

Photosynthetic pathway and morphological functional types in the steppe vegetation from Inner Mongolia, North China

R.Z. WANG

Laboratory of Quantitative Vegetation Ecology, Institute of Botany, the Chinese Academy of Sciences, No. 20 Nanxincun, Xiangshan, Beijing, 100093, China

Abstract

Photosynthetic pathway (C_3 , C_4 , and CAM) and morphological functional types were identified for the forage species from steppe vegetation in Inner Mongolia, China, using the data from both field survey and references. Of the total 136 identified vascular species, in 29 families and 89 genera, 78 % were found with C_3 photosynthesis, including dominant herbs, e.g. *Stipa grandis* P. Smirn., *S. krylovii* Roshev., and *Leymus chinensis* (Trin.) Tzvel. These C_3 species covered about 90 % of the total herbage production in the steppe. 20 % were found with C_4 photosynthesis and 2 % with CAM photosynthesis. Photosynthetic pathway functional types were coarse and may not fit for the studies and land management in small scales, because of the high C_3 photosynthesis composition and the few families in which C_4 species occur. Morphological functional types (e.g. shrubs, high perennial grasses, short perennial graminaceous plants, annual grasses, annual forbs, perennial forbs, and succulents) may be practical for spatial and temporal descriptions of steppe ecosystems in local and region scales. Classification for plant functional types, especially morphological types, may contribute to studying the links between plant species and communities, ecosystems, and global changes, and for steppe management decisions in the region.

Additional key words: annual and perennial plants; C_3 , C_4 , and CAM photosynthesis; dry and wet soils; forbs; grasses; land cultivation.

Introduction

Plant functional types are referred to groups or types of species that share morphological and physiological attributes and play a similar role in ecosystems. They are popular means for studying the logical links between physiological and life-history strategies at plant level, and ecological process at ecosystem and global levels (Chapin 1993, Paruelo and Lauenroth 1996). Classifications of plant functional types were mainly based on plant photosynthetic pathway types (C_3 , C_4 , and CAM) or morphological attributes. Most of studies on plant functional types were focused on photosynthetic pathway identification (Williams and Markley 1973, Downton 1975, Raghavendra and Das 1978, Waller and Lewis 1979, Redmann *et al.* 1995, Wang 2002b), morphological functional type classifications (Smith *et al.* 1993, Aguiar *et al.* 1996, Paruelo and Lauenroth 1996, Pillar 1997, Scholes *et al.* 1997, Diaz *et al.* 1998, McIntyre *et al.* 1999, Duckworth *et al.* 2000), as well as the relationships between plant functional types and global changes (Teeri and Stowe 1976, Teeri *et al.* 1980, Collins and Jones 1985, Takeda and Hakoyama 1985, Ueno and Takeda

1992, Box 1996, Cramer 1997, Diaz and Cabido 1997, Leemans 1997, Yin and Li 1997, Ehleringer *et al.* 1997, Keeley 1998, Collatz *et al.* 1998, Pyankov *et al.* 2000). These works provide strong evidence that the abundance of plant functional types correlates with different vegetation, land use, and climatic attributes in local, region, and global scales.

Inner Mongolian steppe, distributed at the eastern end of the Eurasian steppe zone, covers large continuous areas in Inner Mongolia. The usual growing condition for the steppe herbage is superior both in quality and quantity, so that this type of grassland is one of the best suited in northern China for the range land industry (Jiang *et al.* 1985, Li *et al.* 1988, Xiao *et al.* 1995). Studies on local flora, plant communities, plant biomass, and their responses to environmental changes have been conducted (Liu 1993, Jiang *et al.* 1985, Li *et al.* 1988, Zhao *et al.* 1988, Xiao *et al.* 1995), but plant functional type compositions in Inner Mongolian steppe remain unclear. Plant functional types are the important linkages between plant species and ecosystems, land use, as well as global changes.

Received 27 January 2003, accepted 26 February 2003.

