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Grazing primarily drives the relative abundance change of C_4 plants in the typical steppe grasslands across households at a regional scale

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Abstract. Increases in temperature and grazing intensity are believed to promote the relative abundance of C_4 plants in grassland communities in Inner Mongolia. However, there is a lack of understanding as to which factor is the primary driver at the household scale. The relative abundance of C_4 plants in grassland communities within 32 households was monitored over a 5-year period (2008–12) in the typical steppe region of Inner Mongolia. The relationships between the mean annual temperature, grazing intensity and their combinations on the patterns of the relative abundance of C_4 plants across the land managed by these households were analysed. The results showed that (1) the herbage mass of the typical steppe grassland was mainly composed of C_3 plants (87%); (2) the C_4 plants were more sensitive to, and can be used as indicators of, environmental changes. These C_4 species included *Cleistogenes squarrosa* (Trin.) Keng, *Chenopodium glaucum* Linn. and *Salsola collina* Pall.; (3) both increasing temperature and grazing intensity promoted the relative abundance of C_4 plants. Grazing intensity was the primary driver of the change in relative abundance of C_4 plants in this region. Not only did grazing change the micro-environment of the grasslands, but also the C_3 species were preferentially grazed by the livestock. Comparison of the results with previous studies on the temporal variation in the abundance of C_4 plants suggests that the relative importance of grazing and climatic factors depends on the spatial scales of the studies, with climate being of greater importance at the regional rather than the household scale.

Additional keywords: grazing intensity, grazing preferences, Inner Mongolian grassland, temperature.

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Introduction

Terrestrial vegetation is composed of 95% C_3 plants and 5% C_4 plants (Su *et al.* 2011), but C_4 plants contribute about 20% of global gross primary productivity (Wand *et al.* 1999). The C_4 pathway of photosynthesis in the dicots originated in arid regions at low latitudes and C_4 grasses and sedges dominate nearly all grasslands in the tropics, subtropics and warm temperate zones and are major components of arid landscapes from the temperate regions to the tropics (Archibold 1995; Sage *et al.* 1999). The relative abundance of C_4 plants is not only an aspect of ecosystem structure, but more importantly, it reflects ecosystem functions (Snyder and Tartowski 2006; Sierra *et al.* 2010). Thus, studies on the relative abundance of C_4 plants have become more important in the context of global climate change (Kohn 2010; Wittmer *et al.* 2010; Scheiter *et al.* 2012).

The concentration of CO_2 in the atmosphere, air temperature, and land-use patterns are generally considered to be the main drivers that influence the relative abundance of C_4 and C_3 species (Zech *et al.* 2009; Pushkina *et al.* 2010; Wittmer *et al.* 2010). Compared with C_3 plants, C_4 plants have higher water-use efficiency and greater photosynthetic rates at low atmospheric CO_2 concentrations resulting in greater growth under these conditions (Farquhar *et al.* 1989; Leegood 2013). A series of studies on paleoclimate climate modelling, and vegetation changes have confirmed the fact that the relative abundance of C_4 plants will decrease with increasing atmospheric CO_2 concentration (Cerling *et al.* 1993; Scheiter *et al.* 2012; Ripley *et al.* 2013). However, some studies did not fully support this view (Owensby *et al.* 1999; Tooth and Leishman 2013). Then researchers gradually realised the importance of temperature. On one hand, C_4 plants appear only if the temperature is above a certain threshold (Teeri and Stowe 1976; Sage 2004). The optimum temperatures for many C_4 species are about 35°C and at temperatures lower than about 15°C, the growth of most C_4 species virtually stops. The optimum for many C_3 species is about 20–25°C and growth will continue down to close to 0°C (McWilliam 1978). On the other hand, a temperature rise would directly affect the relative C_3 and C_4 plant growth and dry matter accumulation and would ultimately determine the relative abundance of the two groups in the vegetation (Sage and Kubien 2007; Wittmer *et al.* 2010).

