d) improvement of natural resource management in the buffer zone around the park

The takh is seen as the flagship species for the conservation objective. Much research is conducted at the park to monitor the takh and other dominant species such as marmots, wolves and red deer. Monitoring programs are set-up in order to determine their health, estimate carrying capacities and interactions between species. Hydrological and soil resources are assessed and mapped. Vegetation types are identified and mapped. Studies are made of the food preferences of various herbivores in the park and the impact of grazing on the density and distribution of vegetation. In order to share the experience and knowledge of park management with other national parks in Mongolia and Central Asia, Hustai National Park hosts a month-long park ranger training course and also advises on park management regulations. The park's research staff often collaborates on studies with international scientists and many have travelled to the Netherlands and elsewhere to improve their knowledge of their respective fields.

Yearly an increasing number of tourists visit Hustai National Park and the development of a responsible tourism (ecotourism) is an important source of income for the park. For the national park, however, not only the development of ecotourism is of vital importance, but also the support of sustainable management of the surrounding steppe ecosystems by the local herding communities.

Regular meetings are held in the three soum centres to discuss the latest work at Hustai National Park and resolve any concerns voiced by the local herdsman. Soums are the smallest administrative units in Mongolia, similar to districts in other countries. The local school has an ecology room with equipment and materials supplied by the Hustai National Park Biodiversity Project. The buffer zone project works closely with locals to improve their standards of living, and to increase conservation awareness in the local communities around the national park, using the takh as a flagship species.

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Appendix Field-based dataset of net primary production (ANPP) and mean annual precipitation (MAP).

Site	Latitude	Longitude	MAP(mm)	ANPP(gm ⁻²)	Source
Xilingol (China)	43.7	116.6	182	85	DAAC ORNL
			450	228	
			293	231	
			287	103	
			304	140	
			302	203	
			414	189	
			326	227	
Tuva site (Russia)	51.8	94.4	198	101	DAAC ORNL
			229	82	
			254	162	
			194	25	
			279	105	
			376	128	
			404	136	
			393	120	
Shortandy (Kazakhstan)	51.7	71	319	134	DAAC ORNL
			403	110	
			406	171	
Khomutov (Ukraine)	47.2	38	476	345	DAAC ORNL
			324	281	
			444	391	
			476	446	
Hustai National Park (Mongolia)	47.5	106	187	77	van Staaldunin
			249	179	
			167	106	
Jornada I (NM, USA)	32.6	-106.75	435	33	Herbel et al. (1972)
			195	45	
			207	55	
			233	72	
			110	47	
			230	64	
			138	29	
			212	56	
			162	74	
			91	17	
			161	14	
81	9				

Site	Latitude	Longitude	MAP(mm)	ANPP(gm-2)	Source
			142	6	
Jornada II	32.6	-106.75	180	126	Szarek (1979)
(NM, USA)			321	251	
			237	188	
			394	127	
Sidney	47.4	-104.1	377	128	Wight and Black (1979)
(MT, USA)			326	79	
			527	125	
			342	121	
			330	72	
			493	122	
			424	76	
			394	93	
			368	132	
			376	110	
CPER	40.8	-104.6	117	84	Lauenroth and Sala (1992)
(CO, USA)			339	96	
			325	102	
			371	139	
			490	140	
			205	103	
			288	96	
			296	97	
			338	119	
			193	84	
			341	109	
			299	87	
			330	99	
			353	118	
			301	102	
			122	62	
			328	70	
			244	84	
			415	94	
			331	104	
			307	109	
			175	89	
			404	104	
			399	107	
			338	107	
			107	65	
			371	82	
			292	83	
			588	114	

Site	Latitude	Longitude	MAP(mm)	ANPP(gm ⁻²)	Source
			333	105	
			417	112	
			242	101	
			262	102	
			374	64	
			275	98	
			268	63	
			324	94	
			261	80	
			248	67	
			292	74	
			494	113	
			360	96	
			397	143	
			475	135	
			428	115	
			407	124	
			321	110	
			265	88	
			332	94	
			335	90	
			300	87	
			357	90	
Konza (KS, USA)	39.1	-94.6	513	372	Briggs and Knapp (1995)
			620	235	
			675	260	
			625	370	
			695	383	
			600	472	
			740	468	
			830	370	
			860	420	
			875	415	
			875	405	
			885	395	
			905	560	
			1025	520	
			975	363	
			1105	380	
			1130	395	
			1210	425	
			1435	590	
Hays (KS, USA)	38.9	-99.38	714	774	Hulett and Tomanek (1969)
			752	575	
			411	156	

Site	Latitude	Longitude	MAP(mm)	ANPP(gm ⁻²)	Source
			754	367	
			517	270	
			673	104	
			575	583	
			665	657	
			600	450	
			650	719	
			1100	673	
			340	351	
			535	379	
			471	484	
			537	425	
			234	279	
			720	568	
			793	904	
			621	461	
			520	446	
			719	670	
			586	500	
			563	389	
			502	305	
Salina (KS, USA)	38.4	-97.3	802	485	Piper (1995)
			835	662	
			461	320	
			585	373	
			874	438	
			605	243	
			927	473	

Successive MAP and ANPP data of Hustai National Park are from the years (2000-2003) respectively.

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Chapter 3

Impact of grazing by large and small mammalian herbivores in a Mongolian forest steppe

Submitted for publication

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Abstract

We investigated the impact of the type and intensity of grazing on plant species abundance, plant productivity and plant nutrient concentration. The study was located at Hustai National Park in the forest steppe region of Mongolia.

On the *Stipa* steppe we had built 2 types of exclosures; (1) one type which excluded the grazing by large mammalian herbivores, mainly takh (Prezwalksi horse), and (2) another type that excluded large and small, Siberian marmots, mammalian herbivores. The control plots were fully grazed. We measured species frequencies, tiller densities, plant biomass and nitrogen concentrations of the vegetation.

Grazing significantly decreased the plant standing crop and an increase in intensity led to a successive decrease in standing crop.

Grazing seemed to improve forage quality, as we found a higher N-concentration in the standing crop. However, this is solely the result of the higher live-dead ratio of the vegetation.

Our results did show a higher frequency of the rhizomatous *Leymus chinensis* under a higher grazing intensity, as well as a higher frequency of the total of rhizomatous species. We found a marginally significant decrease in the frequency of *Stipa krylovii*. However, we found reduced basal areas, lower tiller densities and a shift to smaller bunches of *Stipa*, which will lead to an ultimate decline of the *Stipa* population.

A correspondence analysis of species frequencies showed in all treatments a general shift to dryer conditions.

A higher grazing intensity led to a shift in dominance by caespitose species to a dominance by rhizomatous species.

Keywords: Caespitose species; Compensatory growth; *Leymus chinensis*, Rhizomatous species; Species composition.

Nomenclature: Grubov (2001)

Abbreviations: BA = Basal area; CA = Correspondence analysis.

Introduction

Mammalian herbivores play a crucial role in the sustainability of natural grasslands through their influence on the structural and functional properties of the ecosystem. Their grazing often leads to changes in vegetation structure, species composition and abundance, plant productivity and plant nitrogen cycling (Bakker et al. 1983; Detling 1998; McNaughton 1985; Werger et al. 2002).

On the semi-arid steppes of Mongolia there is a long history of grazing by large herbivores. In the forest steppe region, the vegetation of the typical *Stipa* steppe comprises a variety of grasses with different growth forms and several forbs (Hilbig 1995; Wallis de Vries et al. 1996). There are grasses that grow in bunches, such as the caespitose *Stipa krylovii*, and grasses that grow with solitary tillers such the rhizomatous *Leymus chinensis* (*Elymus chinensis*, Grubov 2001).

In studies on the vegetation of the *Stipa* steppe, Hilbig (1995), Fernandez-Gimenez & Allen-Diaz (2001), Gunin et al. (1999) and Xie and Wittig (2003) observed that the caespitose *Stipa* is dominant at sites with a low or moderate grazing intensity, while at sites with a higher grazing intensity the rhizomatous *Leymus chinensis* and *Carex duriuscula* are more abundant. At sites with a very high grazing pressure (situation of overgrazing), the grasses disappear and are replaced by annual *Artemisia* species (Hilbig 1995).

Comparable observations were made in the North American prairies where the originally dominant caespitose species were replaced by rhizomatous species (Eurasian weeds) when grazing pressure increased after the introduction of livestock (Milchunas et al. 1988; Mack and Thompson 1982).

The increased abundance of rhizomatous species under increased grazing intensity suggests a higher grazing tolerance of the rhizomatous species. This could be due to the occurrence of compensatory growth, which might mitigate the potential negative effects of defoliation (Anten et al. 2003; Gold & Caldwell 1989; Oesterheld and McNaughton 1988). In a greenhouse experiment testing the capacity for compensatory growth of *Stipa krylovii* and *Leymus chinensis*, *Leymus* indeed had a much stronger compensatory growth after clipping than *Stipa* (Van Staaldin and Anten, in press 2005). A field experiment also demonstrated the compensatory growth of *Leymus* after clipping (Wang et al. 2004). The decline in bunchgrasses after grazing could be due to fragmentation of individual plants, as reported in the study on the bunchgrass *Schizachyrium scoparium* (Butler and Briske 1987). As a response to herbivory, they found a reduction in plant basal areas and decreased tiller densities, which contributed to the decline in the bunchgrass.

A phenomenon often observed in plants grazed by large herbivores is the increase of the nitrogen concentration of the shoots, which results from an increased N availability (Bakker et al. 1983; Detling 1998; McNaughton 1985; Holland et al. 1992).

Herbivore-induced changes in vegetation characteristics depend not only on the intensity of grazing (Oesterheld 1992), but also on the type of grazing (Detling 1998; Olff and Ritchie 1998). Differences in forage preference and grazing habit between large and small mammalian herbivores showed to have different effects on the veg-

etation structure and composition and plant nutrient concentrations (Detling 1998; Ollf and Ritchie 1998). In studies on the steppe in Mongolia, differences in the food preference between takh (Przewalski horse) and marmots were reported (Takhi reintroduction centre 1998).

We conducted an enclosure experiment on the *Stipa* steppe in Mongolia in which we examined the effects of 3 years exclusion of takh (*Equus przewalskii*) and Siberian marmots (*Marmota sibirica*) on the plant species abundance, plant biomass and plant N-concentration.

We address the following questions: (1) does the abundance of rhizomatous species, and specifically *Leymus chinensis*, increase under a higher grazing intensity; (2) does the abundance of caespitose species, and specifically *Stipa krylovii*, decrease under a higher grazing intensity; (3) is there an increased fragmentation of the bunches of *Stipa krylovii* under increased grazing; (4) is there an increased N-concentration of the shoots under a higher grazing pressure?

Methods

Experimental site

An enclosure experiment was carried out in Hustai National Park, 100 km west of Ulaan Baatar, Mongolia (47°50' N, 106°00' E). In Mongolia the climate is arid and continental (mean annual temperature +2°C), with a short growing season in summer (from June to September) in which most of the precipitation falls (annual precipitation 296 mm in Hustai National Park). The national park is situated in the forest steppe region of Mongolia and occupies 60,000 ha at elevations ranging from 1100 to 1840 m above sea level. About 88% of the area is covered by grassland and shrub land steppe and ca 5% is covered by birch-dominated forest. Native ungulates are free-ranging within the park and include takh (*Equus przewalskii*), red deer (*Cervus elaphus*), wild boar (*Sus scrofa*), roe deer (*Capreolus capreolus*), migrating Argali sheep (*Ovis ammon*) and Mongolian gazelle (*Procapra gutturosa*). In the park live abundant populations of the Siberian marmot (*Marmota sibirica*), an important rodent herbivore. Takh, a rare, endemic species of the steppe, has been re-introduced in Hustai National Park since 1992.

One of the most widespread grassland types in the park is the *Stipa* steppe, which belongs to the *Thermopsis lanceolata*-*Stipa krylovii* community as described by Wallis de Vries et al. (1996). The vegetation is dominated by *Stipa krylovii*, while *Thermopsis lanceolata*, *Poa attenuata* and *Koeleria macrantha* are characteristic species of this community. The soils are kastanozems and the vegetation cover ranges from 45 to 90% with an average of 70%.

In order to select sites where the grazing intensity is rather high, monitoring data of the takh and the Siberian marmots were used (Takhi reintroduction centre, 1998, 1999).

Design

In June 2000, enclosures were built at four locations on the *Stipa* steppe. All four loca-

tions were chosen within the home-ranges of takh harems (area where they generally graze) and within the main local distribution area of the marmots. Treatments were: ungrazed plots (exclusion of both takh and Siberian marmots), marmot-grazed plots (exclusion of takh only) and fully grazed plots (control plots). For each treatment there were four replicates per location, which makes 12 plots on each location. Within a location, four transects at different elevations were selected at regular distances, and on each transect the treatments were distributed randomly.

The enclosures were constructed with fences made of mesh wire and barbed wire around a 4 x 4 m plot. Ungrazed plots were surrounded by a fence of 1.5 m high and the marmot-grazed plots by a fence of 1.5 m high with an opening of 30 cm above the ground. The fully grazed plot had no fence. By excluding the takh and marmots, other large and small mammalian herbivores were excluded as well.

To get an indication of the grazing intensity of the takh at the different locations we counted dung droppings on a 10 x 40 m plot established in between the enclosure plots. The droppings of the takh, and occasionally of deer and cows, were counted and marked by painted sticks. After about 30 days the new droppings were counted and painted. (during dry periods, the interval was 8 to 10 weeks).

Sampling

In the last 2 weeks of July 2002 and 2003, the aboveground biomass was sampled by clipping a 50 cm x 1 m strip in each of the enclosure and control plots (every year another strip was clipped). The vegetation was clipped at ground level and sorted to aboveground biomass, standing dead plant material, and litter. The standing crop, which consists of aboveground biomass and standing dead material, was also determined because that is the forage herbivores graze on. In 2003 the aboveground biomass was sorted into forb biomass and graminoid biomass. The plants were dried in an oven at 70°C for 48 h and weighed.

In July 2003 also the belowground biomass was sampled by taking a root core, 7.9 cm in diameter and 12 cm deep, at three random locations along each strip immediately after clipping. These cores were washed over a 2 mm mesh screen to remove soil and dead or decayed material. After drying of all live material (roots and rhizomes combined) at 70°C for 48 h, dry weight was determined.

To determine soil characteristics soil cores with a diameter of 2.8 cm and 7 cm deep were taken in 2003. Belowground plant parts were removed and the soil was oven dried at 70°C for 48 h.

Total organic nitrogen concentrations in the aboveground biomass, standing dead plant material, litter, roots and soil were determined after Kjeldahl destruction using a continuous flow analyzer (SKALAR, Breda, Netherlands).

In the first half of July 2002 basal areas and tiller densities of *Stipa* bunches were determined in a 1 m² plot inside each of the 4 x 4 m plots of the ungrazed treatment and fully grazed treatment. Per bunch the diameters were measured in two directions and used for calculating the basal area, assuming an ellipse shape of the

bunch. In a 2 cm wide strip in the centre of the bunch the number of live tillers was counted and the tiller density per cm² determined. The number of tillers per bunch was estimated by multiplying the tiller density by the basal area of the bunch.

In a 1 m² permanent plot inside the enclosure plots (4 x 4 m) and in control plots measurements of species frequencies were taken once in the growing season in the second and third week of August 2000, 2002, and 2003. Using a 1 x 1 m grid divided into 10 x 10 cm sections which was laid on the vegetation, the total number of sections was counted in which a certain species was present. Species frequencies of all the species were recorded.

Statistical analysis

Data were statistically analyzed with the statistical package SPSS 10.0 for Windows (SPSS Inc. Chicago, Illinois, USA). A GLM repeated measures was used to analyze the overall effects and the interactions between factors (year *df* = 1, grazing *df* = 2, location *df* = 3) on data of biomass, N-concentrations and species frequency. With a post hoc multiple comparison test and a contrasts test, on which a Bonferroni correction was applied, the differences between the means were tested. In case there were only data available for one year, a one-way Anova was used to test the significance of the effect of grazing. With a chi-squared test the effect of grazing on size distribution of *Stipa* bunches was analyzed. Differences were considered significant at *P* < 0.05.

In order to analyze the effects of the grazing treatments on the overall composition of the vegetation in the enclosures, we performed a correspondence analysis (CA) with species frequency data (2003) (Jongman et al. 1995), using the statistical package MVSP 3.0 (Kovach Computing Services, Anglesey, UK). Species data of 2000 and 2003 were used for a combined CA.

Results

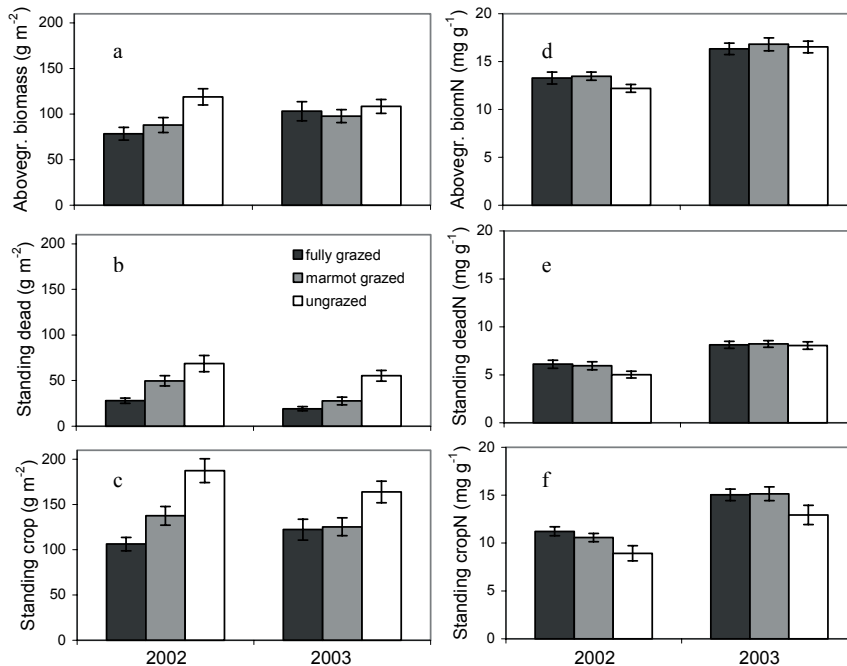
Biomass and grazing intensity

Grazing clearly had a significant effect on the aboveground biomass, standing dead plant material, live/dead ratio and litter of the vegetation in the plots at the time of harvest. As expected the fully grazed plots had significant less (aboveground) biomass (5 to 35% lower) than the ungrazed plots (Figs. 1a, b, Tables 1, 2 and 3). However, no significant difference in biomass was found between the fully grazed and marmot-grazed plots (Table 3).

Standing dead material was more in the ungrazed than in the marmot-grazed (30 to 50% higher) and the fully grazed plots (60 to 65% higher) (Fig. 1b, Table 1 and 3). Also a significant effect of the type of grazing was found; the marmot-grazed plots had more standing dead material (30 to 40% higher) than the fully grazed plots.

In the dry year of 2002 the amount of standing dead material in all the plots was significantly more than in the wet 2003 (Fig. 1b, Table 1, 2 and 3). From May till September in 2003 the precipitation was about three times more than in the same period in 2002 (Table 4a). Year significantly affected the amount of standing dead material in the plots (Table 2).

Fig. 1 Mean and st. error of a) above ground biomass, b) standing dead, c) standing crop, the mean N-concentration in d) above ground biomass, e) standing dead and f) standing crop of vegetation of the fully grazed, marmot grazed and ungrazed treatment in 2002 and 2003.



As a consequence of the stronger decrease after grazing in standing dead material than in biomass, there was a significantly higher live/dead ratio of the standing crop (biomass and dead material) on the fully grazed plots than on the ungrazed plots (Fig. 1c, Table 1 and 3). There was no significant difference in live/dead ratio between the fully grazed and marmot-grazed plots.

No significant difference was found in the amount of litter between the ungrazed plots and the fully grazed or marmot-grazed plots (Table 1 and 3). There was only a significant effect of type of grazing on the amount of litter: the fully grazed plots had a significant smaller amount of litter than the marmot-grazed plots.

Grazing did not have an effect on root biomass (Table 4b).

An indication for the grazing intensity of large herbivores is given by the number of dung droppings counted at the different locations (Table 4c). Location 3 had a higher grazing intensity than location 1 and 4. Between locations 1, 2 and 4 there was no significant difference in grazing intensity.

Nitrogen concentrations

The N-concentrations of the aboveground biomass, standing dead material and standing crop were significantly affected by year (Table 2). In 2003, when there was much more precipitation than in 2002, the N-concentrations were higher than in 2002 (Figs. 1d, e, f, Table 1, 2 and 4a).

Table 1 Mean and st. error of above ground biomass, standing dead, standing crop, live/dead ratio, litter, the mean N-concentration in above ground biomass, standing dead and standing crop, *Stipa* frequency, *Leymus* frequency, *Carex* frequency, bunchgrass frequency and rhizomatous graminoids frequency of the vegetation of the fully grazed, marmot grazed and ungrazed treatment in 2002 and 2003.

	2002 Fully graz		2002 Marm.graz		2002 Ungrazed		2003 Fully graz		2003 Marm.graz		2003 Ungrazed	
(g/m ²)												
Abv biom	78.29	(7.0)	87.93	(8.2)	118.84	(9.0)	103.17	(10.5)	97.71	(7.2)	108.42	(7.6)
St dead	27.94	(2.9)	49.63	(5.6)	68.65	(9.0)	19.10	(2.3)	27.59	(4.3)	55.35	(5.9)
St crop	106.23	(7.5)	137.56	(10.3)	187.50	(13.1)	122.28	(11.5)	125.30	(9.8)	163.78	(11.9)
Live/dead	3.50	(0.5)	2.22	(0.4)	2.44	(0.6)	5.99	(0.6)	4.64	(0.8)	2.23	(0.22)
Litter	31.95	(5.0)	37.12	(4.9)	40.17	(3.8)	22.15	(4.6)	33.25	(6.0)	36.32	(6.2)
(mg/g)												
Abv biom N	13.28	(0.6)	13.47	(0.4)	12.20	(0.4)	16.33	(0.6)	16.81	(0.7)	16.53	(0.6)
St dead N	6.10	(0.4)	5.95	(0.4)	5.02	(0.3)	8.13	(0.4)	8.22	(0.3)	8.05	(0.4)
St crop N	11.22	(0.5)	10.57	(0.4)	8.93	(0.8)	15.04	(0.6)	15.14	(0.7)	12.93	(1.0)
<i>Stipa</i> freq	32.44	(4.5)	23.94	(3.7)	38.67	(6.2)	34.33	(3.8)	25.88	(4.6)	36.33	(5.7)
<i>Ley</i> freq	33.08	(6.0)	48.26	(10.8)	26.63	(5.4)	47.25	(8.9)	59.75	(11.2)	28.33	(3.8)
<i>Carex</i> freq	39.73	(7.7)	32.36	(7.7)	15.64	(2.8)	67.17	(7.8)	56.08	(6.6)	39.54	(6.9)
Bunch freq	55.31	(4.4)	53.69	(3.3)	61.33	(5.3)	61.81	(6.7)	56.19	(5.1)	64.47	(7.8)
Rhiz freq	54.88	(8.0)	62.00	(7.3)	29.87	(4.1)	88.37	(10.1)	98.75	(9.1)	65.13	(7.9)

Table 2 P-values of a repeated measures (test of within- subjects effects) with above ground biomass, standing dead, standing crop, live/dead ratio, litter, above ground biomass N-concentration, standing dead N-concentration, standing crop N-concentration, *Stipa* frequency, *Leymus* frequency, *Carex* frequency, bunchgrass frequency and rhizomatous graminoids frequency as variables and year (df = 1), grazing (df = 2) and location (df = 3) as factors.

