Chapter 1
Abiotic and Biotic Determinants of Steppe Productivity and Performance – A View from Central Asia

Karsten Wesche and Jan Treiber

Abstract With over 13 Mio. km², grasslands of Eurasia form one of the largest continuous terrestrial biomes. They mostly represent environments with low productivity and with a long evolutionary history of natural grazing. Over the last few decades, increasing population sizes and socio-economic changes have subjected these steppes to increasing pressure, and associated degradation. We concentrate on the steppes of Central Asia (Mongolia, northern China and Tibet) and show that land use practice, climate and soil conditions are the most important drivers of change in these grasslands.

Grazing has strongly degrading effects on relatively moist grass and forest-steppes whereas evidence indicates that acute vegetation degradation in semi-arid desert steppes is largely absent. In such environments, precipitation controls community composition and productivity at both the local and regional scales. Recurrent droughts give rise to episodic fodder shortages, which results in animal numbers being maintained at relatively low levels. This may explain the lack of degradation in dry steppes, and supports predictions drawn from the non-equilibrium theory of rangeland science.

On the other hand, soil degradation due to grazing is found across the entire range of hygric conditions without any apparent interaction with precipitation. Soil nutrient contents were recently found to co-limit plant productivity, even at relatively dry sites, indicating that grazing may have indirect effects on steppe performance not predicted by standard theories.

We conclude that moister parts of Central Asia are sensitive to grazing degradation, which directly affects vegetation and soils, while semi-arid parts are mainly and more specifically influenced by soil degradation, which has more indirect effects on plant communities.

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Abbreviations

ANPP	Aboveground (annual) net primary productivity
CV	Coefficient of variation
IMGERS	Inner Mongolian Grassland Ecosystem Research Station
K	Potassium
N	Nitrogen
NEQT	Non equilibrium theory
P	Phosphorus

1.1 Introduction

Together with forests, grasslands and open shrubland constitute the largest terrestrial biomes, with temperate grasslands alone accounting for ca. 8% of land surface (White et al. 2000). They store huge amounts of carbon in their soil, and C-sequestration potential of the world's permanent pastures may be equivalent to 4% of global greenhouse gas emissions (Soussana and Luscher 2007). Asia hosts the largest grassland belt of the world – estimates differ but the most frequently quoted numbers are in the range of 6–9 Mio. km² of (mainly dry) grasslands with broadly similar physiognomy (Photo 1.1), while (mainly eastern) Europe accounts for an estimated 7 Mio. km² (Cressey 1960; White et al. 2000). Together, the Eurasian grasslands may once have formed the largest continuous land biome on the planet, but as in North and South America, they have more recently come under tremendous pressure with vast areas of temperate grassland being converted to arable fields, many of which are now fallow. Moreover, the proportion of former grasslands currently under protection is lower than that afforded to any other major habitat type (Hoekstra et al. 2005; Peart 2008).

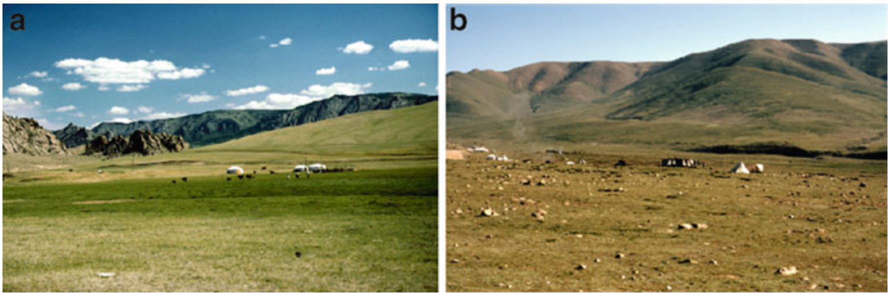

Photo 1.1 Physiognomic resemblance of Central Asian steppes. (**a**) Summer camp in the central Mongolian forest-steppe/grass steppe ecotone. (**b**) Summer camp in the alpine meadows of eastern Tibet (a photos taken by KW unless stated otherwise)

The remaining areas continue to change, and the traditional pastoral grazing systems are successively being replaced. Land use systems are intensifying due to rising human population pressures and new economic constraints that favour sedentary land use systems and larger herds (Sneath 1998; Janzen 2005). This has raised concerns about increasing degradation. However, land use has always been constrained by harsh climates (cold, often dry), and general theory predicts that land use attributes are modified by the overall climate conditions at any given site (Milchunas and Lauenroth 1993; Cingolani et al. 2005; Vetter 2005). This leads to the idea that the relative importance of land use vs. climatic controls change along the aridity gradient (Fernandez-Gimenez and Allen-Diaz 1999; Ellis et al. 2002).

Climate change interacts with land use effects and also introduces new pressures that trigger growing concerns about increasing vulnerability of the Eurasian steppes (Christensen et al. 2004; Angerer et al. 2008). Land use in dry and/or cold environments is especially sensitive to changes in the abiotic conditions (Duraiappah and Naeem 2005), rendering not only the Eurasian grasslands but also their human populations potentially vulnerable. In spite of extensive research on the subject, details of potential effects of changing precipitation and temperatures on ecosystem functioning are far from fully understood (IPCC 2007; Soussana and Luscher 2007). It is even less clear how climate change effects interact with other abiotic controls such as soil conditions. A number of studies have dealt with effects of land use and climate on soil nutrients and carbon contents (see e.g. several chapters in this volume), but their relevance to steppe plant performance has been less commonly studied, particularly for the drier regions of Central Asia.

Research in the grasslands of Asia has traditionally been published in the locally most important languages, i.e. Russian and Chinese, but there are a number of reviews in German and English that provide overviews of the older literature (e.g. Walter 1974; Lavrenko and Karamysheva 1993; Zhu 1993). The last two to three decades have witnessed a rapidly increasing number of publications on various ecosystem functions, with a predominant focus on aboveground net primary production (ANPP, or respective proxies) as the main variable of interest for the prevailing grazing system. Much of this research is now published in easily accessible journals or other outlets, and the older notion that North American prairies are much more comprehensively studied is perhaps no longer valid. Recent reviews covering Central Asia have so far adopted a local or at most part-regional perspective (e.g. Gunin et al. 1995; van Staalduinen and Werger 2006a), while comprehensive evaluations of a given vegetation type, such as the short grass steppes of North America (Lauenroth and Burke 2008), are still lacking. Up-dated overviews and synoptic analyses of the ongoing research in Eurasian grasslands are also scarce.

Compiling the huge literature for all Eurasian grasslands is beyond the scope of a book chapter, and would presumably also require a larger multi-author team. Instead, we present a brief overview of research covering one major part of the Eurasian grasslands, the Central Asian steppes and related communities. While aspects of population ecology and carbon sequestration are merely touched upon in this review and would certainly merit a separate analysis, we focus on the plant community composition and biomass productivity with an emphasis on ANPP.

The main drivers of biomass productivity are discussed with a specific focus on the following three aspects:

- Grazing effects: How does grazing affect plant community composition, and is there evidence for degradation and deteriorating biomass productivity?
- Climate effects: How do precipitation and temperature influence vegetation patterns and ANPP, and are there effects of interannual variability? Do potential climatic constraints influence grazing effects?
- Soil conditions: How does grazing affect soil nutrient conditions, and how are these conditions related to climate? Does soil nutrient availability limit productivity in spite of the strong climatic controls?

We will start with a description of the basic physiogeographic features of the region. The main part of the text will be devoted to a discussion of the specific questions with respect to mostly recent major publications. This is illustrated by already published examples from our own research in the Central Asian drylands and in Tibet.

1.2 Physiogeographic Setting

1.2.1 What and Where Are Central Asian Steppes?

A plethora of literature addressing various aspects of vegetation ecology and grazing ecology reveals both the similarities (Photo 1.1) and the pronounced differences between various types of grassland throughout Eurasia. For the present review, we concentrate on the grasslands of Central Asia, a term which has been somewhat ambiguously used throughout the literature. We adopt the biogeographical approach of Russian scholars rather than taking the simpler topographical view that is now followed by many authors including most publishing in a political context: The region between the Caspian Sea and the western Himalayas, i.e. Kazakhstan and neighbouring countries (Turkmenistan, Uzbekistan, etc.) is in the centre of the Eurasian continent, and is often referred to as Central Asia, terminology which is also found in IPCC reports (IPCC 2007). In contrast, Russian literature traditionally referred to this region as Middle Asia, as opposed to Central Asia, which refers to Mongolia, large parts of China (including most of Tibet) and small adjoining parts of Kazakhstan (Figs. 1.1 and 1.2). Although these regions are no more distant from any ocean than many parts of Middle Asia, they are nonetheless more continental in terms of climate and, consequently, biogeography. The reasons are detailed below and will demonstrate that Middle Asia and Central Asia (and certainly the more oceanic East Asia) should be differentiated, at least if aspects of physical geography are the focus (Cowan 2006).

Grasslands may be referred to as anything from forb-rich grasslands (“meadow steppes”) in the forest-steppe ecotone, to typical “grass steppes” with dense swards,

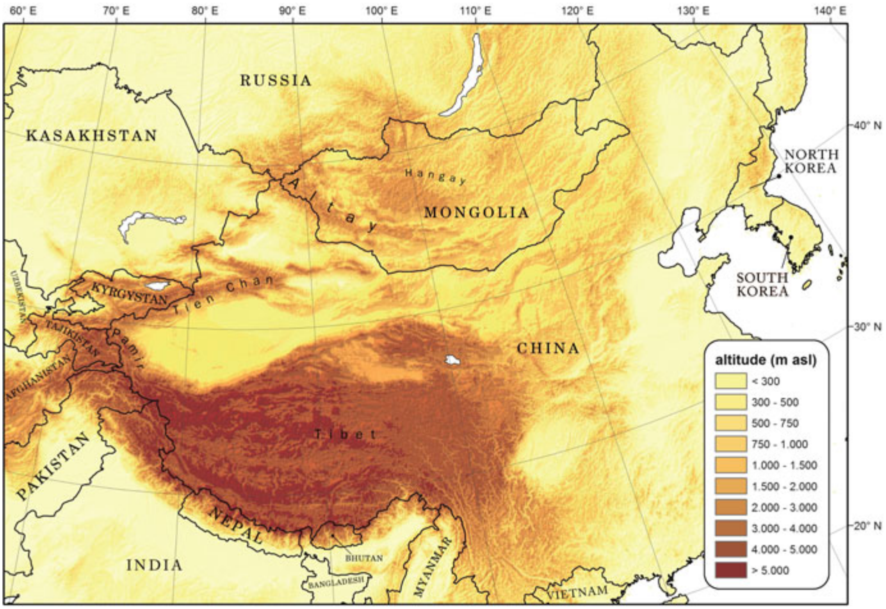

Fig. 1.1 Topographic map of eastern Eurasia (Altitudinal information based on SRTM data)

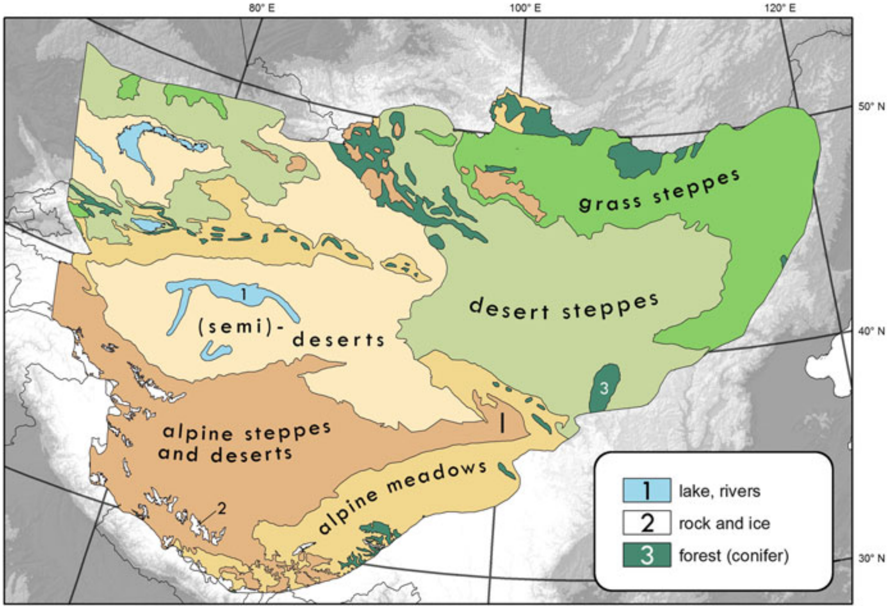

Fig. 1.2 Spatial distribution of the main vegetation types in Central Asia (After Olson et al. 2001, simplified, see Table 1.1 for background environmental data)

or sparse "desert steppes" where vegetation cover is well below 50%. Here, we will mainly review data from vegetation types that have an appreciable cover of graminoids mainly Poaceae and Cyperaceae, and a continuous, though not necessarily closed, vegetation cover. This excludes arid deserts where vegetation is restricted to water surplus sites. Semi-desert communities that have a diffuse vegetation cover are included if they have an appreciable cover of graminoids, mainly Poaceae (desert steppes). On the humid end, mosaics of grass and forest patches (forest-steppes) are transitory to the more semi-humid to semi-arid grass steppes.