Disturbance, including grazing, fire, and roads related to land-use change, also have different effects on the growth and reproduction of C_3 and C_4 plants and can lead to changes in their relative abundance (Pushkina *et al.* 2010; Collins and Calabrese 2012; Scheiter *et al.* 2012; Way 2012). Animal grazing is the most dominant land use of grasslands (Mavromihalis *et al.* 2013). Grazing influence on the relative abundance of C_4 plants has received much attention in the study of grasslands in North and South America (Reeder *et al.* 2004; Altesor *et al.* 2006; Derner *et al.* 2006), Central Asia (Auerswald *et al.* 2012; Ren *et al.* 2012), South Africa (Franz-Odendaal *et al.* 2002), Australia (Bell *et al.* 2012) and New Zealand (Crush and Rowarth 2007). Most of these studies suggest that grazing increases the relative abundance of C_4 species in some plant communities (Reeder *et al.* 2004; Waters *et al.* 2005; Fanselow *et al.* 2011). Two reasons may explain these results. Firstly, grazing may have changed the micro-environment. Secondly, the foraging preferences of herbivores caused by the different palatability of C_3 and C_4 plants (McPherson and Rasmussen 1989), as well as differences in their digestibility could mean that the animals select either C_3 or C_4 plants (Whalley 1994; Norman *et al.* 2009). However, other studies suggested that grazing had no effects on the relative abundance of C_4 plants (Derner *et al.* 2006; Auerswald *et al.* 2012).

Since the household is the basic management unit of the grasslands in Inner Mongolia (Hou *et al.* 2012), the objective of the present work was to understand the relative importance of grazing and temperature in determining the relative abundance of C_4 plants in these grasslands at this scale. Bearing in mind that temperature may affect the relative abundance of C_4 plants at a large temporal-spatial scale, grazing may play a more important role at a smaller temporal-spatial scale (Franz-Odendaal *et al.* 2002; Reeder *et al.* 2004; Bell *et al.* 2012).

We hypothesise that, at the household scale, grazing is the primary driver for the changes in the relative abundance of C_4 plants in grassland communities in Inner Mongolia. To verify this hypothesis, we selected 32 households in the Baiyinxile ranch, located in a typical steppe grassland region in Inner Mongolia, and monitored the relative abundance of C_4 plants during 2008–12. We also determined the mean annual temperature and grazing intensity at each household, and analysed the effects of these two factors and their combinations on the relative abundance of C_4 plants. This study aimed to enrich the understanding of the changes in the relative abundance of C_3 and C_4 plants in response to environmental factors, and provide a better basis for assessing the effects of climate and land-use change on grassland ecosystem structure and functioning, and provide support for the development of improved management strategies.

Materials and methods

Study area

This study was conducted on the Baiyinxile ranch, Xilingol league of Inner Mongolia (Fig. 1), ranging from 116.03°E to 116.79°E and 43.69°N to 44.27°N. Gentle hills and high plains constitute the major terrain with altitude ranging from 1126 m to 1384 m above mean sea level. It is a temperate continental

