Photosynthetic pathway types of forage species along grazing gradient from the Songnen grassland, Northeastern China

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Abstract

Photosynthetic pathway types (C_3 and C_4 species) and their dynamics along grazing gradient were determined for 42 plant species in 30 genera and 13 families from the Songnen grassland, Northeastern China. Of the total, 10 species in 9 genera and 4 families had C_4 photosynthesis; 32 species in 21 genera and 12 families had C_3 photosynthesis. The proportion of C_4 species in total plants and C_4/C_3 increased with grazing intensity, and peaked in overgrazed plot. Most of the increased C_4 species (6 of 10) along the grazed gradient were annual grasses and halophytes. This indicated that the C_4 species had greater capacity to tolerate environmental stresses (*e.g.* drought and saline) caused by animal grazing in the Songnen grassland, Northeastern China.

Additional key words: C_3 and C_4 species; grazing intensity.

Introduction

The classification of plant species into photosynthetic pathway types has received much attention (Downton 1975, Raghavendra and Das 1978, Waller and Lewis 1979, Li 1993, Redmann *et al.* 1995, Tang and Zhang 1999) since the works by Downton and Tregunna (1968) and Black (1971). Theoretical studies by Downton (1975), Raghavendra and Das (1977), Waller and Lewis (1979), Mateu Andrés (1993), Li (1993), Redmann *et al.* (1995), and Sayed and Mohamed (2000) have examined the list of C_4 plants for many types of vegetation or regions. The most researches were focused on the geographical distribution of C_3 and C_4 plants and relations with climate (Williams and Markley 1973, Teeri and Stowe 1976, Teeri *et al.* 1980, Collins and Jones 1985, Takeda and Hakoyama 1985, Ueno and Takeda 1992, Yin and Li 1997, Wang *et al.* 1997). Some have tested the physiological adaptation of C_3 and C_4 plants from grassland region (Redmann *et al.* 1995, Wang *et al.* 1997). Few have advanced hypotheses about latitudinal distribution of C_4 species (Teeri and Stowe 1976, Teeri *et al.* 1980), but no one has looked at the relation of photosynthetic pathway types with vegetation succession and grassland management.

The Songnen grassland is in the central part of Northeastern China (43°30' to 48°40' N; 121°30' to 127°00' E), about 40 % of which is *Leymus chinensis* (Trin.) Tzvel. grassland. Grasslands dominated by this species are widely distributed at the eastern end of the Eurasian steppe zone, the main locations in China being the Songnen plain and the eastern part of the Inner Mongolian plateau. The high palatability of the species and the herbage production superior both in quality and in quantity make the grasslands ideal for grazing and mowing in the area (Wang and Ripley 1997). There has, however, been deterioration and salinization of the grassland since the 1960s. Increasing demand for agricultural land has resulted in both the reduction in size of grassland and the need for it to support more livestock. This increase in grazing pressure has led to a substantial reduction in canopy cover throughout much of the grassland, combining with soil compaction, salinization, and drought.

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Materials and methods

Study site: The study was conducted in a native *L. chinensis* grassland located near the Grassland Ecology Field Station of Northeast Normal University, on the Changling Horse Breeding Farm, Jilin province, China. The site, located at 44°45'N, 123°45'E, is in a flat, low-lying southern part of the Songnen grassland. The soil is a meadow chernozem, having 0.75-4.00 % organic matter in the surface layer, which has developed saline-sodic characteristics because of restricted drainage (Wang 1997, Wang and Ripley 1997). Grazing has been heaviest in the vicinity of gates to grazed area, water supply, and the camp near the centre of the grassland, resulting in large patches of seriously deteriorated vegetation and salinized soil, while elsewhere the vegetation condition varies from fair to very good. Some soil characteristics of the grassland along the grazing succession gradient are shown in Table 1. This spatial pattern of grazing related to the animal diet selection provided the gradient on which this study is based.

Climate: The area has a continental climate, with large seasonal temperature and precipitation changes. The mean annual air temperature is about 5 °C, with monthly changes ranging from −18 °C in January to +23 °C in July. The annual precipitation ranges from 300 to 600 mm, of which 80-90 % falls between May and September. The main characteristics of the climate of the region are: a cold, dry, frequently windy spring; a warm, wet summer, with frequent droughts; early autumn frosts; and a long cold winter with relatively little snowfall. A more detailed description of the climate of the area may be found in Ripley *et al.* (1996).