	Year	Year*loc	Grazing	Graz*loc	year*graz	Yr*graz*loc	Loc
Abv biom	.259	.003*	.015*	.856	.099	.590	.316
St dead	.003*	.116	.000*	.327	.617	.564	.101
St crop	.437	.054	.000*	.902	.227	.594	.243
Live/dead	.001*	.002*	.000*	.052	.204	.772	.037*
Litter	.193	.001*	.016*	.215	.851	.617	.005*
Abv biom N	.000*	.162	.383	.248	.473	.535	.121
St dead N	.000*	.368	.237	.186	.355	.208	.225
St crop N	.000*	.395	.010*	.370	.421	.961	.011*
<i>Stipa</i> freq	.837	.845	.028*	.542	.562	.080	.019*
<i>Ley</i> freq	.001*	.839	.009*	.943	.015*	.135	.651
<i>Carex</i> freq	.000*	.476	.176	.774	.495	.618	.922
Bunch freq	.253	.828	.477	.657	.706	.502	.090
Rhiz freq	.000*	.010*	.030*	.649	.462	.467	.022*

* indicate significant effects $p < 0.05$.

Table 3 P-values of contrasts (repeated measures, tests of within-subjects contrasts) between the means per grazing treatment of the variables: above ground biomass, standing dead, standing crop, live/dead ratio, litter, above ground biomass N-concentration, standing dead N-concentration, standing crop N-concentration, *Stipa* frequency, *Carex* frequency, bunchgrass frequency and rhizomatous graminoids frequency. A Bonferroni correction is applied on the p-values.

	Fully graz - marm graz	Fully graz - ungrazed	Marm graz - ungrazed	(Fully + marm graz) - ungrazed
Abv biom	2.133	0.018*	0.168	0.045*
St dead	0.021*	0.000*	0.000*	0.000*
t crop	0.396	0.000*	0.009*	0.000*
Live/dead	0.075	0.009*	0.039*	0.006*
Litter	0.018*	0.087	1.737	0.333
t biom N	1.431	1.569	0.531	0.630
St dead N	2.148	0.636	0.333	0.282
St crop N	1.458	0.045*	0.096	0.045*
<i>Stip</i> freq	0.108	1.458	0.057	0.279
<i>Carex</i> freq	1.158	0.366	0.189	0.108
Bunch freq	1.005	2.091	0.792	1.296
Rhiz freq	1.158	0.390	0.003*	0.009*

* indicate significant effects $p < 0.05$

Table 4a Total precipitation in Hustai per year and per summer period (May, June, July, August, September) during 2000 – 2003.

	2000	2001	2002	2003
Yearly precipitation (mm)	186.6	249.1	166.9	334.9
Summer precipitation (mm)	149.4	207.9	111	309.9

Table 4b Mean and st. error of root mass, root N-concentration and soil N-concentration of the fully grazed, marmot grazed and ungrazed treatment in 2003. Means followed by a different letter within the same row are significantly different, as results from analysis of variance (1way-ANOVA) with treatment as factor ($df = 2$) ($P < 0.05$).

	Fully grazed	Marmot graz	Ungrazed
Roots (g/m^2)	548.1 (68.2) a	475.1 (37.3) a	555.5 (67.0) a
Root N (mg/g)	9.5 (0.3) a	9.3 (0.5) a	9.15 (0.3) a
Soil N (mg/g)	2.47 (0.0) a	2.49 (0.1) a	2.53 (0.1) a

Table 4c Mean and st. error of the number of dung dropping per 30 days on the 4 locations during the period of 2001 – 2003. Means followed by a different letter are significantly different, as results from analysis of variance (ANOVA) with location as factor ($df = 3$) ($P < 0.05$).

	Location 1	Location 2	Location 3	Location 4
Dung droppings	17.76 (4.9)a	23.25 (3.5)ab	37.13 (2.1)b	15.13 (2.1)a

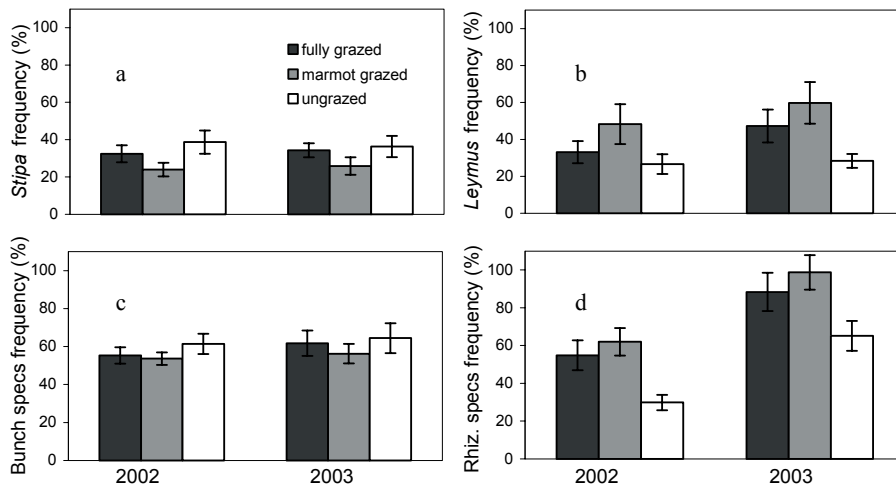
Although there was no effect of grazing on the N-concentrations of the aboveground biomass (biom N) and the standing dead material (st dead N) separately, there was a significant grazing effect on the N-concentrations of the standing crop (st crop N), which consists of aboveground biomass and standing dead material (Table 2). The standing crop is the forage where the large herbivores grazed on. The fully grazed plots had significantly higher N-concentrations of standing crop than the ungrazed plot (Figs. 1f, Table 1 and 3).

Grazing did not affect root N-concentrations and soil N-concentrations (Table 4b).

Shift in species composition

The frequency of the bunchgrass *Stipa krylovii* in the plots was significantly affected by grazing (Table 2). The higher frequency of *Stipa* in the ungrazed plots compared to the marmot-grazed plots was almost significant ($p = .057$) (Fig. 2a, Table 1 and 3).

Fig. 2 Mean and st. error of a) *Stipa* frequency, b) *Leymus* frequency, c) bunchgrass frequency and d) rhizomatous graminoids frequency of the vegetation of the fully grazed, marmot grazed and ungrazed treatment in 2002 and 2003.



For the rhizomatous *Leymus chinensis* an interaction was found between year and grazing (Fig. 2b, Table 2); which means that the effect of grazing depended on the year. Therefore no general grazing effect over the two years could be determined, only for the years separately (Table 5). In 2003 there was an effect of grazing, while in 2002 there was no effect. Species frequency of *Leymus* in 2003 was lower in the ungrazed plots compared to the marmot-grazed plots (Fig. 2b, Table 1 and 5).

Table 5 P-values of the differences between the means of *Leymus* frequencies per grazing treatment.

	Fully graz - marm graz	Fully graz - ungrazed	Marm graz - ungrazed
Ley freq (2002)	.545	1.000	.187
Ley freq (2003)	.921	.353	.039*

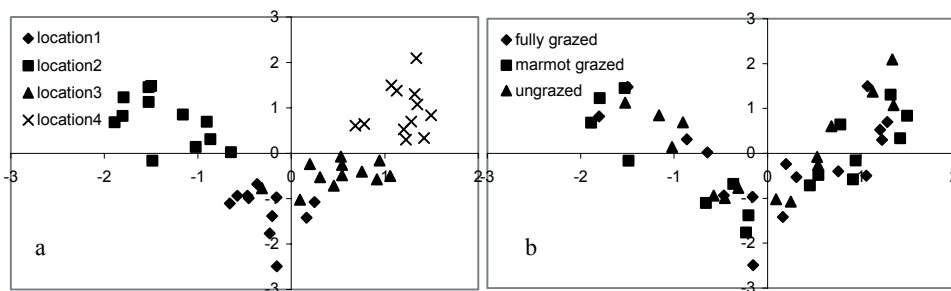
* indicate significant differences $p < 0.05$.

For *Carex duriuscula*, another rhizomatous species, there was no grazing effect on the frequency in the plots (Table 2). Yet there was an effect of year. In the wet summer of 2003 (Table 1d) the species frequency of *Carex* was higher than in 2002 (Table 1 and 2). The frequency of the group of bunchgrasses (total of frequencies of bunchgrass species) was not affected by grazing or any other factor (Fig. 2c, Table 2).

For the rhizomatous species group, there was a significant grazing effect on the frequency (total of frequencies of rhizomatous species) (Table 2). There was a significantly higher species group frequency in the marmot-grazed plots than in the ungrazed plots (Fig. 2d, Table 1 and 3). There also was a higher frequency in the total of fully grazed and marmot-grazed plots than in the ungrazed plots.

In the Figs. 3a and b the scores of a correspondence analysis (CA) of the species data of the exclosures are presented. Fig. 3a shows the site scores (2003) of the different locations along the ordination axes. After 3 years of exclusion the first two ordina-

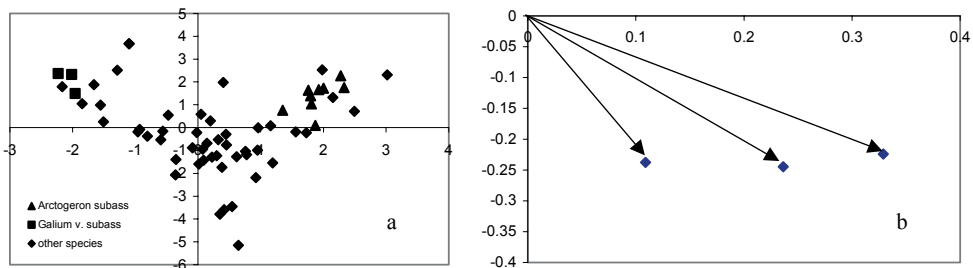
Fig. 3 Site scores a) per location b) per treatment of correspondence analysis (CA) with species frequency data of 2003.



tion axes are still completely determined by the differences between locations. For the site scores per grazing treatment however, no pattern was found (Fig. 3b). In order to evaluate the possible effects of 3 years of exclusion on the vegetation a combined CA of the species data of 2000 and 2003 was performed (Fig. 4a). There was a shift in site scores from 2000 to 2003 (Fig. 4b).

The distribution of the species scores give an indication for the environmental fac-

Fig. 4 Scores of species of the *Arctogeron* subassociation, the *Galium verum* subassociation and other species of a combined CA with data of 2000 and 2003, b) Shift in site scores per treatment from 2000-2003.



tors that are represented by the ordination axes (Fig. 4a) On the right hand side of the first ordination axis species from the *Arctogeron gramineum* subassociation (Hilbig 1995) and other species from sandy and rocky slopes (like *Carex korshinski*) are found. Species of the *Galium verum* subassociation (Hilbig 1995) are found on the left side of this axis. The *Arctogeron gramineum* subassociation occurs on exposed stony and rocky sites with little earth, while the *Galium verum* subassociation occurs on less dry sites and contains many species that are also found on the meadow steppe (Hilbig 1995). This indicates that the first axis represents a gradient from dry (right) to wetter conditions (left). The second axis cannot easily be interpreted.

Fig. 4b shows the vectors representing the average changes in site scores of the three grazing treatments from 2000 to 2003 along the first two axes of the CA. The treatments differ in their shifts along the first CA axis. The direction of the shifts suggests that conditions have become dryer.

Bunch size and tiller density of *Stipa krylovii*

Table 6 shows that grazing does not affect the total number of *Stipa krylovii* bunches in the plots. Grazing however, increased the portion of small bunches (BA<25cm) and decreased the portion of large bunches (BA>25) (Table 6).

Individual bunch basal area and total basal area per plot were significantly reduced by grazing (Table 6). No effect of grazing was found on the tiller density or on the number of tillers per bunch.

Table 6 Means of bunch frequencies, basal area (BA) estimates and tiller densities of *Stipa krylovii* bunches on fully grazed (n = 16) and ungrazed (n = 16) plots (1m x 0.5m). # With a chi-squared test a significant grazing effect on the distribution of small and large bunches within a plot was shown (P<0.05).¹ Means followed by a different letter within the same row are significantly different (P<0.05). * data are SQR transformed to perform an ANOVA.

	Fully grazed	Ungrazed
Bunch frequencies		
Small bunches (BA<25cm ²)	146 [#]	139 [#]
Large bunches (BA>25cm ²)	27 [#]	56 [#]
Tot bunches	173a ¹	195a
Basal areas		
Basal area (cm ²) / bunch *	12.12a	19.46b
Tot basal area (cm ²) /plot*	142.13a	273.93b
Tiller numbers and densities		
Tillers/bunch	40.82a	52.76a
Tillers/(cm ²) BA	5.13a	6.19a
Tillers/plot*	458.25a	742.68b

Discussion

The exclusion of large herbivores and small herbivores led to a higher plant standing crop (which consists of biomass and standing dead material) in the plots. The grazing intensity of the takh and marmots was sufficient to cause significant differences between the different types of exclosures. A successive increase in the amount of standing crop on fully grazed, marmot-grazed and ungrazed plots reflected a successive decrease in grazing intensity.

Grazing seemed to rejuvenate the vegetation, as we found a much lower amount of standing dead material in the grazed plots than in the ungrazed plots. As a consequence, the live-dead ratio of the vegetation was much higher in the grazed plots. Our data showed an improved forage quality after grazing, as reflected in higher N-concentrations of the standing crop. However, this seems solely to be the result of the higher live-dead ratio of the vegetation, as the aboveground biomass had much higher N-concentrations than the dead material, and no increase of the N-concentrations of the biomass or of the dead material after grazing was found. Nor did we find increased N-concentrations of the roots or the soil after grazing. Contrary to the findings of Holland et al. (1992), who found an increased N-mineralization and N-availability leading to higher N-concentrations in the aboveground biomass, our results indicate that the improved forage quality did not result from an increased N-availability.

Weather conditions, however, seemed to affect the N-availability for the plants. We found significantly higher N-concentrations in the aboveground biomass and standing dead in 2003, when there was much more precipitation as compared to 2002 (Table 4a). Presumably a higher moisture content of the soil resulted in an increased microbial activity, a higher N-mineralization and thereby a higher N-availability for the plants.

Although grazing significantly decreased the above ground biomass, it did not affect root biomass in our exclosure experiment. This is consistent with the results of Ferraro and Oosterheld (2001) who analysed the responses of more than 40 individual grass species to defoliation. They found a large negative effect on aboveground biomass and just a minimal effect on root biomass. However, in a greenhouse experiment with *Stipa* and *Leymus* (Van Staaldin and Anten, in press 2005) a large defoliation effect on root biomass was found. Compared to the exclosure experiment, there was a larger decrease of aboveground biomass (30-35% and 70-75% reductions respectively).

Possibly this stronger defoliation effect on biomass production in the greenhouse resulted from the higher nitrogen availability at which the plants were grown. Ferraro and Oosterheld (2001) found that plants grown at high nitrogen levels were more negatively affected by clipping than plants at low nitrogen. Comparing the responses of individual plants (Ferraro and Oosterheld 2002) with responses at ecosystem level (Oosterheld et al. 1999), the effects of defoliation on individual plants

were much more negative. This can be explained by the fact that plants in pot experiments are often grown under high nitrogen levels, while the plants in grazing ecosystems generally experience nitrogen limitation.

As was hypothesized, our results did show a higher frequency of the rhizomatous *Leymus chinensis* under a higher grazing intensity, as well as a higher frequency of the total of rhizomatous species. This is in accordance with studies in North American prairies (Milchunas et al. 1988; Mack and Thompson 1982) where the dominating caespitose species were replaced by rhizomatous species when grazing pressure increased. The increased frequency of *Leymus* and its higher grazing tolerance can be attributed to a much stronger compensatory growth in *Leymus* after defoliation than in *Stipa*, as was shown in a greenhouse experiment (Van Staalduin and Anten, in press 2005). Van Staalduin and Anten (in press 2005) found that compensatory growth in *Leymus* mainly resulted from a higher assimilation rate and the reallocation of stored carbohydrates from its rhizomes. In our enclosure experiment *Leymus* seemed to be benefited more by grazing in the wet year of 2003 than in the dry 2002, as the frequency increased more after grazing in 2003 (Table 4a). For *Stipa* the frequencies remained the same in the 2 years. This is in accordance with Van Staalduin and Anten (in press 2005), who found that in *Leymus* there was more compensatory growth under wet than under dry conditions, while in *Stipa* compensation was decreased under wet conditions.

In our enclosure experiment we found a marginally significant decrease in the frequency of *Stipa krylovii*, but no decrease in the frequency of all the bunchgrasses after grazing. However, we found reduced basal areas, lower tillers densities and a shift to smaller bunches of *Stipa* (Table 6). Ultimately this will probably lead to a decline of the *Stipa* population. Butler and Briske (1988) reported similar results in their research on the population structure of the bunchgrass *Schizachyrium scoparium*. Here the fragmentation of individual bunches and the subsequent decrease in tiller numbers contributed to a decline of the bunchgrass in response to grazing.

Correspondence analysis showed the effect of 3 years of exclusion of the vegetation from grazing even though the qualitative species composition did not yet change. In all treatments species frequencies suggested a general shift to dryer conditions. In Mongolia indeed, there were two extremely dry summers (2000 and 2002) during the period of fieldwork (Table 4a) and large changes in the hydrology in Hustai National Park were reported, with the drying up of streams and a decrease in soil moisture (Hustai National Park, 2000-2002, 2003).

It is remarkable that the drying effect showed stronger in the ungrazed plots than in the marmot-grazed and fully grazed plots (Fig. 1e). This is probably due to the positive effect of grazing on soil water content by reducing the transpiring leaf area and thereby decreasing the transpiration of the vegetation, as was found in studies of Archer and Detling (1986) and Day and Detling (1994).

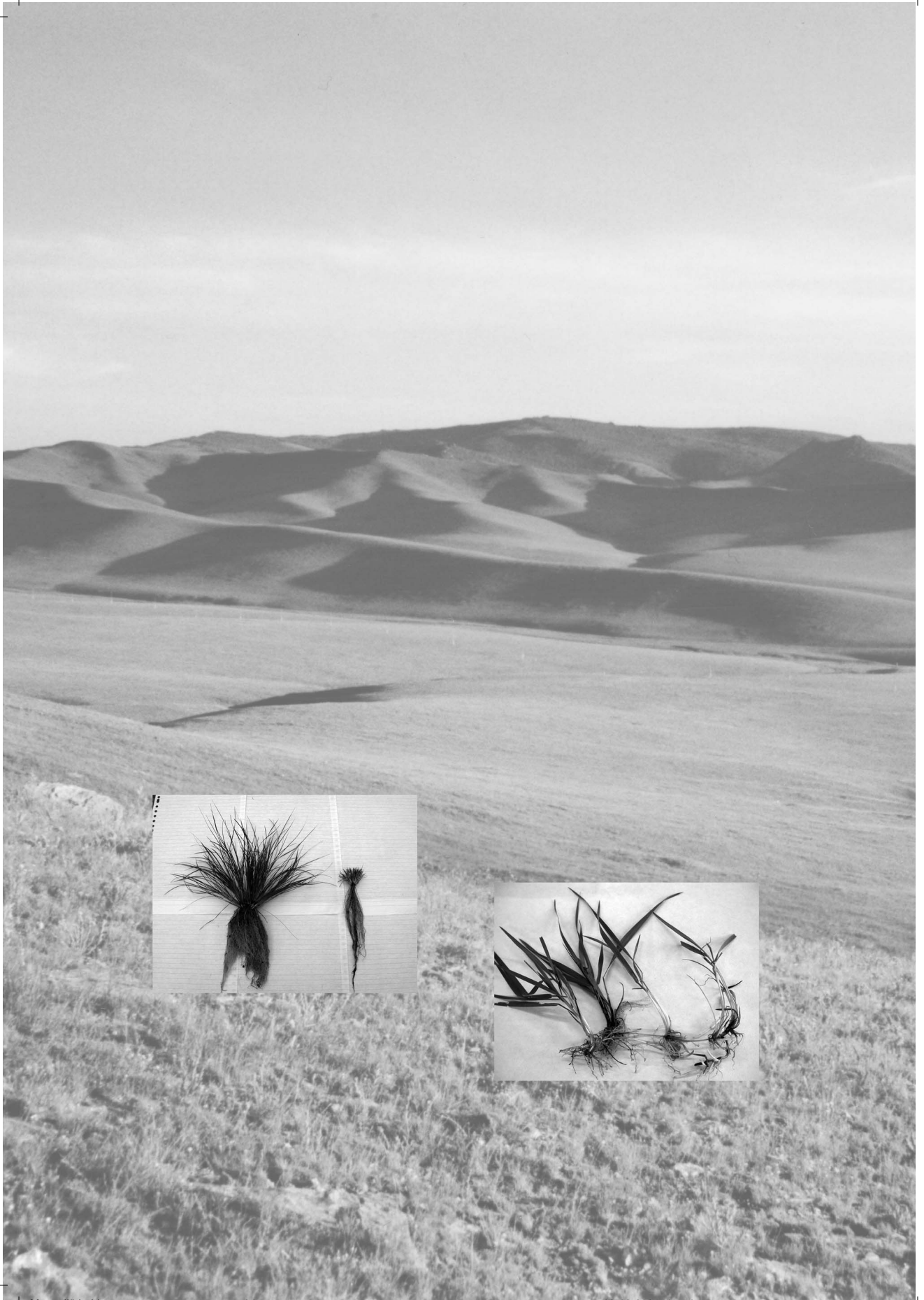
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Chapter 4

Differences in the compensatory growth of two co-occurring grass species in relation to water availability

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Abstract

We compared the potential for compensatory growth of two grass species from the Mongolian steppe that differ in their ability to persist under grazing: the rhizomatous *Leymus chinensis* and the caespitose *Stipa krylovii*, and investigated how this ability might be affected by drought. Plants were grown in a greenhouse under wet and dry conditions and subjected to a clipping treatment (biweekly removal of 75–90% of the aerial mass). *Leymus* exhibited a much stronger compensatory growth after clipping than *Stipa*. *Leymus* showed a significant increase in its relative growth rate (RGR) after clipping, while for *Stipa* RGR was negatively affected. Clipped *Leymus* plants maintained leaf productivity levels that were similar to undamaged individuals, while leaf productivity in clipped *Stipa* dropped to less than half of that of the controls. In *Leymus* there was less compensatory growth under dry than under wet conditions, while in *Stipa* compensation was increased under drought. This difference probably reflects the fact that *Stipa* is more drought tolerant than *Leymus*. The greater compensatory growth of *Leymus* compared to *Stipa* mainly resulted from a greater stimulation of its net assimilation rate (NAR), and its greater capacity to store and re-allocate carbohydrates by clipping. The greater increase in NAR was probably the result of a stronger reduction in self-shading, because *Leymus* shoots were much denser than those of *Stipa*, which resulted in a higher increase in light penetration to remaining leaves after clipping. The results of this study suggest that the greater ability of *Leymus* to persist under grazing is the result of its larger capacity for compensatory growth.