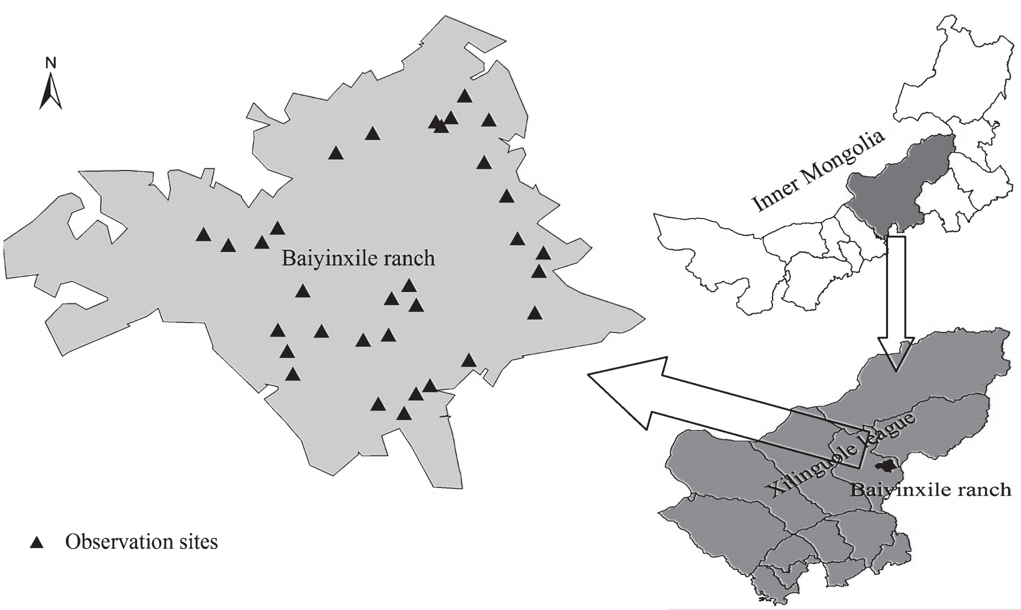

Fig. 1. Location map of Inner Mongolia showing the study region (Xilingol league), the Baiyinxile ranch and the sampling sites.

climate, characterised by a mean annual temperature of –0.1°C, and mean annual precipitation of 350 mm. The main soil type is a chestnut soil. The region is covered by typical steppe vegetation with *Stipa grandis* P.Smirn. and *Leymus chinensis* (Trin.) Tzvel. as the major dominant species. The 'double rights one system' land policy began in 1999 and was fully implemented in 2003. It is the semi-private property rights, which mean that both the livestock and grassland are contracted to herder households, but the grasslands belong to the state (Li *et al*. 2007). Thus, individual households became the basic production and management units at that time. The most common grazing animals were sheep, goats and cattle in this area.

Vegetation survey

Vegetation data were collected from 2008 to 2012 between the end of July and mid-August when the aboveground biomass is at its peak. The grasslands within 32 households (all with long-term grazing from 2003) were investigated. In each household, an area of 10 × 10 m was selected and monitored during the whole period. The grasslands at all these sites were dominated by *Stipa* species (*S. grandis* or *S. krylovii* Roshev). The grazing intensity at each site was estimated based on the distance of the site from the housing and sheepfolds, that is, a greater intensity was estimated for sites close to the housing and sheepfolds. The average distance of a site from housing was 500 m (An and Han 2011). Since topography, grassland community type and plant patches all affect the foraging behaviour of sheep (Senft *et al.* 1987), we selected the monitoring site within each household to ensure that the selected site was representative of the average grazing intensity within the household. Each site was selected (Wang *et al.* 1999) on flat land and in an area where the vegetation reflected, as much as possible, the overall vegetation condition of the household and having the lowest heterogeneity. All sites were located with a global positioning system device. At peak plant biomass, three 1 × 1-m plots were randomly placed at each site to determine aboveground plant biomass by harvesting species by species and drying at 65°C (for ~24 h) in the laboratory. Each year, care was taken to ensure that the new sampling sites were not at the same locations that had been previously sampled. All species were grouped into C_3 or C_4 species (Tang and Liu 2001), and the relative abundance of C_4 species was calculated as their proportion of the total aboveground biomass of the grassland at each site. The monitoring of vegetation on all the 32 sites lasted for 5 years, and during this period, six C_4 species were recorded: *Artemisia sieversiana* Ehrhart ex Willd., *Cleistogenes squarrosa* (Trin.) Keng, *Chenopodium aristatum* L., *Ch. glaucum* L., *Kochia prostrata* (L.) Schrad. and *Salsola collina* Pall. and 53 C_3 species were recorded.