In our view, Central Asian steppes are thus grasslands of the mid-latitudes. They occur in the most continental regions of Eurasia, i.e. Mongolia, China, and parts of Russia and Kazakhstan where winters are cold and dry and precipitation is largely confined to a short growing season in summer. These steppes have an appreciable cover of graminoids (mostly Poaceae, some Cyperaceae) and total vegetation cover may range from a completely closed sward in species-rich meadow steppes to the sparse vegetation cover of desert steppes. Trees are restricted to extrazonal moist sites (along rivers, north-facing slopes), be it due to abiotic factors or human impact.

There are only country-level vegetation maps (Lavrenko et al. 1979; Atlas of Tibet en (Atlas of Tibetan Plateau) Plateau 1990; Anonymous 1996; Vostokova and Gunin 2005) and we thus employed a global map of ecoregions (Olson et al. 2001) and simplified this to depict the main biomes (Fig. 1.2). Central Asia is surrounded by drylands and alpine sites in the west and south, and deciduous forests and coniferous forests in the east and north, respectively. Pronounced precipitation gradients control the vegetation belts, leading to a strong north–south differentiation in Mongolia and northern China (Photo 1.2). At their southern limit, boreal forests are increasingly restricted to north-facing slopes (forest-steppe). The next drier habitat type along the aridity gradient is grass steppe, which is often tall, especially in Eastern Mongolia and north-west China, and similar to the tall grass steppes of North America. Desert steppes and (semi-) deserts occur in the endorheic basins; their driest parts lack any zonal vegetation cover outside of water surplus sites (e.g. Taklimakan, Tsaidam depression).

True high altitude deserts are found in north-western Tibet, while most of the western plateau comprises alpine steppes with *Stipa* spp. In the eastern, moister part of Tibet, *Kobresia* spp. cover 450,000 km² and form the largest homogeneous alpine ecosystem in the world (Miehe et al. 2008). They can be rich in flowering forbs and are, in this sense, similar to the colourful meadow steppes in the northern parts of Central Asia.

1.2.2 Climate and Soils

The continental climate is characterised by pronounced cold, relatively dry conditions (Fig. 1.3) and a marked seasonality (Barthel 1983; Weischet and Endlicher 2000). Winters are typically cold with monthly means as low as –40°C, particularly in the northern parts of the region or at the higher altitudes of Tibet. Cold air

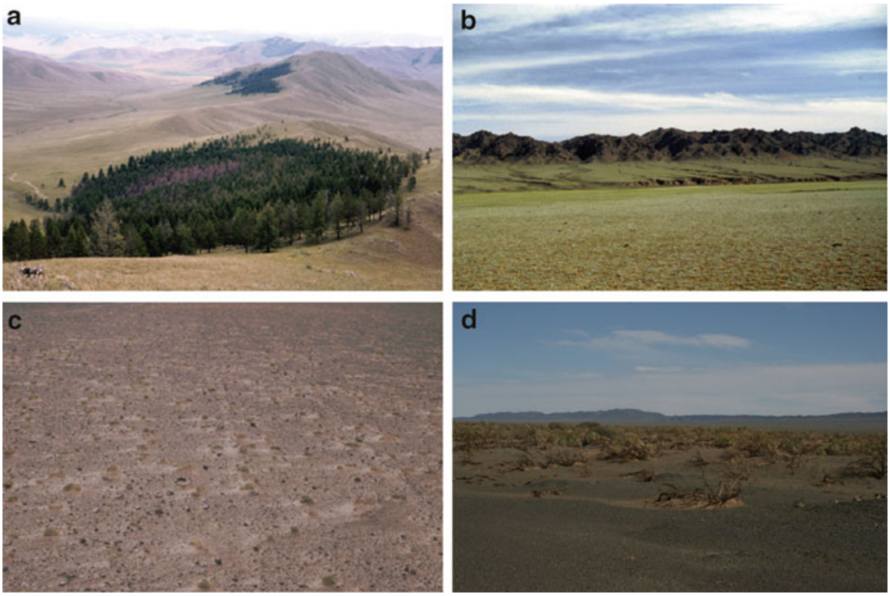

Photo 1.2 Change of plant communities along the zonal precipitation gradient in Mongolia. (**a**) Forest-steppe, i.e. mosaics of forests (north-facing slopes) and meadow steppes near Ulaanbaatar (note defoliation of trees due to outbreak of geometrid moths). (**b**) Grass steppes and mountain steppes on the pediments of the Altay in southern Mongolia. (**c**) Heavily grazed desert steppe in a year of Dzuud. Small nebkhas have formed around bunches of *Stipa glareosa*. (**d**) Semi-desert vegetation dominated by woody Chenopodiaceae in far southern Mongolia, a region that is too dry for livestock grazing

accumulates in the extensive basins while mountain sites are less affected, leading to stable temperature inversions on a local scale. In spring, temperatures rise steeply, but inflow of cold northern air masses can result in occasional frosts up to May. Moreover, strong winds, especially in the Gobi Altay, make living conditions unpleasant. In summer, air partly comes from western circulations but also from the monsoon, resulting in relatively favourable mean temperatures (>20°C) and a frost free period until September.

Precipitation is similarly low as in Middle Asia, but the seasonal distribution is different. Most of the precipitation (typically more than two thirds of the annual mean) falls in the relatively short growing season (Fig. 1.4a). Winter precipitation is very low, and usually springs are also dry (Fig. 1.4b). This contrasts with Middle Asia where moisture availability in spring is much higher, explaining why e.g. geophytes and also evergreen species are more important there. Much of the precipitation is of a convective nature and occurs in spatially and temporally limited events. This results in high spatial and also temporal heterogeneity, where neighbouring sites within a given year, or years at a given site, may differ strongly.

Soils are mostly constituted of fine materials, ranging from typical Loess to almost pure sands. Within substrate groups, soils reflect the availability of moisture

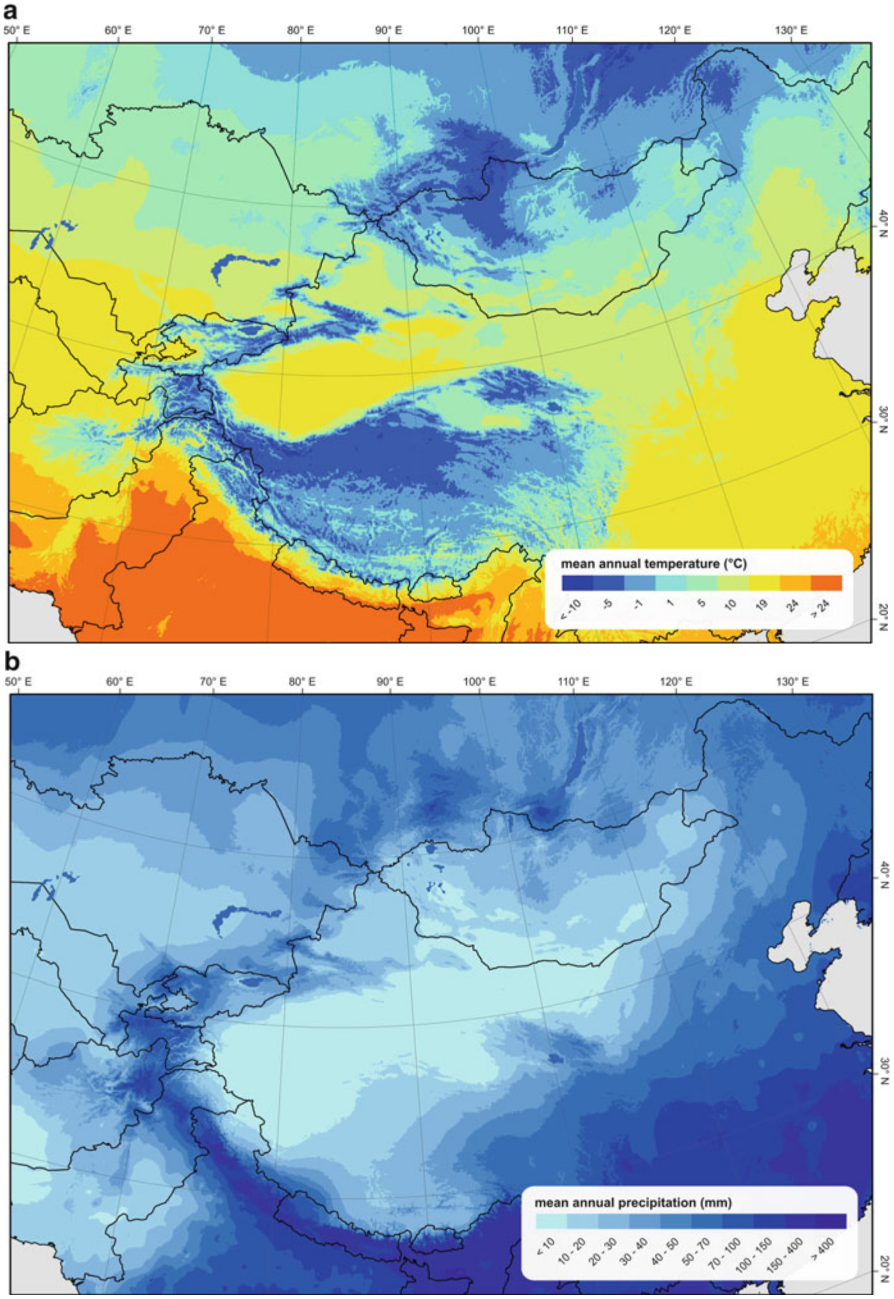

Fig. 1.3 Long-term macroclimate in Central Asia (from the WORLDCLIM model, Hijmans et al. 2005). (**a**) Mean temperatures. (**b**) Mean annual precipitation totals

