

Photosynthetic pathways and life forms in different grassland types from North China

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Abstract

Photosynthetic pathways (C_4 , C_3 , and CAM species) and plant life forms of three grassland types in North China were compared. Of the total 201 species, 144 species in 78 genera and 34 families had C_3 photosynthetic pathway, 56 species in 35 genera and 11 families had C_4 photosynthetic pathway, and 1 species had CAM photosynthetic pathway. The number of C_4 species in Songnen meadow was 70-80 % greater than that in Xilinguole steppe and Hunshandak desert grassland, but that for C_3 species did not differ significantly among the three grassland types. The number of therophytes in the Songnen meadow was relatively greater than that of the other two grassland types, but that of hemicryptophytes was lower. Thus the distribution of C_4 species and plant life form is probably related to precipitation.

Additional key words: C_3 and C_4 species; life forms; meadow; precipitation; steppe and desert grassland.

Introduction

World wide, more than 1 700 C_4 plant species have been identified (Li 1993) since the work of Downton and Tregunna (1968) and Black (1971). Most of these studies focused on the classification of plant species as to their photosynthetic pathway, C_3 , C_4 , or CAM (Williams and Markley 1973, Downton 1975, Raghavendra and Das 1978, Waller and Lewis 1979, Mateu Andrés 1993, Redmann *et al.* 1995, Tang and Zhang 1999, Wang 2002a,b). The geographic distributions of C_4 species and the relation to climatic patterns have also been well documented by many authors (Teeri and Stowe 1976, Teeri *et al.* 1980, Collins and Jones 1985, Takeda and Hakoyama 1985, Ueno and Takeda 1992, Wang *et al.* 1997, Yin and Li 1997). Some studies deal with the differences between C_3 and C_4 species in water use efficiency and drought and salinity adaptation (Williams and Markley 1973, Redmann *et al.* 1995, Wang *et al.* 1997, Yin and Li 1997,

Tang and Zhang 1999). Few researchers have tested the hypothesis about latitudinal distribution of C_4 species (Teeri and Stowe 1976, Teeri *et al.* 1980). But none has yet looked at the differences in plant photosynthetic pathways and life forms between grassland types.

Meadow steppe, steppe, and desert grassland are three main grassland types in North China, which cover an area of about 300 million hectare. More than 1 400 forage species have been identified in 340 genera and 76 families in these areas (Zhang and Liu 1992), but the differences in photosynthetic pathways and life forms between these grassland types remain unclear. The objective of this study was to compare these differences among the three grassland types. The results can be important for the interpretation of variations of grassland ecosystems with climate changes and for grassland management decisions in North China.

Materials and methods

Songnen meadow (43°30'-48°15' N, 122°12'-126°20' E), Xilinguole steppe (41°35'-46°46' N, 111°09'-119°58' E), and Hunshandak desert grassland (42°07'-43°52' N, 111°35'-117°44' E) are three typical grassland types in North China. These grassland types theoretically receive

approximately uniform radiation, but differ in precipitation, vegetation types, soils, and geographical elevation (Table 1). Such environmental differences result in variations in grassland vegetation. The Songnen meadow is located in a semi-arid climate region, which is dominated

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by mesophytes, e.g. *Leymus chinensis* (Trin.) Tzvel and *Cleistogenes squarrosa* (Trin.) Keng, while the Xilinguole steppe and the Hunshandak desert grassland are sited in typical arid region and dominated by xerophytes, e.g. *Stipa grandis* P. Smirn., *S. gobica* Roshev., and *S. krylovii* Roshev. These differences result in changes in photosynthetic pathways and life forms among the three grassland types.

The data on species photosynthetic pathway types and their life forms were compiled from 9 references published between 1979 and 2002 (Commissione Redacto-

rum Flora Intramongolicae 1980, Li 1979, 1993, Shirongdaolji 1991, Liu 1993, Redmann *et al.* 1995, Li and Zheng 1997, Wang 2002a,b). More than 800 for-age plants distributed in the three grassland types were listed on the basis of references by Liu (1993), Li and Zheng (1997), Shirongdaolji (1991), and Wang (2002a,b). The C₄ photosynthetic pathways, life forms, and habitat were recorded according to the literature (e.g. Takeda and Hakoyama 1985, Li 1993, Redmann *et al.* 1995, Wang *et al.* 1997, Yin and Li 1997, Jiang *et al.* 1998, Li 1979, Wang 2002a,b, Wang *et al.* 2002).