Methods: Locations within the grassland were selected using the importance value (IV) of the dominant species (*L. chinensis*) as a scale of deterioration. Areas having IVs of 100, 80-100, 65-80, 45-65, 25-45, and 0-25 % were chosen to represent six grazing treatments: control (CK), lightly grazed (LG), moderately grazed (MG), heavily grazed (HG), overgrazed (OG), and extreme grazed (EG), respectively (Wang 1997, Wang and Ripley 1997). These areas had been grazed at the observed intensities for at least 5 years prior to this study. Plants and soil in each grazing intensity were sampled using 30 randomly located 1×1 m^2 quadrates, in early May and mid-August. All species were recorded in each. C_3 and C_4 plant identification refers to Takeda and Hakoyama (1985), Li (1993), Redmann *et al.* (1995), Yin and Li (1997), and Wang *et al.* (1997). Nomenclature follows Kitagawa (1979) and Redmann *et al.* (1995) (Table 2).

Surface soil samples (0-20 cm) were collected from each of the above plant quadrates and analysed for bulk density, pH, moisture, and organic matter. The pH measurements were taken with a model *HS-3C* pH meter (*Shanghai Rex Instruments Factory*, Shanghai, China). Soil moisture was measured gravimetrically. Soil organic matter was determined using titration method.

Table 1. Properties of grassland soil (0-20 cm depth) in relation to intensity of grazing from Northeastern China. Values for each grazing intensity differ significantly from each other ($p < 0.05$) except those with the same superscript letter. Grazing intensity: CK = ungrazed, LG = lightly grazed, MG = moderately grazed, HG = heavily grazed, OG = overgrazed, EG = extreme grazed.

Soil characteristic	Grazing intensity CK	LG	MG	HG	OG	EG
Bulk density [g m^{-3}]	116 ^{a}	118 ^{a}	121	146	160 ^{b}	163 ^{b}
pH	8.1 ^{c}	8.2 ^{c}	8.5	9.2	9.8 ^{d}	10.0 ^{d}
Moisture [%]	21.44 ^{e}	21.30 ^{e}	19.25	17.25	15.50	13.24
Organic matter [%]	2.77 ^{f}	2.75 ^{f}	2.24	1.76	1.25	0.75

Results

Floristic composition and plant categories: Forty-two species, about 12 % of the total plant species in the Songnen grassland of northeastern China, in 30 genera and 13 families in the grazing area were identified (Table 2). 32 species in 21 genera and 12 families had C_3 photosynthesis; 10 species in 9 genera and 4 families had C_4 photosynthesis. Of the C_4 species, 7 species were found in *Monocotyledonae*, 6 species in *Graminae*, 1 species in *Cyperaceae*, 3 species in *Dicotyledonae*, 2 species in *Chenopodiaceae*, and 1 species in *Amaranthaceae*.

Of the 32 C_3 species, 13 species were non-halophytic perennial species (*e.g.* *L. chinensis*, *C. epigeios*, *Carex duriuscula*), 2 were legumes (*Gueldensfaedtia stenophylla*, *Oxytropis myriophylla*), 11 were halophytes (*e.g.* *Suaeda corniculata*, *S. glauca*, *S. heteroptera*), and 6 were invaders (*e.g.* *Potentilla anserina*, *P. chinensis*, *P. filipendula*). Of the C_4 species which was about 1/3 of the C_4 species identified in the Songnen grasslands, 3 species were annual grasses (*Chloris virgata*, *Echinochloa caudata*, *Setaria viridis*), *E. caudata and S. viridis* were also non-halophytic annual grasses; 3 were invaders (*E. caudata*, *S. viridis*, *Amaranthus retroflexus*), 4 were halophytes (*Aeluropus littoralis*, *Chloris virgata*, *Kochia scoparia*, *K. sieversiana*), and 2 were non-halophytic

Table 2. Photosynthetic pathway (C_3 or C_4) in species along the grazing intensity from grasslands of northeastern China. Grazing intensity: CK = ungrazed, LG = lightly grazed, MG = moderately grazed, HG = heavily grazed, OG = overgrazed, EG = extreme grazed. Nomenclature follows Kitagawa (1979) and Redmann *et al.* (1995). Plant categories: NP = nonhalophytic perennial species, NA = nonhalophytic annual species, LE = legume, HA = halophyte, IN = invader (Wang and Ripley 1997).