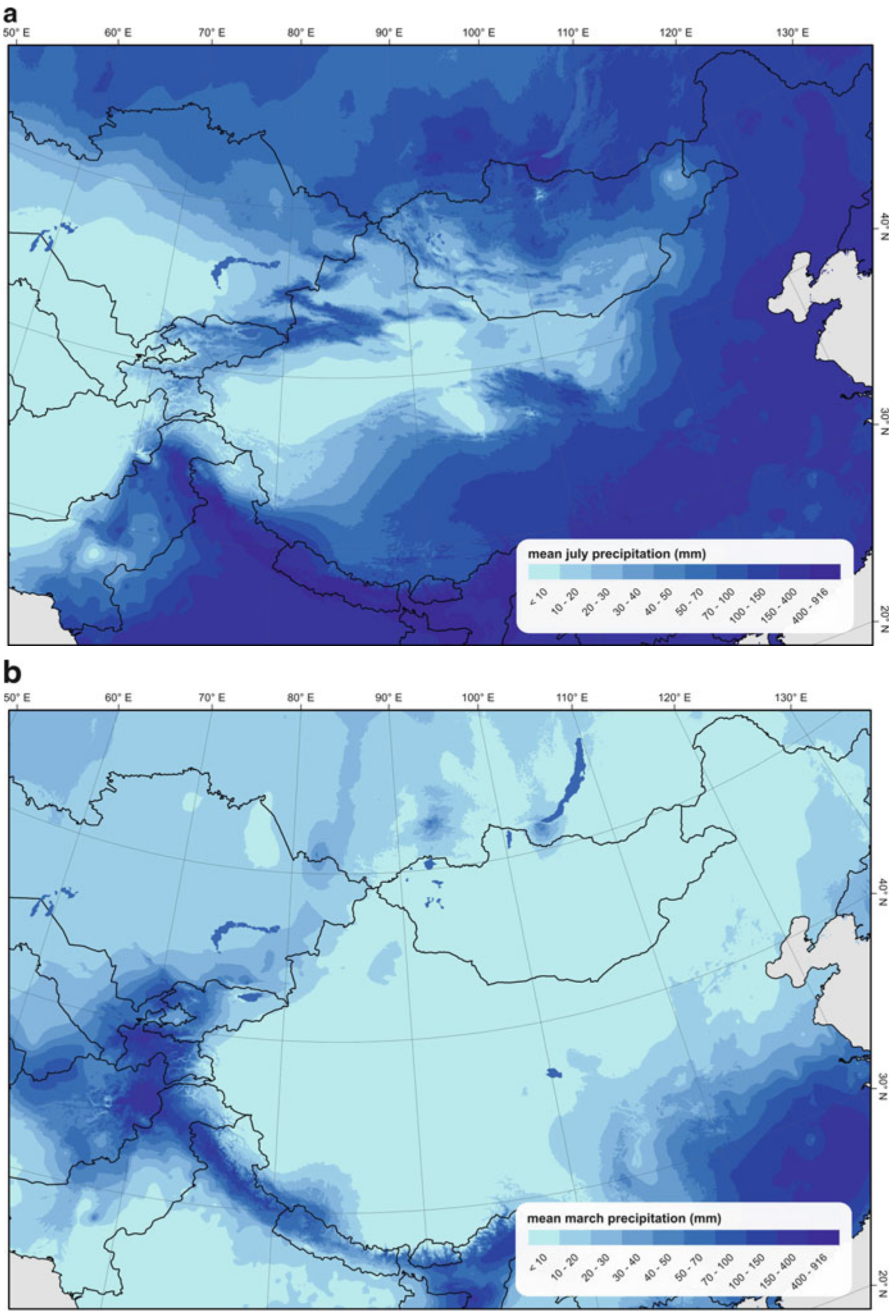

Fig. 1.4 Seasonality in precipitation (Data from Hijmans et al. 2005). (**a**) Mean July precipitation. (**b**) Mean March precipitation

as the main constraint. In Central Asia, Chernozems are distributed along the moister northern and southern parts (Walter 1974; Haase 1983); they have a high organic matter content and typically favourable nutrient concentrations. The typical soils of Central Asian grass steppes are Kastanozems, with an appreciable content of organic matter, though both thickness and C-content of the A-horizon are lower than in the Chernozems. Aridity and permanent, mostly natural, wind erosion in the drier steppes with their sparse vegetation cover result in degradation of Kastonozems, and Burozems become the typical soil of the desert steppes. Topsoils are low in organic matter and high in minerals, reflecting the aridity. On average, water moves upwards rather than downwards in the profile, leading to incomplete leaching and accumulation of minerals, especially carbonates near the soil surface. During rainy summers, more easily soluble salts in the stricter sense (NaCl, etc.) are, however, still transported downwards. In sandy regions, Arenosols and even sand dunes may develop, which constantly shift with the strong winds. Also in these soils salts are washed out. On mountain ranges, where freeze-thaw processes result in heavy weathering and the formation of thick layers of rock scree, weakly developed Leptosols are the prevailing soil type. Salinity is generally not an issue in Central Asian soils, although in basins, pans and oases water accumulation and high evaporation do result in the formation of spatially restricted Solonchaks and Solonez soils.

1.2.3 Plant Biogeography

The Central Asian steppes belong to the Mongolian sub-region of the Central Siberia-Dauria-Mongolian region, as opposed to the desert flora of the Gobi province, which is part of the Central-Asiatic region (Malyshev 2000). However, both the Gobi province and the Mongolian sub-region are sometimes included in the Central-Asiatic region (Meusel and Jäger 1992). Grubov differentiated three phytogeographic provinces in Central Asia: Mongolian, Junggar-Turanian and Tibetan (Fig. 1.5a, Grubov 1999ff). The Mongolian and Jungar regions have a number of species in common, but are differentiated by e.g. *Nanophyton erinaceum* in the recte Jungar-Turanian parts and *Anabasis brevifolia* in the Mongolian parts. The Tibetan province is distinct and the most species-poor. A number of different biogeographical elements constitute the basic species set (Hilbig et al. 1999, 2004; Xie et al. 2004; Dulamsuren et al. 2005). No full-scale analysis has, as yet, been conducted, but the basic patterns are reasonably clear. Broad-range species with Asian, Eurasian and circumpolar temperate distribution enter the region from the Taiga belt in the north where they also mix with boreal species. Arctic-alpine species are mainly restricted to mountain summits. Many of these can tolerate continental temperatures but fade out with increasing dryness. Eastern Asian species extend westwards into northern and eastern Central Asia wherever summer precipitation and temperatures are sufficient. A prominent example is *Ulmus pumila* (Fig. 1.5b), which extends well into the drylands of the central

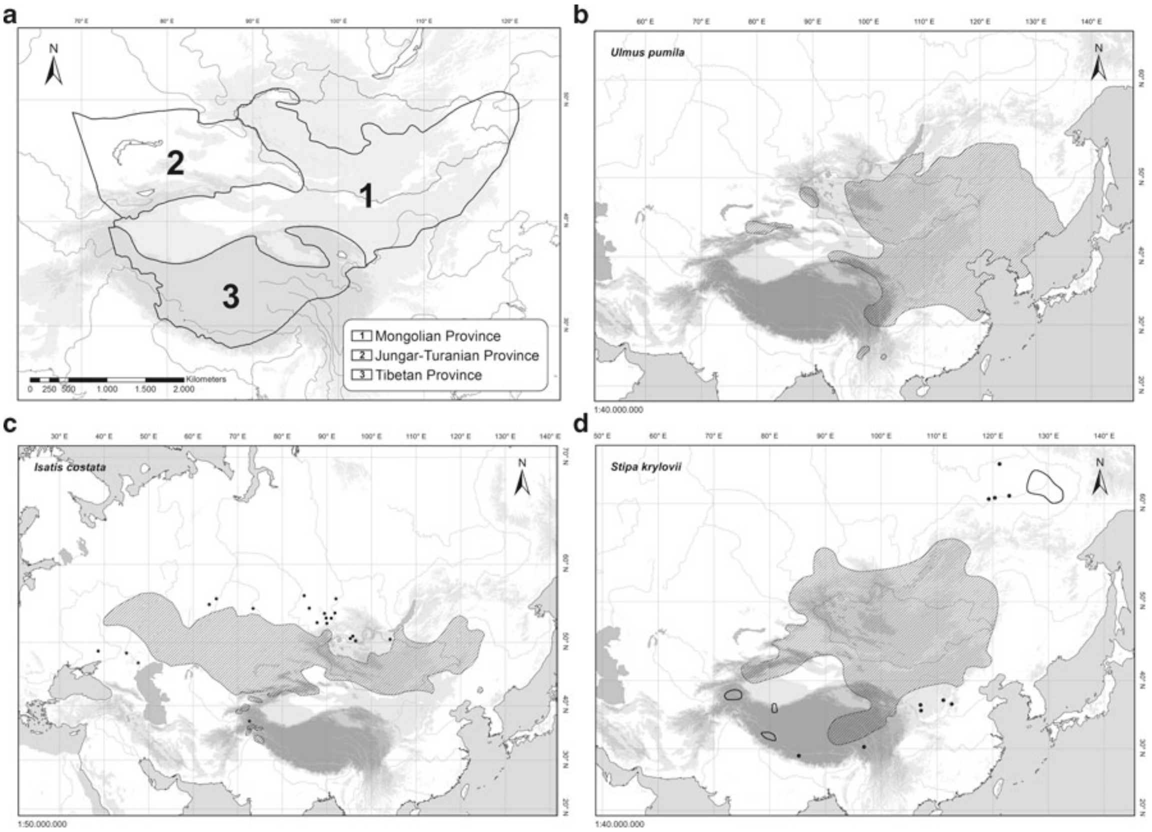

Fig. 1.5 Important biogeographical elements in the flora of Central Asia. (**a**) Outline of the biogeographical regionalization of Central Asia (as delimited by Grubov 1999ff). (**b**) *Ulmus pumila* as an eastern Asian species. (**c**) *Isatis costata* as a Middle and Central Asian species. (**d**) *Stipa krylovii* has a typical Central Asian distribution covering Mongolia, northern China and parts of Tibet

Gobi, but is ultimately replaced by *Populus euphratica*, which is a common tree of more western oases (Wesche et al. 2011). *Isatis costata* is an example of a species with Middle Asian and Central Asian distribution (Fig. 1.5c). One of the region's most common feather grasses *Stipa krylovii* has a typical Central Asian distribution (Fig. 1.5d) that also includes some mountain sites, indicating the close biogeographical links between the Mongolian/northern Chinese grasslands and those of the Tibetan plateau.

1.2.4 Flora – The Species Pool

Poaceae are the most typical constituents of Central Asian steppes. Feather grasses are represented with several sections, with *Stipa krylovii* (section *Leiostipa*) being an example of a species with a wide occurrence in all but the driest steppes (Fig. 1.5d). In Tibet, *Stipa* steppes occur in the drier western parts (Miehe et al. 2011), where *S. purpurea* represents the sect. *Leiostipa*. Other important grass taxa in Central Asia include *Leymus*/*Elymus*, especially *L. chinensis*, which is very abundant in the tall grass steppes of Mongolia and Inner Mongolia. It is often accompanied by *Agropyron cristatum*, which has a wide range along the hygric gradient, perhaps making it the most important forage grass of Central Asian steppes. It has also been introduced to North America, where it partly outperforms the native vegetation (Hansen and Wilson 2006). Cyperaceae rarely form dominance stands at zonal sites, but sedges of the genus *Kobresia* commonly form dense mats in montane and alpine regions. Forbs are diverse, with many genera, and some species occur in the mid-latitudes all over Eurasia and often even North America. Typical taxa include *Potentilla* spp., *Pedicularis* spp. and a huge diversity of legumes. *Astragalus* and *Oxytropis* are the most diverse higher plant genera in the region, with species numbering into the hundreds in Central Asia alone. They are, however, not exceedingly important in terms of vegetation cover. An example comes from the Gobi Gurvan Saykhan region of southern Mongolia that comprises zonal dry steppe communities, while extrazonally moist conditions in the mountains facilitate the occurrence of grass steppes and even meadow steppes (Wesche et al. 2005). In the Gurvan Saykhan, Fabaceae constitute 6% of the average species richness per plot but account for only 2% of its mean vegetation cover. Poaceae in turn represent 17% of the average species numbers, and have a 30% share in the total cover.