Temperature and grazing intensity data collection

The vegetation monitoring started in 2008, but portable weather stations (Kestrel 4500, USA) were not established on the 32 sites until 2012. The mean annual temperature data for 2012 were obtained from these portable weather stations, whereas the information for 2008–11 was derived from the nearby Xilingol meteorological station. All the sites were within 40 km of this station but at different altitudes. The established adiabatic lapse rate is –0.6°C 100 m^{-1}, so the mean annual temperature at each site was estimated using following formula:

$$T_s = T_m - (A_s - 1226.38)/(100 * 0.6)$$

where T_s and A_S are the annual mean temperature and altitude at a site, and T_m (°C) and 1226.4 m are the annual mean temperature and altitude, respectively, at Xilinhot meteorological station.

The accuracy of these calculations was verified by comparing the estimated values for 2012 against that recorded by the portable weather stations. The correlation between the estimated and recorded data across the 32 sites was significant ($P < 0.01$) and indicated the high reliability of the calculation method (Fig. 2).

We calculated the grazing intensity at each of the 32 households for each year, using the pasture area divided by standardised sheep units (SU). The average distance of a site from housing, sheepfolds or a water-point was 500 m. Therefore, we can minimise the error caused by the distance to grazing intensity. The number of different livestock at each household were surveyed along with the vegetation survey each year, and were converted into the number of SU based on their feed requirements (Li and Ji 2004), i.e. for cattle, horses, or mules, 1 animal = 5 SU, and 1 lamb = 0.5 SU.

Data analyses

The sensitivity of C_3 plants, C_4 plants and each of the six C_4 species to environmental factors was tested by calculating the coefficient of variation (CV) of their aboveground biomass across the 32 households from 2008 to 2012. We also calculated Pearson correlation coefficients between grazing intensity, mean annual temperature, and the relative abundance of all and each of the six C_4 species. To examine the effect of temperature and grazing on the relative abundance of C_4 plants, four different detrended canonical correspondence analyses (DCCA) were run based on Borcard points (Borcard *et al.* 1992) using three matrices of data of the relative abundance of C_4 plants, mean annual temperature and grazing intensity (each matrix consisted

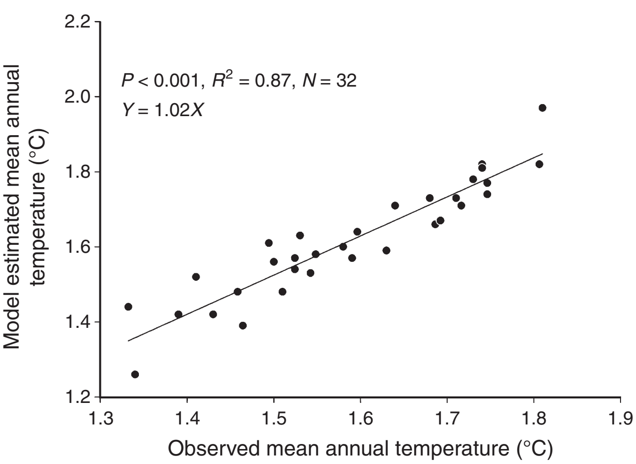

Fig. 2. The relationship between observed mean annual temperature using portable weather stations and the model-estimated mean annual temperature based on the altitude of the studied sites and data from the Xilingol meteorological station.

of 32 households and 5 years). The separate and coupled effect of temperature and grazing, as well as the effects of all other factors on the relative abundance of C_4 plants, were assessed using the ratio of the total variation of the relative abundance of C_4 plants to the variation of temperature, grazing intensity, temperature × grazing intensity, or all other factors. That is, we first calculated the effect of temperature (Et) and grazing intensity (Eg) on the relative abundance of C_4 plants using the constrained ordination analysis with temperature or grazing intensity, respectively, as the constrained factor. Then we calculated the effect of only temperature (Et0) and only grazing intensity (Eg0) by the same approach after exclusion of the effect of grazing (with grazing intensity as a co-variable) or the effect of temperature (with temperature as a co-variable), respectively. Based on these calculations, the coupling effect between temperature and grazing was calculated as (Et-Et0) or (Eg-Eg0), and the effect of all other factors was 1 – (Et + Eg0) or 1 – (Et0 + Eg).

