

Grassland ecosystems in China: review of current knowledge and research advancement

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Grasslands are the dominant landscape in China, accounting for 40% of the national land area. Research concerning China's grassland ecosystems can be chronologically summarized into four periods: (i) pre-1950s, preliminary research and survey of grassland vegetation and plant species by Russians, Japanese and Western Europeans, (ii) 1950–1975, exploration and survey of vegetation, soils and topography as part of natural resource inventory programmes by regional and national institutions mainly led by the Chinese Academy of Sciences, (iii) 1976–1995, establishment of field stations for long-term ecological monitoring and studies of ecosystem processes, (iv) 1996–present, comprehensive studies of community dynamics and ecosystem function integrating multi-scale and multidisciplinary approaches and experimental manipulations.

Major findings of scientific significance in China's grassland ecosystem research include: (i) improved knowledge on succession and biogeochemistry of the semi-arid and temperate grassland ecosystems, (ii) elucidation of life-history strategies and diapause characteristics of the native grasshopper species as one of the key grassland pests, and (iii) development of effective management strategies for controlling rodent pests in grassland ecosystems. Opportunities exist for using the natural grasslands in northern China as a model system to test ecosystem theories that so far have proven a challenge to ecologists worldwide.

Keywords: biogeochemistry; grassland; grasshopper; rodent; China

1. INTRODUCTION

Grasslands are the dominant landscape in China and account for 40% of the national land area. Geographically, about 78% or some 313 million ha of the grasslands in China occur in the northern temperate zone (Sun 2005), constituting an integral part of the Eurasian grassland ecosystem to the east of the continent.

The northern grassland ecosystems of China play important roles in servicing the ecological environment and socio-economics of the region and in supporting diverse species of plants and animals. Traditionally, grasslands have been the major sources of animal products such as meat, milk, wool and pelts, and are home to the majority of the ethnic people. A social function in terms of maintaining cultural diversity and social stability, therefore, has also been a critical component of the grassland ecosystem in China.

An increasing demand for natural resources and animal products to cope with sharply rising human populations has placed tremendous pressures on grassland ecosystems. The accelerated and large-scale degradation and desertification of grassland ecosystems in areas with fragile environmental conditions and poor ecosystem structures have raised concerns

within various organizations and institutions as well as within the scientific community. This has given rise to substantially increased funding and research initiatives in recent decades in an effort to restore degraded lands and seek effective management practices for sustaining the productivity and ecosystem functioning of the grasslands in China. The frequently occurring dust storms since the end of the twentieth century have been considered a direct consequence of degradation and desertification of the northern temperate grassland ecosystems of China.

Owing to their importance in socio-economics, culture, ecology and environmental quality, grassland ecosystems have become one of the most active subjects of research and have attracted much attention from ecologists nationally and internationally. The purpose of this review is to provide an overview of the history, our current knowledge and recent research advancement on the northern grassland ecosystems of China, and to discuss future opportunities that are of significant scientific, environmental and socio-economic importance.

2. CHINA'S GRASSLAND ECOSYSTEMS: TYPES AND DISTRIBUTION

The grassland ecosystems in China are classified into four major types (Sun 2005): meadow steppes, typical steppes, desert steppes and alpine steppes, with a combined distribution ranging from the northeastern

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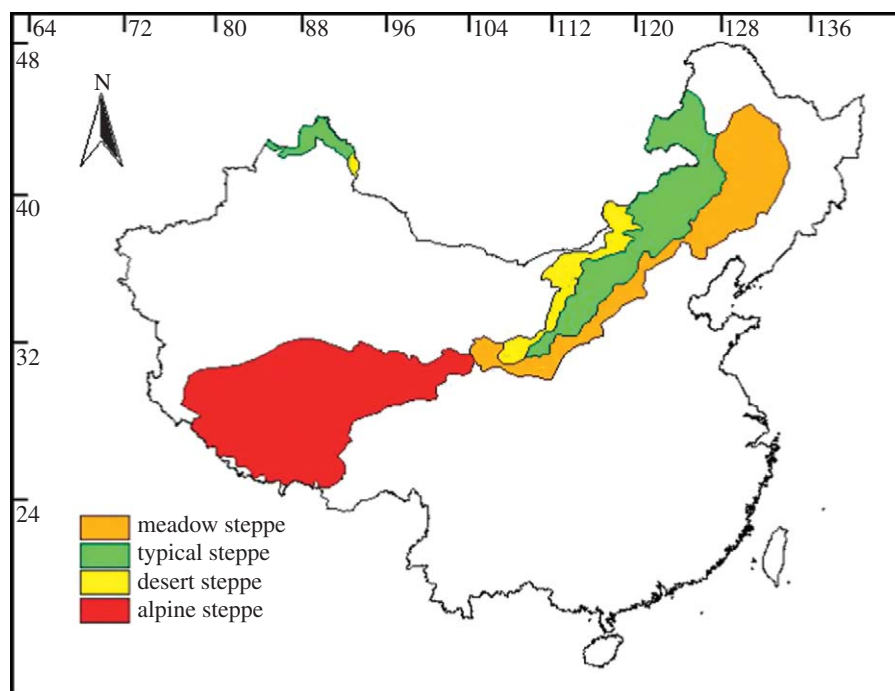


Figure 1. Distribution of grasslands in China by ecosystem types (adapted from the Vegetation Atlas of China compiled by the Editorial Board of Vegetation Map of China 2001).