Allium species are also typical for Central Asia and their relative importance increases under drier climatic conditions; they may have the greatest proportional cover in many desert steppes. Chenopodiaceae have a diversity centre in Central Asia and their relative share of cover increases with aridity. Large parts of the semi-deserts of Central Asia are covered with woody Chenopodiaceae, which are accompanied by drought-tolerant Zygophyllaceae and Solanaceae.

Central Asia hosts a range of wild ungulates and small mammal herbivores, many of which are (now) endemic to the region (Bactrian Camel, Przewalski Horse, Schaller 1998; Gao et al. 2011), and steppes have clearly been grazed over

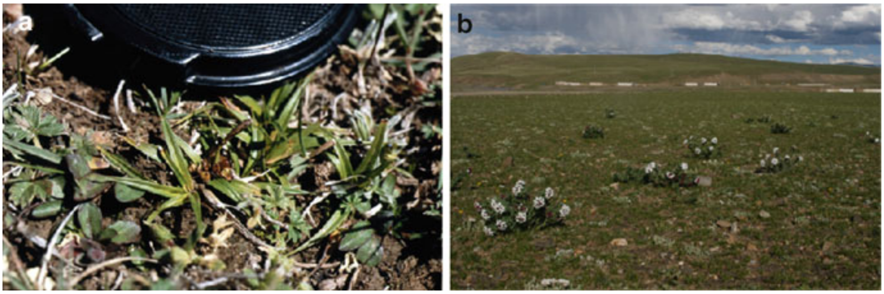

Photo 1.3 Grazing tolerance and avoidance. (**a**) The dwarf sedge *Carex tangulaschanensis* keeps its fruits hidden in the rosette (arrow). (**b**) *Stellera chamaejasme* (Thymelaeaceae) grows as a grazing weed in overgrazed *Kobresia* mats of Tibet and in grass steppes of Central Asia

evolutionary time-scales. The local species pool has been selected under almost omnipresent grazing pressure, and the extant species are, by majority, either tolerant to grazing or they exhibit effective defence strategies. Examples include several Tibetan Cyperaceae, where dwarf species with inflorescences hardly exceed 3 cm in height. Photo 1.3a shows the tiny *Carex tangulaschanensis*, whose fruits are practically hidden in the rosettes and thus beyond the reach of most grazers. Examples of species with an effective defence strategy are *Iris* spp., or *Stellera chamaejasme* (Photo 1.3b), which are poisonous to livestock and may become dominant weeds if steppes are overgrazed. Onions (e.g. *Allium polyrrhizum*) may cause problems if foraged in high quantities, and the Poaceae *Achnatherum splendens* is also mildly toxic. Nevertheless, most of the abundant species, including almost all Poaceae, are of high nutritional value (Jigjidsuren and Johnson 2003).

1.2.5 Land Use

The traditional land use system in Central Asia is nomadic pastoralism, where families migrate with their herds according to availability of livestock forage. Nomadism can be seen as a strategy to buffer temporal variability in climate and forage availability by utilising spatial heterogeneity and moving to less affected regions. Archaeological evidence implies that humans started to roam the steppes at least 6,000 BP (Aldenderfer 2007). Though animal products form the main source of energy, nomads also consume grains traded with sedentary farmers. Nomadic pastoralism in its current form is thus younger than the development of sedentary agriculture in the region, but it may still date back several millennia. Palynological evidence implies that many steppe sites have not changed much in the last millennia (Herzschuh et al. 2004; Miehe et al. 2009), implying that today's rangelands have been grazed since ancient times, with modern land use often merely replacing the natural grazing by wild ungulates and leaving limited impact on the general vegetation physiognomy.

More recently, Central Asia has undergone major social and economic changes. In China, rapid population growth and the rise of sedentary farming practices, even in some of the semi-arid regions, have resulted in tremendous agricultural intensification over the last decades/centuries. Rangelands have partly been degraded resulting in erosion, which has become a problem in some regions where climatic conditions would normally allow for a relatively closed vegetation layer. In the last years, the Chinese government has started to control grazing and has implemented large-scale restoration schemes which have slowed down desertification processes, although not in all territories (Runnström 2000). Mongolia has also experienced rapid population growth in the twentieth century, but overall livestock numbers have remained largely constant at ca. 20 Mio. animals (Janzen 2005). The early 1990s brought a rapid transition to a freer market economy, which caused unemployment to soar, making Mongolia one of the few countries in the world where the number of nomadic pastoralists has risen. The Mongolian economy is still based on agriculture, which is in stark contrast to Middle Asian countries like Kazakhstan where the economy rapidly shifted towards the export of fossil fuels. Fast urbanisation resulted in large tracts of rangeland being abandoned and much less intensive grazing than before the 1990s (Coughenour et al. 2008).

In Mongolia, livestock numbers had risen to 30 Mio. by the end of the 1990s, then collapsed to 20 Mio. in the droughts of 2001/2002 (Janzen 2005; Reading et al. 2006). By 2009, numbers had recovered to >30 Mio., and severe winters in 2009 and 2010 again led to severe losses (up to 50% in some regions; see also Chap. 20 by Baas et al., this volume). We thus seem to have an overall trend of intensification, although heavy fluctuations due to climatic variability partly override this trend. Disentangling the relative importance of socio-economic effects and climatic/abiotic constraints is one of the aims of the main part of this review.

1.3 Factors Controlling Grassland Species Composition and Productivity

1.3.1 Biotic Controls: Grazing Effects on Vegetation

Recent and even ongoing rangeland degradation has been described from a huge number of sites in Mongolia, northern China and Tibet. Authors used a range of indicators for assessing desertification that are not all equally suitable. Lower biomass on grazed sites should not be simply taken as evidence for grazing degradation, as grazing by definition is biomass removal. Lower biomass on grazed rangelands compared to that in exclosures merely confirms the presence of grazing rather than allowing for any conclusions on degradation. In addition, biomass, and also the correlated vegetation cover, is highly variable over the years making inferences on long-term trends difficult. The presence of bare soil alone is also not evidence for degradation, as an assumed closed sward is hardly a suitable reference for a semi-arid rangeland that has naturally low vegetation cover.

Photo 1.4 Effects of grazing exclusion in Central Asia. (**a**) Seven years of grazing exclusion in semi-humid upper montane *Kobresia* mats of northern Tibet (province Qinghai) resulted in replacement of Cyperaceae by tall grasses (mainly *Stipa* spp., right side of the fence, photo by E. Seeber). (**b**) Two years of grazing exclusion in southern Mongolian desert steppes has negligible effects. (**c**) As (**b**), but in the drought year 2002; biomass inside the exclosure is necromass from previous year

From a vegetation perspective, changes in plant community composition, especially in the perennial species, are more suitable indicators. Here, we regard evidence of pronounced changes in plant community composition, often associated with the replacement of palatable species by less preferred weeds, as indicators of degradation. Rangelands can also be seen as degraded where the forage productivity is declining. This introduces a further set of degradation indicators based on the body conditions or productivity of the grazing animals themselves, which reflect changes in forage quality (Allen et al. 2011). The latter criterion is, however, rarely applied in Central Asia.

Long-term records that cover the entire periods of changes in land use are scarcely available from Central Asia. Both experimental data and remote sensing studies typically cover at most three decades and often less, which is relatively short for a harsh, variable environment dominated by slowly growing long-lived perennials. There is, however, a number of fencing studies or short-term monitoring studies that provide clear evidence of grazing-induced degradation. The perhaps most-well studied site is the Inner Mongolia Grassland Ecosystem Research Station (IMGERS), where effects of grazing exclusion on long grass steppes have been studied over almost three decades. A large, continuously growing body of literature shows that intense grazing there has negative effects on rangeland community composition and forage productivity, and that drought can exacerbate the negative effects of overgrazing. However, modest grazing seems to stabilise the functioning of these steppes (Bai et al. 2004; Gao et al. 2009).

Similar results come from central Mongolian steppes where recent increases in animal numbers coupled with reduced mobility result in replacement of grass steppes by weed communities of low forage value (Hilbig 1995). Effects are particularly strong in the sacrifice zone around camps and wells, where heavy trampling adds to the effect of grazing (Sasaki et al. 2008). Evidence from experiments and large-scale surveys in eastern Tibet also points to increasing degradation in the last years. The prevailing *Kobresia* mats are tolerant to traditional Yak grazing, and total grazing exclusion may even lead to a replacement of mats by taller grassland communities (Photo 1.4a). On the other hand, more intensive land use in the last decades has resulted in the gradual breakup of the dense mats and the eventual formation of bare soil that is colonised by often impalatable weeds (Wang et al. 2006; Miehe et al. 2008).

The basic pattern in the examples from the moister region is similar: the current, often zonal communities are composed of perennial hemicryptophytes that tolerate substantial grazing pressure. Overgrazing has occurred in the last decades, leading to a reduction in plant biodiversity, replacement of perennials by short-lived weeds, and deteriorating forage production. ANPP and forage quality decline, with invading weeds (e.g. Chenopodiaceae), having low forage value or being even toxic. The prime example is *Stellera chamaejasme* (Thymelaeaceae), which has become a rapidly spreading grazing weed in grasslands from Mongolia to Tibet. *Stellera* is an exception insofar as it is perennial. Encroachment of larger shrubs, which is a problem in many overgrazed rangeland in other parts of the world, is not important in Central Asian rangelands. Instead, mainly semi-shrubs and dwarf shrubs benefit from increased grazing (e.g. *Artemisia frigida*). Taller shrubs gain dominance at sites with some soil disturbance, especially on small mammal burrows, which is discussed below.

Goats have increased in both relative share and absolute numbers almost everywhere in northern China and Mongolia, and even Tibetan herders increasingly keep goats to produce the relatively high-value Cashmere. In one of the few studies that are specifically devoted to changes in herd species composition, Tsagaan Sankey et al. (2006) showed that goats caused a reduction of tree and shrub growth in the grazed forest-steppes of northern Mongolia. Unfortunately, comparative studies on the effects of goats vs. effects of other animals, such as the traditionally kept camels, are too limited to draw any general conclusions as yet.

Authors working in the drier parts of Central Asia often report contradictory evidence on grazing impact. Li et al. (2011c) describe that grazing exclusion in Saxaul (*Haloxylon ammodendron*) woodlands resulted in increased diversity and carbon sequestration in northern China. In contrast, studies form the Mongolian drylands found minor effects of grazing exclusion. Grazing effects seem to decline with increasing dryness of the sites (Fernandez-Gimenez and Allen-Diaz 2001; Zemmrich et al. 2010; Sternberg et al. 2011), and continued observation of grazed vs. fenced (non-grazed) sites showed that grazing effects were small compared to the effects of annual changes in precipitation (Photo 1.4b, Wesche et al. 2010).