Fax: 0086-01-82591781; e-mail: wangrenzh@sohu.com

Acknowledgements: I am grateful for the funding by Key Projects of Knowledge Innovation of Chinese Academy of Sciences (KSCX2-SW-107) and in part by National Key Basic Research Special Foundation Project (NKBRF project G2000018607).

The objective of the present study was to investigate the photosynthetic pathway type and morphological functional type compositions in Inner Mongolian steppe. This study may contribute new information for better understanding the plant functional types in Inner Mongolian steppe and their relations with ecosystems, climate changes, and land use.

Materials and methods

The study was conducted in Xilingol steppe (41°35'–46°46' N, 111°09'–119°58' E), a typical steppe in the Mid-Inner Mongolia (Fig. 1). The steppe is part of Mongolian Plateau, which covers about 200 000 km² area, on average 1 200 m above sea level, varying from 900 m in the north-east to 1 300 m in the south-west. Most of the region has chestnut, chernozem, and sandy soils. The main determinants of the climate in the region are the Mongolian anticyclone and moist Pacific air mass. In winter, north-east China is dominated by an intense Mongolian anticyclone. The steep pressure gradient between this high- and the Aleutian low-pressure system produces a strong westerly flow of cold, dry continental air, at the surface, over north China. As the anticyclone breaks down in spring, the region comes increasingly under the influence of moist Pacific air mass, reaching a climax in the summer monsoon, which lasts two months. The mean annual air temperature ranges from 0 to 3 °C, varying from –21 °C in January to 21 °C in July. Moisture gradient is very steep, with annual precipitation varying from 100 mm in the west to 400 mm in the east. Precipitation is not distributed evenly over growing season, of which 70 % falls between June and August in this region.

Results

Floristic composition of photosynthetic pathway types: 136 vascular plant species, in 89 genera and 29 families, and about 25 % of the total species in Xilingol steppe were identified with C₃, C₄, and CAM photosynthesis (Table 1). Of these species, 71 % (96 of 136) were found in *Dicotyledoneae*, e.g. *Compositae* (30 species), *Chenopodiaceae* (13 species), *Fabaceae* (9 species), *Rosaceae* (8 species). 29 % (40 of 136) were in *Monocotyledoneae*, e.g. *Gramineae* (31 species), *Cyperaceae* (4 species), *Liliaceae* (3 species), and *Iridaceae* (2 species). As for photosynthetic pathway types, 106 species (78 %) in 66 genera and 25 families were found with C₃ photosynthesis, 27 species (20 %) in 22 genera and 9 families with C₄ photosynthesis, and 3 species (2 %) in 2 genera and 1 family with CAM photosynthesis. For the 96 *Dicotyledoneae* species, 83 % (80 of 96) were C₃ species, 14 % were C₄ species, and 3 % (3 of 96) were CAM species. 35 % *Monocotyledoneae* species, however, were C₄ species, the others (65 %) were C₃ species. This indicated that the occurrence of C₄ species in *Monocotyledoneae* was as high as 2 times than in *Dicotyledoneae* in Xilingol steppe region. But the occurrence of C₄ species was common in *Chenopodiaceae*, 54 % (7 of 13) identified *Chenopodiaceae* were C₄ species. Most of *Chenopodiaceae* species were annual and succulent,

standing the plant functional types in Inner Mongolian steppe and their relations with ecosystems, climate changes, and land use.

tation is not distributed evenly over growing season, of which 70 % falls between June and August in this region.

Floristic species were obtained from 11 references published from 1980 to 2002 (Commissione Redactorum Flora Intramongolicae 1980, Li *et al.* 1988, Liu 1993, Zhang and Liu 1992, Wang 2002b,c,d), as well as from the sampling data conducted from 2000 to 2002 (Wang 2002c,d). The data on photosynthetic pathway types and morphological functional types were compiled from 9 references published between 1985 and 2002 (e.g. Takeda and Hakoyama 1985, Li *et al.* 1988, Zhao *et al.* 1988, Li 1993, Redmann *et al.* 1995, Yin and Li 1997, Pyankov *et al.* 2000, Wang 2002c,d). Plants identified in the region were classified into three photosynthetic pathway types (C₄, C₃, and CAM) by physiological attributes and morphological functional types: shrubs (SHR), high perennial grasses (HPG), short perennial grasses (SPG), annual grasses (ANG), annual forbs (ANF), perennial forbs (PEF), and succulents (SUC), by morphological attributes (Table 1).