Species	C_3/C_4	Category	Grazing intensity
Dicotyledonae			
Amaranthaceae			
Amaranthus retroflexus L.	C_4	IN	MG
Chenopodiaceae			
Kochia scoparia (L.) Schrad.	C_4	HA	OG EG
K. sieversiana (Pall.) C.A. Mey.	C_4	HA	OG EG
Suaeda corniculata (C.A. Mey.) Bunge	C_3	HA	OG EG
S. glauca Bunge	C_3	HA	HG OG EG
S. heteroptera Kitag.	C_3	HA	OG EG
Compositae			
Artemisia anethifolia Weber	C_3	IN	MG HG OG
A. anethoides Mattf.	C_3	HA	HG OG
A. scoparia Waldst.	C_3	IN	HG OG
Ixeris sonchifolia Bunge (*Paraixeris sonchifloia* (Bunge) Tzvelev)	C_3	NP	LG MG HG
Saussurea glomerata Poir.	C_3	NP	CK LG MG
S. runcinata DC	C_3	HA	CK LG MG
S. glabra Rupr.	C_3	NP	CK LG
Taraxacum mongolicum Hand.	C_3	IN	MG HG OG
Fabaceae			
Gueldensfaedtia stenophylla Bunge	C_3	LE	CK LG
Oxytropis myriophylla DC	C_3	LE	CK LG MG
Plumbaginaceae			
Limonium bicolor (Bunge) O. Kuntze	C_3	HA	LG MG HG
Polygonaceae			
Polygonum sibiricum Laxm.(*Pleuropteropyrum sibiricum* Kitag.)	C_3	HA	OG EG
Primulaceae			
Glaux maritima L.	C_3	NP	CK LG
Ranunculaceae			
Clematis hexapetala Pall.	C_3	NP	CK LG
Thalictrum simplex L.	C_3	NP	CK LG
T. squarrosum Steph.	C_3	NP	CK LG MG
Rosaceae			
Potentilla anserina L.	C_3	IN	LG MG HG
P. chinensis Seringe	C_3	IN	LG MG HG
P. filipendula Willd.	C_3	IN	LG MG HG
Sanguisorba officinalis L.	C_3	NP	MG HG
Monocotyledonae			
Cyperaceae			
Bolboschoenus maritimus (L.) Pall.	C_4	NP	MG HG
Carex duriuscula C.A.M.	C_3	NP	MG HG OG
Graminae			
Aeluropus littoralis (Gouan) Parlat	C_4	HA	HG OG
Arundinella hirta (Thunb.) Tanaka	C_4	NP	CK LG MG
Calamagrostis epigeios (L.) Roth	C_3	NP	CK LG MG
Chloris virgata Sw.	C_4	HA	LG MG HG OG EG
Cleistogenes squarrosa (Trin.) Keng	C_4	NP	MG HG OG
Echinochloa caudata Roshev.	C_4	IN	HG OG
Leymus chinensis (Trin.) Tzvel.	C_3	NP	CK LG MG HG OG
Poa pratensis L.	C_3	NP	CK LG
Puccinellia chinampoensis Ohwi.	C_3	HA	OG EG
P. tenuiflora (Turcz.) Scrib. & Merr.	C_3	HA	OG EG

Table 2 (continued).

Species	C_3/C_4	Category	Grazing intensity
Setaria viridis (L.) Beauv.	C_4	IN	MG HG OG
Liliaceae			
Allium polyrrhizum Turcz.	C_3	HA	MG HG OG
A. senescens L.	C_3	NP	MG HG OG
Iridaceae			
Iris ensata Thunb.	C_3	HA	PG EG

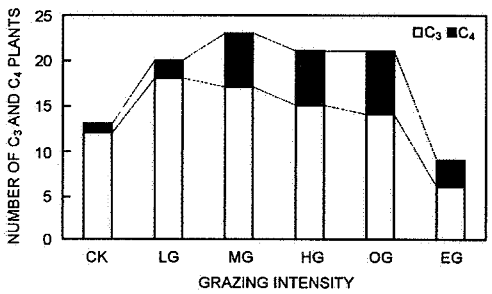

Fig. 1. The number of species of different photosynthetic pathway (C_3 and C_4) along grazing gradient in the Songnen grassland. CK = ungrazed, LG = lightly grazed, MG = moderately grazed, HG = heavily grazed, OG = overgrazed, EG = extreme grazed.