Table 1. Study sites, locations, vegetation, soil types, topography, and precipitation [mm] of the three grassland types in North China.

Site	Vegetation type	Soil type	Elevation [m]	Precipitation [mm]
Songnen meadow	meadow	dark meadow	140-160	434
Xilinguole steppe	steppe	chestnut	900-1 050	303
Hunshandak desert grassland	desert grassland	chestnut	1 400-1 600	326

Results

Floristic composition: 201 plant species, about 25 % of all plant species identified in the three grassland types, belonging to 113 genera and 36 families, were identified (Table 2). Of the total 201 species, 56 species (28 %) in 35 genera and 11 families have C₄ photosynthetic pathway, 144 species (72 %) in 78 genera and 34 families have C₃ photosynthetic pathway, and only 1 species has CAM photosynthetic pathway. 127 species (63 %) belong to *Dicotyledoneae* and 74 (37 %) to *Monocotyledoneae*. As to plant families, 57 species belong to *Gramineae*, 40 to *Compositae*, 17 to *Chenopodiaceae*, and 12 to each of *Fabaceae* and *Rosaceae*. Relatively few species were identified in other families, e.g. *Polygonaceae* or *Portulacaceae*. Of the total 56 C₄ species, 32 % belong to *Dicotyledoneae*, e.g. *Chenopodiaceae* (9 species) or *Amaranthaceae* (3 species); the other 68 % to *Monocotyledoneae*, e.g. *Gramineae* (34 species) and *Cyperaceae* (3 species). Of the 144 C₃ species, 27 % (39 of 144) was in *Compositae*, 16 % (23 of 144) in *Gramineae*, and 8 % (12 of 144) in each of *Rosaceae* and *Fabaceae*. Of the plants identified in the three grassland types, 152 species were found in the Songnen meadow, of which 28 % (43 of 152) were C₄ species and 72 % (109 of 152) were C₃ species. 126 species were found in the Xilinguole steppe, 20 % (25 of 126) were C₄ species and 80 % (102 of 126) were C₃ species. 124 species were identified in the Hunshandak desert grassland, 20 % (25 of 124) were C₄ species, while the other 80 % (99 of 124) were C₃ species. One species belongs to CAM in both the Xilinguole steppe and the Hunshandak desert grassland. Of the total C₄ species, 23 species were distributed only in the Songnen meadow, 4 species only in the Xilinguole steppe, and 3 species only in the Hunshandak desert grassland. Of the species listed in Table 2, 44 % (63 of 144) of the C₃ species and 20 % of the C₄ species (11 of

56) were present in all three grassland types. The number of C₄ species in the Songnen meadow was 70-80 % greater than that in the Xilinguole steppe and the Hunshandak desert grassland, while the differences in C₃ species were not significant among these grassland types.

Plant life forms and habitats: Five plant life forms were identified in the three grassland types (Table 2). 53 % (107 of 201) were hemicryptophytes (H), 27 % (55 of 201) were therophytes (Th), 17 % were geophytes (G), 3 species were chamaephytes (Ch), and 2 species were nanophanerophytes (N). In the Songnen meadow the proportion of Th (28 %) was relatively greater than in the Xilinguole steppe (24 %) and the Hunshandak desert grassland (23 %), but the proportion of H (51 %) was relatively less there than in the Xilinguole steppe (56 %) and the Hunshandak desert grassland (57 %). Of the total 56 C₄ species, 60 % (34 of 56) were Th, 34 % (19 of 56) were H, 4 % (2 of 56) and 2 % (1 of 56) were Ch. 63 % (27 of 43) Th plants were C₄ species in the Songnen meadow, those in the Xilinguole steppe and the Hunshandak desert grassland were 61 % (19 of 31) and 57 % (16 of 28), respectively. The proportions of C₄ species in the other life form types were less than 10 %, except that for H in the Songnen meadow (17 %).