Table 1. Major grassland ecosystem types and construction plant species of China (adapted from Sun 2005).

ecosystem type	construction plant species
meadow steppe	<i>Stipa baicalensis</i> Roshev; <i>Bothriochloa ischaemum</i> L. Keng; <i>Cleistogenes mucronata</i> Keng; <i>Leymus chinensis</i> Tzvel.; <i>L. angustum</i> (Trin.) Pilger; <i>Folifolium sibiricum</i>
typical steppe	<i>Stipa grandis</i> Smirn; <i>S. krylovii</i> Roshev; <i>S. bungeana</i> Trin; <i>S. capillata</i> L.; <i>Festuca sulcata</i> (Hack.) Beck; <i>Cleistogenes squarrosa</i> (Trin.) Keng; <i>Agropyron cristatum</i> (L.) Gaertner; <i>Leymus chinensis</i> Tzvel.; <i>Artemisia frigida</i> Willd; <i>A. intramongolica</i> HC Fu & ZY Zhu; <i>A. gmelinii</i> Webb ex Stechmann; <i>Thymus mongolicus</i> Ronn
desert steppe	<i>Stipa gobica</i> Roshev; <i>S. klemenzii</i> Roshev; <i>S. breviflora</i> Griseb.; <i>S. glareosa</i> P. Smirn.; <i>Cleistogenes songorica</i> (Roshev.) Ohwi; <i>Allium polyrhizum</i> Turcz. ex Regel; <i>Hippolytia trifida</i> (Turcz.) Poljak.; <i>Ajania fruticulosa</i> (Ledeb.) Pojak
alpine steppe	<i>Stipa purpurea</i> Grisebach; <i>S. subsessiliflora</i> (Rupr.) Roshev; <i>S. subsessiliflora</i> var. <i>basiplumosa</i> (Munro ex Hook. f.) PC Kuo & YH Sun; <i>Festuca kryloviana</i> Reverd.; <i>F. pseudovina</i> Hack. ex Wiesb.; <i>F. olgae</i> (Regel) Krovot.; <i>Carex moorcroftii</i> Falc. ex Boott.; <i>Artemisia salsoloides</i> var. <i>wellbyi</i> (Hemsl. & Pearson) Pamp.; <i>A. younghusbandii</i> J.R. Drumm. ex Pamp.; <i>A. minor</i> Jacquem. ex Besser

plain adjacent to Mongolia to south of the Tibetan Plateau, covering a distance of 4500 km in the north-east–southwest direction and 23° latitude (from 28 to 51° N; figure 1). Each type is further classified into different community types based on the construction plant species (table 1). Meadow steppes and typical steppes are the most commonly used ecosystem types for grazing and economic activities related to animal products.

Meadow steppes occur on the most moist and fertile sites among the four grassland ecosystem types, typically in areas with annual precipitation around 450 mm and soils of high organic content (Sun 2005). Construction plant species within this ecosystem type include *Stipa baicalensis* Roshev, *Bothriochloa ischaemum* L. Keng, *Cleistogenes mucronata* Keng, *Leymus chinensis* Tzvel., *L. angustum* (Trin.) Pilger and *Folifolium sibiricum*.

Typical steppes are developed under a semi-arid climate in the temperate zone with annual precipitation

of around 350 mm and the plant species are characteristically drought tolerant (Sun 2005). There are 13 community types generally recognized in the category of typical steppes: most common are the *Stipa* steppes, the *Festuca* steppes, the *Leymus* steppes and the *Artemisia* steppes. Typical steppes are distributed predominantly on plateau between 1000 and 1500 m a.s.l. (Sun 2005).

The desert steppes are the most arid grassland ecosystem type, occurring in areas with annual precipitation between 150 and 250 mm and under the influence of continental climatic conditions (Sun 2005). *Allium polyrhizum* Turcz. ex Regel and several species of *Stipa* form the most widely distributed community types within the desert steppe category.

Alpine steppes are found between 2300 and 5300 m a.s.l. in southwest China. The common construction plant species are cold- and drought-tolerant grasses and small shrubs ranging from locally distributed

species such as *Stipa purpurea* Grisebach, *S. Subsessiliflora* var. *basiplumosa* (Munro ex Hook. f.) P. C. Kuo & Y. H. Sun, *Festuca olgae* (Regel) Krovot., *Carex moorcroftii* Falc. ex Boott. and *Artemisia salsoloides* var. *wellbyi* (Hemsl. & Pearson) Pamp., to common plants of Eurasian grassland ecosystems such as *Festuca kryloviana* Reverd. and *Festuca pseudovina* Hack. ex Wiesb. (Sun 2005).

Most of the meadow steppes and typical steppes are distributed on the Inner Mongolian Plateau, where extensive studies have been conducted on ecosystem structures, function and management strategies, as well as plant–insect and plant–animal interactions.

3. HISTORY OF GRASSLAND ECOSYSTEM RESEARCH IN CHINA

Research on the grassland ecosystems in China can be chronologically summarized into four periods: (i) pre-1950s, preliminary research and survey of grassland vegetation and plant species conducted mostly by Russians, Japanese and Western Europeans, (ii) 1950–1975, large-scale exploration and survey of vegetation, soils and topography as part of the natural resource inventory programmes conducted by various regional and national institutions mainly led by the Chinese Academy of Sciences, (iii) 1976–1995, establishment of field stations for long-term ecological monitoring and studies of ecosystem processes, (iv) 1996–present, comprehensive studies of community dynamics and ecosystem function integrating multi-scale and multi-disciplinary approaches and experimental manipulations with the scientific focus more towards issues concerning ecosystem stability and management, biodiversity and global change.

Research activities on grassland ecosystems in China prior to 1975 were mostly concerned with documentation of plants and natural resources. Since the seventeenth century, missionaries, diplomats and business people from Russia and Western Europe have been collecting and documenting the plants of northern China. Beginning in 1870, the Russian Geographic Society organized many scientific expeditions to China and neighbouring countries and conducted vegetation surveys. Between 1890 and the end of WWII, Japan organized many exploratory tours of northern China and Inner Mongolia, to assess the natural resources of the region. Between 1950 and 1975, more systematic and large-scale surveys of the vegetation, soils and topography of Inner Mongolian grasslands were conducted by Chinese scientists through various institutions and expedition programmes led by the Chinese Academy of Sciences.