and occurred in arid environments, e.g. *Kochia sieversiana* (Pall.) C.A. Mey., *K. prostrata* Schrad., *Salsola collina* Pall., *S. pestifer* A. Nelson, *Suaeda corniculata* (C.A. Mey.) Bunge, and *S. glauca* Bunge. 3 CAM species were identified in the steppe region, e.g. *Orostachys fimbriatus* (Turcz.) Berger, *O. malacophyllus* (Pall.) Fisch., and *Sedum aizoon* L. Succulent and annual attributes were advantage for resistance to ecological stress and conditions in arid steppe.

Photosynthetic pathway type compositions were consistent with habitat conditions in Xilingol steppe region (Fig. 2A,B). Total species numbers dropped significantly from dry steppe (DS) to wet soil (WS), the species numbers in WS was only 8 % of that in DS. This was mostly due to the high composition of xerophytes (e.g. *Stipa grandis* P. Smirn., *S. gobica* Roshev., *S. krylovii* Roshev., *Artemisia intramongolica* H.C. Fu.) in the steppe region. Disturbed and cultivated lands (DB) had the highest number of C₄ species (10 species), which was about 32 % of the total species in this habitat type (Fig. 2B), and most of these species were annual forbs (e.g. *Salsola collina* Pall., *Amaranthus retroflexus* L., *Portulaca oleracea* L.), annual grasses [e.g. *Setaria arenaria* Kitag., *S. glauca* (L.) Beauv., *S. viridis* (L.) Beauv.]. Sandy soil habitats (SS) and meadow steppe (MS) also had relatively more

PHOTOSYNTHETIC PATHWAY IN THE STEPPE VEGETATION FROM INNER MONGOLIA

Table 1. Photosynthetic pathways (C₃, C₄, and CAM) and plant functional types in Inner Mongolian steppe, 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 2002a). Plant functional types: SHR = shrubs, HPG = high perennial grasses, SPG = short perennial graminaceous plants (grasses and sedge), ANG = annual grasses, ANF = annual forbs, PEF = perennial forbs, SUC = succulents.