Keywords: Biomass allocation · Growth analysis · Herbivory · Steppe ecosystem · Sustainable grazing

Introduction

Partial defoliation of plants by herbivores or through physical damage is a common phenomenon in natural habitats. Humans harvest leaves either directly (tea, tobacco) or indirectly by grazing cattle. While partial defoliation entails a loss of photosynthetic area, this rarely results in a proportional reduction in growth. Plants

appear to possess compensatory mechanisms through which they can mitigate potential negative effects of defoliation (Oosterheld and McNaughton 1988; Gold and Caldwell 1990).

Under natural conditions the ability to compensate for leaf losses can give plants a selective advantage (Stowe et al. 2000). In agricultural systems compensatory growth has important consequences for sustainable levels of leaf harvesting or cattle grazing. The latter is particularly important in semi-arid climates which include the large steppe areas of the world. Stimulation of grassland productivity by herbivores has been observed in several studies: the plants exhibited increased photosynthetic rates (Caldwell et al. 1981; Gold and Caldwell 1990; Anten and Ackerly 2001a), and relative growth rates (RGR, growth rate per unit plant biomass) after grazing or clipping (Hilbert et al. 1981; Oosterheld and McNaughton 1988, 1991; Anten et al. 2003). Grazing often leads to changes in vegetation structure, species composition and the productivity of the ecosystem (Werger et al. 2002). These changes will depend on the intensity of grazing (Oosterheld 1992), resource availability and interspecific differences in the ability to compensate for leaf losses.

To quantify the degree to which plants can compensate for potential losses in performance due to defoliation and interspecific differences there in, we used a method developed by Anten et al. (2003), quantifying the performance of defoliated plants relative to the estimated performance of hypothetical noncompensating plants. The difference in performance between species is then used as a measure of the selective advantage of a species. With the method of Anten et al. (2003) the contributions of the different mechanisms of compensatory growth to relative growth rate (RGR) can be assessed. The two components of RGR are net assimilation rate (NAR, growth per unit leaf area) and leaf area ratio (LAR, leaf area per plant biomass) ($RGR = NAR \times LAR$). Defoliation causes an immediate drop in LAR and therefore a reduction in RGR. To compensate for this loss in leaf area, NAR can be enhanced by increased light availability on the remaining leaves (Gold and Caldwell 1990; Anten and Ackerly 2001a) or by increased leaf nitrogen concentration (Nowak and Caldwell 1984; Anten and Ackerly 2001a) and LAR may be increased by increased biomass allocation to new leaf production (Oosterheld and McNaughton 1991; Anten et al. 2003), reallocation of stored carbohydrates (McPherson and Williams 1998) or activation of dormant buds. By these processes the RGR can be increased and the plant can compensate for the loss in biomass. The contribution of these different mechanisms probably differs between species and between plants growing under different growth conditions.

It is often observed that the amount of compensatory growth after defoliation is influenced by the level of resource availability (Hilbert et al. 1981; Coughenour et al. 1990; Oosterheld and McNaughton 1991). Belsky (1993) argued that compensation only occurs under optimal conditions, while Anten et al. (2003) found less compensatory growth for plants growing at low light availability. The model of Hilbert et al. (1981), on the other hand, predicts that plants growing at low-resource availability are more likely to increase production following clipping, than plants growing

under optimal conditions (Hilbert et al. 1981). Several field studies (Oosterheld and McNaughton 1988, 1991; Coughenour et al. 1990) indeed found that plants growing at low nutrient or water availability exhibited stronger compensatory growth than those under more favorable conditions.

In this paper, we investigate the influence of drought stress on compensatory growth. Plants suffering from drought stress can be positively affected by grazing or clipping (McNaughton 1983; Archer and Detling 1986; Coughenour et al. 1990; Day and Detling 1994). The removal of transpiring leaf area can enhance soil water conservation and improve plant water potential (Archer and Detling 1986; Day and Detling 1994). However, it is typically observed in steppe vegetation that overgrazing and its associated negative effects, i.e. changes in species composition and degradation of the vegetation, are more pronounced during cycles of dry years than during wetter periods (Gunin et al. 1999). Because grazing by livestock is common in semi-arid regions it is important to investigate the effect of drought on the amount of compensatory growth.

On the semi-arid steppes of Mongolia there is a long history of grazing by large herbivores and the plants seem to be adapted to the damage by grazing and periods of drought. The vegetation is made up of a variety of grasses with different growth forms (Hilbig 1995; Wallis de Vries et al. 1996). Some grow in bunches, such as the caespitose *Stipa krylovii*, while others grow with long and short rhizomatous tillers, such as *Leymus chinensis*.

Under light or moderate grazing *Stipa krylovii* is the dominant species, but under a higher grazing intensity *Stipa* decreases and the rhizomatous *Leymus chinensis* and *Carex duriuscula* become dominant (Hilbig 1995; Fernandez-Gimenez and Allen-Diaz 2001). This phenomenon where the original dominating caespitose species are being replaced by rhizomatous species when grazing pressure by livestock increases is common in many other semi-arid grassland areas, e.g. Inner Mongolia, Northern China and North American steppe (Mack and Thompson 1982; Milchunas et al. 1988; Xie and Wittig 2003). This shift in dominance could be attributed to either a higher grazing resistance or grazing tolerance (see definitions Stowe et al. 2000) of the rhizomatous species. A higher grazing resistance, i.e. a better avoidance of grazing, can be achieved by characteristics like a prostrate growth form, the possession of spines or defense substances, which make the plants unattractive or unpalatable for grazers. However, *Stipa* and *Leymus* have about the same stature, and the food preference of horses is similar for both species (Takhi reintroduction centre 1998). This suggests that the shift in dominance to *Leymus* is primarily related to its greater grazing tolerance which in turn is associated with a greater compensatory growth. Rhizomatous species have large belowground storage organs and the reallocation of carbohydrates is probably an important mechanism contributing to compensatory growth in these species (Chapin et al. 1990; Kobe 1997; McPherson and Williams 1998). Yet we do not know of any study in which growth characteristics of caespitose and rhizomatous grasses have been quantitatively related to their capacity for compensatory growth.

We conducted a greenhouse experiment with *Leymus chinensis* and *Stipa krylovii*, two co-occurring species of the steppe, on which we performed a clipping treatment and dryness treatment simultaneously. We address the following questions: (1) does the more grazing tolerant *Leymus* have a greater capacity for compensatory growth than *Stipa*, (2) what plant characteristic determine potential interspecific differences in compensatory growth, and (3) how is compensatory growth affected by a reduction in water availability?

Methods

Greenhouse experiment

Tillers of *Stipa krylovii* and *Leymus chinensis* (also known as *Elymus chinensis*) plants were collected from the steppe vegetation in Hustai Nuruu National Park, situated at 100 km west of Ulaan Baatar, Mongolia (47°50' N, 106°00' E). We took tillers from 9 *Stipa* and 14 *Leymus* plants. In Mongolia the climate is arid and continental (mean annual temperature +2° C), with a short growing season in summer (from June to September) in which most of the precipitation falls (annual precipitation 270 mm). The tillers were grown in pots in the greenhouse of Utrecht University, Utrecht, the Netherlands, where the experiment was carried out. In April 2003 tillers were randomly taken from these plants; 47 pots were planted with *Stipa* (3 tillers of one individual plant per pot) and 89 pots with *Leymus* (1 tiller per pot). We took 3 tillers for *Stipa*, because these were smaller than *Leymus* tillers, and we wanted plant mass per pot at the start of the experiment to be as similar as possible between the two species. The pots had a volume of 5 l and were filled with a mixture of sand, clay and humus (4:1:1), and fertilized with 16.4 g/pot Scotts Osmocote-standard (15%N + 9%P + 9%K + 3%Mg + trace elements), total N gift being about 2.5 g N per plant. On 11 June 2003 the experiment was initiated for *Leymus*; 60 *Leymus* plants were selected. These plants were chosen after determining the size of all plants according to the number of tillers and tiller height omitting the smallest and largest individuals. The 60 plants were then divided into 3 size classes and equally assigned over 4 treatments and 1 additional set of plants, which was harvested at the start of the experiment. For *Stipa* the experiment started later, on 25 June 2003 with 45 plants, similarly divided into size classes and assigned to 4 treatments and an initial harvest. This lower number (45 compared to 60) was because of limited availability of plants. At the first harvest, on 11 June 2003 for *Leymus* and on 25 June 2003 for *Stipa*, the roots and rhizomes (of *Leymus*) were carefully washed and separated from other plant parts. Leaf area was determined by using a LI-3100 area meter (Li-Cor inc. Lincoln, Nebraska, USA). Leaves, sheaths, roots and rhizomes were oven-dried for 72 hours at 50° C and weighed.

The pots were placed at random in the greenhouse and we applied two clipping treatments (control and clipped) and two levels of water availability: 500 ml/pot applied every 2 days (wet) and 260 ml/pot every 4 days (dry), with 12 replicate plants per treatment for *Leymus* and 9 replicate plants for *Stipa*. During the experiment measurements on volumetric soil moisture content in the pots were regularly per-

formed with a Delta Thetaprobe (Delta-T Devices, Cambridge, UK). When the pots became too dry in hot and sunny periods, the water gift was more frequent. Under the dry treatment, the water content in the pots was higher for the clipped plants than for the control plants, but these differences were only significant for the *Stipa* plants. We measured significant differences in volumetric soil moisture content on 1 July (5.93% *Stipa*-clip, 5.00% *Stipa*-contr), on 15 July (5.38% *Stipa*-clip, 4.47% *Stipa*-contr), and on 22 July (5.72% *Stipa*-clip, 4.98% *Stipa*-contr).

Plants were grown for 72 days during which the clipping treatment was imposed at day 2, day 29 and day 57. In this way, the plants had about 4 weeks to recover after the first and second clipping, and 2 weeks after the third clipping before the plants were harvested. The *Leymus* plants were clipped at a height of 10 cm, and the *Stipa* plants, which were smaller, were clipped at a height of 7 cm. This resulted in a removal of about 75% of the shoot mass in both species, as estimated from the data of the initial harvest. Leaf areas and dry masses of clipped leaves were determined in the same way as during the initial harvest.

Leymus was harvested on 21 August and *Stipa* on 4 September 2003. Leaf area and the biomass of all the plant parts were determined in the same way as during the initial harvest. Total organic nitrogen, phosphorus and potassium contents of the leaves were determined after Kjeldahl destruction with a continuous flow analyzer (SKALAR, Breda, Netherlands).

For *Stipa* plants carbohydrate concentration in the roots was measured (control and clipped plants). Because of a failure of the cooling system rhizome samples of *Leymus* could not be used for the analysis of carbohydrate content. So, we set up an extra greenhouse experiment with *Leymus* to measure starch content of below ground parts in control and clipped *Leymus* plants. Five control plants and 5 plants with a clipping treatment (similar to former experiment) were placed in the greenhouse on 16 September under similar conditions as the former experiment. At harvest on 26 November biomass of all the plant parts were determined (same procedure as initial harvest) and carbohydrate concentration in the rhizomes was measured. To determine the carbohydrate concentration in the samples, starch was hydrolyzed using DMSO (dimethyl sulphoxide) and thermostable α -Amylase. The resulting starch dextrines were quantitatively hydrolysed by amyloglucosidase to glucose. Thereafter the glucose was colored by Antrone in sulfur acid and measured with a photo-spectrometer.

Growth analysis

The growth analysis method developed by Anten and Ackerly (2001b) was used to estimate the growth parameters: relative growth rate (RGR, $\text{g g}^{-1} \text{day}^{-1}$), net assimilation rate (NAR, $\text{g m}^{-2} \text{day}^{-1}$), lamina mass ratio (LMR, g g^{-1}), lamina area ratio (LAR, $\text{m}^2 \text{g}^{-1}$), the fraction of newly assimilated biomass that is allocated to the production of lamina tissue (f_{lam} , g g^{-1}), specific leaf area (SLA, $\text{m}^2 \text{g}^{-1}$), and the daily change in the average SLA of the plant (γ , day^{-1}) by means of iteration. The method uses a number of growth functions (see Eqs. 1-6 in Anten and Ackerly 2001b) and searches

iteratively the parameter space to find the joint solution of parameter values that yield values for the total plant mass, leaf lamina mass, and lamina area at the end of the growth period that match the measured values. The calculations are based on the dates of the start and the end of the growth period and clipping events, together with the initial biomass, leaf area, and the amounts of leaf area lost during the growth interval. The equations are directly solved for the parameters NAR , leaf allocation (f_{lam}), and daily increase in SLA (γ). For further details see Anten and Ackerly (2001b).

Compensation

The most commonly used definition of compensation states that compensatory growth occurs only when there is an increase in RGR in defoliated plants relative to undamaged individuals. This definition is incomplete (Anten et al. 2003). Immediately after clipping, the plants will have a lower LAR and therefore a reduced RGR. To compensate for this, plants can increase photosynthesis or increase the allocation of assimilates to leaf growth, which results in an increase of the NAR or a partial recovery of LAR. But this response may not be enough to compensate fully for the earlier decrease in RGR. As a result such a plant will have a lower RGR than an unclipped plant, but will have a higher RGR than it would have had without any compensatory response.

We therefore applied the method of Anten et al. (2003), which compares the performance of a clipped plant not only with that of an undamaged plant but also with that of a hypothetical non compensating defoliated plant. The potential negative effect of defoliation (L_{pot}) is the difference between the performance of an undamaged plant and the predicted performance of a hypothetical non-compensating defoliated plant. The real negative effect of defoliation (L_{real}) is the difference between the performance of an undamaged plant and the observed performance of a defoliated one (see Anten et al. 2003).

To estimate the compensation we performed calculations with replicate hypothetical plants. The biomass values of the hypothetical plants were derived from replicate clipped plants and the growth parameters NAR , leaf allocation (f_{lam}), and daily increase in SLA (γ) were derived from replicate undamaged plants. The plants were paired after being arranged to size. Compensation (C) is defined as the fraction of the potential loss (L_{pot}) that is made up for by compensatory growth:

$$C = [(L_{pot} - L_{real}) / L_{pot}] \times 100\% \\ = \{[\Pi_d(x_d) - \Pi_o(x_u)] / [\Pi_u(x_u) - \Pi_o(x_u)]\} \times 100\% \quad (1)$$

where Π is the performance measure (growth, plant size, reproduction etc.), x refers to a series of growth parameters that may change as a result of compensatory mechanisms (e.g., NAR or allocation of mass to leaves), the subscripts d and u indicate whether a plant has been defoliated (d) or not (u). $\Pi_o(x_u)$ refers to the performance of a hypothetical non-compensating defoliated plant with the growth parameters

(x_u) of an unclipped plant. $C > 100\%$ indicates overcompensation, $C = 100\%$ full compensation, $0 < C < 100\%$ partial compensation, $C = 0\%$ no compensation, and $C < 0\%$ negative compensation.

A sensitivity analysis was performed to estimate the relative contributions of changes in each individual parameter to the overall extent of compensation (see Anten et al. 2003). This was done by taking one of the 3 growth parameters to be equal to the measured value for defoliated plants, while the other 2 were taken to be equal to those of the control plants.

Statistical analysis

Data were statistically analyzed with the statistical package SPSS 10.0 for Windows (SPSS Inc. Chicago, Illinois, USA). First, a three-way Anova is used to analyse the overall effects and the interactions between factors (species, clipping and dryness, all $df = 1$). With a one-way Anova the significance of the effect of clipping was tested for the wet and dry treatment of one species separately and in the same way the effect of dryness was tested for the control and clipped treatment separately. Differences were considered significant at $P < 0.05$.

Results

Plant performance, allocation and growth

In all *Leymus* and *Stipa* plants, clipping resulted in a strong reduction in total standing mass, leaf mass and belowground mass at the end of the experiment (Table 1). In *Leymus*, belowground mass consisted of root mass and rhizome mass, while in *Stipa* it consisted only of root mass. The clipping effect was stronger in *Stipa* (75–80% lower) than in *Leymus* (60 to 65% reduction), as was indicated by the significant species*clipping interaction (Table 2). The dry treatment also resulted in a significant lower total mass and leaf mass of *Leymus* and *Stipa*, and a lower belowground mass of *Leymus* (Table 1). The negative effect of dryness on total mass was stronger in *Leymus* (44–51% reduction) than in *Stipa* (33–47% reduction) as indicated by the significant species*dryness interaction (Table 2). For *Stipa* the belowground mass was negatively affected by drought in the control plants but not in the clipped ones (Table 1).

The *Leymus* plants showed a significant increase in their relative growth rates (RGR) after clipping (Table 1, Fig. 1; clipped biomass was included in the calculation). For *Stipa* RGR was negatively affected by clipping, though this reduction was only significant under dry conditions. The difference in effect of clipping on the RGR of the two species was also reflected by the significant interaction between species and clipping (Table 2). In *Leymus* net growth per unit leaf area (NAR) was two-fold higher in the clipped than in the unclipped plants; in *Stipa* this increase was no more than 30% (Table 1, Fig. 1). The *Stipa* plants grown under wet conditions showed an increase in NAR after clipping (increase of 29%), but apparently this increase did not fully compensate for the initial reduction in LAR. Under dry conditions the increase in NAR of *Stipa* plants was not significant. In both species clipped plants allocated a 30%

Table 1 Mean and std. error (in parentheses) of measured values at the final harvest, including leaf area ratio (LAR), estimated relative growth rate (RGR), net assimilation rate (NAR), fraction of biomass allocated to lamina growth (f_{lam}) and specific leaf area (SLA), and results of analysis of variance (ANOVA) with clipping (df = 1) as factor and an ANOVA with dryness (df = 1) as factor.

	<i>Leymus</i> Control	<i>Leymus</i> Clipped	<i>Leymus</i> Clipping effect	<i>Stipa</i> Control	<i>Stipa</i> Clipped	<i>Stipa</i> Clipping effect
Total mass (g) (excluding clipped)						
Wet	52.21 (1.3)	20.91 (1.1)	***	21.18 (1.3)	4.23 (0.5)	***
Dry	29.28 (0.5)	10.25 (0.6)	***	11.22 (0.8)	2.83 (0.3)	***
Drying effect		***	***		***	*
Leaf mass (g) (excluding clipped)						
Wet	36.15 (1.1)	12.57 (0.8)	***	13.95 (1.2)	2.89 (0.4)	***
Dry	20.14 (0.7)	6.04 (0.4)	***	6.59 (0.4)	1.75 (0.2)	***
Drying effect		***	***		***	*
LAR (m ² mg ⁻¹)						
Wet	5.65 (0.2)	4.91 (0.2)	*	2.70 (0.1)	2.56 (0.1)	n.s.
Dry	4.66 (0.2)	4.16 (0.3)	n.s.	2.38 (0.1)	2.26 (0.1)	n.s.
Drying effect		***	*		n.s.	n.s.
Belowground mass (g)						
Wet	16.06 (0.9)	8.34 (0.5)	***	7.23 (0.4)	1.34 (0.2)	***
Dry	9.14 (0.5)	4.21 (0.2)	***	4.63 (0.3)	1.08 (0.1)	***
Drying effect		***	***		***	n.s.
RGR (g g ⁻¹ d ⁻¹) * 100						
Wet	3.46 (0.1)	5.16 (0.1)	***	4.91 (0.2)	4.27 (0.2)	n.s.
Dry	2.63 (0.1)	3.16 (0.1)	*	4.18 (0.3)	3.25 (0.3)	*
Drying effect		***	***		*	*
NAR † (g m ⁻² d ⁻¹)						
Wet	5.94 (0.2)	12.58 (0.5)	***	18.95 (0.7)	24.42 (0.1)	**
Dry	5.09 (0.3)	9.19 (0.9)	***	17.79 (0.8)	19.28 (2.0)	n.s.
Drying effect		*	**		n.s.	n.s.
f_{lam} (g g ⁻¹)						
Wet	0.43 (0.01)	0.58 (0.01)	***	0.45 (0.01)	0.59 (0.02)	***
Dry	0.35 (0.01)	0.57 (0.01)	***	0.38 (0.01)	0.61 (0.02)	***
Drying effect		***	n.s.		**	n.s.
SLA (m ² mg ⁻¹)						
Wet	12.87 (0.3)	14.91 (0.4)	*	6.09 (0.3)	7.31 (0.3)	n.s.
Dry	12.69 (0.3)	12.25 (0.8)	n.s.	6.32 (0.2)	6.85 (0.2)	n.s.
Drying effect		n.s.	*		n.s.	n.s.