Of the total 201 species, 67 species (33 %) were distributed in dry steppe, 64 species (32 %) in meadow steppe, 55 species (27 %) in disturbed land and old fields, 50 species (25 %) in sandy soil, 18 species (9 %) in saline meadow, and 10 species (5 %) in wet soil. Of the 56 C₄ species, 25 species (45 %) were distributed in disturbed land and old fields, 13 species (23 %) in sandy soil, 11 species (20 %) in meadow steppe, 10 species (18 %) in dry steppe, 8 species (14 %) in wet soil, and 4 species (7 %) in saline meadow.

Table 2. Photosynthetic pathway (C_3 or C_4) in species in Xilinguole steppe (XS), Songnen grasslands (SG), and Hunshandak desert (HD) of North China. Nomenclature follows Kitagawa (1979) and Yin and Wang (1997). Habitat types: DB = disturbed and cultivated land, DS = dry steppe, MS = meadow steppe, SM = saline meadow, SS = sandy soil, WS = wet soils (Wang 2002). Life forms: M = macrophanerophyte, N = nanophanerophyte, Ch = chamaephyte, H = hemicryptophyte, G = geophyte, Th = therophyte.

Species		C_3/C_4	Habitat	Life form	Distribution
<i>Dicotyledoneae</i>					
<i>Polygonaceae</i>	<i>Polygonum aviculare</i> L.	C_3	DB	Th	SG XS HD
	<i>P. sibiricum</i> Laxm.	C_3	SM	G	SG XS HD
<i>Chenopodiaceae</i>	<i>Agriophyllum pungens</i> (Vahl) Link A. Dietr.	C_4	SS	Th	XS HD
	<i>Atriplex sibirica</i> L.	C_4	SM SS	Th	XS HD
	<i>Axyris amaranthoides</i> L.	C_3	DB	Th	SG XS
	<i>Bassia dasyphylla</i> O. Kuntze	C_4	SS	Th	SG XS
	<i>Chenopodium album</i> L.	C_3	DB	Th	SG XS
	<i>Ch. acuminatum</i> Willd.	C_3	DB	Th	SG XS
	<i>Ch. glaucum</i> L.	C_3	DB SM	Th	SG XS
	<i>Ch. urbicum</i> subsp. <i>sinicum</i>	C_3	DB	Th	SG
	<i>Kochia prostrata</i> Schrad.	C_4	DB SS	Ch	SG XS HD
	<i>K. scoparia</i> (L.) Schrad.	C_4	DB	Th	SG HD
	<i>K. sieversiana</i> (Pall.) C.A. Mey.	C_4	SS	Th	SG XS
	<i>Salsola collina</i> Pall.	C_4	DB	Th	SG XS HD