During the period from 1976 to 1995, major efforts were directed at establishing field research facilities and stations for long-term ecological monitoring and in-depth studies of ecosystem processes. In 1979, the Chinese Academy of Sciences established the Inner Mongolian Grassland Ecosystem Research Station (IMGERS) on typical steppes of Xilingol. The IMGERS is now affiliated with the Chinese Ecological Research Network (CERN) administered by the Chinese Academy of Sciences (CAS) and was recently selected as one of 36 national field

monitoring and scientific research stations. The IMGERS harbours some of the longest, fully protected research plots of natural grassland ecosystem worldwide (Bai *et al.* 2004) and hosts extensive research activities and a broad range of international collaborative research projects on grassland ecosystems of the Eurasian continent.

Following the establishment of the IMGERS, the Institute of Botany of the CAS established more research stations in the grasslands of Inner Mongolia jointly with local governments, forming a network of research stations for grassland ecosystem research. These include the Ordus Sandland Ecological Station (established in 1991; also a member of CERN), the Duolun Restoration Ecology Research and Demonstration Station (established in 2000), the Hunshandak Sandland Ecological Station (established in 2002) and the East Ujumchin Grassland Ecosystem Management Research Station (established in 2005).

Many of the key research initiatives on grassland ecosystem research in China took place after the mid-1990s. The latest decade represents a period of research initiatives more focused on broad ecological issues such as grassland management for sustainable productivity and ecosystem stability, and changes in structure and function in the context of global change. Advancement in research techniques and utilization of multidisciplinary approaches involving field experimental manipulations have promoted more in-depth understanding of the grassland ecosystem function and succession of northern China. The large and continuously distributed grasslands of the Inner Mongolian Plateau provide a unique opportunity for grassland ecosystem studies at various scales.

Despite its long history, grassland ecosystem research of scientific and socio-economic significance has progressed most during recent decades, especially the most recent decade. Therefore, our review has been focused mainly on the most recent research outcomes.

4. STRUCTURE AND FUNCTION OF GRASSLAND ECOSYSTEMS

The structure and function of the northern temperate grassland ecosystems have been studied extensively using the network of grassland research stations on the Inner Mongolian Plateau by Chinese grassland ecologists. Much of the research has been conducted in the Xilingol grasslands of Inner Mongolia, where the landscape is largely meadow and typical steppes and livestock grazing has been the traditional land-use practice supporting the regional economy. The latest research efforts have been mostly concerned with vegetation structure and succession, biogeochemistry, ecophysiology and the greenhouse gas (GHG) dynamics of the region.

(a) *Vegetation structure and succession*

Research on grassland vegetation structure and succession in northern China has benefited the most from long-term data collections from the grasslands in Inner Mongolia managed by the IMGERS. On the basis of a 24-year study of the Inner Mongolian grasslands, Bai *et al.* (2004) made two important

discoveries: (i) ecosystem stability increases progressively along the hierarchy of organizational levels (i.e. from species to functional group to whole community) and (ii) the community-level stability arises from compensatory interactions among major components at both species and functional group levels. Bao *et al.* (2004) studied the dynamics of community composition based on plant functional groups (PFGs) using field experimental data of a 17-year mowing succession of *L. chinensis* steppe of Inner Mongolia, and found that during these 17 years, changes in both community structure and function occurred but with different patterns. Their study demonstrated that the role of different PFGs varied with mowing succession: the dominance of rhizome grasses would be replaced successively by annuals and biennials, tall bunch grasses and short bunch grasses. The aboveground primary productivity (ANPP) of the community displayed resilience to mowing disturbance and remained relatively stable initially through internal regulation of PFGs, declined to a lower level with structural changes of the community after 5 years, and then again maintained a stable level through structural regulation (Bao *et al.* 2004). These findings indicate that the community may rely on constantly regulating its structure to maintain functional stability in grassland ecosystems. In a recent study, Zhou *et al.* (2006) found that land-use could affect the relationship between species diversity and ANPP at the local scale in the semi-arid grassland ecosystems of Inner Mongolia, and suggested that the mode and severity of disturbance are important factors for interpreting the relationship between species diversity and productivity.

Water has been demonstrated as one of the most profound factors that determine the species composition of grassland ecosystems. Research from the Xilin River Basin of the Inner Mongolian Plateau shows that in wetter habitats, hygromesophytes and hygrophytes are more abundant and account for the majority of aboveground biomass, whereas xerophytes and meso-xerophytes become more conspicuous in dryer habitats (Chen *et al.* 2003d). This finding has significant implications for vegetation succession in the northern temperate grassland ecosystems with predicted changes in spatio-temporal patterns of precipitation under the influence of global climate change.

Land-use and land-cover changes at the regional scale are most relevant to policy making and issues concerning sustainable management of natural resources. Availability and rapid progress of remote-sensing techniques and geographical information systems have advanced the research in these areas. For example, many satellite-based remote-sensing products such as the normalized difference vegetation index (NDVI), derived from the NOAA and Landsat-TM or ETM+ and MODIS imageries, have been useful in detecting vegetation dynamics of terrestrial ecosystems. Although remote-sensing techniques have been used in detecting vegetation dynamics in grassland ecosystems of northern China (e.g. Chen *et al.* 2003e; Li *et al.* 2003; Yamano *et al.* 2003), the work to date is still only preliminary in terms of practicality and technical capability. Advancement is expected in this line of research in conjunction with multi-scale studies

and analysis of spatio-temporal vegetation dynamics of the grassland ecosystems.

(b) *Biogeochemistry*

Energy and matter flow among components of ecosystems and exchange with the environment are the central functions of ecosystems. Factors affecting those processes regulate ecosystem productivity and function. Apart from climatic factors such as temperature and precipitation, soil nutrients are the most likely limiting factors to the productivity of the temperate grasslands in northern China.