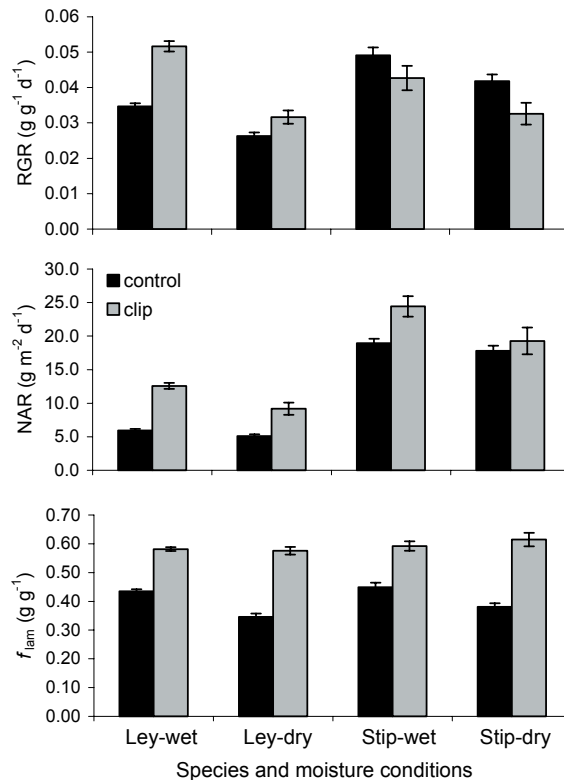
† variable ln transformed. n.s. indicate no significant effects $p > 0.05$. *, ** and *** indicate significant effects $p < 0.05$, $p < 0.01$ and $p < 0.001$, respectively.

Table 2 Results of a three-way ANOVA with (species*dryness*clipping*, df = 1) as factors. † and ‡ indicate variable were ln transformed and square root transformed, respectively. n.s. indicates no significant effects $p > 0.05$. *, ** and *** denote significant effects $p < 0.05$, $p < 0.01$ and $p < 0.001$, respectively.

	Sp	Dry	Clip	S*D	S*C	D*C	S*D*C
RGR	***	***	n.s.	n.s.	***	*	n.s.
NAR †	***	***	***	n.s.	***	*	n.s.
f_{lam}	*	***	***	n.s.	n.s.	***	n.s.
Total mass ‡	***	***	***	***	*	***	n.s.
Productivity	***	***	***	***	n.s.	***	***
Leaf Productivity ‡	***	n.s.	***	***	***	***	***
N-conc.	***	n.s.	***	n.s.	n.s.	n.s.	n.s.
P-conc.	**	*	***	n.s.	n.s.	n.s.	n.s.
K-conc.	***	*	***	**	***	n.s.	n.s.

Notes: RGR is relative growth rate, NAR is net assimilation rate, f_{lam} is fraction of biomass allocated to lamina growth and N-conc., P-conc. and K-conc. are the N-, P- and K-concentrations in the leaves respectively.

Fig. 1 The estimated average relative growth rate (RGR), net assimilation rate (NAR), and biomass fraction allocated to lamina growth (f_{lam}) of *Leymus* and *Stipa* at two clipping levels and under wet and dry conditions. Bars indicate ± 1 std error (*Leymus* n=12, *Stipa* n=9)

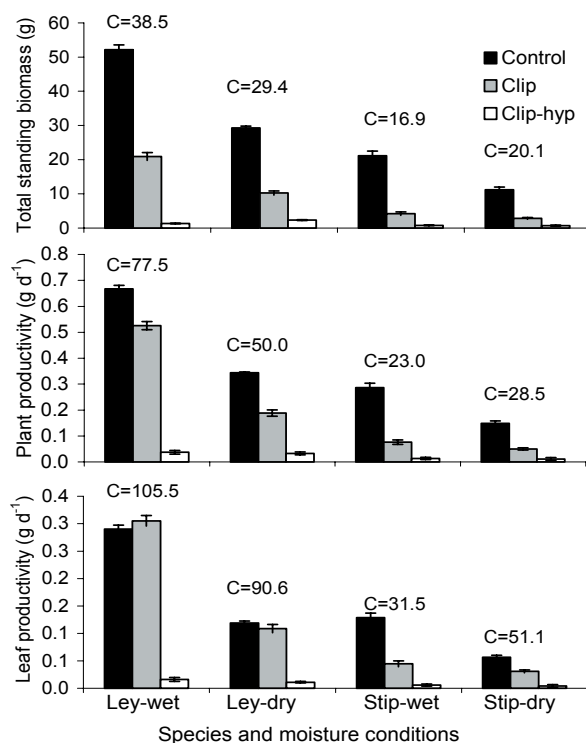


greater fraction of their mass to lamina growth (f_{lam} , Table 1, Fig. 1). The SLA of both species was hardly affected by clipping, only the *Leymus* plants under wet conditions showed a little increase (8%) in SLA after clipping (Table 1).

Compensatory growth

In both species and under both treatments clipped plants were estimated to perform much better in terms of final biomass, productivity and leaf productivity than non-compensating hypothetical plants (Fig. 2). With Eq.(1) it was hence estimated that changes in net assimilation rate (NAR), leaf allocation (f_{lam}), and daily increase in SLA (γ) enabled clipped *Leymus* plants to compensate for a large part of the potential loss caused by defoliation. The degree of compensation depended on the species, the performance measure and the water availability.

Fig. 2 Total standing biomass, estimated plant productivity, and leaf productivity at final harvest of *Leymus* and *Stipa* at two clipping levels (Control and Clip), and the estimated values of these parameters of a hypothetical clipped plant without compensatory mechanisms (Clip-hyp) under wet and dry conditions. Numbers under the columns indicate the calculated values for compensation (C values). Bars indicate ± 1 std error (*Leymus* n = 12, *Stipa* n = 9). See main text for the calculation procedures.



Clipped plants of both species partly compensated for the loss in productivity but this compensation was much stronger in *Leymus* than in *Stipa* (C = 50-77% and 23-28%, respectively; Fig. 2). Taking only the leaf productivity into account the com-

compensation effect was much stronger (Fig. 2), *Leymus* exhibited a full compensation (C about 100%), and *Stipa* a partial compensation of about 50 % under dry conditions and about 30% under wet conditions (Fig. 2).

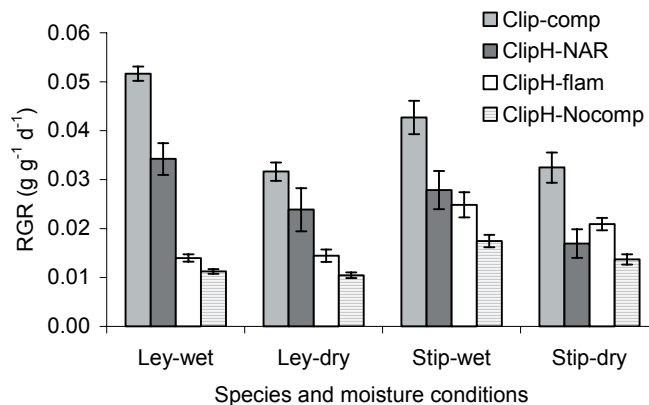
Effect of drought stress

The increase in RGR of *Leymus* after clipping was higher under wet conditions than under dry conditions (Fig. 1). This was further indicated by the significant interactive effect of clipping and dryness on RGR (Table 2). The comparatively greater stimulation of RGR by clipping in wet conditions resulted from a similarly greater stimulation of NAR (Fig. 1, Table 1), also indicated by a significant interaction between clipping and dryness (Table 2). By contrast, enhancement of leaf allocation (f_{lam}) by clipping was greater under dry conditions. In *Stipa* the decrease in RGR after clipping was not significant for the wet treatment (Table 1, Fig. 1), while the change in NAR after clipping was not significant for the dry treatment (Table 1, Fig. 1). There was only a significant increase in NAR for the wet treatment.

For *Leymus* and *Stipa* plants there was a significant increase in f_{lam} after clipping (Table 1, Fig. 1). For both species this increase was higher under dry conditions than under wet conditions, as further indicated by the significant interactive effect of dryness and clipping on f_{lam} (Table 2).

A significant interaction of clipping*dryness was found for total biomass, productivity and leaf productivity (Table 2). In *Leymus*, under dry conditions, the compensation (C) for total biomass, productivity and leaf productivity after clipping was lower (Fig. 2). For *Stipa*, on the contrary, the compensation for total biomass, productivity and leaf productivity after clipping was higher under dry conditions (Fig. 2). A significant interaction of species*clipping*dryness was found for productivity and leaf productivity (Table 2).

Fig. 3 The estimated average relative growth rate (RGR) of clipped plants (Clip-comp), hypothetical clipped plants compensating either for NAR (ClipH-NAR), f_{lam} (ClipH- f_{lam}), or not compensating at all (ClipH-Nocomp) of *Leymus* and *Stipa* plants under wet and dry conditions. Bars indicate ± 1 std error (*Leymus* n = 12, *Stipa* n = 9)



Sensitivity analysis

The contributions of increases in the growth parameters NAR and leaf allocation (f_{lam}) in response to clipping to RGR are shown in Fig. 3. For the *Leymus* plants the NAR had a much greater effect on RGR than f_{lam} had under both wet and under dry conditions, but under wet conditions the relative contribution of NAR was much higher than under dry conditions. For the *Stipa* plants the contributions of NAR and f_{lam} to the RGR were more or less equal.

Starch and nutrient contents

For the *Leymus* plants, clipping had a significant negative effect on the concentration of starch (Fig. 4). In the rhizome and roots it dropped by more than 60%. There was no significant clipping effect on the concentration of starch in the roots of *Stipa*. For *Leymus* there was a significant increase in leaf nitrogen contents after clipping,

Fig. 4 Starch content in belowground organs of *Leymus* and *Stipa* at two clipping levels. Bars indicate ± 1 std error (*Leymus* n = 5, *Stipa* n = 5). * indicate significant clipping effects $p < 0.05$

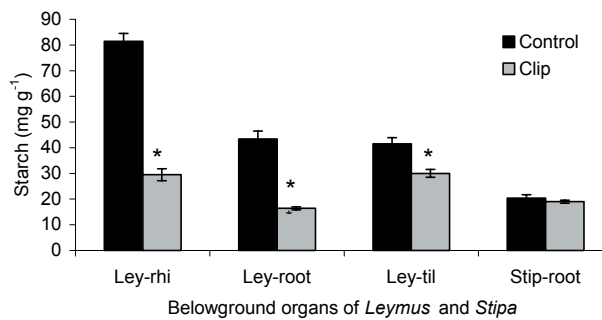


Table 3 Mean and std. error (in parentheses) of N-, and P-concentrations in the leaves of *Leymus* and *Stipa*, and results of analysis of variance (ANOVA) with clipping (df = 1) as factor and an ANOVA with dryness (df = 1) as factor. n.s. indicate no significant effects $p > 0.05$. *, ** and *** denote significant effects $p < 0.05$, $p < 0.01$ and $p < 0.001$, respectively.

	<i>Leymus</i> Control	<i>Leymus</i> Clipped	<i>Leymus</i> Clipping effect	<i>Stipa</i> Control	<i>Stipa</i> Clipped	<i>Stipa</i> Clipping effect
N-concentration (mg g ⁻¹)						
Wet	39.72 (0.6)	43.07 (1.2)	*	34.03 (1.2)	36.84 (1.0)	n.s.
Dry	41.12 (0.9)	44.99 (0.8)	*	33.44 (0.9)	35.84 (0.8)	n.s.
Drying effect	n.s.	n.s.		n.s.	n.s.	
P-concentration (mg g ⁻¹)						
Wet	1.84 (0.1)	2.73 (0.1)	***	1.59 (0.1)	2.84 (0.2)	***
Dry	1.83 (0.1)	2.67 (0.1)	**	1.44 (0.1)	2.29 (0.1)	***
Drying effect	n.s.	n.s.		n.s.	*	

while for *Stipa* there was no significant clipping effect found on the N content (Table 3). Leaf phosphorus contents of both species increased after clipping while in *Stipa* they were lower in the dry than in wet treatment.

Discussion

Interspecific differences in compensation

As expected, *Leymus chinensis* exhibited a much stronger degree of compensatory growth after clipping than *Stipa krylovii*. Clipped *Leymus* plants maintained leaf productivity levels that were similar to undamaged individuals, while leaf productivity in clipped *Stipa* dropped to less than half of that of the controls. Apparently *Leymus* is more tolerant to clipping (and by extrapolation to grazing) than *Stipa* (see definitions in Stowe et al. 2000) and this could explain the shift in dominance from *Stipa* to *Leymus* when grazing pressure increases in the Mongolian steppe.

In this paper we used the method of Anten et al. (2003), which estimates compensation relative to a hypothetical non-compensating defoliated plant rather than relative to undamaged plants in the standard approach (Hilbert et al. 1981). If we had used the standard approach we would have concluded that while *Leymus* exhibits compensatory growth *Stipa* plants did not, because the relative growth rate (RGR) of defoliated plants was lower than that of the controls. However, we estimated that clipped *Stipa* plants had a considerably higher RGR than hypothetical noncompensating plants and compensated for a large percentage of the potential loss in performance (Fig. 2).

Our sensitivity analysis showed that enhancements of net assimilation rate (NAR) after clipping contributed more to the increase in RGR than the enhancements of leaf allocation (f_{lam}) in *Leymus*, especially under wet conditions (Fig. 3). In *Stipa* on the other hand NAR increased only by 20%. Its contribution to stimulation of RGR relative to non-compensating plants was comparable to that of f_{lam} . It appears that the greater compensatory growth of *Leymus* compared to *Stipa* was mostly due to the stimulation of its NAR by clipping.

Various mechanisms may contribute to increases in NAR after leaf losses (see Introduction). Reductions in self-shading might have played a role in the large NAR stimulation of *Leymus* found here and also in the difference between the two species. In this experiment *Leymus* formed large tussocks and there was probably a strong degree of self-shading within the shoot. Removing a big part of the shoot by clipping can result in a considerable increased light intensity on the remaining leaves. *Stipa* shoots on the other hand are relatively open while their leaves are much thinner than those of *Leymus*. In a greenhouse experiment (M.A. Carrillo-Gavilán, unpublished data) with *Leymus* plants that were similar in form as the ones used here, it was measured that two weeks after clipping, average light intensity on the leaves was 40% greater than in controls. Similar results have been obtained with other grass species (Gold and Caldwell 1990; Senock et al. 1991).

Increases in photosynthetic capacity are another way through which plants can enhance NAR after defoliation (Nowak and Caldwell 1984). The photosynthetic

capacity of leaves is strongly related to their N-concentration (Evans 1989). We only found a small increase in leaf N-concentration after clipping (Table 3) suggesting that changes in photosynthetic capacity are not important for the increase in NAR. The realized photosynthetic rates however, also depend on stomatal conductance and hence on the amount of water available per unit leaf area. Clipped plants had a greater amount of roots per unit leaf area and they could therefore achieve a higher average stomatal conductance. However, the stimulation of NAR by clipping was greater under wet than under dry conditions suggesting that this mechanism did not play a very important role.

We predicted that the greater ability of *Leymus* to store carbohydrates in its rhizomes would contribute to its greater capacity for compensatory growth as compared to the caespitose *Stipa*, as these reserves could be used to support new leaf growth after clipping (see Introduction). Consistent with this prediction, *Leymus* exhibited a greater carbohydrate concentration in its below ground structures, particularly its rhizomes, while there was also a stronger reduction in carbohydrate concentration after clipping (Fig. 4). It is often observed that plants are not able to use a large proportion of their stored carbohydrates in response to clipping (Davidson and Milthorpe 1966; Richards and Caldwell 1985). This could be caused by a limitation of regrowth by the nutrients nitrogen and phosphorus rather than carbon (Trlica and Cook 1971; Chapin et al. 1990). Our results show a significant increase of the N content of the leaves after clipping for *Leymus* and a significant increase of the P content for both species (Table 3). This indicates that probably there was no nutrient limitation.

In short *Leymus* exhibited a greater capacity for compensatory growth than *Stipa*. This advantage was to a large extent probably due to the ability of this species to store carbohydrates and reallocate them after leaf losses, and due to the stronger positive effect of defoliation on light penetration through the canopy.

Response to drought stress

In *Leymus* compensation of plant productivity after clipping was less under dry conditions than under wet conditions. This is contrary to previous studies (Archer and Detling 1986; Coughenour et al. 1990; Day and Detling 1994) where compensation was found to increase under dry conditions and where it was argued that this was because clipping removes transpiring leaf area, enhances soil water conservation and improves plant water potential.

The higher compensation of plant productivity for *Leymus* under wet conditions is mainly caused by the higher increase in net assimilation rate (NAR). Under dry conditions *Leymus* shoots were more open than under wet conditions, self-shading was probably much less, and the greater increase in NAR might therefore partly be due to greater improvements in light penetration through the canopy by clipping. It could also be that under dry conditions *Leymus* plants have fewer carbohydrates that can be reallocated to support growth.

As noted conservation of soil moisture has been considered to contribute to stronger

compensatory growth under dry than under wet conditions because of the removal of transpiring leaves. Indeed volumetric soil moisture contents in the pots were higher after clipping compared to the control pots (see Methods). Because pots have a restricted volume, this effect is probably stronger than under field conditions. However, *Leymus* lower compensation for plant productivity found under dry conditions seems contrary to what one would expect if pot size were to play an important role. In contrast to *Leymus*, *Stipa* exhibited a greater compensation for losses in plant productivity under dry conditions than under wet conditions. Overall, *Stipa* appears to be more drought tolerant than *Leymus*, as was indicated by the significantly smaller effect of drought on growth and final standing mass in *Stipa* (Fig. 2, Table 2). Furthermore, on the steppes of Eurasia, *Stipa* is generally more abundant at drier sites than *Leymus* (Xiao et al. 1995). Thus, our results suggest that the effect of drought on compensation can differ between species and that it depends on the overall drought tolerance of the species in question.

Stimulated productivity

Under wet conditions clipped *Leymus* plants exhibited almost full compensation (C about 80%) for the potential loss in plant productivity. In the case of *Stipa* and that of *Leymus* under dry conditions the compensation was much lower. When we only consider the leaf productivity, which is forage for wild ungulates and livestock, there was a full compensation (about 100 %) in *Leymus* under both water availabilities, while *Stipa* exhibited only partial compensation (Fig. 2). Note however, that our analysis does not distinguish between compensatory mechanisms that arise from an active response by the plant and mechanisms that are a direct result of defoliation. An increase of nitrogen concentration in the leaves, the breaking of dormancy of buds, and the reallocation of carbohydrates are all active responses of the plant, while an increase of light availability on the remaining leaves or an increase of water availability are direct results of defoliation.

The carrying capacity of the steppe areas, i.e. the maximum number of herbivores which can be supported in an area, is an important issue for pasture management in many parts of the world (Mongolia, China etc). Our data clearly show that when estimating the carrying capacity the effect of compensation should be accounted for. Productivity levels of actually clipped plants were considerably higher than what they would have been in absence of compensatory growth (compare clipped to clipped-hyp in Fig. 2), because the compensatory mechanisms contribute enormously to the productivity of plants after clipping. Disregarding compensatory growth would result in a considerable overestimation of the carrying capacity of *Stipa* grasslands, while for *Leymus* grasslands the estimation should be correct, because of the effect of full compensation.

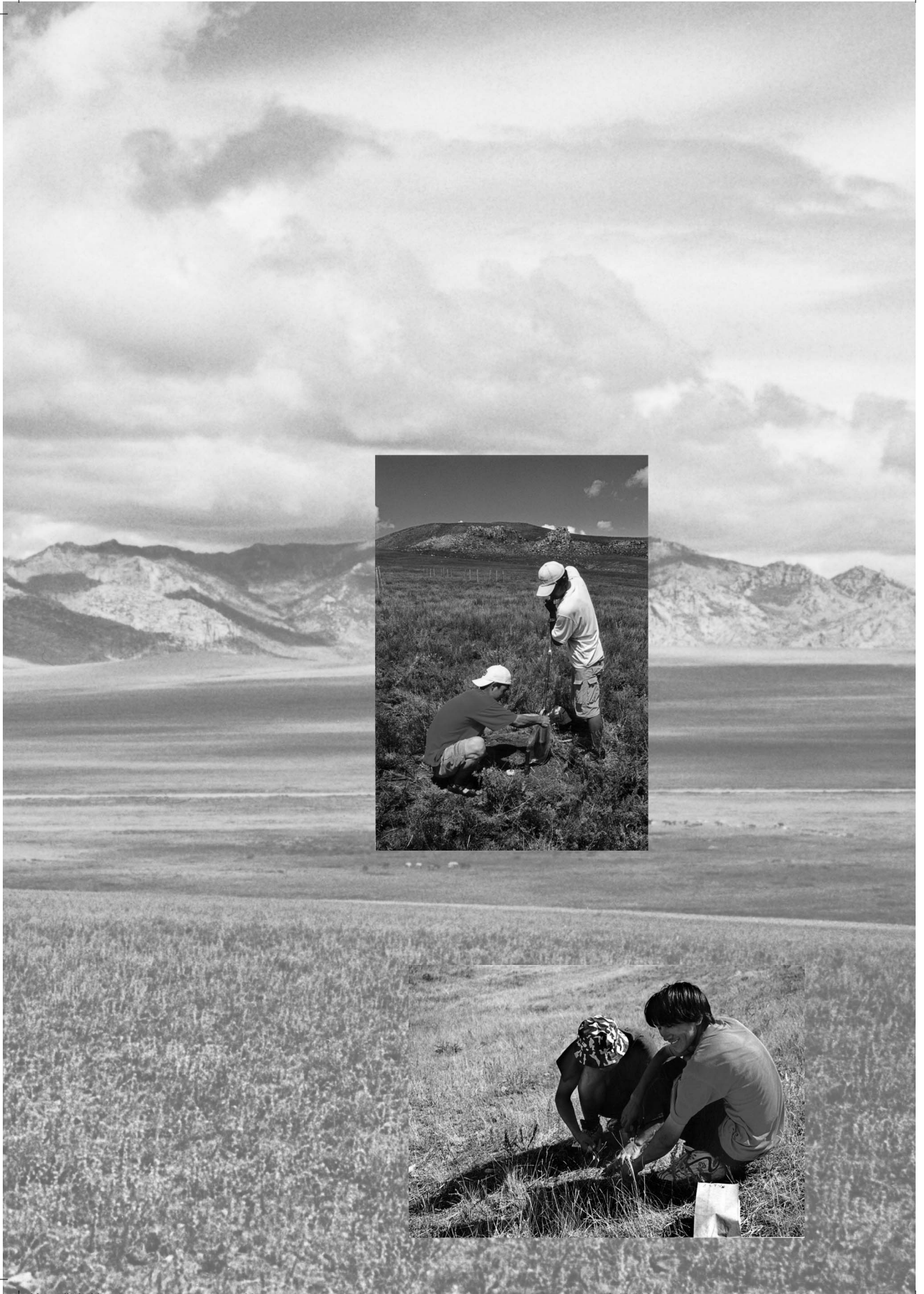
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Chapter 5

Marmot disturbances in a Mongolian steppe vegetation

Submitted for publication

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Abstract

We conducted a study in Mongolia on the *Stipa* steppe, which is the main habitat for the Siberian marmot (*Marmota sibirica*). The marmots create mounds that differ greatly in vegetation cover. We examined the relation between different types of marmot mounds and the species composition, species cover, diversity, plant biomass and soil- and plant- N-concentrations of the local vegetation.