	<i>S. foliosa</i> (L.) Schrad.	C_4	DB	Th	SG
	<i>S. pestifer</i> Litv.	C_4	SS	Th	XS HD
	<i>Suaeda corniculata</i> (C.A. Mey.) Bunge	C_3	SS	Th	SG XS HD
	<i>S. glauca</i> Bunge	C_3	SS	Th	SG XS HD
	<i>S. heteroptera</i> Kitag.	C_3	SS	Th	SG
<i>Amaranthaceae</i>	<i>Amaranthus ascendens</i> Lois.	C_4	DB	Th	SG
	<i>A. blitoides</i> S. Watson	C_4	DB	Th	SG
	<i>A. retroflexus</i> L.	C_4	DB	Th	SG XS
<i>Portulacaceae</i>	<i>Portulaca oleracea</i> L.	C_4	DB	Th	SG XS HD
<i>Caryophyllaceae</i>	<i>Dianthus amurensis</i> Jacq.	C_4	DS	H	SG
<i>Ranunculaceae</i>	<i>Clematis hexapetala</i> Pall.	C_3	SS DS MS	G	SG XS HD
	<i>Ranunculus japonicus</i> Thumb.	C_3	MS	G	SG XS HD
	<i>Thalictrum petaloedum</i> L. var. <i>supr.</i> (Nakai) Kitag.	C_3	DS	G	SG XS HD
	<i>Th. simplex</i> L.	C_3	MS	G	SG XS HD
	<i>Th. squarrosum</i> Steph.	C_3	SS DS	G	SG XS HD
<i>Cruciferae</i>	<i>Lepidium apetalum</i> Willd.	C_3	DB SM	H	SG XS HD
<i>Crassulaceae</i>	<i>Orostachys fimbriatus</i> (Turcz.) Berger	CAM	SS	Th	XS HD
<i>Rosaceae</i>	<i>Geum aleppicum</i> Jacq.	C_3	MS	H	XS HD
	<i>Potentilla acaulis</i> L.	C_3	DS	H	XS HD
	<i>P. anserina</i> L.	C_3	MS	H	SG XS HD
	<i>P. bifurca</i> L.	C_3	DS	H	XS HD
	<i>P. bifurca</i> L. var. <i>major</i> Ledeb.	C_3	DS	H	HD
	<i>P. chinensis</i> Seringe	C_3	DS	H	SG HD
	<i>P. discolor</i> Bunge	C_3	DS	H	SG
	<i>P. filipendula</i> Willd.	C_3	SS	H	SG
	<i>P. flagellaris</i> Willd.	C_3	MS	H	SG XS HD
	<i>P. fragaricoides</i> L.	C_3	DS	H	XS
	<i>Sanguisorba officinalis</i> L.	C_3	MS	H	SG XS HD
	<i>S. tenuifolia</i> Fisch	C_3	MS	H	SG
<i>Fabaceae</i>	<i>Caragana microphylla</i> Lam.	C_3	DS SS	N	XS HD
	<i>C. stenophylla</i> Pojark.	C_3	DS SS	N	XS HD
	<i>Gueldensfaedtia stenophylla</i> Bunge	C_3	MS	H	SG XS HD
	<i>Kummerowia stipulacea</i> (Maxim.) Makino	C_3	DB	Th	SG
	<i>K. striata</i> (Thunb.) Schindler	C_3	DB	Th	SG
	<i>Lespedeza davurica</i> Schindler	C_3	DS	Ch	SG XS HD