All statistical analyses were performed using SPSS 17.0 and Canaco 4.5 (Braak and Smilauer 2002).

Results

The status of C_3 and C_4 plants

Averaged over all 32 sites, the percentage of C_3 plants in the plant biomass was 87.7% (Fig. 3). The contribution of C_4 plants to community biomass decreased from 28.2% in 2008 to 6.9% in 2012, and was 12.3% on average.

Variation of C_3 and C_4 plants across the 32 households

We calculated the CV of aboveground biomass of C_3 and C_4 plants at the 32 sites from 2008 to 2012. The CV of C_4 plants (69%) was greater than that of C_3 plants (53%) (Fig. 4). There were also differences in CV among the six C_4 species: *C. squarrosa*, *Ch. aristatum*, *Ch. glaucum* and *S. collina* had a higher CV, while *A. sieversiana* and *K. prostrata* had a lower CV. The lower CV of these latter two species was mainly related to their lower frequency in the studied grasslands. *Artemesial sieversiana* only appeared at two sites in 2009 and 2011, and *K. prostrata* appeared at three sites in 2008, 2009 and 2012.

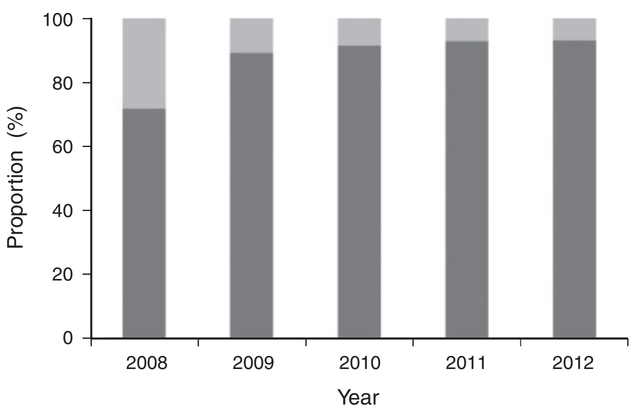

Fig. 3. The proportion of C_3 (dark shading) and C_4 (light shading) plants in the aboveground biomass of grassland from 2008 to 2012.

Relationships between grazing intensity, mean annual temperature and the relative abundance of C_4 plants

The relative abundance of all the C_4 plants showed a positive correlation with grazing intensity and with mean annual temperature across the 32 households (Fig. 5*a1*, *a2*). The relative abundance of *C. squarrosa*, *Ch. glaucum*, and *S. collina* was also significantly correlated with grazing intensity or mean annual temperature, respectively (Fig. 5*b1*, *c1*, *d1*, *b2*, *c2* and *d2*). These results showed that the relative abundance of these three C_4 species was higher with a high grazing intensity and a high mean annual temperature.

Contribution of temperature and grazing to change in the relative abundance of C_4 plants

Based on four different DCCA analyses, we determined the separate effects of temperature alone, grazing intensity alone and the coupling effects of temperature and grazing intensity, as well as the effects of all other factors on the variation in the relative abundance of C_4 species (Table 1). Grazing intensity