Research to date into the biogeochemistry of the grasslands of the Inner Mongolian Plateau has been predominantly concerned with the elements of biogeochemical significance, e.g. N and P (Pan *et al.* 2004, 2005; Zhang *et al.* 2004a; Wang *et al.* 2006). Field fertilization experiments and N : P stoichiometry have both been used to identify the most limiting nutrient elements at the species level in typical steppes with and without livestock grazing, using *L. chinensis* and *Carex korshinskyi* Kom as model plants. It has been found that *L. chinensis* is N limited on sites where animal grazing is excluded for only a brief period, whereas P is more likely a limiting factor to the growth of *C. korshinskyi* on sites where animal grazing is excluded for a prolonged period (Zhang *et al.* 2004a). There exists a significant synergistic relationship between tissue N and P concentrations of grassland plants (Zhang *et al.* 2004a). Growth of *L. chinensis* is generally N limited in typical steppes of the Inner Mongolian Plateau (Pan *et al.* 2005). After one growth season, the plant pool of *L. chinensis* grassland can accumulate an average of 32% supplementary N as found by using ¹⁵N-labelling (Pan *et al.* 2004). Nitrogen addition may alter the effect of defoliation on growth such that plants growing at higher N levels would be more negatively affected by defoliation than plants with no supplementary application of N (Yuan *et al.* 2004). Grazing was found to negatively affect the soil N pools in grassland ecosystems (Wang *et al.* 2006). However, increased N deposition due to anthropogenic activities combined with increasing precipitation, as predicted to occur for some of the arid and semi-arid regions, may possibly accelerate plant litter decomposition (Liu *et al.* 2006), hence facilitating faster N transfer from the plant to soil pools in the grassland ecosystems of northern China.

Many studies demonstrated significant growth response to N addition at the plant community level on the typical steppes of the Inner Mongolian Plateau, indicating a great potential for increased grassland productivity with increasing N deposition as a result of global change.

(c) *Ecophysiology*

Ecophysiological characteristics reflect both the genetic control and the environmental modification of plant performance. Research into the ecophysiology of grassland plants on the Inner Mongolian Plateau has focused mostly on photosynthesis and water relations at individual levels in various habitats. Photosynthetic gas exchange and plant water potential have been the most commonly studied traits of plant performance in response to environmental constraints such as drought

and high temperatures (Liu *et al.* 2003a–c, 2004; Niu *et al.* 2003a,b). Generally, C₄-photosynthetic-pathway plants display more negative values of leaf osmotic potential compared with C₃ and crassulacean acid metabolism plants. Studies with 104 plant species by Liu *et al.* (2003b) showed that leaf osmotic potentials became more negative with increasing rooting depth and decreasing leaf water content across different habitats. Such findings may explain the long-term adaptation strategies of various plants to frequent droughts on the temperate grasslands of northern China.

In recent years, the stable isotope technique has become a popular tool for studying carbon cycle and water relations of grassland plants (Chen *et al.* 2002, 2003d, 2004c,d). Promising outcomes may be achieved in the future on the response and adaptation strategies of grassland plants and plant communities to changing climatic conditions.

(d) Greenhouse gas dynamics

Research on GHG in the grassland ecosystems of northern China has focused on carbon fluxes of soils. Soil respiration is an important component of the carbon cycle, the quantification of which has significant implications in models to predict anthropogenic carbon emissions resulting from land-use and land-cover changes. In the typical steppes of Inner Mongolia, soil respiration displays clear seasonal patterns, driven most probably by seasonal patterns of primary production as found in other ecosystem types in temperate climates (Campbell *et al.* 2004). The peaks of soil respiration often occur in summer (Li *et al.* 2000; Chen *et al.* 2003b) corresponding to the maximal temperature of the season. The daily average of soil respiration during growing seasons has been found to be in a range between 565 and 1350 mg C m⁻² d⁻¹ for different plant communities (Chen *et al.* 2003b).

Temperature and soil water are both important in determining seasonal variations in soil respiration of the grassland ecosystems. Generally, soil respiration increases with temperature; exponential (Chen *et al.* 2003b,c, 2004b; Zhang *et al.* 2003a), power (Li *et al.* 2000) and linear functions, can be used to describe the temperature function of soil respiration in the grassland ecosystems of Inner Mongolia.

Q₁₀, the amount of CO₂ exchange due to a 10°C temperature rise, can indicate the sensitivity of soil respiration response to changing environmental conditions. A positive relationship between Q₁₀ and soil moisture has been detected along a soil water gradient in the grasslands of the Inner Mongolian Plateau (Chen *et al.* 2004b), which indicates severe water limitation effects on carbon cycling of the grassland ecosystems in this region. Moreover, interaction between temperature and soil water better explains the seasonal variation in soil respiration than each of the factors alone (Li *et al.* 2000; Chen *et al.* 2003b). In addition to abiotic factors, live-shoot biomass dynamics could contribute greatly to the seasonal variation in soil respiration in the *L. chinensis* and *Stipa grandis* Smirn community, but a significant functional relationship between soil respiration and

total aboveground biomass or root biomass is lacking (Chen *et al.* 1999; Li *et al.* 2002).

The biogenic volatile organic compounds (VOC) emitted by vegetation of terrestrial ecosystems play a key role in both regional air quality and tropospheric chemistry. Most plants in the typical steppes of the Inner Mongolian Plateau have relatively low VOC emission potential at the species level, especially some of the dominant plants such as *L. chinensis*, *S. grandis* and *Agropyron cristatum* (L.) Gaertner (He *et al.* 2005). Research indicates that at the PFG level, the lowest VOC emission potential could be expected from perennial rhizome grasses, a major PFG in a typical temperate grassland ecosystem. Overgrazing is likely to increase VOC emission as a result of increasing the proportion of PFGs with high VOC emission (He *et al.* 2005).

Studies on GHG dynamics on the Inner Mongolian Plateau suggest that changes in climatic conditions are more likely to alter the patterns of carbon fluxes of the grassland ecosystems of northern China.