This pattern becomes clearer when a larger number of studies is analysed. We surveyed our own literature database for studies on grazing effects in Central Asian rangelands (numbering several hundred). We took care to report only one sample from any given site (i.e. the mentioned IMGERS site was included once), and we also excluded studies where the “grazing” effect was mainly restricted to the heavily trampled inner sacrifice zone of a piosphere (e.g. Sasaki et al. 2008). We considered only fencing experiments or studies with a sound sampling design along grazing gradients. Studies were checked for evidence on lasting effects on vegetation composition or productivity (for soils see below), which were classified on a simple three-level scale: no/negligible effects; modest effects, severe effects. We simplified further by disregarding more subtle effects that may only be apparent on the population scale. In woody species, effects of grazing may widely differ depending on the given demographical stages, and can have, e.g. detrimental effects on seedlings and positive effects on juveniles (Li 2010). Zemmrich (2007) showed that the

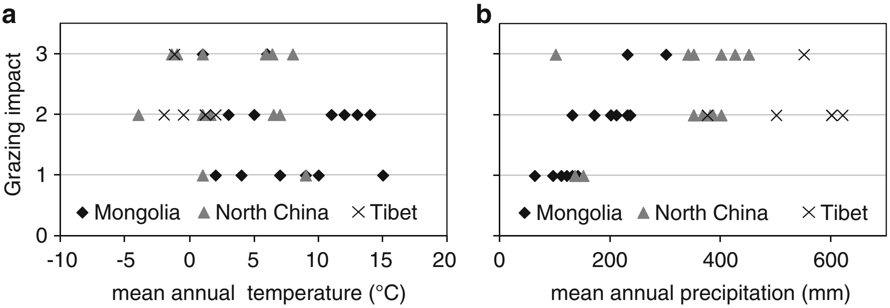

Fig. 1.6 Grazing impact on plant community composition and diversity in Central Asian rangelands. Effects were classified on a simple, three-level scale (*1*: no/negligible, *2*: modest, *3*: severe) and plotted against modelled climate data for a given site (Hijmans et al. 2005). (**a**) Grazing effects plotted against mean annual temperature. (**b**) Grazing effects plotted against mean annual precipitation

demographical structure of the rangeland species *Artemisia xerophytica* may reflect detrimental effects of grazing, while community level species composition and diversity are not affected. Similarly, the production of propagules often suffers heavily from grazing, even though communities have shown no responses as yet (Bläß et al. 2008). Our assessment is therefore probably somewhat conservative.

We plotted data against mean annual temperatures and found no relation to grazing effects (Fig. 1.6a). Annual precipitation of the given site served as a proxy for moisture availability (Fig. 1.6b), which covered a gradient in mean annual precipitation from <100 to 600 mm. Even this simple classification of the grazing impact produced a clear pattern. Studies that report no or negligible effects were restricted to dry regions of Mongolia and northern China, where precipitation is well below 200 mm. Conversely, severe grazing impact was restricted to regions with >300 mm mean annual precipitation. Modest grazing impact is found over the full range of hygric conditions. The sole exception to this pattern is the already mentioned study on *Haloxylon* woodlands in northern China (Zou et al. 2010), where 26 years of grazing exclusion resulted in a pronounced increase in diversity at a mean annual precipitation of ca. 100 mm. The site is somewhat untypical as the majority of species, and all those that were responsive, were short-lived, while the dominant Saxaul trees showed limited responses.

The example nonetheless raises the question as to whether effects of grazing reduction/exclusion are simply missed in many of the other experimental studies from drylands that typical lasted 10 years or often less. There are, however, a number of studies that are not based on fences but on transects that radiate away from permanent water sources or camps (Fernandez-Gimenez and Allen-Diaz 1999; Stumpp et al. 2005; Zemmrich 2007; Sasaki et al. 2009). The high-impact ends of these transects have typically been used for extended periods of time (decades). Thus, even slowly responding species should have had sufficient time to respond. The lack of grazing related patterns in these studies adds some confidence to the results described above.

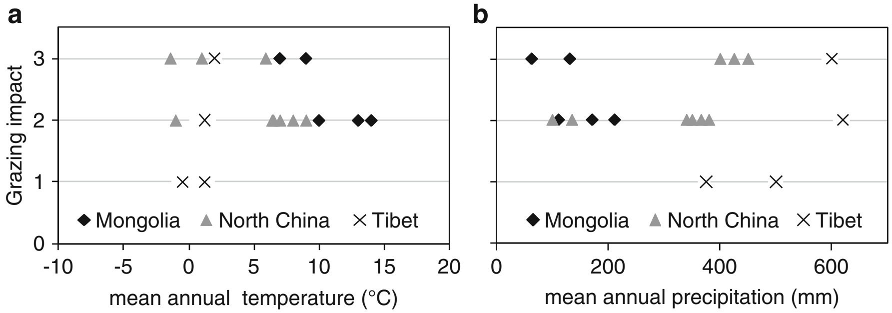

Fig. 1.7 Grazing effects on soil contents of nutrients and carbon in Central Asian rangelands. Effects were classified on a simple, three-level scale (*1*: no/negligible, *2*: modest, *3*: severe) and plotted against climate data for a given site (Hijmans et al. 2005). (**a**) Grazing effects plotted against mean annual temperature. (**b**) Grazing effects plotted against mean annual precipitation

1.3.2 Biotic Controls: Grazing Effects on Soil Conditions

A number of studies screened for Fig. 1.6 also reported grazing effects on soil nutrient contents, but response patterns differed considerably compared to vegetation. Of those that commented on soil conditions, almost all studies described at least modest and often severe losses of soil fertility with increased grazing intensity (Fig. 1.7). Surprisingly few authors comment on positive effects of grazing on soil nutrient availability. Comparison of wild ungulate vs. domestic livestock grazing in the Indian Transhimalaya indicated that wild herbivores facilitated biomass turnover and nutrient availability while the introduction of livestock resulted in losses and reduced availability (Bagchi and Ritchie 2010). In Inner Mongolian steppes, livestock grazing also increased N-turnover and N-availability; the effect was, however, most pronounced at intermediate grazing intensities (Xu et al. 2007). Grazing also increased N in standing crop of central Mongolian steppes, but this was apparently related to increased uptake rather than directly improved availability (van Staalduinen et al. 2007).

There was no apparent relation between the severity of effects and mean annual temperatures (Fig. 1.7a), nor between grazing effects and mean precipitation totals (Fig. 1.7b). There are nonetheless other principal patterns. Nutrient depletion in the course of degradation is sometimes associated with increased heterogeneity and formation of fertile islands under shrubs and other larger perennials (Pei et al. 2006; Cheng et al. 2007). This may at least partly reflect increased erosion as a consequence of reduced plant cover under intense grazing (Li et al. 2005). Relatively few studies report on losses in potassium, but reduced levels of (plant-available) nitrogen and phosphorus are commonly described (Su et al. 2005; Cheng et al. 2007; Zemmrich 2007). Losses in top soil due to erosion inevitably result in losses of carbon, but also nitrogen and phosphorus, which are often concentrated in the upper parts of the profile. Direct grazing impact exacerbates these losses because

Photo 1.5 Fuel sources in Central Asia. (**a**) In the semi-humid alpine meadows of Tibet, Yak dung is smeared on the sward to dry. (**b**) At Mongolian winter places, dung of small livestock accumulates in corrals and can be later cut as fuel. (**c**) In the drylands of Mongolia, Saxaul trees (*Haloxylon ammondendron*) grow at sites with available groundwater and are heavily exploited as fuel wood (pile in the foreground)

animals take up nutrients with their forage. Under grazing, many, but not all, Central Asian rangeland plants show compensatory growth and shift the belowground-aboveground ratio towards higher aboveground productivity. Nutrients in the tissues are largely taken from the soil – or – as is the case in carbon, can at least not be allocated belowground, resulting in lower soil stocks and also reduced carbon sequestration potential (Gao et al. 2008).

Net effects of grazing on carbon source/sink dynamics, may, however, vary. In Tibetan alpine meadows, grazing favours sedges of the genus *Kobresia*, which tend to allocate the majority of their biomass belowground ultimately forming very dense turfs that store huge amounts of carbon. Grazing exclusion may result in the suppression of these sedges by taller Poaceae, which have a larger fraction of their biomass aboveground, effectively reducing carbon sequestration potential of ungrazed sites (Becker et al. submitted).

The extraction of livestock products, such as milk, meat and wool, causes nutrient loss from the rangelands, which are not closed systems as products are exported or consumed by humans and are thus not re-dispersed over time. Perhaps even more important is the extremely widespread practice of dung collection. Dung has been the main fuel source in large parts of treeless Central Asia, and the importance of dung production for pastoral economies is enormous (Photo 1.5a). For Tibetan pastoralists, the provision of dung by Yaks may be as important as the provision of milk (Rhode et al. 2007). Today, many people on the plateau have stopped animal husbandry, but still rely on dung as the main source of energy (pers. observation).

Livestock usually discards phosphorus in faeces and not in urine, while nitrogen is excreted in both urine and faeces (Clark and Woodmansee 1992). Collection of faeces, especially of larger livestock species, therefore results in losses of P and partly of N. Dung of smaller ruminants (sheep, goat) is hardly collected and nutrient withdrawal due to this pathway is probably limited. Transect studies have, however, been performed in a number of grazing systems that are dominated by small ruminants, and these usually find pronounced spatial patterns of decreasing concentrations of P and (sometimes less clearly) N (Fernandez-Gimenez and Allen-Diaz 2001; Stumpp et al. 2005; Holst et al. 2007). Small ruminants are usually herded at night time in corrals (Photo 1.5b). Simple geometric considerations imply that faeces tend to be concentrated around these corrals (Manthey and Peper 2010), and this is aggravated by animal behaviour as a large fraction of the faeces, and also of urine, is preferentially deposited at night time. They are concentrated in a spatially very restricted spot from where a fraction is lost as N_2O; a larger fraction is finally burned by farmers, and very little is redistributed to the steppes (Holst et al. 2007). Operating on a scale of a few hundred meters to a few kilometres, small ruminants thus translocate nutrients from the steppes to the centre of the piosphere, where trampling prevents plant growth rendering the accumulated nutrients effectively unavailable for forage production.

Figure 1.7 implies that grazing may have strong effects on soils, even where the aboveground vegetation shows no direct response. This renders assessments of grazing degradation that are solely based on aboveground vegetation questionable, because they may fail to detect grazing effects. Our data imply that this problem could be particularly severe in drier regions where vegetation responses to grazing are limited. The very fact that changes in soil nutrient contents are not reflected in the vegetation composition suggests an alternative view. In dry regions, growth should be limited by water availability rather than by nutrient supplies, rendering potential changes in terms of soil nutrient contents irrelevant for ecosystem functioning. This question will be addressed under “abiotic controls” later in this review, but first we have to consider small mammals as the second most important group of herbivores.

1.3.3 Biotic Controls: Effects of Other Herbivore Groups

Small mammals are abundant in steppes worldwide, and those of Central Asia are no exception. Rodents and, to a lesser extent, lagomorphs occur with a considerable diversity and colonise Central Asia from the desert lowlands to the alpine *Kobresia* mats. Species numbers tend to be higher in the more productive environments such as the tall grass steppes (Wang et al. 1999). Some species show high densities and rapid population increases; the microtine vole *Microtus brandtii* is perhaps the most studied example. Brandt’s vole occurs in grass steppes of Mongolia and north-eastern China, where populations show boom and bust cycles that may be triggered by large-scale climate phenomena (Zhang et al. 2003b). Outbreaks have increased in frequency, presumably associated with increased grazing, because voles prefer habitats with short vegetation. During outbreaks, vole burrows can rapidly cover the larger part of the steppe surface. Voles consume biomass, and cause massive soil disturbance, eventually leading to the suppression and even disappearance of the otherwise dominant perennial hemicryptophytes (Zielinski 1982; Peterson 1994; Samjaa et al. 2000). Vole burrows carry a small cover of poorly palatable short-lived species. Burrows are abandoned after a few weeks or months and are subsequently colonised by shrubs, which benefit from the lack of competition by hemicryptophytes. Shrubs have comparatively deep roots

Photo 1.6 Pikas (*Ochotona* spp., Lagomorpha) in Central Asia. (**a**) Tibetan pika (*O. curzoniae*) in a disturbed *Kobresia* meadow, characterised by *Leontodon* and *Anaphalis* spp. with low forage value. (**b**) Burrow of the Mongolian pika (*O. pallasi*) characterised by a high abundance of shrubs (*Artemisia* spp.) and annuals (Chenopodiacae). (**c**) Adjacent desert steppe in the southern Mongolian Gobi dominated by herbaceous perennials (*Agropyron cristatum*, *Stipa krylovii*, *Allium* spp.)