Depending on the species which dominate the vegetation on the mounds, three types of mounds were distinguished: an *Artemisia* type of mound which represents the highest level of disturbance, a *Leymus* type which is found at an intermediate level and a *Stipa* type, which together with the off-mound communities, has the lowest level of disturbance. In this sense the three types of mounds represent a series of succession.

The activities of the marmots lead to enhanced forage quality on the *Artemisia* and *Leymus* types of mound, as indicated by increased nitrogen concentrations in the on-mound vegetation of these types of mound. Our results suggest that these higher nutrient concentrations can be largely explained by higher mineralization rates following disturbance. A significantly lower amount of organic matter in the soil of the *Artemisia* mound is consistent with this interpretation.

Keywords: Burrowing activity; Forage quality; Nutrient concentration; Rodent; Species composition; Succession

Introduction

Disturbances that open up gaps in vegetation are common. In grasslands the burrowing of animals create gaps of open space. These are sites where species newly establish and small scale-successions take place, resulting in a mosaic of successional and undisturbed patches across the landscape (Bormann and Likens 1979).

The burrowing activities and grazing of rodents can have significant effects on plant species abundance and community structure, as was shown for kangaroo rats who play a key role in the maintenance of desert grasslands (Brown and Heske 1990; Fields et al. 1999; Heske et al. 1993), and for the prairie dogs in the North American grasslands. The prairie dog colonies provide large and distinct patches differing in species composition, species diversity and forage quality (Archer et al 1987; Coppock et al 1983;

Detling 1998). In the Negev desert of Israel, porcupine diggings strongly disturb the vegetation and determine the succession (Gutterman and Herr 1981; Gutterman 2001). Marmots are widespread in the steppes, deserts and mountain steppe belts of Mongolia (Gunin et al., 1999), where they have a great impact on the landscape by creating mounds and altering the vegetation structure and composition. One of the two occurring marmot species in Mongolia is the Siberian marmot (*Marmota sibirica*), which is distributed in eastern and northeastern Mongolia and in the Hangai, Mongol Altai and Gobi Altai (Rogovin 1992). Siberian marmots are large herbivorous rodents that burrow and live colonially. They graze mainly on grasses and herbs and during summer they are an important prey for grey wolves and eagles (Takhi reintroduction centre, 2001). For Mongolian people they are a favorite animal for its meat and therefore severely hunted. This has enormously diminished the population. These marmots also carry bubonic plague and that puts pressure on the marmot populations.

In the forest steppe region of Mongolia, the typical *Stipa* steppe is one of the main habitats of the marmots. The vegetation is made up of a rich variety of grasses and herbs and dominated by the bunchgrass *Stipa krylovii* (Hilbig 1995; Wallis de Vries et al. 1996).

The mounds created by marmots on the *Stipa* steppe can differ greatly in vegetation cover; there are mounds covered with bare soil, mounds covered by a vegetation more or less similar to the surrounding *Stipa* vegetation, and mounds dominated by the grass *Leymus chinensis* or the herb *Artemisia adamsii* (Takhi reintroduction centre 2001). It is likely that these different types of mounds reflect the extent of disturbance and represent different stages in the regeneration process from bare soil to the original *Stipa* vegetation. It is also likely that the animals' activities cause local differences in nutrient availability compared to the surrounding steppe (Whicker and Detling 1998; Holland and Detling 1990).

We conducted a study on the *Stipa* steppe in which we examined the relation between the different types of marmot mounds and the species composition, species cover, diversity, plant biomass and soil- and plant- N-concentrations of the local vegetation. We addressed the following questions: (1) how does the species composition and species dominance on the different types of marmot mounds compare to the surrounding vegetation (2) does the nutrient concentration in the vegetation on the different types of mounds differ (3) does the nutrient concentration differ in the soil of the different types of marmot mounds?

Methods

Study area

The study was conducted at Hustai National Park, located at 100 km west of Ulaan Baatar, Mongolia (47° 50' N, 106° 00' E). The climate in Mongolia is arid and continental, with a short growing season in summer (from June to September) in which most of the precipitation falls (annual precipitation 296 mm in Hustai National Park). Summers are generally hot, and winters cold.

Hustai National Park is situated in the forest steppe region of Mongolia and occupies 60,000 ha at elevations ranging from 1100 to 1840 m above sea level. About 88% of the area is covered by grassland and shrub land steppe and ca 5% is covered by birch-dominated forest. Native ungulates are free-ranging within the park and include the takh (*Equus przewalskii*), red deer (*Cervus elaphus*), wild boar (*Sus scrofa*), roe deer (*Capreolus capreolus*), migrating Argali sheep (*Ovis ammon*) and Mongolian gazelle (*Procapra gutturosa*). The takh, the last wild-living horse species of the steppe, has grown to a population of about 150 individuals, since it was successfully re-introduced in Hustai National Park in 1992. In addition there live several small rodent species, such as the long tailed souslik (*Citellus undulates*), the grey - and the striped hamster (*Cricetulus migratorius* and *barabensis*), the Brandt's vole (*Lasiopodomys brandtii*) and the Siberian jerboa (*Allactaga sibirica*), together with the bigger Siberian marmot (*Marmota sibirica*) that is very abundant. The overall marmot density in the national park was 1.16 marmots per ha in 1998, which is normal for most of the steppe in Mongolia (Takhi reintroduction centre 1998). In the central and best protected areas of the park the density was higher and reached a level of 3.85 marmots per ha. For the population of about 60 grey wolves (*Canis lupus*) that live in the Park, the marmots are an important prey during summer when the wolves hunt individually.

The areas selected for this study were located in the *Stipa* lowland steppe, which belongs to the *Artemisia adamsii*-*Stipa krylovii*-community as described by Wallis de Vries et al. (1996). This community was also distinguished by Hilbig (1995), but he described it as *Cymbario-Stipetum krylovii*. The vegetation is dominated by the bunch-grass *Stipa krylovii*, with *Artemisia adamsii*, *Artemisia frigida*, *Agropyron cristatum* and *Cymbario dahurica* as typical species. The soils are kastanozems and the vegetation cover ranges from 45 to 80%.

Mound selection

Areas on the *Stipa* lowland steppe with a rather high density of marmots (3.85 marmots/ha) were selected (Takhi reintroduction centre, 1998). Three types of mounds were distinguished: a type in which the vegetation on the mounds was dominated by *Artemisia adamsii*, a type in which the mounds were dominated by *Leymus chinensis* (*Elymus chinensis*, Grubov 2001), and a type in which the mounds were dominated by *Stipa krylovii*. From each type of mound, 3 marmot mounds were selected randomly and two plots were established on each mound with an additional two plots in the common steppe vegetation 3 meters away from the mound.

The on-mound location was characterized by an entrance of a marmot hole with a small patch of bare soil around the entrance, and a surrounding vegetation which was distinct from the normal steppe vegetation and showed signs of disturbance activities of the animal. Marmot dung in front of the entrance indicated that the mound was still in use by marmots.

The off-mound location consisted of the normal steppe vegetation, without burrows of marmots.

Sampling

In the first 2 weeks of August 2002 and 2003, measurements of species frequency and species cover were performed on 2 plots in the vegetation of the on-mound location and 2 plots in the off-mound location of the selected mound. The plots of the off-mound location were established at a distance of 3 m from the on-mound location. A 0.5 x 1 m grid divided into 10 x 10 cm sections was laid on the vegetation, and the occurrences of all species in each of the sections was recorded, giving the species frequencies (max. 50). For all species with a cover of $\geq 1\%$ in the entire plot, the percentages cover were estimated.

Species diversity is calculated as the number of species that occur within one plot. The aboveground biomass was sampled by clipping 2 strips of 50 x 50 cm in each of the on-mound and off-mound plots. The vegetation was clipped at ground level and dried in an oven at 70°C for 48 h and weighed.

To determine soil characteristics 1 soil core per strip with a diameter of 2.8 cm and 7 cm deep was taken. Belowground plant parts were removed and the soil was oven dried at 70°C for 48 h.

Total organic nitrogen, phosphorus and potassium concentrations in the aboveground biomass and soil were determined after Kjeldahl destruction using a continuous flow analyzer (SKALAR, Breda, Netherlands).

Organic matter content of the soil was determined by ignition of the organic material in an oven at 550°C for 2.5 h and determining weight loss.

Statistical analyses

The data were analyzed with the statistical package SPSS 10.0 for Windows (SPSS Inc. Chicago, Illinois, USA).

A two-way analysis of variance (ANOVA) was used to analyze the effects and the interactions between factors 'type of mound' (*Artemisia*, *Leymus*, *Stipa*, $df=2$) and 'sampling location' (on-mound, off-mound, $df=1$). With a one-way ANOVA the significance of the effect of 'sampling location' was tested for the three types of mound separately and in the same way the effect of 'type of mound' was tested for on-mound and off-mound separately. A Bonferroni correction was applied to correct for multiple comparisons.

Species cover values showed great differences between the variances of the means. Therefore an ANOVA was not suitable to apply and we tested nonparametrically for the significance of 'type of mound' and 'sampling location' on cover of the vegetation. The dependent variables (type of mound $df=2$, sampling location $df=1$) were tested separately with the Mann-Whitney test. A Bonferroni correction was applied to correct for multiple comparisons. Differences were considered significant at $P < 0.05$.

In order to classify the vegetation of the on- and off-mound plots of the 3 types of mound, we performed a two-way indicator species analysis (Twinspan 1997; Jongman et al., 1995). Default cut levels (0,2,5,10,29) were used.

We performed a correspondence analysis (CA) with species frequency data of 2002

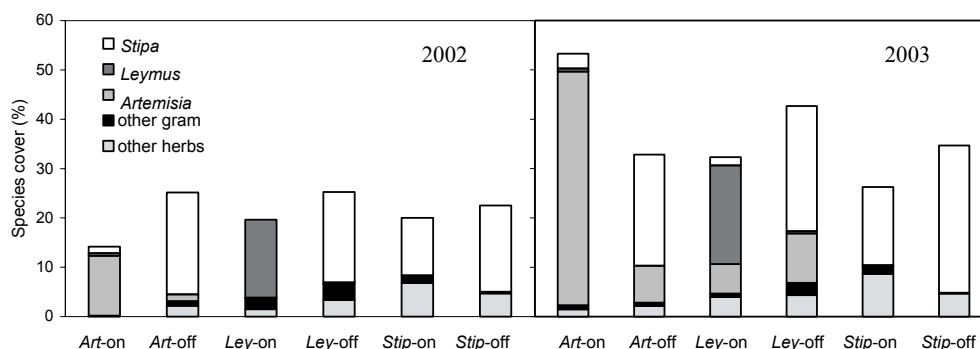
and 2003 (Jongman et al. 1995), to analyze the effect of disturbance by marmots on the overall composition of the on- and off-mound vegetation of the different types of mounds, using the statistical package MVSP 3.0 (Kovach Computing Services, Anglesey, UK). The correlation coefficients between the concentrations of N and P in the vegetation and soil (Nveg, Pveg, Nsoil, Psoil) and the first and second ordination axis were calculated to evaluate which factors determine these axes.

Results

Species cover and frequencies

The total plant cover on and off the *Leymus* and *Stipa* types of mounds did not differ significantly in either year (Fig. 1, Table 1), but for the *Artemisia* type of mound it was significantly higher off-mound than on-mound in 2002 and lower in 2003. Clear differences in cover of different species were found between the on-mound and off-mound vegetation of the *Artemisia* and the *Leymus* type of mounds in 2002 and 2003, but not for the *Stipa* type of mound (Fig.1, Table 1). The cover of the other graminoids and herbs did not differ between on- and off-mound nor between years (Fig.1, Table 1).

Fig. 1 Species cover on the different types of marmot mounds (*Artemisia*-, *Leymus* and *Stipa*-type) on the mound and off the mound in 2002 and 2003.



The three name-giving species each dominated the on-mound vegetation of each of the three types of mounds, respectively, but *Stipa krylovii* dominated the off-mound vegetation of all the three types of mounds. *Artemisia* and *Leymus* had higher cover in the on-mound vegetation than the off-mound vegetation of their mound types, while the cover of *Stipa* did not differ between on- and off-mound in the *Stipa* type of mound.

Table 2 summarizes the species frequencies and diversity in the on- and off-mound vegetation of the three types of mounds. There were several species (*Astragalus brevis-folius*, *Bupleurum bicaule*, *Allium bidentatum*, *Haplophylum dauricum*), which were present in the on-mound vegetation of the *Stipa* type of mound and the off-mound of all

Table 1 Mean and standard error of canopy cover (%) for *Stipa krylovii*, *Leymus chinensis*, other graminoids, *Artemisia adamsii*, other herbs, and the total for the different types of marmot mounds, on the mounds and off the mounds. Dependent variables were tested with the Mann Whitney test separately, and a Bonferroni correction was applied. Similar superscripts indicate there are no significantly different means between on- and off-mounds within marmot mound types. Similar subscripts indicate there are no significantly different means between types of marmot mounds within on- or off-mounds ($P < 0.05$).

	Artemisia mound		Leymus mound		Stipa mound	
	On- mound	Off- mound	On- mound	Off-mound	On-mound	Off-mound
Stipa 2002	1.33 ^a _a (.3)	20.67 ^b _a (1.7)	.00 ^a _b (.0)	18.33 ^b _a (1.7)	11.67 ^a _a (2.3)	17.50 ^a _a (2.1)
Stipa 2003	3.00 ^a _a (2.0)	22.50 ^a _a (2.8)	1.67 ^a _a (.7)	25.33 ^b _a (2.4)	15.83 ^a _b (3.1)	29.83 ^a _a (4.8)
Ley 2002	.50 ^a _a (.5)	.00 ^a _a (.0)	15.83 ^a _b (2.2)	.25 ^b _a (.3)	.00 ^a _a (.0)	.00 ^a _a (.0)
Ley 2003	.60 ^a _a (.6)	.00 ^a _a (.0)	20.00 ^a _b (2.8)	.50 ^b _a (.3)	.00 ^a _a (.0)	.00 ^a _a (.0)
Ogram 2002	.00 ^a _a (.0)	1.00 ^a _{ab} (.5)	2.17 ^a _a (1.6)	3.33 ^a _a (.9)	1.50 ^a _a (.9)	.33 ^a _b (.3)
Ogram 2003	.83 ^a _a (.5)	.67 ^a _a (.7)	.67 ^a _a (.4)	2.50 ^a _a (1.7)	1.50 ^a _a (.8)	.17 ^a _a (.2)
Artem 2002	12.17 ^a _a (1.0)	1.33 ^b _a (.9)	.17 ^a _b (.2)	.00 ^a _a (.0)	.00 ^a _b (.0)	.00 ^a _a (.0)
Artem 2003	47.33 ^a _a (5.2)	7.50 ^b _a (2.6)	6.00 ^a _b (4.0)	10.00 ^a _a (.0)	.25 ^b _b (.3)	.00 ^a _a (.0)
Oherb 2002	.17 ^a _a (.2)	2.17 ^a _a (1.6)	1.50 ^a _{ab} (1.2)	3.33 ^a _a (1.5)	6.83 ^a _b (3.5)	4.67 ^a _a (.6)
Oherb 2003	1.50 ^a _a (.7)	2.17 ^a _a (.9)	4.00 ^a _{ab} (1.0)	4.33 ^a _a (2.4)	8.70 ^a _b (2.7)	4.67 ^a _a (1.5)
Total 2002	13.50 ^a _a (1.2)	25.17 ^b _a (2.0)	19.67 ^a _b (1.1)	25.17 ^a _a (1.8)	20.00 ^a _{ab} (4.7)	22.50 ^a _a (2.0)
Total 2003	51.70 ^a _a (4.2)	30.33 ^b _a (3.3)	27.50 ^a _b (2.7)	36.00 ^a _a (4.9)	26.20 ^a _b (2.8)	34.70 ^a _a (5.4)

three types of mounds, while they were absent or had a lower frequency in the *Artemisia* and the *Leymus* type of mound (Table 2). Therefore, species diversity was highest in the on-mound vegetation of the *Stipa* type of mound and also relatively high in the off-mound vegetation of all the types of mound, while the species diversity in the on-mound vegetation of the *Artemisia* type of mound and of the *Leymus* type of mound was much lower (Table 2). A Twinspan classification (not shown) reproduced the division in the three types of on-mound vegetation, and included all off-mound plots with the *Stipa* on-mound vegetation. In the first subdivision of the *Stipa* vegetation the on-mound and off-mound vegetation was distinguished, with *Astragalus brevifolius*, *Saussurea salicifolia* and *Allium bidentatum* positively discriminating the off-mound vegetation from the on-mound vegetation.

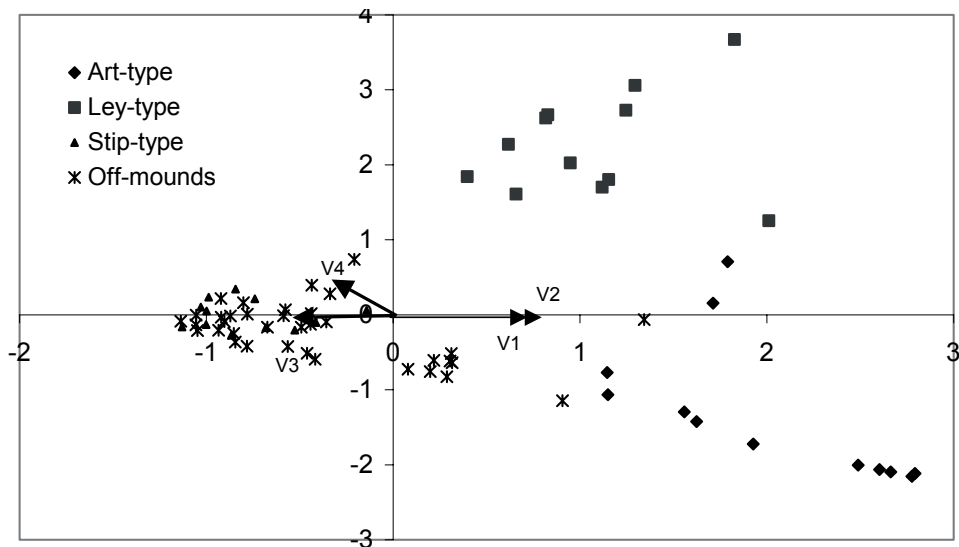
The correspondence analysis confirms the Twinspan classification (Fig. 2): the on-mound *Artemisia* and *Leymus* plots are clearly separated from the *Stipa* plots and the off-mound plots along the first axis, while the second axis separates the *Artemisia* and *Leymus* on-mound plots. The first axis explains 15.7% of the variation; the second axis explains 13.1%.

Plotting the N- and P-concentrations in vegetation and soil as vectors in the ordination diagram of Figure 2 identifies the first axis as a gradient from low (left) to high (right) N- and P-mineralization (Fig. 2).

Table. 2 Species frequencies and species diversity for the different types of marmot mounds, on the mound and off the mound (n=12).

	Art type Freq	Ley type Freq	Stip type Freq	Art off- mound Freq	Ley off-mound Freq	Stip off- mound Freq
Graminoids						
<i>Stipa krylovii</i>	4.7	3.3	23.1	27.8	26.5	28.3
<i>Leymus chinensis</i>	3.5	31.2	0.8	1.3	2.5	.
<i>Poa attenuata</i>	.	0.2	0.2	0.4	3.3	0.6
<i>Agropyron cristatum</i>	.	3.3	7.0	0.6	3.5	4.6
<i>Cleistogenes squarrosa</i>	0.4	0.2	1.1	1.3	3.9	0.7
<i>Koeleria macrantha</i>	.	0.2	4.1	2.0	2.8	2.3
<i>Stipa sibirica</i>	.	.	1.4	.	.	1.1
<i>Carex duriuscula</i>	5.8	4.5	8.5	4.9	13.4	7.1
Forbs						
<i>Artemisia adamsii</i>	33.3	4.3	.	11.0	3.2	0.2
<i>Thermopsis dahurica</i>	.	0.1	.	.	0.1	.
<i>Caragana pygmaea</i>	.	0.9	2.3	1.7	1.1	0.8
<i>Astragalus brevifolius</i>	0.1	.	1.7	5.7	3.6	6.7
<i>Oxytropis myriophylla</i>	0.1
<i>Artemisia frigida</i>	.	1.1	8.5	3.8	4.2	10.2
<i>Potentilla acaulis</i>	.	.	2.3	.	0.1	3.3
<i>Potentilla bifurca</i>	.	1.0	11.6	0.8	3.5	0.8
<i>Cymbaria dahurica</i>	2.4	0.3	1.7	1.9	2.7	1.6
<i>Ptilotrichum canescens</i>	2.0	.	0.5	0.3	0.8	0.6
<i>Gonolimon speciosum</i>	.	0.1	0.1	.	0.3	.
<i>Bupleurum bicaule</i>	.	.	0.8	0.4	0.1	0.4
<i>Pulsatilla bungeana</i>	0.3	.
<i>Saussurea salicifolia</i>	0.1	.	0.3	.	0.3	0.8
<i>Haplophyllum dauricum</i>	0.1	.	0.3	0.8	0.7	1.0
<i>Androsace incana</i>	.	.	0.1	.	.	.
<i>Allium bidentatum</i>	.	0.1	0.8	2.4	0.5	5.3
<i>Iris trigida</i>	.	.	0.9	.	0.3	1.1
<i>Veronica incana</i>	.	0.4	.	.	2.3	.
<i>Heteropappus biennis</i>	0.1	2.4	2.9	0.3	1.5	2.5
<i>Amblynotus rupestris</i>	.	1.6	1.9	0.1	0.3	5.6
<i>Chenopodium album</i>	1.9	1.4	3.6	1.5	3.7	3.9
<i>Bupleurum scorzonerifolium</i>	.	.	0.7	.	0.6	0.5
<i>Stellera chamaejasme</i>	0.4	.
<i>Potentilla conferta</i>	0.3	0.1	0.3	.	0.8	0.6
<i>Orostachis malacophylla</i>	.	.	1.6	.	.	4.9
<i>Potentilla multifida</i>	.	1.7	0.2	.	0.6	0.3
<i>Sibbaldianthe adpressa</i>	0.6	0.4	.	0.8	0.5	.
<i>Arenaria capillaris</i>	.	.	.	0.5	0.4	.
<i>Potentilla tanacetifolia</i>	0.1
<i>Allium spec</i>	.	.	0.5	.	.	0.6
<i>Cirsium esculentum</i>	0.1	.
<i>Ephedra sinica</i>	0.1
Species diversity	4.5	6.2	10.9	8.3	10.3	11.3

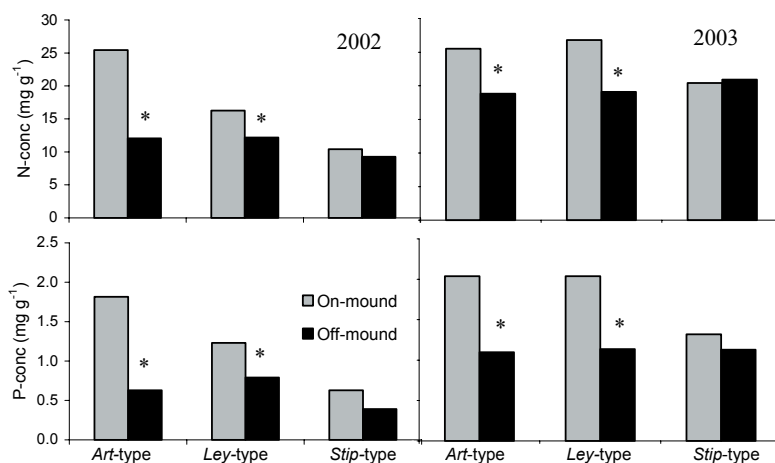
Fig. 2. Scores of a correspondence analysis (CA) of the on- and off-mound sites of the *Artemisia*-, *Leymus* and *Stipa*-type of mounds. V_1 =vector of N-concentration in the vegetation (0,68; -0,04); v_2 =vector of P-concentration in the vegetation (0,78; 0,00); v_3 =vector of N-concentration in the soil (-0,56; 0,05); v_4 =vector of P-concentration in the soil (-0,31; 0,37).