5. ECOLOGY OF GRASSHOPPERS AS GRASSLAND PESTS

Grasshoppers have been the subject of particular research emphasis in China owing to their importance in grassland ecosystem processes and functioning. Grasshoppers, as the primary consumers, affect grassland productivity and compete with domestic animals for food resources. The biogeography of some 150 species of grasshopper fauna on the Inner Mongolian Plateau has been studied, of which 10–15 species are considered as grassland pests (Li & Kang 1991). Long-term studies of grasshopper ecology have been conducted at the IMGERS since 1979, with earlier work mainly focused on the fauna and food selections, and on the economic thresholds as control guidelines for the major grasshopper species of the region. During the past two decades, more research efforts have been directed at understanding the life-history strategies, chemical ecology, niche differentiation and community dynamics in response to the grazing of grasshoppers. Notable progress has been made in understanding the grasshopper ecology of the grassland ecosystems in northern China. Such knowledge is fundamental to developing alternative methods to pesticides for controlling outbreaks of grasshopper populations in the grassland ecosystems.

(a) Life-history strategies and diapause characteristics

Understanding life-history strategies and diapause characteristics is useful for improving predictive models and developing management guidelines for grasshopper control. In the grassland ecosystems of Inner Mongolia, nearly all the grasshopper species have only one generation per annum, but occur in different seasons and form sequential development cohorts. In the latest research on grasshoppers, life-history strategies and diapause characteristics are used in an attempt to explain the seasonal patterns of egg diapause and over-wintering in response to temperature variations. Temperature has been identified as one of the

key controlling factors of the life-history and diapause characteristics of grasshoppers. The diapause and non-diapause eggs of different grasshopper species have been found to respond and adapt to seasonal temperature fluctuations (Hao & Kang 2004a-c). Irrespective of their seasonal occurrence, all species of grasshoppers on the Inner Mongolian Plateau over-winter as eggs and enter diapause in embryo stage 19, but eggs deposited by adult grasshoppers in different seasons enter the winter at different embryological developmental stages (Hao & Kang 2004a,b; Zhao *et al.* 2005). Therefore, the over-wintering eggs can be either diapause or non-diapause.

Interspecific differences have been found in the over-wintering embryonic stages, developmental rates, survival curves and cumulative hatching probabilities of six grasshopper species, including one early-season hatching species (*Omocestus haemorrhoidalis*), three mid-season hatching species (*Oedaleus decorus asiaticus*, *Anagaracris barabensis* and *Calliptamus abbreviatus*) and two late-season hatching species (*Chorthippus dubius* and *Chorthippus fallax*; Hao & Kang 2004a,b; Zhao *et al.* 2005). Great variations have been observed in the embryonic stages of over-wintering eggs in grasshopper species of the Inner Mongolian grasslands. Generally, the early-season hatching species are able to reach a much more advanced stage of development (embryonic stage 19) before the onset of winter than the late-season hatching species due primarily to cumulative growth temperatures; the developmental stage at which the eggs of a species over-winter varies greatly within the mid-season hatching species such that both diapause and non-diapause eggs are found during the winter season (Zhao *et al.* 2005). The late-season hatching species over-winter as eggs at early embryonic stages (Zhao *et al.* 2005). Although differences have been found among the above six grasshopper species in the low developmental threshold temperature and sum of effective thermal units for the post-diapause development of eggs, they are insufficient to explain the seasonal sequence of the grasshoppers.

Research by Hao & Kang (2004a,b) revealed species-specific adaptation to different temperature ranges for egg hatching in grasshoppers of the Inner Mongolian grasslands. The egg development of the early-season hatching species tends to adapt to a lower temperature range, the mid-season hatching species to a middle temperature range and the late-season hatching species to a higher temperature range. The late-season hatching species have a wider adaptive temperature range than the early- and mid-season hatching species for egg development (Hao & Kang 2004a,b). The springtime temperature has not been found to be an obvious factor affecting the differences in hatching time among grasshopper species. In fact, the timing of diapause determines the sequential development of grasshopper species through growth seasons (Hao & Kang 2004b). It was postulated that the temporal separation of niches, as a result of adaptation to prevailing environmental conditions over a long period of evolutionary history, could eliminate severe competition for the food supply among different grasshopper species (Kang & Chen 1994a,b).

Eggs are the only form of over-wintering strategy known in the Chinese grasshoppers (Lockwood *et al.* 1994). Therefore, cold tolerance is a critical trait in the life history of grasshopper species in the grassland ecosystems of China. Using *C. fallax* as a model insect, Hao & Kang (2004c) demonstrated that within the same grasshopper species the cold tolerance of individual eggs could differ. Their study showed that supercooling points (SCP) of the *C. fallax* eggs could vary from -6 to -32.4°C , apparently separating them into higher and lower SCP groups. The supercooling capacity differed among the pre-diapause, diapause and post-diapause embryonic stages (Hao & Kang 2004c). Studies of cold hardiness and supercooling capacity in eight grasshopper species showed that the pre-diapause and diapause eggs could survive to temperatures as low as -27°C (Hao & Kang 2004c; Zhao *et al.* 2005). Considering the local climate on the Inner Mongolian Plateau, the pre-diapause and diapause, low SCP eggs can safely survive the severe winter seasons, but not the post-diapause, high SCP eggs. *C. fallax* has been empirically proven to be a true cold-tolerant insect having low SCP eggs (Hao & Kang 2004c).

Although the grasshopper eggs over-winter as diapause and non-diapause or in different embryonic stages, most eggs can safely survive the winter season. Differences in cold tolerance have no apparent influence on the sequential development of cohorts of grasshoppers (Hao & Kang 2004a-c). Post-diapause eggs are sensitive to low temperatures, especially the abrupt decline in temperature heralding spring. Therefore, for monitoring and predicting grasshopper populations, particular attention should be paid to the temperature and the mortality of post-diapause eggs the following spring (Jing & Kang 2004). Photoperiod is also known to be an important factor influencing diapause characteristics of grasshopper eggs. Further insights could be gained into understanding mechanisms of the occurrence and termination of diapause of grasshopper eggs based on genomic studies of the locust (Kang *et al.* 2004).

(b) Chemical and behavioural ecology

Grasshoppers' antennae play an important role in host orientation, food selection and oviposition site selection. The numbers and distribution of various structural and functional types of antennal sensilla can be peculiar to a grasshopper life form and are related to development, habits or habitats for a given grasshopper species. Interrelations between grasshoppers' antennal sensilla and their food preferences and habits reflect the evolution of taxonomic groups with specialized food habits.