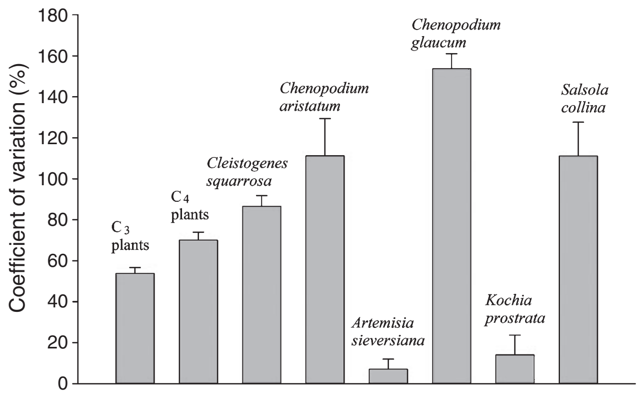

Fig. 4. The coefficients of variation of all C_3 plants, all C_4 plants and six C_4 species: *Cleistogenes squarrosa* (Trin.) Keng, *Chenopodium aristatum* L., *Ch. glaucum* L., *Salsola collina* Pall., *Artemisia sieversiana* Ehrhart ex Willd., and *Kochia prostrata* (L.) Schrad. across 32 grassland sites during 2008–12.

Table 1. Results of detrended canonical correspondence analyses and partitioning of the variation of the relative abundance of C_4 plants among different variables

Total variation of the relative abundance of C_4 plants	0.1999
Sum of canonical eigenvalues for:	
Temperature-constrained analysis	0.0852
Grazing-constrained analysis	0.1071
Temperature-constrained analysis after removing effect of grazing	0.0602
Grazing-constrained analysis after removing effect of temperature	0.0821
Variation of the relative abundance of C_4 plants explained by:	Percentage
Temperature	42.6
Grazing	53.4
Temperature only	30.1
Grazing only	41.1
Coupled effect of temperature and grazing	12.5
All other factors	16.3