Table 2 (continued)

	Species	C ₃ /C ₄	Habitat	Life form	Distribution
	<i>Melilotus suaveolens</i> Ledeb.	C ₃	MS	H	SG XS HD
	<i>Melilotoides ruthenica</i> (L.) Sojak	C ₃	DS SS	G	XS HD
	<i>Oxytropis hirta</i> Bunge	C ₃	SS	H	SG XS HD
	<i>O. filiformis</i> D.C.	C ₃	DS SS	H	XS HD
	<i>O. myriophylla</i> D.C.	C ₃	MS DS SS	H	SG XS HD
	<i>Thermopsis lanceolata</i> R.Br.	C ₄	MS DS	H	SG XS HD
Geraniaceae	<i>Erodium stephanianum</i> Willd.	C ₃	DS SS	G	SG XS HD
Zygophyllaceae	<i>Tribulus terrestris</i> L.	C ₄	SS	Th	SG XS HD
Rutaceae	<i>Haplophyllum dauricum</i> Juss.	C ₃	DS	H	SG XS HD
Polygalaceae	<i>Polygala tenuifolia</i> Willd.	C ₃	DS MS	H	SG XS HD
Euphorbiaceae	<i>Euphorbia esula</i> L.	C ₃	SS	G	SG XS HD
	<i>E. humifusa</i> Willd.	C ₄	SS DB	Th	SG XS HD
Violaceae	<i>Viola dissecta</i> Ledeb.	C ₃	SS DB DS	H	SG XS HD
Thymelaeaceae	<i>Diarthron linifolium</i> Turcz	C ₃	SS	Th	SG XS
	<i>Stellera chamaejasme</i> L.	C ₃	SS	H	SG XS HD
Umbelliferae	<i>Bupleurum scorzonrifolium</i> Willd.	C ₃	DS	H	SG XS HD
	<i>Siler divaricatum</i> Benth. et Hook	C ₃	DS SS	G	SG XS HD
Primulaceae	<i>Glaux maritima</i> L.	C ₃	SM	Th	SG XS HD
Plumbaginaceae	<i>Limonium bicolor</i> O. Kuntze	C ₃	SM	H	SG XS HD
Apocynaceae	<i>Apocynum lancifolium</i> Russan	C ₃	SM	H	SG
Asclepiadaceae	<i>Cynanchum amplexicaule</i> Hemsl.	C ₃	MS	G	SG XS HD
	<i>C. chinensis</i> R.Br.	C ₃	DS	G	SG
	<i>Pycnostelma paniculatum</i> K. Schum.	C ₃	DS	G	SG XS HD
Convolvulaceae	<i>Calystegia pellita</i> Ledeb.	C ₃	MS	G	SG
Boraginaceae	<i>Cynoglossum divaricatum</i> Steph.	C ₃	SS	G	SG XS HD
	<i>Lappula echinata</i> Gilib.	C ₃	SS	H	SG
Labiatae	<i>Phlomis tuberosa</i> L.	C ₃	MS	H	XS HD
	<i>Scutellaria baicalensis</i> Georgi	C ₃	MS	H	SG XS HD
	<i>S. ikonnikovii</i> Juz.	C ₃	MS	H	XS HD
	<i>Thymus serpyllum</i> L.	C ₃	DS	Ch	
Solanaceae	<i>Datura stramonium</i> L.	C ₃	DB	Th	HD
	<i>Solanum nigrum</i> L.	C ₃	DB	Th	SG HD
Bignoniaceae	<i>Incarvillea sinensis</i> Lamark.	C ₃	DS MS	Th	SG
Plantaginaceae	<i>Plantago asiatica</i> L.	C ₃	DB	H	SG XS HD
	<i>P. depressa</i> Willd.	C ₃	DB	H	SG XS HD
Rubiaceae	<i>Galium verum</i> L.	C ₃	MS	H	SG XS
Campanulaceae	<i>Adenophora stenophylla</i> Hemsley	C ₃	MS	G	SG
	<i>Platycodon grandiflorum</i> D.C.	C ₃	DS	G	SG
Compositae	<i>Artemisia anethoides</i> Mattf.	C ₃	DB SS	H	SG HD
	<i>A. anethifolia</i> Weber	C ₃	SG	H	SG XS HD
	<i>A. annua</i> L.	C ₃	SS	H	XS HD
	<i>A. argyi</i> Levl. et Vant.	C ₃	MS	H	XS HD
	<i>A. desertorum</i> Spreng.	C ₃	SS	H	SG XS HD
	<i>A. dracunculus</i> L.	C ₃	DB DS	H	XS HD
	<i>A. frigida</i> Willd.	C ₃	DS SS	H	SG HD
	<i>A. integrifolia</i> L.	C ₃	MS	H	SG HD
	<i>A. japonica</i> Thunb. var. <i>manshurica</i> Kom.	C ₃	MS SS	H	SG XS
	<i>A. laciniata</i> Willd.	C ₃	MS	H	SG
	<i>A. mongolica</i> Fisch.	C ₃	MS	H	SG
	<i>A. pectinata</i> Pall. (<i>Neopallasia pectinata</i>) Polsak.	C ₃	DS SS	H	XS HD

Table 2 (continued)