Five major types of antennal sensillae have been identified for 12 species in the subfamilies of Pamphaginae, Catantopinae, Oedipodinae and Gomphocerinae in the grasslands of Inner Mongolia (Chen *et al.* 2003a): trichoid, long basiconic, short basiconic, slender and short basiconic, and coeloconic sensillae. Total numbers of antennal sensillae vary with sex, subfamilies, feeding groups, life forms and eco-types (Chen *et al.* 2003a). Males have more sensillae than females due to the presence of greater numbers of

short basiconic and coeloconic sensillae. Species in the subfamily Catantopinae have longer basiconic sensillae than others, while the subfamily Oedipodinae has the greatest number of slender and short basiconic sensillae and coeloconic sensillae, followed by Catantopinae and Gomphocerinae, with Pamphaginae having the fewest. Species which prefer to stay on the ground possess fewer antennal sensillae than species that stay on plants. Moreover, species feeding on grasses possess more antennal sensillae, particularly coeloconic sensillae, compared with other feeding groups (Chen et al. 2003a).

Detection of plant odours is one way grasshoppers identify potential food sources. Electroantennogram (EAG) studies on the role of olfaction in host-plant location exhibited some specificity of grasshoppers to host-plant odours. *Oedaleus d. asiaticus* and *A. barabensis* from the subfamily Oedipodinae are major pests in the natural grasslands of the Inner Mongolian Plateau. They have sympatric distribution and synchronous seasonal activity, but different host-plant preference with *O. d. asiaticus* being graminivorous and *A. barabensis* forbivorous. Experimental studies showed that the male *O. d. asiaticus* had much stronger EAG responses than conspecific females and both sexes of *A. barabensis*, and that sexual differences in EAG responses corresponded to different numbers of antennal sensilla of both sexes and certain behavioural and morphological factors (Chen & Kang 2000). The female graminivorous *O. d. asiaticus* possessed significantly higher olfactory sensitivities for gramineous plant species than the forbivorous *A. barabensis*, whereas *A. barabensis* displayed significantly higher EAG responses to *Allium sensescens* and a tendency for high responses to mixed plant species.

Similar EAG response profiles to 37 plant volatile compounds have been found for *O. d. asiaticus* and *A. barabensis* as well as for both sexes of the same species (Chen et al. 2004a). Most of the green leaf volatiles induce higher EAG responses in both sexes of grasshoppers than terpenic compounds and some aromatic compounds. Strong EAG responses can be induced by 6-carbon alcohols (1-hexanol, Z-hexen-2-ol-1, E-2-hexen-1-ol, E-hexen-3-ol-1), an aldehyde (E-2-hexen-1-al), an ester (Z-hexen-3-yl acetate) and 7-carbon alcohols (1-heptanol) in *O. d. asiaticus* and *A. barabensis* regardless of sex. Monoterpenes with functional groups of alcohols and aldehydes are more stimulating than other monoterpenes (Chen et al. 2004a). Of the aromatics benzaldehyde induces the greatest responses from both grasshopper species. *Oedaleus d. asiaticus* has been found to have greater EAG responses than *A. barabensis* to the green leaf volatiles such as 1-decanol, 1-nonanol, 1-pentanol, hexanol, Z-hexenyl-3-yl acetate, and the sesquiterpene (–)-trans-caryophyllene (Chen et al. 2004a). Coexisting grasshopper species differentiate not only in food selection but also in olfactory responses to host plants.

(c) Ecological niche and divergence

Ecological niche and divergence determine species distribution and composition in ecosystems both spatially and temporally. For grasshoppers, physical

habitats and food sources are likely determinants of their ecological niche. Kang & Chen (1992) studied the spatial and temporal heterogeneity of grasshoppers in two grassland types of the typical steppes, *L. chinensis* and *S. grandis*, on the Inner Mongolian Plateau using multivariate analysis and diversity indices, and categorized 11 grasshopper species based on guild or assemblage. They found that three dominant grasshopper species, *Dasyhippus barbipes*, *Myrmeleotettix palpalis* and *C. dubius*, were temporally separated into early-, mid- and late-season hatching species with distinct temporal developmental sequences. The richness of grasshopper species in the temporal dimension has been found to be greatest during the mid-growth seasons for plants and lower in the early and late seasons (Kang & Chen 1992). Spatially, the richness of grasshopper species is generally greater in the *L. chinensis* steppes (approx. 11 grasshopper species) than in the *S. grandis* steppes (approx. 9 grasshopper species) due to the difference in the richness of plant species between the two grassland types.

Examination of niche differentiation shows that grasshopper species with a broad niche along at least one dimension have a narrow niche along another (Kang & Chen 1994a). Xerophytous and geocole grasshopper species usually have a wider spatial niche than mesophytous and phytocole species. Sufficient differences exist between grasshopper species for the overall overlap associated with resource use to explain coexistence in the assemblages by resource segregation. Experimental evidence suggests that the species-specific use of resources may be due primarily to niche differentiation and to coevolutionary interactions between grasshoppers and plants, rather than to interspecific competition among grasshopper species (Kang & Chen 1994a). The differentiation of spatial, temporal and trophic niches avoids interspecific competition for resources.

Microscopic dietary analysis of grasshoppers identified 31 species of vascular plants, one species of fungus and mites as food sources in the typical steppes of the Inner Mongolian Plateau (Kang & Chen 1994b). On the basis of partitioning in utilization of food resources, grasshopper species can be categorized into five feeding groups (Kang & Chen 1994b): graminivorous, mixed graminivorous, mixed forbivorous, forbivorous, and phytocarnivorous. In the grasslands of the Inner Mongolian Plateau, the grasshopper species from Pyrgomorphae and Pamphaginae are mainly forbivorous, whereas those from Gomphocerinae and other groups are graminivorous (Kang et al. 1999). The grasshopper communities on the Inner Mongolian grasslands are dominated mainly by Gomphocerinae and are principally graminivorous (Lockwood et al. 1994). Although the grasshopper species of the Inner Mongolian Plateau differ from those of Europe and North America, the evolution of taxonomic groups with specialized food habits is comparable. The mandible structures of graminivorous and forbivorous forms of these grasshopper species entirely agree with their food habits. Though the herbivorous mandibles are not distinctive, the depth of the central concavity in the molar surface is positively correlated with the proportion of dicot plants in the grasshopper diet (Kang et al. 1999).