(Kutschera et al. 1997; Liu et al. 2003) enabling them to use water that moves rapidly down in the disturbed burrow soils. *Microtus brandtii* may convert relatively productive grassland into stands of weeds or into scrub, which have limited value as pasture. Not surprisingly, the species is seen as a pest and control schemes have been implemented, including large-scale aerial poisoning (Shi et al. 2002), which has severe side-effects on other organisms.

Marmots (*Marmota* spp.) are also abundant in grass steppes, but they have much slower population dynamics and larger burrows that are less easily abandoned and more permanent. Marmots do not demonstrate outbreaks and never devastate entire regions through burrowing activity (van Staalduinen and Werger 2006b). Plant diversity is lower on burrows compared to open steppe, but even active burrows are partly covered by perennial grasses (*Stipa krylovii*, *Leymus chinensis*). Plant tissues have a higher concentration of nitrogen and phosphorus, ANPP is also higher, and burrows thus present valuable forage. Zokors (*Myospalax* spp.) are the main fossorial rodents on the Tibetan plateau, and have similar mixed effects on rangelands. The diversity of plants is lower on burrows, but biomass productivity and nutrient availability is higher (Zhang et al. 2003a; Wang et al. 2008). Burrows also provide special microhabitats for a number of organisms, and zokors are sometimes seen as ecosystem engineers rather than pests.

Pikas (*Ochotona* spp., Lagomorpha) are widespread from the drylands of southern Mongolia to the alpine meadows of Tibet. They have been considered as pests because they compete with livestock for forage and dig burrows like voles. In Tibet, they tend to be associated with disturbed *Kobresia* mats (Photo 1.6a), but whether they cause the fragmentation of sods or just benefit from sod disturbance by livestock or climatic conditions is not clear (Pech et al. 2007; Miehe et al. 2008). Pikas may even have positive effects on rangeland conditions. In Mongolia, pikas do not show population outbreaks and they live in permanent burrows that usually cover only a fraction of the surface (Nadrowski 2006). Diversity on burrows may be higher or lower than on the surrounding steppes depending on the soil substrate (Photo 1.6b, c, Wesche et al. 2007). Pikas are important herbivores and they consume

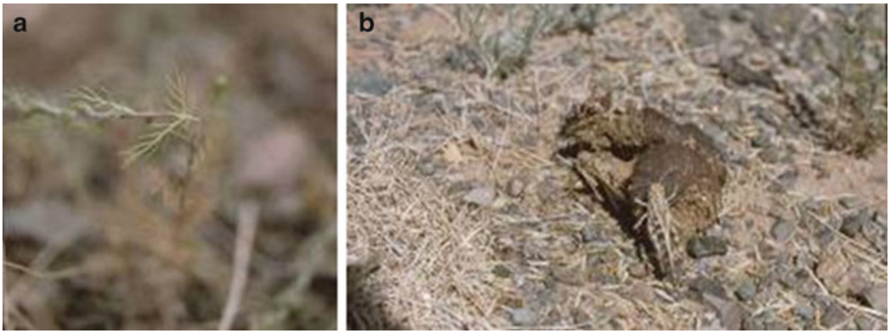

Photo 1.7 In years of outbreaks, Orthoptera can be important herbivores in southern Mongolian desert steppes. (**a**) Tiny stem of the annual *Artemisia* (*Neopallasia*) *pectinata*, that is avoided by livestock but has been cut by grasshoppers. (**b**) During outbreaks, herbaceous forage becomes so scarce that grasshoppers feed on dung

a similar share of the ANPP as livestock (Lai and Smith 2003; Retzer 2007). In Mongolia, in addition to storing forage for winter, pikas concentrate faeces on their burrows, thereby counteracting the large-scale nutrient withdrawal by livestock described above. As a consequence, pika burrows have higher plant available soil nutrient contents, and plants on burrows are more nutritious and productive. Burrows therefore represent preferred forage sources for livestock (Wesche et al. 2007), independent of soil associated moisture. Pikas and livestock can co-exist in the long run (Komonen et al. 2003; Retzer and Reudenbach 2005). Given that burrows also offer microhabitats for other biota, pikas should be seen as ecosystem engineers, that occur under particularly dry (southern Mongolia) and cold (Tibet) conditions (Smith and Foggin 1999). Large-scale poisoning is thus inappropriate and has largely been stopped now.

Much less well studied are other herbivore groups such as insects. Ongoing research is still largely devoted to taxonomy and distribution patterns, while effects on pasture conditions are only known by anecdotal evidence. Even under the generally cold conditions of Central Asia, the warm summer conditions allow for considerable insect diversity. In particular, Orthoptera occur with great diversity and in surprisingly large sizes (Photo 1.7). Abundance levels also appear to be high, but quantitative data are lacking. In southern Mongolian desert steppes, Orthoptera were encountered each year between 2000 and 2008, but feeding effects seemed mostly negligible (pers. obs.). In 2004, we witnessed one of the rare outbreaks, when Orthopterans numbered dozens/m² with considerable impact on the steppe vegetation. Grasshoppers clip vegetation even closer to the ground than pikas (Photo 1.7), resulting in the almost complete removal of above-ground forage and inflorescences. Sound measurements are not available and will be hard to obtain due to the irregular nature of such outbreaks, but it seems certain that insect herbivory can have an effect, at least in some years (Zhang et al. 2011).

1.3.4 Abiotic Controls – Climatic Constraints

It is established that herbivores have a strong impact on site conditions, particularly on soil nutrient availability, while direct effects on vegetation composition are mediated by the climate, especially precipitation. Differences in temperatures were of limited importance, partly because entire Central Asia has low mean temperatures (Table 1.1) and cold winters. Rapidly dropping temperatures in September and early October usually terminate the growing season (von Wehrden et al. 2010). The time at which C4 grasses commence growth is dependent on sufficiently high temperatures being reached, which may not be until summer during years with cooler springs (Liang et al. 2002). The dominant C3 species may respond even negatively to warm spring temperatures (Yuan et al. 2007; Yu et al. 2010), presumably due to lack of water in spring. Snow depths have increased in most of the Central Asian grasslands over the last decades (Peng et al. 2010) and analysis of satellite images implies that this results in enhanced growth in summer. This highlights the critical importance of early spring moisture availability. In fact, growth in spring is usually delayed until the onset of summer rains in May/June, although temperatures are well above zero from late April onwards. Together, precipitation and temperature restrict the growing season in much of Central Asia to 3 months or even less.

Precipitation is the crucial factor for all biota in Central Asia, which can be seen at various levels. Large-scale precipitation patterns control the spatial distribution of major vegetation belts in Mongolia and northern China (Table 1.1, Fig. 1.2). Temperature is only a mediating factor, even in Tibet where the *Kobresia* meadows of the moist western half cover an altitudinal range of almost 3,000 m, corresponding to 15–18 K difference between the lowest and the highest occurrence. Still, the vegetation of these eastern Tibetan mats is astonishingly homogenous. The western parts of Tibet have a very different vegetation, dominated by alpine steppes with *Stipa* and *Allium*, but this is related to lower precipitation rather than to different temperatures (Miehe et al. 2008, 2011).

Precipitation patterns are much more continental than in neighbouring Middle Asia, but also compared to North American prairies with their occasional winter precipitation. The prairies are less cold and have a longer growing season (Lauenroth and Milchunas 1992; Lauenroth 2008). A short grass steppe in North America receives around 320 mm/a as compared to 120 mm mean precipitation in the southern Mongolian desert steppes, that also have a continuous but sparse cover of short grass (data from station Dalandzadgad, National Meteorological Service Mongolia). Rain use efficiency (RUE) – in this context the ratio between ANPP and annual precipitation total – is therefore clearly higher in Central Asian steppes (Xiao et al. 1996). This is at least partly an effect of seasonality, as shown by data from the Dalandzadgad station. On average, 90 mm (75%) of the precipitation falls between May and August, resulting in an average of 20–30 mm per month for the growing season. This is not exceedingly low compared to many semi-deserts and explains why appreciable growth and land use practices persist in these desert steppes.

Table 1.1 Overview of spatial extent and altitudinal distribution of major biomes (see Fig. 1.2), and modelled mean annual climatic values (Hijmans et al. 2005)

	Area	Altitude			Temperature (°C)			Precipitation total (mm)		
Biome	(Mio. km²)	Mean	Lowest cell	Highest[a] cell	Mean	Coldest cell	Warmest cell	Mean	Driest cell	Wettest cell
Desert steppe	1.953	1,280	250	3,970	4.2	−9.2	10.9	170	25	695
(Semi-) desert	1.559	1,310	−150	5,200	7.6	−10.5	14.8	105	10	505
Alpine steppes and deserts	1.266	4,540	670	6,550	−3.8	−17.8	11.4	195	230	1,585
Grass steppes	1.153	1,220	500	3,510	−0.4	−10.9	11.1	280	100	715
Alpine meadows	0.865	3,760	190	6,430	−2.2	−17.6	11.4	345	40	1,740
Forest	0.305	2,080	560	5,370	−1.4	−11.7	13.1	275	60	2,375
Lake, rivers	0.101	810	250	1,730	9.8	4.6	12.6	110	20	405
Rock and ice	0.059	5,570	3,830	6,970	−7.2	−15.5	4.4	225	40	1,035

[a] Figures were extrapolated from a relatively crude biome map and extreme values should be treated with care

Precipitation also exerts a strong influence at the local scale, where plot-level species richness (α-diversity) and species composition are correlated to mean annual precipitation (Bai et al. 2007; von Wehrden and Wesche 2007; Ma et al. 2010). This reflects the fundamental diversity – productivity correlation (Wang et al. 2011). According to Ni (2004), aboveground net primary production in northern China ranges between 15 and 1,647 g/m². The latter is clearly an extreme value showing that water surplus sites such as saline meadows were included. The precipitation range for these data was approximately 80–620 mm annual mean, and the correlation between ANPP and precipitation was $r = 0.32$. The correlation was even stronger in an analysis that covered biomass measurements from all Chinese grasslands including Tibet, but which excluded untypical water surplus sites (ANPP range 10–360 g/m², precipitation 100–500 mm, Bai et al. 2007). Mean annual precipitation explained ca. 36% of the differences in ANPP (mean annual temperature only ca. 3%) and 44% of the variation in species richness. Correlations differed in detail between major grassland types, but ANPP/precipitation and species richness showed linear relationships with no evidence of hump-shaped patterns or levelling at the higher precipitation levels. Even moister regions of Central Asia have still limited productivity compared to e.g. monsoonal eastern Asia, and may still represent the rising part of the productivity-diversity relationship (von Wehrden and Wesche 2007).

Mean values do, however, poorly reflect the huge interannual variability in precipitation, which is an inherent feature of most drylands. Coefficients of variation (CV, interannual standard deviation expressed as percentage of the annual mean) are typically high in the semi-arid parts of Mongolia and China (Zhou et al. 2007). Climate stations in southern Mongolia have interannual CVs of 35–55%, and growing season variability may be even higher (von Wehrden et al. 2010). In a given year, the aforementioned Dalandzadgad station may report anything between 30 and 150 mm precipitation (mean 120 mm). With water as the main limiting factor, ANPP shows related changes, as is evidenced by plot-level studies (Hilbig et al. 1993; Xiao et al. 1996; Wang 2004; Munkhtsetseg et al. 2007) but also in larger-scale remote-sensing based approaches (Piao et al. 2004; von Wehrden and Wesche 2007; Zhou et al. 2007). The example in Fig. 1.8 shows the development of standing crop in an exclosure experiment conducted in southern Mongolia (Wesche and Retzer 2005; Retzer 2007, supplemented). At ungrazed sites, standing crop varied between ca. 25 (2001) and 55 g/m² (2004). 2001 and 2002 were drought years with very low ANPP, while 2003 and the following years were relatively moist. ANPP thus showed a moderately strong correlation with summer precipitation at the neighbouring Dalandzadgad station ($r = 0.46$). Precipitation and ANPP are often not perfectly correlated, even in drylands (Fernández 2007), indicating that plants may need time to recover or are intermittently constrained by other limitations. Moreover, there is also evidence that a few more pronounced rain events may be more important than a higher number of lighter rains (Ronnenberg et al. 2008); an issue which is addressed in the fertilization studies discussed later in this review.