	Species	C ₃ /C ₄	Habitat	Plant functional type
Dicotyledoneae				
Polygonaceae	<i>Polygonum aviculare</i> L.	C ₃	DB	ANF
	<i>P. sibiricum</i> Laxm.	C ₃	SM	ANF
Chenopodiaceae	<i>Agriophyllum pungens</i> (Vahl) Link A. Dietr.	C ₄	SS	ANF
	<i>Atriplex sibirica</i> L.	C ₄	SM SS	ANF
	<i>Axyris amaranthoides</i> L.	C ₃	DB	ANF
	<i>Bassia dasyphylla</i> O. Kuntze	C ₄	SS	SUC
	<i>Chenopodium album</i> L.	C ₃	DB	ANF
	<i>Ch. acuminatum</i> Willd.	C ₃	DB	ANF
	<i>Ch. glaucum</i> L.	C ₃	DB SM	ANF
	<i>Kochia prostrata</i> Schrad.	C ₄	DB SS	SHR
	<i>K. sieversiana</i> (Pall.) C.A. Mey.	C ₄	SS	SUC
	<i>Salsola collina</i> Pall.	C ₄	DB	SUC
	<i>S. pestifer</i> A. Nelson	C ₄	SS	SUC
	<i>Suaeda corniculata</i> (C.A. Mey.) Bunge	C ₃	SS	SUC
	<i>S. glauca</i> Bunge	C ₃	SS	SUC
Amaranthaceae	<i>Amaranthus retroflexus</i> L.	C ₄	DB	ANF
Portulacaceae	<i>Portulaca oleracea</i> L.	C ₄	DB	ANF
Ranunculaceae	<i>Clematis hexapetala</i> Pall.	C ₃	SS DS MS	PEF
	<i>Ranunculus japonicus</i> Thumb.	C ₃	MS	PEF
	<i>Thalictrum petaloedum</i> L. var. <i>supr.</i> (Nakai) Kitag.	C ₃	DS	PEF
	<i>Th. simplex</i> L.	C ₃	MS	PEF
	<i>Th. squarrosum</i> Steph.	C ₃	SS DS	PEF
Cruciferae	<i>Lepidium apetalum</i> Willd.	C ₃	DB SM	ANF
Crassulaceae	<i>Orostachys fimbriatus</i> (Turcz.) Berger	CAM	SS	SUC
	<i>O. malacophyllus</i> (Pall.) Fisch.	CAM	SS	SUC
	<i>Sedum aizoon</i> L.	CAM	DS	SUC
Rosaceae	<i>Armeniaca sibirica</i> (L.) Lam.	C ₃	SS	SHR
	<i>Geum aleppicum</i> Jacq.	C ₃	MS	PEF
	<i>Potentilla acaulis</i> L.	C ₃	DS	PEF
	<i>P. anserina</i> L.	C ₃	MS	PEF
	<i>P. bifurca</i> L.	C ₃	DS	PEF
	<i>P. flagellaris</i> Willd.	C ₃	MS	PEF
	<i>P. fragaricoides</i> L.	C ₃	DS	PEF
	<i>Sanguisorba officinalis</i> L.	C ₃	MS	PEF
Fabaceae	<i>Caragana microphylla</i> Lam.	C ₃	DS SS	SHR
	<i>C. stenophylla</i> Pojark.	C ₃	DS SS	SHR
	<i>Gueldensfaedtia stenophylla</i> Bunge	C ₃	MS	PEF
	<i>Lespedeza davurica</i> Schindler	C ₃	DS	SHR
	<i>Melilotus suaveolens</i> Ledeb.	C ₃	MS	ANF
	<i>Melilotoides ruthenica</i> (L.) Sojak	C ₃	DS SS	PEF
	<i>Oxytropis hirta</i> Bunge	C ₃	SS	PEF
	<i>O. filiformis</i> D.C.	C ₃	DS SS	PEF
	<i>O. myriophylla</i> D.C.	C ₃	MS DS SS	PEF
	<i>Thermopsis lanceolata</i> R. Br.	C ₄	MS DS	PEF
Geraniaceae	<i>Erodium stephanianum</i> Willd.	C ₃	DS SS	ANF
Zygophyllaceae	<i>Tribulus terrestris</i> L.	C ₄	SS	ANF
Rutaceae	<i>Haphophyllum dauricum</i> Juss	C ₃	DS	PEF
	<i>Polygala tenuifolia</i> Willd.	C ₃	DS MS	PEF

Table 1 (continued)