(d) Livestock grazing and grasshopper population dynamics

Owing to the impact of grasshoppers on grassland vegetation, understanding the relationships between population dynamics of grasshoppers and grazing is vitally important. Studies of 34 species of grasshoppers from 16 types of habitat in the Xilin River Basin of the Inner Mongolian Plateau have suggested that vegetation type and moisture conditions are the main factors influencing the distribution of grasshoppers in the region (Kang *et al.* 1989).

Livestock grazing can alter the environmental conditions for grasshoppers by affecting their food resources and the spatio-temporal heterogeneity of their habitats. Changes in the plant community resulting from livestock grazing directly affect the grasshopper species composition and community structure (Kang 1994, 1995; Kang & Chen 1995). Species composition of grasshopper populations has been found to relate largely to plant biomass rather than species diversity and evenness of plants. For example, the species diversity of plants was found to be higher on moderately grazed sites (Zhou *et al.* 2006) whereas a higher species diversity of grasshoppers tended to occur on non-grazed or lightly grazed sites (Kang 1995).

Species-specific relationships between grasshoppers and plants have been found in the grasslands of the Inner Mongolian Plateau. Kang (1995) found that the biomass of grasshoppers in the subfamily Catantopinae was correlated positively with the biomass of tall grasses and negatively with the biomass of forbs and short grasses, while the biomass of grasshoppers in the subfamily Oedipodinae was correlated negatively with the biomass of grasses and total plants and positively with the biomass of forbs and leguminous plants. In the subfamily Gomphocerinae, some species are closely associated with overgrazed sites and some with floral conditions. Soil compactness and water content also significantly affect grasshopper density and community composition. Grazing at moderate intensity tends to preserve the highest plant diversity and a more diverse grasshopper community with a lower proportion of the pest species (Kang 1994, 1995). With increasing grazing intensity, the xerophytous grasshopper species become more abundant, but the mesophytous and hydrophytous species markedly decline (Kang & Chen 1995). Overgrazing often results in decreased species richness and density of grasshoppers. There also exists a species–area relationship in grasshopper assemblages which is affected by grazing (Kang & Zhang 1996). Therefore, effective grazing management can minimize the outbreaks of xerophytous grasshopper species (Kang 1995).

6. RODENTS AND GRASSLAND ECOSYSTEMS

(a) Damage to grassland

Population outbreaks of rodents frequently occur in the grassland ecosystems of China. It is estimated that 10–20% of grasslands are heavily infested by rodents causing a 20 billion kg loss of grasses every year. In the grasslands of the Inner Mongolian Plateau it has been found that each vole can eat 40 g of fresh plant material

per day, and in high-density years with up to 1384 individuals ha^{-1} , 15–44% of grass production can be consumed by voles (Zhong *et al.* 1999). In the Qinghai–Tibet Plateau, natural grasslands cover about 1.4 million km^2 ; the area of degraded grassland is up to 0.71 million km^2 of which 0.37 million km^2 are damaged by rodents. The average density of the plateau pika (*Ochotona curzoniae*) is greater than 4.29 individuals ha^{-1} and the density of plateau zokor (*Myospalax baileyi*) is about 1.07 individuals ha^{-1} (Zhang 1999). Their eating and excavating activities cause degradation of the grasslands and turn the infested area into black sandy soil. So far, the area covered by black sandy soil is estimated at about 40 000 km^2 due to infestation by plateau pika and zokor. One plateau zokor can produce about 240 mounds each year, covering 22.5 m^2 of grassland.

(b) Impact of livestock grazing

Overgrazing by livestock and the irrational use of grasslands have been identified as important factors in worsening rodent and weed infestations (Zhang *et al.* 2003d). Overgrazing facilitates rodent infestations by providing suitable habitats and food. Many rodent species in grasslands prefer to live in habitats with open spacing and avoid high grasses; plateau pikas prefer open habitats and avoid dense shrubs or thick vegetation (Fan *et al.* 1999). Grazing at high intensity can severely reduce the height and cover of vegetation and produce habitats more suitable for Brandt's vole and Mongolian gerbil (*Meriones unguiculatus*; Zhong *et al.* 1999). Substantially increased livestock numbers over the past 50 years have increased the frequency of outbreaks of Brandt's vole (Zhang *et al.* 2003c).

Under conditions of overgrazing by livestock, the succession of the degraded grasslands can be changed into a vicious circle (Zhang *et al.* 2003d): overgrazing → grassland degradation → rodent infestation → further grassland degradation.

In the grasslands of the Xilin River Basin of Inner Mongolia, the dominance of plant species changes from *L. chinensis* and *Stipa krylovii* → *Artemisia frigida*, *L. chinensis* and *Cleistogenes squarrosa* → *A. frigida*, *Potentilla acaulis* and *C. squarrosa* → *Planta annua* under light, heavy and excessive overgrazing by livestock (Zhong *et al.* 1999). Accordingly, dominance in the rodent community changes from *Cricetulus barabensis*, *Citellus dauricus* and *Ochotona daurica* → *O. daurica*, *C. barabensis* and *C. dauricus* → *Microtus brandti* → *Meriones unguiculatus* under light, heavy and excessive overgrazing. In the alpine meadow of the Qinghai–Tibet Plateau, it has been reported that both pika and zokor populations increase rapidly with increasing grazing intensity (Shi 1983; Jing *et al.* 1991; Liu *et al.* 1991; Bian *et al.* 1994; Su 2001).