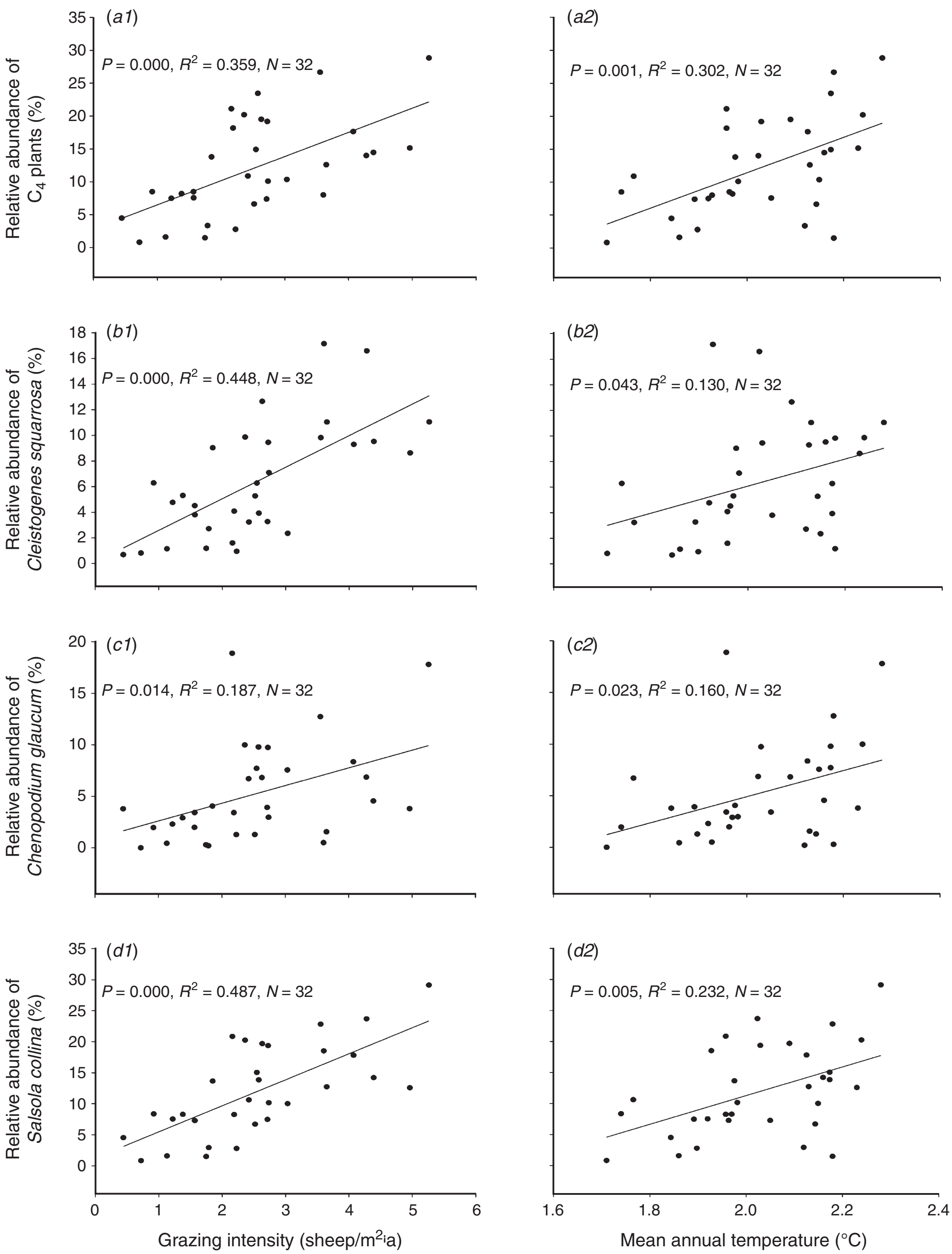

Fig. 5. Changes in the relative abundance of all C_4 plants plus the relative abundance of three individual C_4 species in the aboveground biomass with increasing grazing intensity or increasing mean annual temperature at the Baiyinxile ranch, Inner Mongolia.

explained 53.6% of the variation, among which 41.1% was explained by grazing intensity alone. Temperature explained 42.6% of the variation, and 30.1% of which was explained by temperature alone. Only 12.5% of the variation was explained by the coupled effects of temperature and grazing; and all other factors explained the rest (16.3%). Thus grazing and temperature together led to the differences in relative abundance of C_4 species, and the effects of grazing was greater than those of temperature.

Discussion

Both temperature and grazing can promote the abundance of C_4 plants

It is widely considered that higher temperatures are generally associated with greater abundance of C_4 plants (Zheng *et al.* 2011; Auerswald *et al.* 2012). Our data supported this statement in that there was a decrease in the abundance of C_4 species associated with a decrease in temperature over the years 2008–12 (Figs 3 and 5*a*2). This is because C_4 species have a competitive advantage in environments with higher temperatures, lower CO_2 concentrations, higher solar radiation, and lower soil moisture contents (Sage and Kubien 2007). The rising temperatures and associated climatic aridity predicted by climate-change scenarios (Kang *et al*. 2011) are therefore likely to lead to an increase in the abundance of C_4 species in the Inner Mongolia grasslands.