Biomass, nutrient concentrations and organic matter

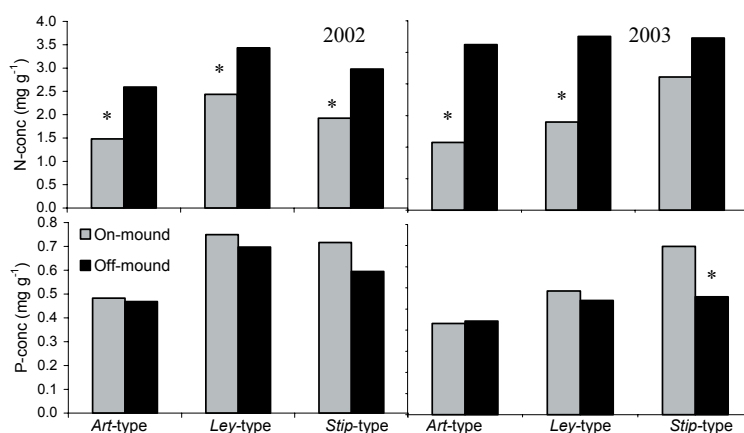
The amount of biomass on and off the mounds (Table 3) showed a similar pattern as the total plant cover (Table 1). The amount of biomass on and off the *Leymus* and *Stipa* types of mounds did not differ significantly in either year (Table 3). For the *Artemisia* type of mound the biomass was significantly higher on-mound than off-mound in 2003, while in 2002 there was no difference.

Fig. 3 N- and P-concentrations in the vegetation of the different types of marmot mounds (*Artemisia*-, *Leymus*- and *Stipa*-type) on the mound and the off the mound in 2002 and 2003.



* indicate a significant difference between the on- and off-mound location $p < 0.05$

Fig. 4 N- and P-concentrations in the soil of the different types of marmot mounds (*Artemisia*-, *Leymus*- and *Stipa*-type) on the mound and off the mound in 2002 and 2003.



* indicate a significant difference between the on- and off-mound location $p < 0.05$.

The N- and P-concentrations in the on-mound vegetation of the *Artemisia* and *Leymus* type of mounds were significantly higher than in the off-mound vegetation (Fig. 3, Tables 3 and 4), as was also indicated by a significant effect of sampling location and type of mound on the nitrogen and phosphorus concentration in the vegetation

Table 3 Mean and standard error of aboveground biomass, nitrogen, phosphorus and potassium concentration in biomass, and N, P, and K concentrations respectively in the soil for the different types of marmot mounds, on the mounds and off the mounds. Dependent variables were tested with an ANOVA test separately, and a Bonferroni correction was applied. Similar superscripts indicate there are no significantly different means between on- and off-mounds within marmot mound types. Similar subscripts indicate there are no significantly different means between types of marmot mounds within on- or off-mounds ($P < 0.05$).

	<i>Artemisia</i> mound		<i>Leymus</i> mound		<i>Stipa</i> mound	
	On- mound	Off- mound	On- mound	Off-mound	On-mound	Off-mound
Biom (g m^{-2}) 2002	53.37 ^a _a (5.2)	43.97 ^a _a (3.8)	81.00 ^a _{ab} (10.0)	93.78 ^a _b (6.1)	95.10 ^a _b (14.0)	99.80 ^a _b (6.9)
Biom (g m^{-2}) 2003	142.57 ^a _a (10.7)	92.25 ^b _a (8.1)	76.26 ^a _b (5.6)	91.43 ^a _a (6.7)	77.25 ^b _b (5.6)	75.91 ^a _a (9.6)
Nveg (mg g^{-1}) 2002	25.43 ^a _a (.9)	12.04 _a (.8)	16.25 ^a _b (1.1)	12.18 ^b _a (.7)	10.41 ^a _c (.9)	9.27 ^b _b (.4)
Nveg (mg g^{-1}) 2003	25.53 ^a _a (1.2)	18.82 _a (.4)	26.79 ^a _a (.8)	19.08 ^b _a (.9)	20.39 ^a _b (1.0)	20.91 ^a _a (.6)
Pveg (mg g^{-1}) 2002	1.82 ^a _a (1.4)	.63 ^b _a (.0)	1.23 ^a _b (.1)	.79 ^b _a (.0)	.63 ^a _c (.1)	.39 ^a _b (.0)
Pveg (mg g^{-1}) 2003	2.04 ^a _a (.2)	1.10 ^b _a (.0)	2.04 ^a _a (.1)	1.14 ^b _a (.1)	1.32 ^a _b (.1)	1.13 ^a _a (.0)
Kveg (mg g^{-1}) 2002	18.82 ^a _a (1.8)	8.78 ^b _a (.8)	16.53 ^a _a (.6)	9.20 ^b _a (.5)	6.06 ^a _b (1.1)	4.26 ^a _b (.4)
Kveg (mg g^{-1}) 2003	19.19 ^a _a (2.3)	7.96 ^b _a (.1)	16.74 ^a _a (.6)	8.70 ^b _a (1.1)	10.26 ^a _b (1.4)	8.66 ^a _b (.4)
Nsoil (mg g^{-1}) 2002	1.48 ^a _a (.9)	2.59 ^b _a (.2)	2.43 ^a _b (.1)	3.43 ^b _a (.3)	1.92 ^a _{ab} (.2)	2.98 ^b _b (.2)
Nsoil (mg g^{-1}) 2003	1.07 ^a _a (.2)	2.62 ^b _a (.1)	1.40 ^a _{ab} (.1)	2.75 ^b _a (.2)	2.11 ^a _b (.2)	2.73 ^a _a (.2)
Psoil (mg g^{-1}) 2002	.48 ^a _a (.1)	.47 ^a _a (.1)	.75 ^a _b (.0)	.70 ^a _b (.0)	.72 ^a _b (.0)	.59 ^a _{ab} (.0)
Psoil (mg g^{-1}) 2003	.43 ^a _a (.0)	.44 ^a _a (.0)	.58 ^a _a (.0)	.54 ^a _{ab} (.0)	.80 ^a _b (.1)	.55 ^b _b (.0)
Ksoil (mg g^{-1}) 2002	6.71 ^a _a (.6)	5.97 ^a _a (.3)	8.65 ^a _b (.3)	9.04 ^a _b (.4)	7.05 ^a _{ab} (.3)	6.19 ^a _a (.3)
Ksoil (mg g^{-1}) 2003	5.28 ^a _a (.3)	5.36 ^a _a (.2)	6.07 ^a _a (.6)	5.49 ^a _a (.3)	6.69 ^a _a (.8)	5.25 ^a _a (.2)
Org mat % 2003	4.70 ^a _a (.9)	8.06 ^b _a (.6)	6.70 ^a _a (.9)	8.39 _a (.6)	5.99 ^a _a (.3)	7.21 ^a _a (.5)

(Table 4). In this respect the *Stipa* type of mound differed from the other two types of mounds, as there were no on- and off mound differences in N- and P- concentration of the vegetation. This was supported by the significant interaction between type of mound and sampling location (Table 4).

Contrary to the higher N-concentrations in the on-mound vegetation of the *Artemisia* and *Leymus* type of mounds, we found lower N-concentrations in the soil on-mound (Figs. 3 and 4, Tables 3 and 4). There were no differences in on- and off-mound P-concentrations in the soil, except for the *Stipa* type of mound in 2003, when the P-concentration on-mound was significantly higher (Fig. 4, Table 3).

We also found a significant lower percentage of organic matter in the on-mound soil of the *Artemisia* type of mound (Table 3). This was also indicated by the significant effect of sampling location (Table 4).

Table 4 Results of a two-way ANOVA with factors type of mound (*Artemisia*, *Leymus*, *Stipa*, $df=2$) and sampling location (on-mound, off-mound, $df=1$). Biomass is aboveground biomass, Nveg is nitrogen concentration in biomass, Pveg is phosphorus concentration in biomass, Nsoil, Psoil and Ksoil are N, P, and K- concentrations respectively in soil.

	Type of mound	Sampling location	Type of m* samp.loc
Biom 2002	.000*	.697	.420
Biom 2003	.000*	.071	.001*
Nveg 2002	.000*	.000*	.000*
Nveg 2003	.039*	.000*	.000*
Pveg 2002	.000*	.000*	.000*
Pveg 2003	.001*	.000*	.001*
Kveg 2002	.000*	.000*	.001*
Kveg 2003	.006*	.000*	.002*
Nsoil 2002	.002*	.000*	.968
Nsoil 2003	.016*	.000*	.044*
Psoil 2002	.000*	.111	.514
Psoil 2003	.000*	.010*	.011*
Ksoil 2002	.000*	.221	.232
Ksoil 2003	.359	.096	.271
Org mat 2003	.194	.001*	.253

*indicate significant effects $p < 0.05$.

Discussion

The extent to which the species cover and composition of the on-mound vegetation differ from its surrounding vegetation seems to reflect the extent of disturbance at the mound after burrowing activities of the marmots. Such activities have been reported to lead to important changes in species dominance of the vegetation (Fields et al. 1999; Gunin et al. 1999; Detling 1998). On the North American prairies, the colonies of prairie dogs comprised different plant community types, which were indicative of the extent of disturbance and represented different stages of colonization (Archer et al. 1987; Coppock et al. 1983; Whicker and Detling 1988). Graminoids

dominated the vegetation on the uncolonized and lightly colonized sites, while they decreased on the medium sized towns and became nearly nonexistent on the large, densely populated dog towns. The large prairie dog towns were dominated by forbs and shrubs.

In our study the mounds dominated by *Artemisia adamsii* or *Leymus chinensis* were very distinct in species cover and composition from the surrounding off-mound vegetation. Such drastic changes in vegetation might result from disturbance. The vegetation on the *Stipa* type of mound, however, was similar to its surrounding vegetation and dominated by *Stipa krylovii*. This suggests either that these mound were less disturbed, because of less burrowing, or that the actual disturbance was longer ago and the vegetation had already recuperated from the disturbances. Visual inspection suggested the latter, as was also noted by Gunin et al. (1999) who reported that abandoned marmot mounds were dominated by *Stipa krylovii*.

In Hilbig (1995) the *Leymus* community is mentioned as a grazing facies of the *Stipa* steppe, with *Leymus chinensis* and *Artemisia frigida* as characteristic species. According to this author, under higher grazing intensity *Leymus chinensis* becomes the dominant species and replaces *Stipa krylovii*. Further degradation promotes the abundance of species of the *Carex duriuscula* facies, with *Carex duriuscula*, *Artemisia adamsii*, *Sibbaldianthe adpressa*, *Potentilla bifurca* and annual *Chenopodiaceae* as characteristic species. Our *Artemisia* type has much in common with Hilbig's *Carex duriuscula* facies.

Considering the growth habit of the three species dominating the three types of mounds, these mound types may well represent a successional series. When a mound is created by burrowing marmots, the mound is initially covered by bare soil. This can be colonized most easily by *Artemisia adamsii*, a perennial forb, generally occurring in the steppe vegetation. It produces many, easily dispersed seeds that establish well on degraded vegetation and bare soil (Yankai and Shunji, 1990; Hilbig, 1995).

The perennial grasses *Leymus chinensis* and *Stipa krylovii* do produce seeds, but under the relatively dry conditions of Hustai National Park (annual precipitation 296 mm) seedlings are not commonly found and do not establish well (Min et al. 1990; Wang et al. 2001) (*Leymus chinensis* = *Aneurolepidium chinensis*). In a field study of *Leymus*, Wang et al. (2001) found a diminished allocation to reproductive shoots and an increased allocation to rhizomes under dryer conditions. For both species, vegetative growth is by far their most common way of site colonization. *Leymus* shows a fast lateral spread by forming rhizomes (Jigjidsuren and Johnson 2003; Min et al. 1990; Wang et al. 2001). *Stipa*, however, is a caespitose grass with a much slower lateral spread. It does not make long rhizomes but it relatively slowly increases its bunch size by growing more tillers (Grubov 2001). *Stipa* bunches can break up as part of the bunch die off (Van Staaldunin and Werger, submitted).

The activities of the marmots lead to enhanced forage quality on the *Artemisia* and *Leymus* types of mound, as indicated by increased nitrogen concentrations in the

on-mound vegetation of these types of mound (Fig. 3). The total above ground nitrogen yield also was greater on these mounds, because the above ground biomass was similar or greater than in the surrounding off-mound vegetation (Table 3). Whicker and Detling (1988) also found higher nitrogen concentrations in plant shoots on prairie dog towns due to the activities of the rodent. Beside this, grazing as such was also found to induce increases in N-concentrations in shoots (Coppock et al., 1983; McNaughton, 1985; Jaramillo and Detling, 1988; Van Staaldunin and Werger, submitted).

The gradient in plant nutrient-concentrations from low in the *Stipa* and the off-mound plots to higher in the *Artemisia* and *Leymus* on-mound plots most probably reflects a similar gradient in mineralization rates (Fig. 3). Simultaneously, the N-concentrations in the soil exhibited a (more or less) reverse gradient (Fig. 4). Holland and Detling (1990) also reported lower soil N-concentrations and higher N-mineralization rates in the soils of prairie dog colonies in the Colorado prairies. The higher N-mineralization rates allowed higher N-uptake rates and resulted in higher N-concentrations in the plants and lower concentrations in the soil.

In summary, our results suggest that higher mineralization rates following disturbance largely explain the higher nutrient concentrations in the plants on the *Artemisia*- and *Leymus*-mounds. The significantly lower amount of organic matter in the soil of the *Artemisia* mound is consistent with this interpretation (Table 3).

The results of the correspondence analysis showing the direction of the vectors of Nveg and Pveg indicates that the first axis represents a gradient from low nitrogen mineralization (left) to higher N-mineralization (right) in the soil (Fig. 2). This is also indicated by the direction of the vectors of Nsoil and Psoil, which show an increase in N- and P-concentrations in the soil to the left side of the first axis. The second axis reflects the separation of the *Leymus chinensis*- and *Artemisia adamsii*-dominated plots.

The *Artemisia* type of mound represents the highest level of disturbance, with the *Leymus* type at an intermediate level and the *Stipa* type, together with the off-mound communities, at the lowest level of disturbance. In this sense the three types of mounds represent a series of succession.

Marmots locally destroy the *Stipa* steppe vegetation when they are actively building new mounds. This leads to patches with an *Artemisia adamsii*-dominated vegetation. *Artemisia adamsii* easily colonizes bare, disturbed sites and thrives well under conditions of increased nutrient availability (Gunin et al. 1999; Hilbig 1995). The leaves of the species are only scarcely eaten by the marmots (Takhi reintroduction centre 1998), but the seeds are eaten in great amounts at the end of summer (personal observation). Once the marmots decrease their burrowing activities the vegetation cover regenerates and becomes dominated by *Leymus chinensis*. This species tolerates fair levels of grazing pressure resulting from strong compensatory growth (Van Staaldunin and Anten, in press) and expands through rhizomes. At much lower

levels of grazing or after abandonment the vegetation returns to the *Stipa krylovii*-dominated steppe vegetation, which is much richer in species than the disturbed types.

Thus, the activities of the Siberian marmots create a dynamic and patchy vegetation cover by frequently creating differently vegetated patches, which can easily regenerate into the more stable *Stipa* steppe.

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Chapter 6

General discussion and summary

Herbivores play a key role in the sustainability of steppe grasslands through their influence on the structural and functional properties of the ecosystem. Their grazing often leads to changes in vegetation structure, species composition and abundance, plant productivity and plant nitrogen cycling.

In the natural situation plants are often damaged by partial defoliation by herbivores, but this rarely results in a proportional reduction in growth. They appear to be adapted to grazing and possess compensatory mechanisms through which they can mitigate potential negative effects of defoliation.

Natural grasslands can support large populations of (wild) herbivores, which may locally consume more than 50% of the aboveground net primary production. However, in Mongolia too high stocking rates of livestock led to a situation of overgrazing, and a deterioration of the steppe vegetation took place.

In order to be able to develop a sustainable pasture management, a better understanding is needed of the role of herbivory in the sustainability of the ecosystem, and of the mechanisms underlying the grazing effects on the vegetation.

The aim of the study described in this thesis is to gain insight in the impact of different types of herbivores, a large and a small, on the steppe vegetation. To this end, an enclosure experiment was set up on the *Stipa* steppe, in which we examined the effects of 3 years of exclusion of tahr (*Przewalski horse*) and Siberian marmots on plant species abundance, plant biomass and plant N-concentration. We investigated whether shifts in plant species dominance occur with increased grazing, and if this can be explained by differences in growth responses to clipping. We tried to establish a link between the plant species dynamics in the Mongolian steppe and physiologically based plant characteristics observed in a greenhouse experiment. In that greenhouse experiment we compared the potential for compensatory growth of *Leymus chinensis* and *Stipa krylovii*, two co-occurring grass species of the steppe, using a recently developed technique of growth analysis. On the *Stipa* steppe we studied the impact of marmot disturbances. The main results are summarized in this chapter.

Plant species composition, abundance and diversity affected by herbivores

The typical *Stipa* steppe comprises a variety of grasses with different growth forms and several forbs. There are grasses that grow in bunches, and grasses that grow with solitary tillers. A change in grazing intensity can lead to a shift in dominance of species with different growth forms.

Under light or moderate grazing the caespitose *Stipa krylovii* is the dominant grass species, but when grazing pressure increases this leads to a dominance by rhizomatous species. We found a higher frequency of the rhizomatous grass *Leymus chinensis*,

and a (weak) decrease of the caespitose *Stipa krylovii* under a higher grazing intensity (chapter 3). The total of rhizomatous species also had a higher frequency.

The increased frequency of *Leymus* and its higher grazing tolerance can be attributed to a much stronger compensatory growth in *Leymus* after defoliation than in *Stipa*, as was shown in the greenhouse experiment (chapter 4). We found that the compensatory growth in *Leymus* mainly resulted from a higher assimilation rate and the reallocation of stored carbohydrates from its rhizomes.

Although the decrease in the frequency of *Stipa krylovii* was only marginally significant, the reduced basal areas, lower tillers densities and the shift to smaller bunches of *Stipa* (chapter 3) we found after grazing, makes it probable that ultimately this will lead to a marked decline of the *Stipa* population.

Burrowing activities of marmots lead to important changes in the vegetation of the *Stipa* steppe. They create mounds that differ greatly in vegetation cover; there are mounds covered with bare soil, mounds covered by a vegetation more or less similar to the surrounding *Stipa* vegetation, and mounds dominated by the grass *Leymus chinensis* or the herb *Artemisia adamsii* (chapter 5).

Mounds dominated by *Artemisia adamsii* or *Leymus chinensis* are very distinct in species cover and composition from the surrounding off-mound vegetation, and this probably results from disturbance. The vegetation on the *Stipa* type of mound however, is similar to its surrounding vegetation and dominated by *Stipa krylovii*. This suggests either that these mounds are less disturbed, because of less burrowing activities, or that the actual disturbance was longer ago and the vegetation has already recuperated from the disturbances. Visual inspection suggested the latter.

Disturbance by marmots decreases species diversity as it was found that species diversity was highest in the surrounding *Stipa* vegetation and on the *Stipa* dominated mounds, while it was much lower on the more disturbed *Artemisia* and *Leymus* dominated mounds.

It is likely that the different types of mounds represent a series of succession, considering the growth habit of the species dominating the different types of mounds. When a mound is created by burrowing marmots, the mound is initially covered by bare soil. This can be easiest colonized by *Artemisia adamsii*, a perennial forb, generally occurring in the steppe vegetation. It produces many, easily dispersed seeds, that establish well on degraded vegetation and bare soil. The perennial grasses *Leymus chinensis* and *Stipa krylovii* do produce seeds, but under the relatively dry conditions seedlings are not commonly found and do not establish well. For both species, vegetative growth is by far their most common way of site colonization. *Leymus* shows a fast lateral spread by forming rhizomes. *Stipa*, however, is a caespitose grass with a much slower lateral spread. It does not make long rhizomes but it relatively slowly increases its bunch size by growing more tillers. *Stipa* bunches can break up as part of the bunch die off (chapter 3).