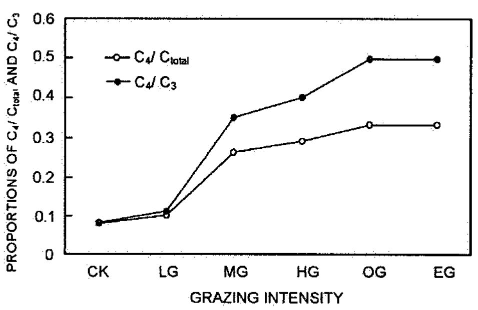

Fig. 2. The proportion of C_4/C_{total} and C_4/C_3 plant species along grazing gradient in the Songnen grassland, Northeastern China. CK = ungrazed, LG = lightly grazed, MG = moderately grazed, HG = heavily grazed, OG = overgrazed, EG = extreme grazed.

perennial species (*Bolboschoenus maritimus*, *Arundinella hirta*). This implied that most of the increased C_4 species (6 of 10) along grazing gradient were annual grasses and halophytes in the region (Table 2).

Dynamics with grazing intensity: The numbers of C_3 and C_4 species varied with the grazing intensity due to the plant succession caused by animal grazing (Fig. 1). The total numbers of plant species increased from CK (13 species) to MG (23 species) with the increase of grazing intensity, then dropped significantly from HG to EG. The numbers of C_3 species increased from 12 species in CK to 18 species in LG, and then dropped slightly as grazing intensity increased, reduced to 6 species in EG. The numbers of C_4 species increased with grazing intensity, peaked in OG (7 species), and fell off rapidly in EG (3 species). This indicated that the moderately grazed plot had the 'species-richest' plant composition, and overgrazed and extreme grazed plots had the greatest C_4 plant composition in the Songnen grassland.

The proportion of C_4 species in flora also varied with grazing intensity (Fig. 2). Both proportions of the C_4/C_{total} and C_4/C_3 rose rapidly, increased by 160 % and 218 % in MG respectively, and peaked in OG and EG (0.50 and 0.33, respectively). The proportions of C_4/C_{total} and C_4/C_3 in OG and EG were 6 times higher than those in the CK treatment, and the differences between the two grazing intensities were not significant. This suggests that proportion of C_4 plants in the region floras increased with the grazing intensity in the Songnen grassland.

Discussion

The C_4 species, with high photosynthetic rate and greater tolerance to environmental stresses, were most common in meadow steppe saline grasslands in the Northeastern China (Redmann *et al.* 1995, Yin and Wang 1997). Most *L. chinensis* grasslands, distributed in the Songnen plain, Northeastern China, were saline meadow grasslands, with many rhizome perennial mesophytes (such as *L. chinensis*, *C. epigeios*, and legumes), annual grasses (especially *C. virgata*, *E. caudata*, *S. viridis*), and halophytes (*e.g. S. corniculata*, *Puccinellia tenuiflora*). The number of identified C_4 species was about 10 % of the total forage plants in the Songnen grassland region, but in this study site it was as high as 24 %. This most likely resulted from grazing impacts on both soil moisture and salinity. The previous studies (Wang *et al.* 1997, Yin and Wang 1997) found that the C_4 species had relatively higher water use efficiency and salt tolerance. 20 % of C_4 species were distributed in the salinized grasslands in Northeastern China, while the number of C_3 species was about 18 % (Yin and Wang 1997). Both the soil moisture and organic matter contents reduced significantly with the grazing intensity in the grazing plot, but the soil pH rose remarkably (Table 1), indicating the grassland conditions were getting worse. This may result in the increase of invaders (*e.g. E. caudata*, *S. viridis*, *A. retroflexus*, *P. anserina*), and halophytes (*e.g. A. littoralis*, *C. virgata*, *K. scoparia*, *K. siev-*

ersiana, S. corniculata), and most of these species were C_4 plants. Most C_4 species (6 of 10) distributed in HG, OG, and EG were annual grasses (*e.g. E. caudata, S. viridis, C. virgata*) and halophytes (*e.g. C. virgata, K. scoparia, K. sieversiana*). This suggests that these species may be more fit for drought and saline caused by animal grazing in the region. This also can be proved by the observation that the proportions of C_4/C_{total} and C_4/C_3 increased with grazing intensity in this study (Fig. 2). The increase of high photosynthesis C_4 plants in grazing deteriorated and salinized grassland may be advantage for the grassland restoration.

This and previous studies (Williams and Markley 1973, Wang and Ripley 1997) clearly document the effects of grazing on plant distribution in grassland. Grazing management decisions must take into account grassland grazing succession (Wang and Ripley 1997) and seasonal development patterns (warm season and cool season), which are closely related to the distribution of C_4 and C_3 species (Williams and Markley 1973). Knowledge of the photosynthetic pathway types could be useful in developing forages for dry and saline grassland in Northeastern China.

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