Standing crop at sites grazed by the two main herbivore groups (livestock, pikas) was also highly variable, indicating that both herbivore groups were not able to

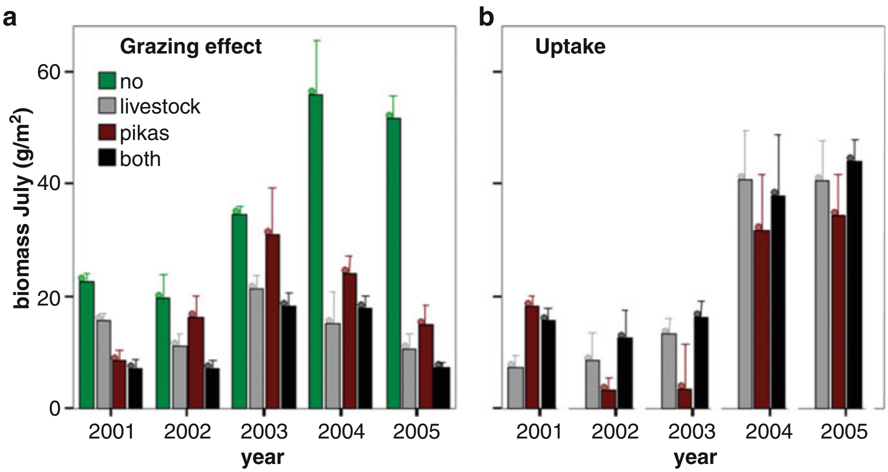

Fig. 1.8 Fencing experiment in desert steppes of southern Mongolia. The experiment comprised four blocks with differential exclusion of the two main herbivore groups (livestock – mainly sheep/goat; pikas – *Ochotona* spp.). (**a**) Amount of aboveground standing crop in July. (**b**) Uptake, estimated as the difference between grazing treatments and the respective ungrazed control (mean, standard deviation, after Wesche and Retzer 2005, supplemented)

track interannual changes in forage availability. Uptake was low during droughts in the first 2 years but remained low in the more favourable year of 2003 (Fig. 1.8b). It took a further year for herbivores to increase uptake and utilise the larger part of the available forage again. The patterns differed between groups: Pikas were able to maintain higher feeding pressure than livestock in the first year of the drought while livestock became the more active group in the following years. This is most easily explained by changes in numbers (Retzer and Reudenbach 2005): Herders moved away from the drought region in 2001, experiencing heavy losses but saving at least part of their herds. Pikas are sedentary but were able to survive quite well during the first year (partly because they had reserve fodder in their burrows). Resources were consumed in the second year and the sedentary pika populations collapsed (Nadrowski 2006).

The correlation between livestock numbers and weather conditions is also evident in an analysis of governmental livestock statistics for the region (Fig. 1.9, Begzuren et al. 2004; Retzer and Reudenbach 2005). Correlation analyses showed that occasional snow cover in winter may cause severe losses (Begzuren et al. 2004). Harsh winters of 2002, and more recently 2009/2010, resulted in massive losses (up to >30%, national livestock statistics), simply because snow cover prevented access to forage on winter pastures (see Chap. 20 by Baas et al., this volume). Winter snow may occasionally hit all sites in Central Asia, including the drier parts (Batjargal et al. 2002; Tachiiri et al. 2008). Such catastrophic conditions are called “Dzuud” or “Zud” by Mongolians. Collapses due to summer drought (called “char Dzuud” – black Dzuud) are mostly restricted to the drier parts of Central Asia, such as southern

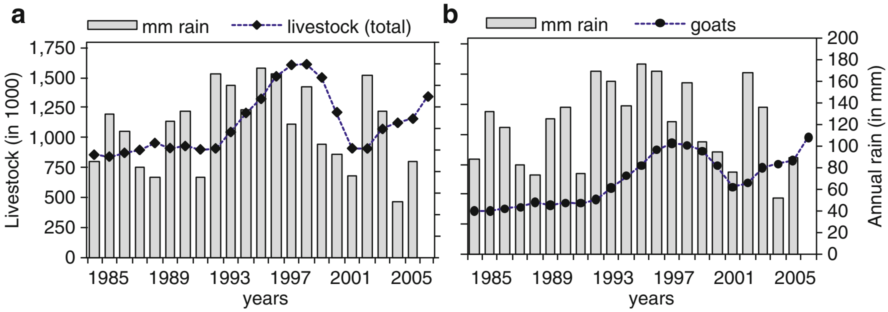

Fig. 1.9 Relationship between animal numbers and precipitation in the South Gobi Aymak, southern Mongolia (data National Statistical Yearbook). (**a**) Total livestock numbers (*dotted line*). (**b**) Goat numbers only (note that precipitation showed no long-term trend over the years; $r^2 < 0.01$)

Mongolia or the alpine steppes of Tibet. The moister tall grass steppes, forest and alpine meadows have more predictable precipitation patterns (interannual CV <25%), resulting in a more equal ANPP. This allows livestock herds to build up without suffering from regular droughts, eventually leading to high numbers and, often, overgrazing.

Such phenomena offer an explanation for the patterns observed in Fig. 1.6. Strong impact of grazing on vegetation is more commonly found under relatively moist conditions, typically >200 mm/a in Central Asia (Ellis et al. 2002). At drier sites livestock numbers are kept relatively low due to recurrent droughts, so that grazing in these steppes often only has a negligible impact on the vegetation. This is described by the non-equilibrium theory (NEQT) of rangeland science: Herds show strong fluctuations as a consequence of highly variable precipitation and thus forage availability. Relatively frequent collapses result in relatively small populations and a lower risk of grazing degradation (Ellis and Swift 1988; Sullivan and Rohde 2002; Vetter 2005). In contrast, moister sites have less variability and allow for more or less permanently high livestock numbers, which may eventually exceed carrying capacity and trigger degradation. This conceptual model describes conditions in large parts of Central Asia reasonably well and has consequently been embraced by a number of authors (Fernandez-Gimenez and Allen-Diaz 1999; Zemmrich 2007; Wesche et al. 2010).

There are, however, unsolved questions, such as the relatively limited impact of grazing in low productive rangelands with a long evolutionary history of grazing (Milchunas and Lauenroth 1993; Cingolani et al. 2005; Milchunas et al. 2008), which are often explained in terms of evolutionary adaptations without any emphasis being placed on stochastic events. The discussion among schools of thought remains intense, particularly because of the far-fetching implications of the NEQT for the evaluation of human impact in dry rangelands such as e.g. the Sahel. No consensus has been reached as yet (Gillson and Hoffman 2007; Hambler et al. 2007). From a Central Asian perspective, there are also contradictory examples including the apparent grazing degradation in dry Saxaul stands described under grazing effects above (cf. Photo 1.5c). An example of a larger-scale analysis is given by Ho (2001), who analysed livestock statistics in northern Chinese grasslands and found no apparent correlation with precipitation. Even our simple example from southern Mongolia indicates that the NEQT is too simple (Fig. 1.9b): Goat numbers have more or less steadily increased, irrespective of the climate conditions, implying that socio-economic aspects (in this case the interest in producing Cashmere that can be sold at relatively high prices to the international market), also play a role. The NEQT in its strictest sense is an oversimplification, as is the assumption of widespread grazing degradation everywhere in Central Asia. The true nature of such trends lies somewhere in between, with NEQ and steady-state conditions representing only two extremes in an overall more complex system.

Perhaps more importantly, much of the discussion on the NEQT ignores belowground conditions. The relation between precipitation patterns and belowground productivity/total productivity is not necessarily close in Central Asia (Ni 2001). Both remote sensing data and actual measurements in Chinese grasslands show that carbon stocks in soils show moderately strong correlations with precipitation patterns (Ni 2001; Yang et al. 2010b). Plants may allocate 50–98% of their growth belowground, with decreasing precipitation resulting in more belowground allocation within a given habitat type such as steppe (Fan et al. 2008; Yang et al. 2009a). The precipitation effect on allocation disappears if all grassland types in China are analysed jointly, which results in specific biological traits becoming more relevant. *Kobresia* spp. in alpine meadows of Tibet have very low aboveground-belowground ratios in phytomass, and build up huge soil carbon sinks. They occur mostly at high altitudes and consequently at low temperatures, explaining why mean annual temperature and altitude emerge as a decisive factor for sizes of soil carbon pools in large-scale comparisons in Chinese grasslands (Ni 2001; Piao et al. 2004; Dai and Huang 2006; Yang et al. 2010b). Clearly, below-ground conditions are not solely controlled by precipitation.

1.3.5 Abiotic Controls – Nutrient Availability

In our context, the main question is whether soil conditions matter at all for steppe plant performance, especially for the crucial forage productivity. Most of Central Asia is cold and dry, implying that plant growth should be limited by climate rather than by soil conditions. The NEQT, but also key reviews on dryland ecology (Noy-Meir 1973; Breman and De Wit 1983), emphasise the overwhelming role of precipitation, regarding e.g. soil nutrient availability as a secondary factor for growth in drylands. More recent reviews have, however, shown that soil nutrients may limit plant growth over a wide range of precipitation (and temperature) conditions (Breman and De Wit 1983; Hooper and Johnson 1999; LeBauer and Treseder 2008). Nitrogen has most commonly been assessed as a limiting factor, but where tested, P is usually found to be co-limiting. In the moister grass steppes (mean annual precipitation >300 mm) experimental nitrogen fertilization under ambient precipitation

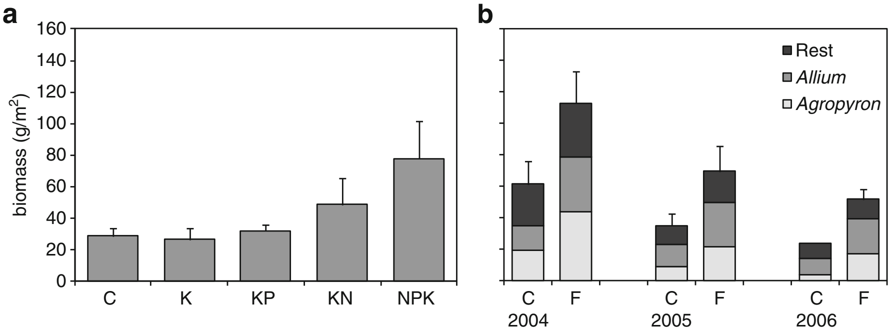

Fig. 1.10 Effects of fertilization in Central Asian grasslands. (**a**) Effects of fertilization in Tibetan *Kobresia pygmaea* mats (n = 4; station Kema, 4,450 m asl, Seeber, Miehe and Wesche unpublished). Macronutrients were applied at annual rates of 10 g N, 5 g P and 34 g K per m², and under ambient precipitation. (**b**) Effects of fertilization in southern Mongolian desert steppes (after Wesche and Ronnenberg 2010 changed). NPK fertilizer was applied at equivalents of 10 g N, 3.3 g P and 33 g K per m², plus Mg and various micronutrients at an annual base (*F* fertilized, *C* controls, n = 9)

usually results in a significant increase in ANPP (Pan et al. 2005; Bai et al. 2009; Fanselow et al. 2011), improved tissue N contents (Liu et al. 2007; Huang et al. 2008) but also slow changes in dominance patterns, due to differing responses to fertilization among species. Patterns in belowground productivity are less widely studied but may even be opposite (Li et al. 2011a).