Effects of herbivores on plant productivity, forage quality and nitrogen cycling

Grazing significantly decreased the plant standing crop (which consists of above-ground biomass and standing dead material) of the *Stipa* vegetation (chapter 3). The exclusion of takh and marmots led to a higher plant standing crop in the enclosure plots, and the intensity of grazing by takh and marmots was sufficient to cause significant differences between the different types of enclosures. A successive increase in the amount of standing crop on fully grazed, marmot-grazed and ungrazed plots reflected a successive decrease in grazing intensity.

That grazing should stimulate the growth of the vegetation, and thereby compensate for the loss of leaf area, is a phenomenon often reported to occur. However, in our field experiment we were not able to determine the growth of the vegetation after grazing, since we could only measure plant biomass, which is a result of growth and partial defoliation by grazing.

Therefore we designed an experiment in the greenhouse, in which we determined the effect of partial defoliation by clipping on plant growth. We performed a growth analysis on two species of the steppe: *Leymus chinensis* and *Stipa krylovii* (chapter 4). *Leymus* showed a significant increase in its relative growth rate (RGR) after clipping, while for *Stipa* RGR was negatively affected.

Grazing by takh and marmots seemed to improve forage quality, as was reflected in higher nitrogen (N) concentrations of the standing crop after grazing, which indicates a higher protein content of the forage. However, this seems solely to be the result of the higher live-dead ratio of the standing crop, as the aboveground biomass had much higher N-concentrations than the dead material, and no increase of the N-concentrations of the biomass or of the dead material after grazing was found. Nor did we find increased N-concentrations of the roots or the soil after grazing. Contrary to other studies, in which an increased N-mineralization and N-availability was found to lead to higher N-concentrations in the aboveground biomass, our results indicate that the improved forage quality did not result from an increased N-availability.

Disturbances by marmots led to enhanced forage quality on the *Artemisia* and *Leymus* types of mound, as indicated by increased nitrogen concentrations in the vegetation of these types of mound. Our results suggest that these higher nutrient concentrations can be largely explained by higher mineralization rates following disturbance. We found a gradient in plant nutrient concentrations from low on the *Stipa* mounds to higher in the *Artemisia* and *Leymus* mounds, while the N-concentrations in the soil exhibited a (more or less) reverse gradient. The gradient in plant nutrient concentrations most probably reflects a similar gradient in mineralization rates. The higher N-mineralization rates should have allowed higher N-uptake rates and higher N-concentrations in the plants and lower concentrations in the soil. A significantly lower amount of organic matter in the soil of the *Artemisia* mound is consistent with this interpretation.

Besides the higher nitrogen concentration in the above ground biomass, the total above ground nitrogen yield also was greater on the *Artemisia* and *Leymus* mounds. This was because the above ground biomass was similar or greater on the mounds than in the surrounding off-mound vegetation.

Compensatory growth

Plants possess compensatory mechanisms through which they can mitigate potential negative effects of defoliation. They exhibit increased photosynthetic rates and relative growth rates (RGR) after grazing or clipping. The two components of RGR are net assimilation rate (NAR, growth per unit leaf area) and leaf area ratio (LAR, leaf area per plant biomass) ($RGR = NAR \times LAR$). The contribution of these different mechanisms differ between species and between plants growing under different environmental conditions.

Compensatory growth was much stronger for the rhizomatous *Leymus chinensis* than for the caespitose *Stipa krylovii*, as we found in the greenhouse experiment (chapter 4). *Leymus* showed a significant increase in its relative growth rate (RGR) after clipping, while for *Stipa* RGR was negatively affected. Clipped *Leymus* plants maintained leaf productivity levels that were similar to undamaged individuals, while leaf productivity in clipped *Stipa* dropped to less than half of that of the controls. The greater compensatory growth of *Leymus* compared to *Stipa* mainly resulted from a greater stimulation of its net assimilation rate (NAR), and its greater capacity to store and re-allocate carbohydrates by clipping. The greater increase in NAR was probably the result of a stronger reduction in self-shading, because *Leymus* shoots stood much denser than those of *Stipa*. The strong decrease in self-shading in *Leymus* resulted in a higher increase in light penetration to remaining leaves after clipping.

Apparently *Leymus* is more tolerant to clipping (and by extrapolation to grazing) than *Stipa* and this could explain the shift in dominance from *Stipa* to *Leymus* when grazing pressure increases in the Mongolian steppe (chapter 3).

In *Leymus* there was more compensatory growth under wet than under dry conditions, while in *Stipa* compensation was increased under dry conditions (chapter 4). This probably reflects the fact that *Stipa* is more drought tolerant than *Leymus*.

In accordance with these results, we found in our grazing experiment (chapter 3) a higher increase in frequency of *Leymus* after grazing in the wet year of 2003 than in the dry 2002, while for *Stipa* the frequencies remained the same in these two years. Our results suggest that the effect of drought on compensation can differ between species and that it depends on the overall drought tolerance of the species in question.

Sustainable pasture use and carrying capacity

The carrying capacity of the steppe areas, i.e. the maximum number of herbivores which can be supported in an area, is an important issue for pasture management on the Mongolian and Eurasian steppes. When estimating the carrying capacity the

effect of compensation should be accounted for. Our results showed that compensatory mechanisms contribute enormously to the productivity of plants after clipping. Disregarding the effects of compensatory growth would result in a considerable overestimation of the carrying capacity of *Stipa* grasslands, while for *Leymus* grasslands the estimation should be correct, because of the effect of full compensation. Further research on the effect of different levels of clipping on compensation can give more insight in the degree of compensation that occurs under different grazing intensities. Together with the investigation of the effect of nitrogen availability on compensation this can give valuable information for a sustainable pasture use.

6 дугаар бүлэг

Хураангуй

Өвсөн тэжээлтэн экосистемийнхээ бүтэц, үйл ажиллагаанд нөлөөлөх замаар тал хээрийн бэлчээрийн тогтвортой байдалд голлох үүрэг гүйцэтгэдэг. Тэдний бэлчээрлэлтээр ургамалжлын бүтэц, зүйлийн бүрдэл, арви, ургамлын бүтээмж, азотын эргэлт байнга өөрчлөгддөг.

Өвсөн тэжээлтэн амьтад ургамлын эрхтэн, хэсгүүдийг байнга идэж сүйтгэдэг ч, энэ нь ургамлын өсөлтөнд онц нөлөөлдөггүй. Ургамал үүнд зохилдож, өөрийгөө нөхөн сэргээх хариу механизмтай болсон байдаг.

Аливаа байгалийн бэлчээр нь экосистемийн анхдагч цэвэр бүтээмж болох газрын дээрх босоо массын 50 гаруй хувийг хэрэглэх хэмжээний томоохон популяциудийг даах чадвартай боловч, Монголд малын тоо толгой хэт өсөж, бэлчээрийн даац хэтэрснээс бэлчээр талхлагдаж, ургамалжилт доройтож байна. Бэлчээрийн тогтвортой менежмент бий болгохын тулд экосистемийн тэнцвэрт байдалд өвсөн тэжээлтэн ямар үүрэгтэйг, тэдний бэлчээрлэлт ургамлан бүрхэвчинд нөлөөлөх далд механизмийг сайтар мэдэх шаардлагатай.

Бид судалгаагаараа тал хээрийн том, жижиг янз бүрийн өвсөн тэжээлтэн амьтад ургамалжилд хэрхэн нөлөөлдгийг тодруулахыг зорилоо. Хялганат хээрийн бэлчээрт тахь (*Equus Przewalskii*) болон Сибирь тарвага (*Marmota sibirica*)-наас хамгаалсан туршлагын хашаанууд барьж, тэдгээр өвсөн тэжээлтэн бэлчээрийн ургамлын зүйлийн арви, биомасс, ургамлын азотын агууламжинд хэрхэн нөлөөлөхийг гурван жил дараалан судлав. Ингэхдээ бэлчээрийн зонхилогч ургамал солигдох нь бэлчээрлэлт ихсэхтэй холбоотой эсэх, энэ нь зүйлүүдийн нөхөн ургах чадварын зөрүүгээр тайлагдах эсэхийг шинжилсэн болно. Мөн Монголын хээр тал дахь ургамлын зүйлийн динамик болон хүлэмж дэх ургамлын физиологийн шинж төлөвийн хоорондох холбоог илрүүлэхийг оролдов. Хүлэмжийн туршилтанд ургалтын анализийн сүүлийн үеийн арга зүй ашиглан тал хээрийн бэлчээрт зэрэгцэн оршдог Нангиад түнгэ (*Leymus chinensis*) болон Шивээт хялгана (*Stipa krylovii*)-ын нөхөн ургах чадварыг харьцуулж судаллаа. Түүнчлэн хялганат хээрийн ургамалжилд тарваганы нүх, дошны нөлөөг авч үзэв. Судалгааны гол үр дүнг энэ бүлэгт нэгтгэн дүгнэлээ.

Өвсөн тэжээлтэн ургамлын зүйлийн бүрдэл, арви, баялагт нөлөөлөх нь Хялганат хээрийн ургамалжлын түгээмэл хэвшил нь янз бүрийн амьдралын хэлбэртэй, дэгнүүлт болон дэгнүүлгүй олон зүйлийн үетэн, зарим зүйлийн сөөг сөөгөнцөрөөс бүрдэнэ. Бэлчээрлэлт хэр байгаагаас хамааран бэлчээрийн ургамлын зонхилогч зүйлүүд солигддог.

Бэлчээрлэлт хэвийн байхад дэгнүүлт *Stipa krylovii* зонхилж байдаг ч бэлчээр талхлагдаж ирэхэд үндэслэг ишт зүйлүүд зонхилогч болдог. Бидний

судалгаагаар ийм бэлчээрт үндэслэг ишт *Leymus chinensis* олширч, *Stipa krylovii*-ийн дэгнүүл цөөрч байгаа нь ажиглагдсан юм (3 дугаар бүлэг). Ерөнхийдөө үндэслэг ишт зүйлүүд олширч байв.

Leymus-ийн тохиолдоц олширч, тэрээр бэлчээрийн талхлагдлийг сайн тэсвэрлэж чаддаг нь түүний нөхөн ургах чадвар сайнтай холбоотой байж болох юм.

Хүлэмжийн туршилтаар ийм байдал ажиглагдсан юм (4 дүгээр бүлэг). *Leymus*-ийн нөхөн ургалт илүү байгаа нь түүний өөриймшүүлэх чадвар сайн, үндэслэг ишээрээ дамжуулан нүүрс-ус нөөцөлдгөөс үүдэлтэйг бид илрүүлэв.

Stipa krylovii талхлагдлын улмаас суурь нь багасаж, бут нь сийрэгшиж, дэгнүүл нь жижгэрснээр (3 дугаар бүлэг) эцсийн бүлэгт популяцийн нягтшилыг мэдэгдэхүйц буурахад хүргэж байна.

Хялганат хээрийн ургамлын бүлгэмдэлд тарваганы нүхний дошжилт үлэмж нөлөөлдөг. Дошны ургамалжил янз бүрийн үе шаттай бөгөөд, зарим дош нүцгэн, заримынх нь ургамалжил орчны хялганат хээрийн бүлгэмдэлд нилээд дөхсөн, зарим нь *Leymus chinensis* юмуу *Artemisia adamsii* зонхилсон ургамлан бүрхэвчтэй байдаг (5 дугаар бүлэг).

Artemisia adamsii юмуу *Leymus chinensis* зонхилсон ургамалжилтай дош зүйлийн бүрдэл, бүтцээрээ дошноос гадуурх орчны ургамалжлаас эрс ялгаатай бөгөөд энэ нь талхлагдлын үр дагавар байх талтай. Харин *Stipa* хэвшлийн бүлгэмдэлтэй дош нь орчныхтойгоо төстэй ургамалжилтай байна. Ийм дош нь нэг бол дөнгөж дошжиж байгаагаас бага талхлагдсан эсвэл талхлагдалд өртөөд удаж байгаа учраас байгалийн бүлгэмдэл эргэн сэргэж буй хэрэг. Бидний ажигласанаар энэ нь эргэн сэргэж буй бүлгэмдэл юм.

Хавийн хялганат хээрийн бэлчээрт болон *Stipa* зонхилсон дошинд зүйлийн баялаг харьцангуй илүү байхад их талхлагдаж, *Artemisia* болон *Leymus* зонхилсон дошных дээрхээс доогуур байгаа нь тарвага зүйлийн бүрдлийг цөөрүүлдгийг харуулж байна.

Янз бүрийн бүлгэмдэлтэй дошнууд дахь зонхилгогч зүйлүүдийн ургах онцлогийг аваад үзэхэд эдгээр бүлгэмдлүүд сукцессийн хөгжлийн янз бүрийн шатанд байгаа нь ажиглагдаж, Амьдралтай, шинэхэн дош эхлээд ургамлан бүрхэвчгүй, нүцгэн хөрс байдаг. Тал хээрийн бүлгэмдэлд тохиолдох *Artemisia adamsii* ийм нүцгэн хөрсийг эзлэн ургахдаа сайн. Энэ нь түүний тархалт сайтай, талхлагдсан бэлчээр болон нүцгэн хөрсөнд амархан соёолдог олон үр боловсруулдагтай нь холбоотой. *Leymus chinensis*, *Stipa krylovii* мэт олон настуудын үр хуурай, гандуу нөхцөлд соёолох чадвар муутай. Энэ хоёр зүйлийн хувьд хүрээгээ тэлж ургах гол арга нь ургал үржил юм. *Leymus* нь үндэслэг иш үүсгэн эрчимтэй тархдаг. Харин *Stipa* нь маш удаан тархалттай дэгнүүлт ургамал юм. Энэ нь үндэслэг ишээр биш харин нахиа нэмэх замаар дэгнүүл нь нягтшиж томордог. *Stipa*-гийн дэгнүүлийн хэсгүүд үхэж үрэгдэхэд дэгнүүл хуваагдах нь бий (3 дугаар бүлэг).

Өвсөн тэжээлтэн ургамлын бүтээмж, тэжээллэг чанар, азотын эргэлтэд нөлөөлөх нь

Бэлчээрлэлтийн улмаас хялганат хээрийн бэлчээрийн босоо ургац (газрын дээрх биомасс болон босоо хагд) мэдэгдэхүйц багасаж байна (3 дугаар бүлэг). Тахь болон тарваганаас тусгаарласан хашаан доторх ургац орчныхоосоо их байсан бөгөөд тахь, тарваганы нөлөө өөр хоорондоо ялгаатай байлаа. Тахь, тарвага хоёулаа идэшлэсэн талбайд ургац хамгийн бага, зөвхөн тарвага идэшлэсэн талбайд арай илүү, аль нь ч идэшлээгүй талбайд ургац өндөр байлаа.

Бэлчээрлэлт нь ургалтыг өдөөж, түүгээр ургамал алдсан навчныхаа талбайг нөхдөг зүй тогтолтойг хааяагүй дурдсан байдаг. Гэвч бид хээрийн туршилтаараа бэлчээрлэлтийн дараа ургамлын ургалтыг тодорхойлж чадаагүй зөвхөн ургамлын биомассыг хэмжсэн болно.

Тиймээс бид ургамлын өсөлтөд тайралт хэрхэн нөлөөлөхийг хүлэмжийн туршилтаар судаллаа. Ингэхдээ тал хээрийн бүлгэмдлийн хоёр зүйл *Leymus chinensis*, *Stipa krylovii*-ийн ургалтад анализ хийв.(4 дүгээр бүлэг). Тайралтын дараа *Leymus*-ийн харьцангуй өсөлтийн хурд (RGR) нэмэгдэж байсан бол, *Stipa*-д тайралт сөрөг нөлөөлж байв.

Тахь, тарваганы бэлчээрлэлт нь ургамлын тэжээллэг чанарыг сайжруулж байгаа нь босоо ургацын азотын агууламж их болсноос харагдана. Азот ихсэж байгаа нь ургамал дахь уургын хэмжээг нэмэгдүүлж байгаа гэсэн үг юм. Гэхдээ энэ нь босоо ургац дахь ногоо-хагд хоёрын харьцаанаас л хамаарна. Яагаад гэвэл, ногоон өвсний азотын агууламж хагдныхаас их, нөгөөтэйгүүр ногоон өвс, хагд хоёрын аль алиных нь азотын агууламж бэлчээрлэлтийн дараа нэмэгддэггүй. Түүнчлэн бэлчээрлэлтийн дараа газрын доорх үндсэнд ч, хөрсөнд ч азотын агууламж өөрчлөгдөөгүй. Урьд хийгдсэн бусад судалгаануудад газрын дээрх босоо массын азотын агууламж нэмэгдэх нь азот эрдэсжиж, элбэгшихээс үүдэлтэй гэжээ. Гэвч бидний судалгаа азотын хэмжээ нэмэгдсэнээс бэлчээрийн тэжээллэг чанар сайжирдаггүйг харуулж байна.

Artemisia, *Leymus* хэвшилтэй дошны ургамалжлын азотын агууламж өссөн нь тарваганы нөлөөгөөр ургамлын тэжээллэг чанар нэмэгддэгийг харуулж байна. Судалгааны дүнгээс үзэхэд тарваганы нөлөөгөөр эрдэсжилт ихэссэнээр ургамлын тэжээллэг чанар дээшилдэг байна. *Stipa* хэвшилтэй дошноос эхлээд *Artemisia*, *Leymus* хэвшилтэй дош хүртэл ургамлын шим тэжээлийн агууламж өсөх шатлал байгааг бид илрүүлэв. Харин хөрсөнд азотын агууламжийн энэ шатлал тодорхой хэмжээгээр урвуу, өөрөөр хэлбэл буурах чиглэлтэй байв. Ургамлын шимт чанарын ихсэлт эрдэсжилтийн явцтай төстэй байна. Азот эрдэсжих эрчим нэмэгдэхийн хэрээр ургамал хөрснөөс азот авах хэмжээ нэмэгдэж, улмаар ургамал дахь азотын агууламж ихсэж, хөрсөнд багасна. *Artemisia* хэвшилтэй дошны хөрсөн дэх органик бодисын хэмжээ мэдэгдэхүйц бага байсан нь үүгээр тайлбарлагдана.

Artemisia болон *Leymus* хэвшилтэй дошнуудын газрын дээрх биомассын азотын

агууламж их байхын сацуу нийт азотын хэмжээ ч бас их байв. Энэ нь эдгээр хэвшилтэй дошны газрын дээрх биомасс дош хавийн ургамалжилтай адил юмуу арай илүү байгаатай холбоотой.

Нөхөн ургалт

Ургамал идэгдэж, гэмтэхээс үүсэх сөрөг үр дагавраас өөрийгөө хамгаалж нөхөн ургах механизмтай байдаг. Идэгдэх юмуу тайрсны дараа ургамлын фотосинтезийн эрч нэмэгдэж, харьцангуй өсөлтийн хурд (RGR) нь өсдөг. Харьцангуй өсөлтийн хурд ($RGR = NAR \times LAR$) нь: цэвэр өөриймшүүлэлтийн хурд (NAR, навчны нэгж талбайд ноогдох өсөлт), навчны талбайн харьцаа (LAR, ургамлын нэгж биомассад ноогдох навчны талбай) гэсэн хоёр хэсгээс бүрддэг. Эдгээр хоёр механизмийн үйлчлэх нь зүйлүүдийн хооронд болон өөр өөр орчинд ургадаг ургамлуудад ялгаатай байна.

Үндэслэг ишт *Leymus chinensis*-ийн нөхөн ургах чадвар дэгнүүлт *Stipa krylovii*-гийнхээс хавьгүй илүү байгааг бид хүлэмжид хийсэн туршилтаараа үзүүлсэн билээ (4 дүгээр бүлэг). Тайрсны дараа *Leymus*-ийн харьцангуй өсөлтийн хурд (RGR) илэрхий нэмэгдэж, *Stipa*-гийнх буурч байв. Тайрагдсан *Leymus*-ийн навчны бүтээмжийн түвшин хэвийн бодгалийнхтай адил байхад, *Stipa*-гийнх хяналтынхаас бараг тал хагасаар доогуур байв. *Stipa*-тай харьцуулахад *Leymus*-ийн нөхөн ургах чадвар сайн байгаа нь түүний цэвэр өөриймшүүлэлтийн хурд (NAR) илүү, нүүрс-ус нөөцлөх, тайралтын үед дахин хуваарилах чадвар илүүтэй нь холбоотой. Тайралтаар *Leymus*-ийн цэвэр өөриймшүүлэлтийн хурд (NAR) илүү нэмэгддэг нь сүүдэрлэх хэсгүүд алга болсонтой холбоотой байж болох юм. *Leymus* нь *Stipa*-г бодоход илүү нягт ургадаг тул өөрийгөө сүүдэрлэх нь илүү билээ. *Leymus*-ийн сүүдэрлэх хэсэг багасах тусам үлдсэн навчист гэрлийн хүртээмж сайжирна.

Монголын тал хээрт бэлчээр талхлагдахад бэлчээрийн зонхилогч *Stipa Leymus*-аар солигддог нь *Leymus* тайралтад (идэгдэхэд мөн адил) *Stipa*-гаас тэсвэртэй байгаагаар тайлбарлагдана (3 дугаар бүлэг).

Stipa-ийн нөхөн ургах чадвар хуурай нөхцөлд сайжирч байхад *Leymus*-ийнх чийглэг орчинд хуурайгийнхаас илүү байлаа (4 дүгээр бүлэг). Энэ нь магадгүй *Stipa* ганд илүү тэсвэртэйг харуулж байна.

Дээрх үр дүнд тулгуурлан бид (3 дугаар бүлэг) идээшлэлттэй талбайд *Leymus*-ийн тоо хэмжээ гантай 2002 оныхтой харьцуулахад хур тунадас сайтай 2003 онд нэмэгдсэн байхад *Stipa*-гийнх энэ 2 жилд өөрчлөгдөөгүйг илрүүлсэн билээ. Агаарын хуурайшилт зүйлүүдийн нөхөн ургах чадварт харилцан адилгүй нөлөөлөх бөгөөд энэ нь тухайн зүйлийн ганг тэсвэрлэх чанараас хамаардаг болохыг бидний судалгаа харууллаа.