Although there is some dispute about whether grazing can affect the relative abundance of C_4 plants (Derner *et al.* 2006; Fanselow *et al.* 2011), a series of studies carried out in the Inner Mongolian steppe have found that grazing intensity can indeed increase the relative abundance of C_4 plants (Wang 2002; Fanselow *et al.* 2011; Zheng *et al.* 2011). Our results at the household scale also support these earlier findings (Fig. 5). Three reasons may explain these results. Firstly, grazing suppresses C_3 plants more than C_4 plants and C_4 plants turn generally green later than C_3 plants (by 6 weeks, see Liang *et al.* 2002), and thus avoid grazing damage in early spring. In addition, C_4 species (mainly *C. squarrosa*) also have a lower canopy (<10 cm) than C_3 plants (20–50 cm) and thus avoid being grazed by cattle (Wang *et al.* 2003). Secondly, removal of the biomass of C_3 plants through grazing enhances the intensity of light reaching the ground and the action of wind, creating a drier and warmer micro-environment (Teeri and Stowe 1976; Li *et al.* 2000), which facilitates the development of C_4 plants (Sage 2004). The shade from tall C_3 plants not only reduces the light availability for short grasses, but also changes the proportion of infrared/far-infrared (Casal *et al.* 1987). Controlled experiments have demonstrated that the proportional reduction of infrared/far-infrared light can reduce the tillering of *C. squarrosa* (Deregibus *et al.* 1985; Casal *et al.* 1987), the major C_4 species in the studied grassland. Infrared light intensity diminishes to a greater extent than far-infrared when light is filtered through the plant canopy, thus removal of the upper plant canopy by grazing will increase the infrared/far-infrared ratio of the light reaching the short grasses, and will enhance the tillering of *C. squarrosa*. The last and perhaps the most important reason is the differences in the preference (McPherson and Rasmussen 1989) and digestibility (Norman *et al.* 2009) of the C_3 and C_4 species. Yokohama *et al*. (2011) reported that the species most preferred by grazing livestock on the Mongolian plateau [*S. glareosa*, *P. smirnov*, *S. krylovii*, *Achnatherum splendens* (Trin.) Nevski, *Agropyron cristatum* (L.) Gaertn., *Elytrigia repens* (L.) Nevski, *L. chinensis*, *Poa pratensis* L., *Artemisia frigid* Willd., and *Caragana pygmaea* (L.) DC. etc.] are all C_3 species. These species maintain the forage production of Inner Mongolian grasslands. The results of Norman *et al.* (2009) indicated that the C_4 species in the region have lower digestibility values than C_3 species and so the grazing livestock tend to prefer the C_3 species.

Grazing affects the relative abundance of C_4 plants more than temperature at the household scale

Scale is widely considered to be the main cause of differences among ecological models because of the operation of different mechanisms at different scales (Wu and Loucks 1995). Temperature is the most important factor in the evolution of paleoclimates (Zhang *et al.* 2003; Pushkina *et al.* 2010) and the change in relative abundance of C_4 plants on a large scale (Sage 2004; Wittmer *et al.* 2010). Auerswald *et al.* (2012) found that C_4 abundance in an Inner Mongolia grassland system is driven by a temperature-moisture interaction, not grazing pressure. Our study shows that grazing had a greater effect than temperature in altering the abundance of C_4 plants at the small scale across households, which is in agreement with similar conclusions in other studies (Fanselow *et al.* 2011). Scale must be taken into account when defining the relative effects of different factors on ecological processes and functions, including the effects on the abundance of C_4 plants.

However, our results are different from those of Auerswald *et al.* (2012). In their study, the temporal variation in the abundance of C_4 plants was measured at one site that experiences large inter-annual variation in climate (temperature as well as precipitation) but under a small range of grazing intensities (02.25 SU ha^{-1}), while our study considered the spatial variation in the abundance of C_4 plants on grasslands across 32 households, where the variation in mean annual temperature was small, and the range of grazing intensities was large (0–5.25 SU ha^{-1}). The contrasting results of Auerswald *et al*. (2012) and ours indicate that the relative importance was dependent on the relative scales of the different factors. For the same group of factors, those with more variation would have greater effects than those with less variation.

C_4 plants, especially C. squarrosa*,* Ch. glaucum*, and* S. collina*, can be used as important indicators for monitoring Inner Mongolian grasslands*

Changes in a range of environmental factors, including grazing, temperature, road construction and precipitation, at both large scale and small scales, can affect changes in the biomass of C_4 plants (Jolly and Haxeltine 1997; Pushkina *et al.* 2010; Sinninghe Damsté *et al.* 2011; Collins and Calabrese 2012; Scheiter *et al.* 2012; Way 2012). In our study, the CV of C_4 species was higher than that of C_3 species (Fig. 4) implying that C_4 plants exhibited a greater sensitivity to environmental change than the C_3 plants. In particular, three C_4 species: *C. squarrosa*, *C. glaucum*, and *S. collina*, not only showed more sensitivity to environmental change (Fig. 4), but they also all showed an increasing abundance with increased grazing pressure and temperature (Fig. 5). Thus, the changes in the abundance of these species could be used as indicators for detecting climate change and human disturbance in Inner Mongolian grasslands.

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