Species	C ₃ /C ₄	Habitat	Life form	Distribution
<i>Artemisia pubescens</i> Ledeb.	C ₃	SS	H	XS HD
<i>A. scoparia</i> Waldst. et Kit.	C ₃	DB DS	H	SG XS HD
<i>A. selengensis</i> Turcz. ex Bess.	C ₃	MS	H	XS HD
<i>A. sieversiana</i> Willd.	C ₃	DB	H	SG XS HD
<i>Aster alpinus</i> L.	C ₃	DS	H	XS HD
<i>Filifolium sibiricum</i> Kitam.	C ₃	DS SS	H	SG XS HD
<i>Heteropappus altaicus</i> (Willd.) Novopokr.	C ₃	DS SS	H	SG XS HD
<i>H. altaicus</i> (Willd.) Novopokr. var. <i>millefolium</i> (Vant.) Wang	C ₃	DS	H	XS
<i>Hypochaeris grandiflora</i> Ledeb.	C ₄	MS WS	H	SG
<i>Inula britanica</i> L. var. <i>sublanata</i> Kom.	C ₃	MS	H	SG XS HD
<i>I. britanica</i> L. var. <i>japonica</i> (Thunb.) Franch. et Sav.	C ₃	MS	H	SG
<i>I. japonica</i> Thunb.	C ₃	MS	H	XS
<i>Ixeris chinensis</i> Nakai subsp. <i>graminifolia</i> Kitag.	C ₃	DB	H	SG XS HD
<i>I. chinensis</i> Nalai var. <i>intermedia</i> Kitag.	C ₃	DB	H	SG
<i>I. sonchifolia</i> Hance	C ₃	DB	H	SG XS HD
<i>Lactuca indica</i> L.	C ₃	MS	G	SG
<i>Leontopodium leontopodioides</i> Reauv.	C ₃	MS DS SS	H	SG XS HD
<i>Picris japonica</i> Thunb.	C ₃	MS DS DB	H	SG XS
<i>Saussurea glomerata</i> Poir.	C ₃	SM	G	SG
<i>S. japonica</i> (Thunb.) D.C.	C ₃	MS SS	G	XS HD
<i>S. runcinata</i> D.C.	C ₃	SM	G	SG XS HD
<i>Scorzonera glabra</i> Rupr.	C ₃	DS	G	SG
<i>Senecio ambracens</i> Turcz.	C ₃	MS	H	SG
<i>S. integrifolius</i> Claiville	C ₃	MS	H	SG
<i>Serratula yamatsutana</i> Kitag.	C ₃	MS DS	G	SG
<i>Taraxacum mongolicum</i> Hand.	C ₃	MS DB	H	SG XS HD
<i>T. ohwianum</i> Kitam.	C ₃	MS DB	H	SG XS
<i>Xanthium strumarium</i> L.	C ₃	DB	Th	SG XS HD
<i>Monocotyledoneae</i>				
<i>Cyperaceae</i>				
<i>Bolboschoenus maritimus</i> (L.) Pall.	C ₄	MS WS	H	SG
<i>Carex dahurica</i> Kükenth.	C ₃	DS	H	XS
<i>C. duriuscula</i> C.A.M.	C ₃	DS	H	SG XS HD
<i>C. enervis</i> C.A.M.	C ₄	DS	H	XS
<i>C. lanceolata</i> Boott.	C ₃	DS MS	H	HD
<i>C. neurocarpa</i> Maxim.	C ₃	MS WS	H	SG
<i>C. pediformis</i> C.A.M.	C ₄	DS SS	H	XS HD
<i>Gramineae</i>				
<i>Achnatherum avinoides</i> (Honda) Chang	C ₄	DS	H	SG
<i>A. splendens</i> (Trin.) Nevski	C ₄	MS SM	H	XS HD
<i>Aeluropus littoralis</i> (Gouan) Parlat	C ₄	SM	H	SG
<i>Agropyron cristatum</i> (L.) Gaertner	C ₃	MS DS SS	H	SG XS HD
<i>A. desertorum</i> (Fisch.) Schult.	C ₃	DS SS	H	HD
<i>Aristida adscensionis</i> L.	C ₄	DS	H	HD
<i>Arthraxon hispidus</i> (Thunb.) Makino	C ₄	DB WS	H	SG
<i>Arundinella hirta</i> (Thunb.) Tanaka	C ₄	MS WS	H	SG
<i>Avena fatua</i> L.	C ₃	DB	Th	SG XS HD
<i>Beckmannia syzigachne</i> (Steud.) Fernald	C ₃	MS	Th	XS HD
<i>Bromus inermis</i> Leyss.	C ₃	MS	H	XS HD
<i>Calamagrostis epigeios</i> (L.) Roth	C ₃	MS WS	H	SG XS HD
<i>Chloris virgata</i> Sw.	C ₄	SM WS	Th	SG XS HD
<i>Cleistogenes chinensis</i> (Maxim.) Keng	C ₄	DS	H	SG
<i>C. squarrosa</i> (Trin.) Keng	C ₄	MS	H	SG XS HD
<i>Digitaria ciliaris</i> (Rotz.) Koel	C ₄	DB	Th	SG
<i>D. ischaemus</i> (Schreb.) Schreb. ex Muhl.	C ₄	DB	Th	SG XS HD
<i>D. lineis</i> (Krock.) Crep	C ₄	DB	Th	SG
<i>D. sanguinalis</i> (L.) Scop.	C ₄	DB	Th	SG
<i>Echinochloa candata</i> Roshev.	C ₄	MS WS	Th	SG
<i>E. crus galli</i> (L.) Beauv.	C ₄	MS WS	Th	SG XS HD

Table 2 (continued)