Бэлчээрийн тогтвортой ашиглалт ба даац

Хээрийн бэлчээрийн даац, өөрөөр хэлбэл, тодорхой хэмжээний газарт нутагт

амьдрах өвсөн тэжээлтний дээд тоо толгой гэдэг ойлголт бол Монгол болон Евразийн хээрийн бэлчээрийн менежментийн гол асуудал юм. Бэлчээрийн даац тодорхойлохдоо ургамлын нөхөн ургалтыг тооцоолуштай. Нөхөн ургалтын механизм нь идэгдсэний дараах ургамлын бүтээмжид асар их түлхэц өгдгийг бидний судалгаа харууллаа. Хэрэв нөхөн ургалтыг тооцоолохгүй бол хялганат хээрийн бэлчээрийн даацыг хэтрүүлж тооцохоор байхад *Leymus*-тай бэлчээрийн хувьд нөхөн ургалт өндөртэй учир даацыг нь нэмж тооцвол зөв болно. Цаашид тайралтыг янз бүрийн түвшинд хийж нөхөн ургалтад яаж нөлөөлөхийг үзэж судалбал, бэлчээрлэлт нөхөн ургалтад нөлөөлөх зүй тогтлын талаар ойлголтыг өргөжүүлэх юм. Үүний зэрэгцээ азотын хэмжээ нөхөн ургалтад хэрхэн нөлөөлдгийг судлах нь бэлчээрийн тогтвортой ашиглалтад чухал болно.

Nederlandse samenvatting

Herbivoren spelen een sleutelrol in het duurzame behoud van steppe graslanden door hun invloed op structurele en functionele eigenschappen van het ecosysteem. Hun begrazing leidt vaak tot veranderingen in vegetatiestructuur, soorten-samenstelling en -abundantie, productiviteit en stikstofkringloop van planten. Onder natuurlijke omstandigheden worden planten door gedeeltelijke ontbladering door herbivoren vaak beschadigd, maar dit leidt zelden tot een proportionele afname in de groei. Planten lijken aangepast te zijn aan begrazing en bezitten compenserende mechanismen, waarmee ze de potentieel negatieve effecten van ontbladering kunnen afzwakken.

Natuurlijke graslanden kunnen grote populaties van (wilde) herbivoren onderhouden, en plaatselijk kunnen die meer dan 50% van de bovengrondse netto primaire productie consumeren. In Mongolië echter heeft een te grote veestapel geleid tot een situatie van overbegrazing, waardoor er een achteruitgang van de steppevegetatie plaatsvond.

Om in staat te zijn een duurzaam weidebeheer te ontwikkelen, is er een beter begrip nodig van de rol van herbivorie in de duurzaamheid van het ecosysteem en van de onderliggende mechanismen van begrazingseffecten op de vegetatie.

Het doel van het onderzoek beschreven in dit proefschrift is inzicht in de invloed van verschillende typen herbivoren, een grote en een kleine, op de steppe vegetatie te verkrijgen. Hiertoe is een begrazingsexperiment op de *Stipa*-steppe opgezet, waarin we het effect van 3 jaar uitsluiting van takh (*Przewalski paard*) en de Siberische marmot op abundantie van plantensoorten, plantenbiomassa en de N-concentratie van planten onderzochten. We onderzochten of er met toenemende begrazing een verschuiving in de dominantie van plantensoorten plaatsvindt en of dit uit de verschillen in groeiresponses na ontbladering kan worden verklaard. We probeerden een verband te leggen tussen de dynamiek van de plantensoorten op de Mongoolse steppe en fysiologisch gefundeerde planteneigenschappen, die we in het kasexperiment waarnamen. In dat kasexperiment vergeleken we de potentie voor compenserende groei van *Leymus chinensis* en *Stipa krylovii*, twee naast elkaar voorkomende grassoorten van de steppe, daarbij gebruik makend van een recent ontwikkelde techniek van groei-analyse. Op de *Stipa*-steppe bestudeerden we de invloed van verstoringen door marmotten. De belangrijkste resultaten worden hier samengevat.

Soortensamenstelling, abundantie en diversiteit van planten, beïnvloed door herbivoren

De typische *Stipa*-steppe bestaat uit een verscheidenheid aan grassen met verschillende groeivormen en verscheidene kruidachtigen. Er zijn grassen die in pollen groeien en grassen met apart staande spruiten, die ondergronds met een wortelstok met elkaar verbonden zijn. Een verandering in begrazingsintensiteit kan leiden tot een verschuiving in dominantie van soorten met verschillende groeivormen.

Onder lichte of matige begrazing is de caespitose (pollenvormende) *Stipa krylovii* de dominante grassoort, maar wanneer de begrazingsdruk toeneemt leidt dit tot een dominantie van rhizomateuze (met een wortelstok groeiende) soorten. We vonden een hogere frequentie van het rhizomateuze gras *Leymus chinensis* en een (zwakke) afname van de caespitose *Stipa krylovii* onder een hogere begrazingsintensiteit (hoofdstuk 3). Het totaal van rhizomateuze soorten vertoonde ook een hogere frequentie.

De toegenomen frequentie van *Leymus* and zijn hogere begrazingstolerantie kan worden toegeschreven aan een veel sterkere compenserende groei in *Leymus* na ontbladering dan in *Stipa*, zoals aangetoond in een kasexperiment (hoofdstuk 4). We vonden dat de compenserende groei in *Leymus* voornamelijk het gevolg was van een hogere assimilatiesnelheid en herallocatie van opgeslagen koolhydraten vanuit de rhizomen.

Hoewel de afname in de frequentie van *Stipa krylovii* slecht marginaal significant was, maken de gereduceerde basale oppervlakten, lagere spruitdichtheden en de verschuiving naar kleinere pollen van *Stipa* (hoofdstuk 3), die we na begrazing vonden, het aannemelijk dat dit uiteindelijk zal leiden tot een merkbare afname van de *Stipa* populatie.

Graaactiviteiten van marmotten leiden tot belangrijke veranderingen in de vegetatie van de *Stipa*-steppe. Ze creëren heuvels die zeer verschillen in vegetatiebedekking; er zijn heuvels bedekt met kale bodem, heuvels bedekt met een vegetatie min of meer gelijk aan de omringende *Stipa*-vegetatie en heuvels gedomineerd door het gras *Leymus chinensis* of het kruid *Artemisia adamsii* (hoofdstuk 5).

Heuvels gedomineerd door *Artemisia adamsii* of *Leymus chinensis* zijn zeer verschillend in vegetatiebedekking en samenstelling ten opzichte van de omringende vegetatie, hetgeen waarschijnlijk het gevolg is van verstoring. De vegetatie op een *Stipa* heuvel is echter gelijk aan de omringende vegetatie en wordt gedomineerd door *Stipa krylovii*. Dit suggereert dat deze heuvels minder verstoord zijn, vanwege minder graaactiviteiten, of dat de actuele verstoring langer geleden plaatsvond en dat de vegetatie alweer hersteld is van de verstoring. Visuele inspectie suggereert het laatste.

Verstoring door marmotten leidt tot afname van de soortenrijkdom. We vonden dat de soortenrijkdom het hoogst was in de omringende *Stipa*-vegetatie en op de door *Stipa* gedomineerde heuvels, terwijl het veel lager was op de meer verstoorde door *Artemisia* en *Leymus* gedomineerde heuvels.

Waarschijnlijk representeren de verschillende typen van heuvels een successiereeks. Wanneer door gravende marmotten een heuvel is gemaakt, is de heuvel in eerste instantie bedekt door kale bodem. Deze kan het gemakkelijkst worden gekoloniseerd door *Artemisia adamsii*, een perenne kruidachtige plant die algemeen voorkomt in de steppe-vegetatie. Deze plant produceert vele, gemakkelijk verspreidbare zaden, die zich gemakkelijk in een gedegradeerde vegetatie en op een kale bodem vestigen. De perenne grassen *Leymus chinensis* en *Stipa krylovii* produceren zaden, maar onder relatief droge omstandigheden worden er over het algemeen geen kiemplanten

gevonden en kunnen deze zich niet goed vestigen. Voor beide soorten is vegetatieve uitbreiding verreweg de meest algemene manier van kolonisatie. *Leymus* vertoont een snelle laterale uitbreiding door de vorming van rhizomen. *Stipa* is echter een caespitooos gras met een veel langzamere laterale uitbreiding. Het maakt geen lange rhizomen maar neemt slechts relatief langzaam in polgrootte toe door de groei van meer spruiten. *Stipa*-pollen kunnen fragmenteren wanneer een deel van de pol afsterft (hoofdstuk 3).

Effect van herbivoren op plant productiviteit, voedselkwaliteit en stikstof kringloop

Begrazing verminderde significant de 'plant standing crop' (die bestaat uit bovengrondse biomassa en staand dood materiaal) van de *Stipa*-vegetatie (hoofdstuk 3). De uitsluiting van takh en marmotten leidde tot een hogere 'plant standing crop' in de onbegraasde vakken en de intensiteit van begrazing door takh en marmotten was voldoende om significante verschillen tussen de verschillende typen van onbegraasde vakken te veroorzaken. Een successieve toename in de hoeveelheid 'standing crop' op volledig begraasde, marmot begraasde en onbegraasde vakken weerspiegelde een successieve afname in begrazingsintensiteit.

Dat begrazing de groei van de vegetatie zou stimuleren en daarmee compenseren voor het verlies aan bladoppervlak, is een fenomeen dat vaak is gerapporteerd. In ons veldexperiment echter waren we niet in staat om de groei van de vegetatie na knippen te bepalen, aangezien we alleen de momentane 'standing crop' konden meten, wat het resultaat is van groei en gedeeltelijke ontbladering door begrazing. Daarom hebben we een experiment in de kas ontworpen, waarin we het effect van gedeeltelijke ontbladering door knippen op plantengroei bepaalden. We voerden een groei-analyse uit op twee soorten van de steppe: *Leymus chinensis* en *Stipa krylovii* (hoofdstuk 4). *Leymus* vertoonde na knippen een significante toename in zijn relatieve groeisnelheid (RGR), terwijl voor *Stipa* de RGR negatief beïnvloed werd.

Begrazing door takh en marmotten lijkt de kwaliteit van het voedsel te verbeteren, zoals weerspiegeld werd door hogere stikstof (N) concentraties van de 'standing crop' na begrazing, wat een hoger eiwitgehalte van het voer indiceert. Dit lijkt echter slechts het gevolg van een hogere levend-dood verhouding van de 'standing crop' te zijn, omdat de bovengrondse biomassa veel hogere N-concentraties had dan het dode materiaal en er geen toename van de N-concentraties in de biomassa of het dode materiaal na begrazing werd gevonden. Evenmin vonden we na begrazing toegenomen N-concentraties in de wortels of de bodem. In tegenstelling tot andere studies, waarin een gevonden toename in N-mineralisatie en N-beschikbaarheid tot een hogere N-concentratie in de bovengrondse biomassa bleek te leiden, wijzen onze resultaten erop dat de verbeterde voedselkwaliteit niet het gevolg van een toegenomen N-beschikbaarheid was.

Verstoringen door marmotten leidden tot verbeterde voedselkwaliteit op de *Artemisia* en *Leymus* heuvels, zoals geïndiceerd door een toegenomen stikstofconcentratie in de vegetatie van deze typen heuvels. Onze resultaten suggereren dat deze hogere stik-

stofconcentraties grotendeels uit hogere mineralisatiesnelheden volgend op verstoring verklaard kunnen worden. We vonden een gradiënt in nutriëntenconcentraties in de planten van laag op de *Stipa* heuvels tot hoger op de *Artemisia* en *Leymus* heuvels, terwijl de N-concentraties in de bodem een (min of meer) omgekeerde gradiënt vertoonden. De gradiënt in nutriëntenconcentraties in de planten weerspiegelt hoogst waarschijnlijk een zelfde gradiënt in mineralisatiesnelheden. De hogere N-mineralisatiesnelheden zouden hogere N-opnamesnelheden toelaten en tot hogere N-concentraties in de planten en lagere concentraties in de bodem leiden. Een significant lagere hoeveelheid aan organisch materiaal in de bodem is consistent met deze interpretatie.

Naast de hogere stikstofconcentratie in de bovengrondse biomassa, was de totale bovengrondse stikstofopbrengst ook groter op de *Artemisia* en *Leymus* heuvels. Dit omdat de bovengrondse biomassa op de heuvels gelijk of groter was dan in de omliggende vegetatie.

Compenserende groei

Planten bezitten compenserende mechanismen waarmee ze potentieel negatieve effecten van ontbladering ongedaan of minder ernstig kunnen maken. Ze vertonen verhoogde fotosynthese en relatieve groei-snelheden (RGR) na begrazing of knippen. De twee componenten van de RGR zijn netto assimilatie snelheid (NAR, groeisnelheid per eenheid bladoppervlak) en bladoppervlak verhouding (LAR, bladoppervlak per eenheid biomassa van de plant) ($RGR = NAR \times LAR$). De bijdrage van deze verschillende componenten verschilt tussen soorten en tussen planten die onder verschillende omstandigheden groeien.

Compenserende groei was veel sterker voor de rhizomateuze *Leymus chinensis* dan voor de caespitose *Stipa krylovii*, hetgeen bleek uit een kasexperiment (hoofdstuk 4). *Leymus* vertoonde na knippen een significante toename in de relatieve groeisnelheid (RGR), terwijl voor *Stipa* de RGR negatief werd beïnvloed. Geknipte *Leymus*-planten behielden bladproductiviteitsniveau's die gelijk waren aan onbeschadigde planten, terwijl de bladproductiviteit in geknipte *Stipa* tot minder dan de helft van de controle planten daalde. De sterkere compenserende groei van *Leymus* in vergelijking tot *Stipa* was voornamelijk het gevolg van een sterkere stimulatie van de netto assimilatie snelheid (NAR), en een groter vermogen tot het opslaan en heralloceren van koolhydraten bij knippen. De sterkere toename in NAR was waarschijnlijk het gevolg van een sterkere afname in zelfbeschaduwning, omdat de *Leymus*-spruiten veel dichter op elkaar stonden dan die van *Stipa*. De sterke afname in zelfbeschaduwning van *Leymus* bladen na knippen had een grotere toename in de lichtval op de overblijvende bladen tot gevolg.

Klaarblijkelijk is *Leymus* toleranter voor knippen (en bij extrapolatie voor begrazing) dan *Stipa* en kan dit de verschuiving in dominantie van *Stipa* naar *Leymus*, wanneer de begrazingsdruk op de Mongoolse steppe toeneemt, verklaren (hoofdstuk 3).

In *Leymus* was er meer compenserende groei onder natte dan onder droge omstan-

digheden, terwijl in *Stipa* de compensatie toenam onder droge omstandigheden (hoofdstuk 4). Dit weerspiegelt waarschijnlijk het feit dat *Stipa* een grote tolerantie voor droogte heeft dan *Leymus*.

In overeenstemming met deze resultaten vonden we in ons begrazingsexperiment (hoofdstuk 3) een hogere toename in de frequentie van *Leymus* na begrazing in het natte jaar van 2003 dan in het droge 2002, terwijl voor *Stipa* de frequenties in deze twee jaar hetzelfde bleven.

Onze resultaten suggereren dat het effect van droogte op compensatie tussen soorten kan verschillen en dat dit van de algehele droogtetolerantie van de betreffende soorten afhangt.

Duurzaam weidebeheer en draagkracht

De draagkracht van steppegebieden, dit is het maximum aantal herbivoren dat kan leven in een gebied, is een belangrijk onderwerp voor weidebeheer op de Mongoolse en Euraziatische steppen. Wanneer er schattingen van de draagkracht gemaakt worden zou er rekening met het effect van compensatie moeten worden gehouden. Onze resultaten laten zien dat compenserende mechanismen enorm aan de productiviteit van planten na knippen bijdragen. Negeren van de effecten van ontbladering en compenserende groei zou een behoorlijke overschatting van de draagkracht van *Stipa*-graslanden tot gevolg hebben, terwijl voor *Leymus*-graslanden de schatting correct zou zijn, vanwege het effect van volledige compensatie.

Verder onderzoek naar het effect van verschillende niveaus van knippen op compensatie kan meer inzicht geven in de mate van compensatie die onder verschillende begrazingsintensiteiten plaatsvindt. Samen met onderzoek naar het effect van stikstofbeschikbaarheid op compensatie kan dit waardevolle informatie voor een duurzaam weidebeheer geven.



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Сувдаа, Сээнэг, Мягаа, Бямбаа, Цэцгээ, Бурмаа, Соёлоо, Болд, Гандорж, Сэржээ нартаа баярласнаа хэлье. Та бүхний сайхан хоол, халамж ялангуяа намайг өвдөхөд халамжилж байсныг тань хэзээ ч мартахгүй.

Олон үйл ажиллагаануудыг маань сайн зохион байгуулж өгсөн Я.Амаржаргалдаа талархъя. Гэрт минь зочилж, тусалж байсан Цэрэннадмид гуайд талархснаа хэлье. Тэрээр биологийн багш байсан болохоор миний ажлыг үргэж сонирхдог байсныг нь би их хүндэтгэдэг.

Намайг Монголд ирэх бүр нисэх буудал дээрээс халуун дотноор тосч авч тусалдаг байсан Ц.Дашпүрэв (Пүүжээ), Ц.Бороо хоёртоо талархал илэрхийлье. Та нар миний бүхий л албан бичиг баримтаас эхлэн концертийн билетийг минь хүртэл зохицуулж өгдөг байсанд их баярлалаа.

In Mongolia I like to thank all the people of Hustain Nuruu and Macne office in Ulaan Baatar. It was an unforgettable time, the four years I lived in the ger camp in Hustai during the summer, together with the staff members, project workers, researchers and eco-volunteers. I enjoyed your friendliness and hospitality very much, and felt like being part of a family.

With great respect I memorize Dr. Jachin Tserendeleg, who told me much about the history of the Mongolian people and how the culture interweaves with nature. I am grateful for his hospitality and that of Badmaa. His passing felt as a great loss.

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Fantastic were the parties with the dancing of Mongolian waltzes, the singing and funny competitions. The Naadam festivals along the Tuul river with all the staff members were really wonderful. Togtokhsuren, Enkthur, Enkhuyac, Sukh, Serge-len, Chimeg, Erdentsimeg, Batnassan, Batxuy, Xongoroo, Oyunbayar, Monaa and

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have a chat and a drink after a hard day working in the field. To learn from you about grasses and grasslands, and your experience of nature conservation was of great value for me.

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To my friends from far, Pep in Australia and Enkhee in Japan, thanks for your support. In times when I was down, the mails with pep-talk from Australia gave me new spirit, and the correspondence about climate change helped me to put the Mongolian situation in a broader perspective. Enkhee, I thank you for the Mongolian translation of the summary and for your friendship; here in the Netherlands, in Mongolia and now from Japan.

Tenslotte wil ik mijn ouders, familie en vrienden bedanken voor de warme belangstelling die ze voor mijn onderzoek getoond hebben. Voor de mails die ik van hen kreeg gedurende de zomers dat ik in Hustai zat en die me op de hoogte hielden van hoe het thuis ging.

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Willem, het was leuk dat jij gelijk het eerste jaar al meekwam voor een aantal weken in Mongolië. Zo kon ik trots zijn op mijn 'grote' zoon, die voor het eerst op een paard gezeten, er meteen al in galop vandoor ging.

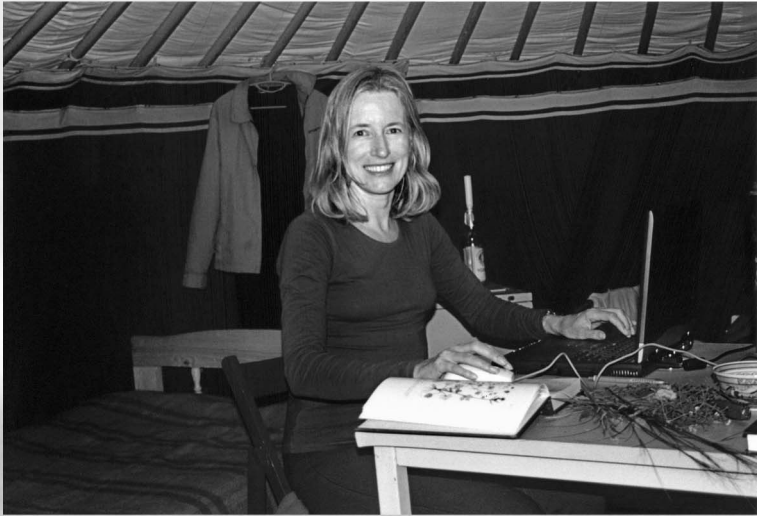
Degene aan wie ik het meest te danken heb, is Peter. Het eerste idee, om zelf een onderzoeksvoorstel te gaan schrijven, was van jou afkomstig. Heel erg bedankt Peet, voor je nauwe betrokkenheid en steun van het begin tot eind van het project.

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the research, but especially for the people from Mongolia. I always felt stimulated by you and strengthened to travel again to Hustai, even while you and Dad grew older and were more and more in need of my attention. I regret that Dad did not live long enough to share in this moment of celebration. My memories go back to the period in which I helped Dad with the work on the grapes in our greenhouses. How he explained to me Liebig's law, showing the long list of elements on the bag of fertilizer. His lessons so well taught awakened my interest in plants and their physiology. Willem, I very much appreciated your visit to Mongolia, that first year. I was very proud to see my big son riding a horse for the first time and immediately taking off in a gallop.

The one to whom I am most grateful is Peter. Initially it was your idea Peet, that I should write a PhD-proposal myself. Many, many thanks for your close commitment and support from the beginning till the end of the project.



Curriculum vitae

Marja van Staalduinen was born in 1956 in 's Gravenzande in the Netherlands. She went to high school in The Hague at the Dalton Scholengemeenschap, which she finished in 1974. In the same year she started as a student of biology at the University of Utrecht, where she specialized in ecology, but which study she did not complete at that time.

After earning a living in various jobs for several years and giving birth to her son, she decided in 1986 to change her career to IT. Here she worked for seven years, finishing as an information analyst.

In 1993 she decided to continue her study biology at Utrecht University during which she carried out two research projects. The first project was an experimental field research on the effect of atmospheric N-deposition on the decomposition of *Carex acutiformis* in a fen area. The other project was the development of a dynamic model that simulated the growth and competition of two plant species in a chalk grassland.

In 1995 she graduated and worked for nearly three years on a research contract at Wageningen University and Research Centre (WUR). There she performed a scenario study with a dynamic simulation model on the effect of increased atmospheric CO₂ concentration and temperature on the species richness of terrestrial ecosystems.

In 1999 she wrote a PhD research proposal on plant animal interactions in a Mongolian steppe and in 2000 she started with this project at the Plant Ecology Group, Utrecht University. There she worked for five years on this project, partly in Mongolia and partly in Utrecht. She lives in Utrecht and is planning to move to Spain.