(c) Pest management

Control of rodents is critical for restoring degraded grassland (Zhang *et al.* 2003d). On the Qinghai–Tibet Plateau, after chemical eradication, control of overgrazing and weeds, and the resultant increase in grasses have been very effective in containing plateau pika and zokor (Fan *et al.* 1999). In the grasslands of the Inner Mongolian Plateau, control of overgrazing reduced the

population density of Brandt's vole by 78% and increased the grass production by 40% from 1987 to 1989 (Zhong *et al.* 1999). Since the rodent population can recover quickly after chemical control, fertility control of the rodents has been recommended as an alternative method. As mating system alters the effect of fertility control, for monogamous or polygynous rodent species it is more effective if both sexes are sterilized due to mating interference (Zhang 2000b; Zhang & Zhang 2003).

Simulation by modelling indicates that fertility control offers great potential for managing populations of Brandt's vole in the grasslands of the Inner Mongolian Plateau (Shi *et al.* 2002). A mixture of the contraceptive compounds levonorgestrel and quinestrol has been demonstrated to be effective in reducing fertility of some grassland rodents like Brandt's voles (*M. brandti*), grey hamster (*Cricetulus migratorius*), striped hamster (*C. barabensis*), *Phodopus sungorus* and mid-day gerbils (*Meriones meridianus*; Zhang *et al.* 2004b).

(d) *Impact of climate change*

In the northwestern grasslands of China, precipitation has been widely recognized as a critical factor in controlling primary production. Population outbreaks of Mongolian gerbil are often closely linked to abundant precipitation due to increased food resources. Plagues usually occur immediately after rodent outbreaks. Using historical records collected between 1948 and 1998, Zhang *et al.* (2003c) found that there was significant correlation between years for which the monthly averages of the Southern oscillation index (SOI) were consistently higher and years in which outbreaks occurred. Stone *et al.* (1996) found that the SOI phases could be used to predict precipitation over central China. In general, abundant precipitation is linked to high SOI values in the grasslands of the Inner Mongolian Plateau. An El Niño Southern Oscillation (ENSO) hypothesis has been proposed to explain outbreaks of rodent pests (Zhang *et al.* 2003c), which suggests that climate anomalies affect the abundance of rodents through the availability of food, and that rodents may have developed feedback mechanisms triggered by climatic factors which are related to the irregular signals of ENSO.

(e) *Ecosystem function*

Rodents can affect the functioning of grassland ecosystems by modifying the physical environment through their feeding and nesting activities. For example, zokors deposit mounds of nutrient-poor soil on the ground surface when excavating their foraging tunnels, which facilitates nutrient cycling on infested sites. It is estimated that one plateau zokor can deposit at least 1024 kg of nutrient-poor soil on the soil surface of alpine meadow steppes each year (Wang & Fan 1987). The soil N of fresh mounds is often higher than the average N content of the adjacent soils (Wang *et al.* 1993; Zhang 2000a).

Zokor mounds change plant biomass and species composition by altering soil nutrient composition, surface irradiance and interspecific competition

among grassland plants (Wang & Du 1990; Zhang *et al.* 1994). The flora in zokor mounds clearly differs from the surrounding areas (Wang & Du 1990; Bian *et al.* 1991; Zhang *et al.* 1994; Zhang 2000a). The aboveground biomass of plants around the zokor mounds is higher than in other areas (Wang *et al.* 1993). Forbs are often more abundant on the zokor mounds (Bian *et al.* 1991; Zhang *et al.* 1994). However, long-term colonization by zokors could result in grassland degradation with reduced plant biomass and species diversity. It was found that the biomass, heights and cover of vegetation declined significantly in a habitat colonized by plateau zokors for over 10 years, and that the growth of monocotyledons was constrained (Zhang *et al.* 2003b). Toxic plants such as *Ajania tenuifolia* and *Elsholtzia calycocarpa* become dominant in areas with prolonged colonization by zokors (Zhang *et al.* 2003b).

The burrows of zokor and pika provide suitable habitats for many other species. Some rodent species, such as root voles (*Microtus oeconomus*) and Gansu pikas (*O. cansus*), depend on abandoned burrows for breeding and escaping from predators. Many birds such as the ground jay (*Pseudopodoces humilis*) and several species of snow finch (*Montifringilla adamsi*, *M. blanfordi*, *M. davidiana*, *M. ruficollis* and *M. taczanowski*), also depend on the burrows of pika and zokor for nests or reducing predation risks (Zhang 1982; Smith *et al.* 1990; Smith & Foggin 1999).

Clearly, rodents have certain beneficial effects on the grassland ecosystem; they are not just pests.

7. FUTURE RESEARCH OUTLOOKS

To date, research on the grassland ecosystems of China has been mostly single-discipline-based and at a relatively small scale. Future research needs to adopt holistic approaches to interactions between plants and insects, plants and animals, plants and micro-organisms, and the system responses and feedbacks to global climate change. More attention should be paid to utilizing multidisciplinary and integrative research approaches linking the processes at multiple scales, e.g. from molecular, through species to communities, to landscape and regional scales.

There are continued efforts to understand the belowground processes, in particular interactions among plant roots, soil fauna and micro-organisms, and the associated biophysical and biochemical processes of the grassland ecosystems. Currently, one of the largest multi-factor experiments involving manipulations of precipitation, soil temperature and nutrients, and simulated grazing in a grassland ecosystem has been established in an agro-pastoral ecotone of Inner Mongolia. The experiment brings together a large team of scientists in the research fields of soils, vegetation, insects, grassland animals and global change, and provides a unique platform for increased international collaborations and multi-national research projects led by Chinese grassland ecologists.

As an integral part of the Eurasian grassland ecosystem and one of the largest continuously distributed grasslands, opportunities exist for using the natural grasslands on the Inner Mongolian

Plateau of northern China as a model system to test ecosystem theories that so far have proven a challenge to ecologists worldwide. Future research of significant socio-economic benefit may include large-scale resource management incorporating sustainability.

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