	Species	C ₃ /C ₄	Habitat	Life form	Distribution
	<i>Elymus dahuricus</i> Turcz.	C ₃	MS DS	H	SG XS HD
	<i>Enneapogon borealis</i> (Griseb.) Honda	C ₄	DS	Th	XS
	<i>Eragrostis cilianensis</i> (All.) Link.	C ₄	DB	Th	SG HD
	<i>E. filiformis</i> Link.	C ₄	DB	Th	SG
	<i>E. minor</i> Host	C ₄	DS DB	Th	XS
	<i>E. pilosa</i> (L.) P. B.	C ₄	MS	Th	SG HD
	<i>E. poaeoides</i> Beauv.	C ₄	MS	Th	HD
	<i>Eriochloa villosa</i> (Thunb.) Kunth L.	C ₄	DB	Th	SG
	<i>Festuca ovina</i> L.	C ₃	DS	H	SG HD
	<i>F. rubra</i> L.	C ₃	SS DS	H	XS HD
	<i>Hemarthria sibirica</i> (Gand.) Ohwi.	C ₄	MS	H	SG
	<i>Hierochloa glabra</i> Trin.	C ₄	SS DB	H	SG
	<i>Hordeum brevisubulatum</i> (Trin.) Link	C ₃	SM	H	SG XS HD
	<i>H. brevisubulatum</i> var. <i>hirtellum</i> Cheng ex Skv.	C ₃	SM	H	SG
	<i>Imperata cylindrica</i> (L.) P. B.	C ₄	SS	G	SG
	<i>Koeleria cristata</i> (L.) Pers.	C ₃	DS MS	H	SG XS HD
	<i>Leymus chinensis</i> (Trin.) Tzvel.	C ₃	SM DS	H	SG XS HD
	<i>Miscanthus sacchariflorus</i> (Maxim.) Hack.	C ₄	SS	H	SG
	<i>Panicum ruderae</i> (Kitag.) Cheng	C ₄	DB WS	Th	SG
	<i>Pennisetum centrasiaticum</i> Tzvel.	C ₄	DB	H	XS
	<i>P. flaecidum</i> Griseb.	C ₄	SS	G	SG HD
	<i>Phragmites communis</i> Trin.	C ₃	MS	H	SG XS HD
	<i>Poa annua</i> L.	C ₃	MS DB	Th	HD
	<i>P. pratensis</i> L.	C ₃	MS	H	SG XS HD
	<i>Puccinellia chinampoensis</i> Ohwi.	C ₃	SM	H	SG
	<i>P. jeholensis</i> Kitag.	C ₃	SM	H	SG
	<i>P. tenuiflora</i> (Turcz.) Scrib. et Merr.	C ₃	SM	H	SG XS HD
	<i>Setaria arenaria</i> Kitag.	C ₄	DB	Th	SG XS
	<i>S. glauca</i> (L.) Beauv.	C ₄	DB	Th	XS HD
	<i>S. lutescens</i> Weigel. F. T. Hubb.	C ₄	DB	Th	HD
	<i>S. viridis</i> (L.) Beauv.	C ₄	DB	Th	SG XS HD
	<i>Spodiopogon sibiricus</i> Trin.	C ₄	MS DS	H	SG HD
	<i>Stipa baicalensis</i> Roshev.	C ₃	DS	H	SG XS HD
	<i>S. gobica</i> Roshev.	C ₃	DS	H	XS HD
	<i>S. grandis</i> P. Smirn.	C ₃	DS	H	SG XS HD
	<i>S. krylovii</i> Roshev.	C ₃	DS SS	H	XS HD
Commelinaceae	<i>Commelina communis</i> L.	C ₄	DB	Th	SG
Liliaceae	<i>Allium macrostemon</i> Bunge	C ₃	DB	G	SG HD
	<i>A. polyrrhizum</i> Turcz.	C ₃	SM	G	SG XS HD
	<i>A. senescens</i> L.	C ₃	DS MS	G	SG XS HD
	<i>A. tenuissimum</i> L.	C ₃	DS SS	G	XS
	<i>Lilium tenuifolium</i> Fisch.	C ₃	MS DS	G	SG
	<i>Scilla thunbergii</i> Miyabe et Kudo	C ₃	DS MS	G	SG
Iridaceae	<i>Iris dichotoma</i> Pall.	C ₃	DB DS	G	XS HD
	<i>I. ensata</i> Thunb.	C ₃	MS DS	G	SG
	<i>I. ruthenica</i> Ker. Gawl.	C ₃	DB	G	XS