	Species	C ₃ /C ₄	Habitat	Plant functional type
<i>Euphorbiaceae</i>	<i>Euphorbia esula</i> L.	C ₃	SS	PEF
	<i>E. humifusa</i> Willd.	C ₄	SS DB	ANF
<i>Violaceae</i>	<i>Viola dissecta</i> Ledeb.	C ₃	SS DB DS	PEF
<i>Thymelaeaceae</i>	<i>Diarthron linifolium</i> Turcz.	C ₃	SS	ANF
	<i>Stellera chamaejasme</i> L.	C ₃	SS	PEF
<i>Umbelliferae</i>	<i>Bupleurum scorzonrifolium</i> Willd.	C ₃	DS	PEF
	<i>Saposhnikovia divaricatum</i> (Turcz.) Schischk.	C ₃	DS SS	PEF
<i>Primulaceae</i>	<i>Glaux maritima</i> L.	C ₃	SM	ANF
<i>Plumbaginaceae</i>	<i>Limonium bicolor</i> O. Kuntze	C ₃	SM	PEF
<i>Asclepiadaceae</i>	<i>Cynanchum amplexicaule</i> Hemsl.	C ₃	MS	PEF
<i>Boraginaceae</i>	<i>Cynoglossum divaricatum</i> Steph.	C ₃	SS	ANF
<i>Labiatae</i>	<i>Scutellaria baicalensis</i> Georgi	C ₃	MS	PEF
	<i>S. ikonnikovii</i> Juz.	C ₃	MS	PEF
	<i>Thymus serpyllum</i> L.	C ₃	DS	PEF
<i>Solanaceae</i>	<i>Solanum nigrum</i> L.	C ₃	DB	ANF
<i>Plantaginaceae</i>	<i>Plantago asiatica</i> L.	C ₃	DB	PEF
	<i>P. depressa</i> Willd.	C ₃	DB	PEF
<i>Rubiaceae</i>	<i>Galium verum</i> L.	C ₃	MS	PEF
<i>Compositae</i>	<i>Artemisia anethifolia</i> Weber	C ₃	SM	ANF
	<i>A. annua</i> L.	C ₃	SS	ANF
	<i>A. argyi</i> Levl. et Vant.	C ₃	MS	PEF
	<i>A. desertorum</i> Spreng.	C ₃	SS	SHR
	<i>A. dracunculus</i> L.	C ₃	DB DS	ANF
	<i>A. frigida</i> Willd.	C ₃	DS SS	SHR
	<i>A. japonica</i> Thunb. var. <i>manshurica</i> Kom.	C ₃	MS SS	ANF
	<i>A. pectinata</i> Pall. (<i>Neopallasia pectinata</i>) Polsak.	C ₃	DS SS	ANP
	<i>A. pubescens</i> Ledeb.	C ₃	SS	ANF
	<i>A. scoparia</i> Waldst. et Kit.	C ₃	DB DS	ANF
	<i>A. selengensis</i> Turcz. ex Bess.	C ₃	MS	ANF
	<i>A. sieversiana</i> Willd.	C ₃	DB	ANF
	<i>Aster alpinus</i> L.	C ₃	DS	ANF
	<i>Filifolium sibiricum</i> Kitam.	C ₃	DS SS	FEF
	<i>Heteropappus altaicus</i> (Willd.) Novopokr.	C ₃	DS SS	PEF
	<i>H. altaicus</i> (Willd.) Novopokr. var. <i>millefolium</i>	C ₃	DS	PEF
	<i>Hypochaeris grandiflora</i> Ledeb.	C ₄	MS WS	PEF
	<i>Inula britanica</i> L. var. <i>sublanata</i> Kom.	C ₃	MS	PEF
	<i>I. japonica</i> Thunb.	C ₃	MS	PEF
	<i>Ixeris chinensis</i> Nakai subsp. <i>graminifolia</i> Kitag.	C ₃	DB	PEF
	<i>I. sonchifolia</i> Bunge	C ₃	DB	PEF
	<i>Leontopodium leontopodioides</i> Reauv.	C ₃	MS DS SS	PEF
	<i>Picris japonica</i> Thunb.	C ₃	MS DS DB	ANF
	<i>Saussurea japonica</i> (Thunb.) D.C.	C ₃	MS SS	PEF
	<i>S. runcinata</i> D.C.	C ₃	SM	PEF
	<i>Scorzonera austriaca</i> Willd.	C ₃	DS	PEF
	<i>Serratula yamasutana</i> Kitag.	C ₃	DS	PEF
	<i>Taraxacum mongolicum</i> Hand.	C ₃	MS DB	PEF
	<i>T. ohwianum</i> Kitam.	C ₃	MS DB	PEF
	<i>Xanthium strumarium</i> L.	C ₃	DB	ANF
<i>Monocotyledoneae</i>				
<i>Cyperaceae</i>	<i>Carex dahurica</i> Kukenth.	C ₃	DS	SPG
	<i>C. duriuscula</i> C.A.M.	C ₃	DS	SPG
	<i>C. enervis</i> C.A.M.	C ₄	DS	SPG
	<i>C. pediformis</i> C.A.M.	C ₄	DS SS	SPG