Positive effects of N and/or P addition in the moister steppes of Central Asia are not surprising from a theoretical point of view, and they are important in view of the nutrient losses under heavy grazing discussed above. Together, these observations imply that land management should consider conservation of soil nutrient stocks in the Central Asian steppes. Otherwise, the slow degradation of soils will worsen the direct degradation effects apparent in the above-ground vegetation, resulting in severe and lasting losses in steppe productivity.

Less clear is the importance of soil nutrient availability under more severe climatic conditions, such as those found at high altitude sites in Tibet. Studies from other alpine sites (Theodose and Bowman 1997) and data from Central Asia described above suggest that annual mean temperatures are not necessarily decisive for growth. Nutrient shortage may affect plant growth in high altitude Central Asia, and this is supported by fertilization experiments (Fig. 1.10a). Because initial studies pointing to a certain macro-nutrient as the most limiting factor were not available, we tested full NPK fertilization in *Kobresia* meadows of eastern Tibet (ambient precipitation 400–500 mm). We found strong evidence of N-limitation, and biomass productivity was increased even further when NPK were jointly added. Alpine meadows thus suffer from nutrient constraints (N, followed by P), which may have been aggravated by traditional land use and associated nutrient withdrawal. This is also supported by a large-scale comparison of rain use efficiency (unit aboveground biomass productivity per unit of precipitation) in Tibetan grasslands that also demonstrated positive effects of more fertile soils on productivity (Yang et al. 2010a). Studies on the drier alpine steppes of Tibet are, unfortunately, not available.

Not only low temperatures but also low water availability may interact with nutrient constraints. There is contrasting evidence as to whether the relative importance of nutrient availability, especially N, declines with increasing dryness of the sites (Breman and De Wit 1983; Xia and Wan 2008) or is independent of precipitation (Hooper and Johnson 1999; LeBauer and Treseder 2008). Surprisingly few fertilization studies have, however, been performed in drylands with <200 mm annual mean precipitation. Recent publications from North America (James et al. 2005; Harpole et al. 2007) and anecdotal evidence from Central Asia (Slemnev et al. 2004) implied that nutrients may limit plant growth even under dry conditions. This was also supported by our own fertilization experiments in southern Mongolian desert steppes (Wesche and Ronnenberg 2010). Again, we had to opt for NPK fertilization performed under ambient precipitation (120–180 mm). There was clear evidence of nutrient limitation as fertilization more than doubled ANPP (Fig. 1.10b). The valuable forage grass *Agropyron cristatum* showed a particularly strong response. Tissue contents of N, and therefore raw protein contents, increased and flowering was also facilitated. The absolute magnitude of effects was higher in the moist year of 2004 (180 mm precipitation) than in the more average years of 2005 and 2006 (110, 130 mm), indicating co-limitation by water availability.

In a second experiment at the same sites, fertilizers were applied in factorial combination with irrigation equivalent to 100 mm, which is more than the average summer precipitation at the site (Ronnenberg and Wesche 2011). Fertilization again showed strong effects on ANPP, while irrigation had no significant effect. This is in contrast to findings of relatively stronger irrigation effects in moister Inner Mongolia (Fanselow et al. 2011; Li et al. 2011a), but may simply indicate that timing is important. In our experiment, water was only applied in summer (July, August) and in relatively small daily doses (5 mm). The discussion on winter and spring precipitation above implies that precipitation in late summer may have generally limited effects in the dry grasslands. Moreover, there is also evidence that a few large precipitation events may be more relevant than a number of small events (Ronnenberg et al. 2008), a pattern that has recently been described for North American dry steppes as well (Knapp et al. 2008; Heisler-White et al. 2009).

While cations are usually present in sufficiently high concentrations in the grassland soils, it remains unclear whether P or N is the more crucial limiting factor. To our knowledge, differential fertilization experiments have hardly been performed in dry Central Asia, and there is thus only indirect evidence. Plant tissue NP ratios in southern Mongolia were >20–30, which is high compared to measurements on plants all over China (Han et al. 2005; He et al. 2008). Wide NP ratios point to P rather than N as the limiting factor, although this is only an initial indication (Drenovsky and Richards 2004; Güsewell 2004). The pronounced effects of NPK fertilization on flowering activity may also point towards P limitation (Marschner 1995), and low numbers of legumes in the vegetation (see introduction on flora above) suggest that factors other than N limit growth. Indeed, the generally high pH values in the desert steppes will result in quick immobilisation of P, aggravating already low contents of P in bedrock in several parts of Central Asia (e.g. Inner Mongolia, He et al. 2008). These inferences are, however, speculative, and there is evidence in the literature that the addition of N alone may have positive effects on plant growth in dry Central Asia (Slemnev et al. 2004; Li et al. 2011b).

In any case, the data demonstrate clearly that land-use mediated loss of nutrients may constrain steppe productivity, even at relatively dry and/or cold sites. Due to the productivity-diversity relationship discussed above, low levels of nutrients may also affect species richness in the long run (Bai et al. 2007). Large-scale fertilization of steppes is certainly not feasible (due to very low nitrogen use efficiency; Wesche and Ronnenberg 2010), but future studies should address how different forms of grazing such as sedentary vs. nomadic, or goat-dominated herds vs. traditional camels, affect nutrient flows in the landscape. The comprehensive data from the well researched IMGERS station (including the MAGIM project) in Inner Mongolia shows that land use has tremendous effects on soils and vegetation in the landscape, at population and individual levels. Similar data are needed from other climatically different sites, because nutrient constraints have to be taken into account if realistic scenarios on future land use and the effects of climate change in Central Asia are to be developed.

1.4 Conclusion – Central Asia and Global Change

We have restricted our discussion to relatively simple response variables such as productivity and growth, but even these have revealed complicated patterns. These differed strongly between sites, in spite of the general similarity in physiognomy of the Central Asian grasslands. Grazing, precipitation and temperature may all have an influence, be it in isolation or through interaction. As a consequence, predictions in respect of ongoing land use and climate change remain difficult.

A main problem is that trends in key aspects of global change are not clear. In terms of land use change, intensity has increased over the last few decades and is likely to increase further with respect to current population growth in Mongolia and in the ethnic minorities of China. Animal numbers are already high and will probably increase, at least locally; although strong interannual fluctuations as shown for Mongolia render detection of trends difficult. Sedentarisation complicates the picture even further: Movements have largely ceased in Inner Mongolia, sedentarisation has commenced in Tibet, and prospects in Mongolia depend on outcomes of ongoing political discussions (Sneath 1998; Janzen 2005; Long et al. 2008; Ptackova 2011). With respect to the inherently high variability of conditions, sedentarisation is a risky strategy, and may cause higher ecological and, potentially, economic vulnerability. In particular, dry steppes, with their unpredictable conditions, deserve attention in this respect. Management schemes based on steady-state conditions and local carrying capacities are of questionable value for these regions. On the other hand, the assumption of continuous increases in herd numbers and associated degradation certainly is too simple.

Global climatic change is resulting in rising temperatures being reported by the majority of weather stations in the region, and this is also supported by models (Klein Tank et al. 2006; IPCC 2007; Dagvadorj et al. 2009). Rates of increase have widely been >2 K in the last century, triggering concerns about increasing (physiological) aridity. This is surprising in view of the discussion above that provides no evidence for an unequivocal importance of temperature controls. A warming experiment in northern China also showed that precipitation is more important than temperature alone (Niu et al. 2008). An experiment in northern Tibet described severe negative effects of warming (Klein et al. 2004), but this was conducted at the lower altitudinal (and therefore upper thermal) limit of the dominant *Kobresia* spp. More data from the core alpine sites are needed, especially in combination with water addition. Yu et al. (2010) claim that warm temperatures in Tibetan grasslands lead to a lack of winter chilling and an associated delayed onset of the growing season. This may, however, also be related to precipitation patterns: We correlated values reported by Yu et al. (2010) on the start of the growing season with precipitation in March and found a conspicuous trend (Spearman $\text{rho} = -0.41$, $p < 0.05$). Simulation model studies also imply that trends in aridity in steppe vegetation largely depend on trends in precipitation (Christensen et al. 2004) and rising CO_2 reduces drought sensitivity in grassland plants (Soussana and Luscher 2007). With no extra rain, increased temperatures may offset positive effects of higher CO_2 availability and thus higher water use efficiency; but again, moisture availability rather than temperature alone is the key variable.

This is also in line with results described above, where precipitation emerged as the perhaps single most important factor in the region. Unfortunately, trends in precipitation patterns are much less well understood than those for temperature, and congruence between model simulations over Central and Middle Asia is limited (Lioubimtseva et al. 2005; IPCC 2007). Most stations in Central Asia have reported no change or increased annual precipitation totals over the last decades (Wei et al. 2005; Klein Tank et al. 2006; Shi et al. 2007). In Mongolia, some stations show decreased precipitation (Dagvadorj et al. 2009; Dulamsuren et al. 2010), but the spatial heterogeneity is huge and, on average, total precipitation seems to be stable (Angerer et al. 2008). Future reductions in the intensity of the Indian monsoon due to warming and increasing air pollution in South Asia have been predicted for parts of the Tibetan plateau (May 2004; Zickfeld et al. 2005), while other studies imply increases of precipitation in (eastern) Tibet (Cui and Graf 2009; Yu et al. 2010). Taken together, general scenarios on moisture availability over Central Asia should therefore be taken with caution.

There is a trend towards increasing winter precipitation and snow cover (Peng et al. 2010). This may have disastrous effects on livestock herds if access to winter pastures is prevented (Dzuud), but may have positive consequences if spring moisture availability is improved. In fact, early summer growth shows positive trends to increasing snow depths in northern Chinese grasslands, while effects in Tibet are not significant, possibly due to cold conditions (Peng et al. 2010). Several authors also report increased variability and higher frequency of extreme events in precipitation (Klein Tank et al. 2006; Dagvadorj et al. 2009). This is usually regarded as critical as severe rains result in more runoff. While effects of more extreme rain events are indeed usually negative in relatively moist regions, they may be positive in dry environments, where small water doses may evaporate quickly and not even become effective for plant growth (see above, Knapp et al. 2008). Therefore, at present, neither knowledge on trends in timing of precipitation patterns, nor understanding of the potential effects seems sufficient in our region.

Finally, effects of climate and land use change on productivity and plant performance are further complicated by soil nutrient effects. We have seen that nutrient availability is likely to constrain growth in dry and moist sites alike. Atmospheric nitrogen deposits will increase over Central Asia, but rates may be too small to exert any major impact (Galloway et al. 2004; Kinugasa et al. 2008). Matter fluxes due to livestock grazing may be much more important, but this is a topic that has been explored at very few sites so far, and trends in the future are unclear.

Carbon stocks in soils are not only relevant for local phenomena but also in terms of sequestration and global carbon cycles. Recent publications imply that carbon stocks have remained largely stable in soils of northern China and Tibet (Yang et al. 2009b, 2010b). There is, however, spatial heterogeneity, and there are reports of contradictory patterns (Cao et al. 2003; Xie et al. 2007), but there is at least no unequivocal evidence for declining carbon pools in Central Asian soils. The same holds true for vegetation, where recent studies describe increasing cover in Central Asia (Piao et al. 2004; Yang et al. 2009a), while there is also evidence for severe declines (Wei et al. 2005; Angerer et al. 2008; Dagvadorj et al. 2009). Whether these are due to climate change or land use effects is still open to debate.

It is clear that knowledge on the ecology of Central Asian grasslands has vastly improved in the last two to three decades. It is, however, equally clear that we still lack a comprehensive understanding of most of the involved processes and the potential drivers for changes in plant community composition or productivity. The successively published and surprisingly often negative scenarios on future development in the course of global land use and climate change should thus be viewed with extreme caution. Central Asia is a huge region and it would be very surprising if it did not show complicated and often unexpected responses.

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