Discussion

Plant photosynthetic pathways are consistent with grassland environments and grassland management in North China (Yin and Wang 1997, Wang 2002a,b). More than one half of the C₃ species (59 %) belong to *Compositae* (27 %), *Gramineae* (16 %), and *Rosaceae* and *Fabaceae* (16 %), 77 % C₄ species to *Chenopodiaceae* (16 %) and *Gramineae* (61 %). This indicated that the C₃ and C₄ for-

age species in these grassland types mostly belong to a few families. More C₄ species were found in the Songnen meadow than in the other two sites, mainly due to high precipitation and soil salinisation in the region. Yin and Li (1997) documented that the distribution of C₄ species is significantly related with precipitation in China. The early studies (Redmann *et al.* 1995, Wang *et al.* 1997, Yin

and Wang 1997, Wang 2002a) also found that the C_4 species had relative higher water use efficiency and salt tolerance. 20 % of C_4 species, e.g. *Aeluropus litoralis* (Gouan) Parlat and *Chloris virgata* Sw., were distributed in the salinised meadows in Northeastern China (Wang 2002a,b), while the distribution of C_3 species was about 18 % (Yin and Wang 1997). The presence of more C_4 species in the Songnen meadow may also result from the increase of invader species, e.g. belonging to *Amaranthaceae* (*Amaranthus ascendens* Lois., *A. blitoides* S. Watson), *Gramineae* [*Digitaria lineis* (Krock.) Crep, *D. sanguinalis* (L.) Scop., *Commelina communis* L., *Miscanthus sacchariflorus* Hack., *Panicum ruderales* (Kitag.) Cheng]. Grassland management, such as grazing, mowing, and cultivation (Wang 2002a,b), causes the increase in presence of these invader species. There are no significant differences in both the C_4 and C_3 species between the Xilinguole steppe and the Hunshandak desert grassland, likely due to the low precipitation and similar soil types for the two sites. The decrease of amount of C_4 species from mesic Songnen meadow to dry steppe supports the hypothesis that the distribution of C_4 species is significantly related to precipitation (Teeri and Stowe 1976, Teeri *et al.* 1980, Yin and Li 1997).

Life form compositions of the total plants identified in the three sites were not consistent with that for C_4 species in North China (Wang 2002a,b). Of the total 201 species, more than one half (53 %) were hemicryptophytes (H). This may result from the high composition of graminaceous plants (*Gramineae* and *Cyperaceae*) for the grassland types, because over 60 % of the total forage plants were of the H life form in the meadows in North China (Li, 1979, Wang 2002a,b). Only 27 % of the total species

in Table 2 were therophytes (Th), while more than 60 % C_4 species was Th in these three grassland types. Relatively more Th C_4 species is an advantage for this photosynthetic pathway type to diffuse far away, because this type of plants has a high capacity for seed production and dispersal (Wang 1997, 2002a,b). The relatively high amount of C_4 species with H life form in the Songnen meadow may result from the mesic grassland environments, because most H species were hygrophytes or mesohydrophytes, e.g. *Hypochaeris grandiflora* Ledeb, *Bolboschoenus maritimus* (L.) Pall., *Arthraxon hispidus* (Thunb.) Makino, or *Arundinella hirta* (Thunb.) Tanaka. Also these plants are C_4 species.

High proportions of the species identified in Table 2 were distributed in dry steppe (33 %) and meadow steppe (32 %), which is consistent with steppe and meadow conditions. 27 % of the total species and 45 % of C_4 species, e.g. *Chenopodiaceae*, *Amaranthaceae*, and annual grasses, were pioneer plants in the disturbed and cultivated land which may be the early grassland succession stages or old fields caused by overgrazing and cultivation. More C_4 species in the disturbed and cultivated land support the hypothesis that the C_4 species have greater tolerance to environmental stress (Wang and Yin 1997), because the early succession stages may be characterised by a lower soil moisture content and higher soil pH (Wang and Ripley 1997). Plant photosynthetic pathways strongly respond to grassland types, environments, and dynamics in North China (Wang 2002a,b). Therefore grassland management decisions must take into account photosynthetic pathway composition, which is closely related to grassland production.

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