PHOTOSYNTHETIC PATHWAY IN THE STEPPE VEGETATION FROM INNER MONGOLIA

Table 1 (continued)

	Species	C ₃ /C ₄	Habitat	Plant functional type
Gramineae	<i>Achnatherum splendens</i> (Trin.) Nevski	C ₄	MS SM	HPG
	<i>Agropyron cristatum</i> (L.) Gaertner	C ₃	MS DS SS	HPG
	<i>Avena fatua</i> L.	C ₃	MS DB DS	ANG
	<i>Beckmannia syzigachne</i> (Steud.) Fernald	C ₃	MS	ANG
	<i>Bromus inermis</i> Leyss.	C ₃	MS	HPG
	<i>Calamagrostis epigeios</i> (L.) Roth	C ₃	MS WS	HPG
	<i>Chloris virgata</i> Sw.	C ₄	SM WS	ANG
	<i>Cleistogenes squarrosa</i> (Trin.) Keng	C ₄	MS	SPG
	<i>Digitaria ischaemum</i> (Schreb.) Schreb. ex Muhl.	C ₄	DB	ANG
	<i>Echinochloa crus galli</i> (L.) Beauv.	C ₄	MS WS	ANG
	<i>Elymus dahuricus</i> Turcz.	C ₃	MS DS	HPG
	<i>Enneapogon borealis</i> (Griseb.) Honda	C ₄	DS	ANG
	<i>Eragrostis minor</i> Host.	C ₄	MS	ANG
	<i>Festuca ovina</i> L.	C ₃	DS	HPG
	<i>F. rubra</i> L.	C ₃	SS DS	HPG
	<i>Hierochloa glabra</i> Trin.	C ₄	MS	SPG
	<i>Hordeum brevisubulatum</i> (Trin.) Link	C ₃	SM	HPG
	<i>Koeleria cristata</i> (L.) Pers.	C ₃	DS MS	HPG
	<i>Leymus chinensis</i> (Trin.) Tzvel.	C ₃	SM DS	HPG
	<i>Pennisetum centrasiaticum</i> Tzvel.	C ₄	DB	HPG
	<i>Phragmites communis</i> Trin.	C ₃	MS	HPG
	<i>Poa pratensis</i> L.	C ₃	MS	SPG
	<i>Puccinellia tenuiflora</i> (Turcz.) Scrib. et Merr.	C ₃	SM	HPG
	<i>Roegneria turczaninowii</i> (Drob.) Nevski.	C ₃	MS	HPG
	<i>Setaria arenaria</i> Kitag.	C ₄	DB	ANG
	<i>S. glauca</i> (L.) Beauv.	C ₄	DB	ANG
	<i>S. viridis</i> (L.) Beauv.	C ₄	DB	ANG
	<i>Stipa baicalensis</i> Roshev.	C ₃	DS	HPG
	<i>S. gobica</i> Roshev.	C ₃	DS	HPG
	<i>S. grandis</i> P. Smirn.	C ₃	DS	HPG
	<i>S. krylovii</i> Roshev.	C ₃	DS SS	HPG
Liliaceae	<i>Allium polyrrhizum</i> Turcz.	C ₃	SM	PEF
	<i>A. senescens</i> L.	C ₃	DS MS	PEF
	<i>A. tenuissimum</i> L.	C ₃	DS SS	PEF
Iridaceae	<i>Iris dichotoma</i> Pall.	C ₃	DB DS	PEF
	<i>I. ruthenica</i> Ker. Gawl.	C ₃	DB	PEF

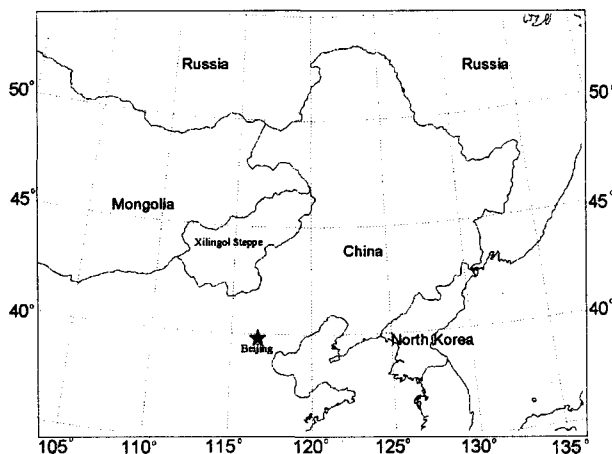


Fig. 1. Location of the Xilingol steppe in north China.

C₄ species (9 and 7 species, respectively). Saline meadow (SM) and wet soil habitats (WS) had the lowest number of C₄ species (3 species), but WS had the highest percentage of C₄ species, due to the low C₃ species composition in the habitat. Hence the photosynthetic pathway type compositions were not only related with climate changes in region and global scales, but also responded to habitats in small scale.

Morphological functional types: According to plant morphological attributes and life-span, the identified plant species were classified into 7 functional types, e.g. perennial forbs (PEF), annual forbs (ANF), high perennial grasses (HPG), short perennial graminaceous plants (grasses and sedge) (SPG), annual grasses (ANG), shrubs (SHR), and succulents (SUC) (Table 1 and Fig. 3A). Of the 7 functional types in Xilingol steppe, PEF type had the greatest number of species (40 % of the total species),

followed by ANF type (23 %), HPG type (15 %), SUC (7 %), ANG type (6 %), SPG type (5 %), and SHR type (5 %), respectively. Of the total 136 species, 63 % were found in PEF and AEF, 26 % in HPG, ANG, and SPG, 5 % in SHR, and 7 % in SUC. This suggested that forbs were the leading plant functional type in this steppe region, but most of these forbs were companion species, few could be dominant in specific habitats, e.g. *Agriophyllum pungens* (Vahl) Link A. Dietr. and *Artemisia desertorum* Spreng. in mobile dunes, and *Suaeda corniculata* (C.A. Mey.) Bunge and *S. glauca* Bunge in saline meadows. Graminaceous plants were the common dominants, producing 70 % of the total herbage in the steppe region, e.g. *Leymus chinensis* (Trin.) Tzvel., *Stipa grandis* P. Smirn., and *S. krylovii* Roshev. This indicated that the plant functional type with most species may not be the key type in the steppe region.

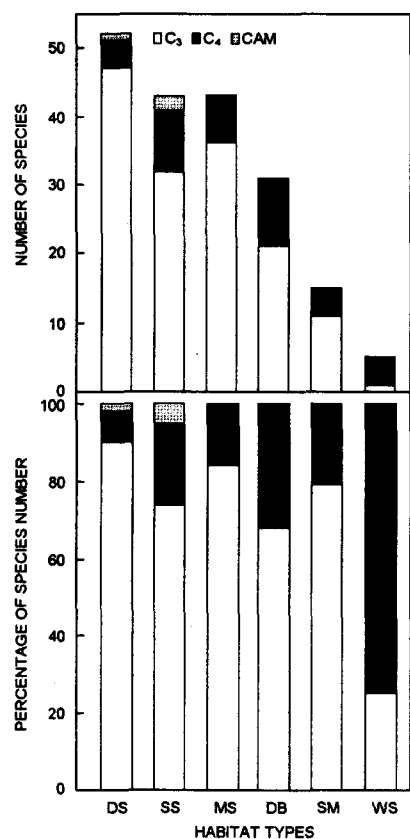


Fig. 2. The numbers of photosynthetic pathway types (C₃, C₄, and CAM) (top) and their percentages (bottom) in different habitats in Inner Mongolian Steppe, China. Habitat types: DB = disturbed and cultivated land, DS = dry steppe, MS = meadow steppe, SM = saline meadow, SS = sandy soil, WS = wet soils.

Photosynthetic pathway type compositions varied in each morphological functional types in Xilingol steppe

(Fig. 3A,B). ANF and ANG types had greatest number of C₄ species (6 species in each), followed by SPG and SUC (4 species in each), HPG and PEF (2 species in each), and SHR (1 species). Relatively more C₄ species in ANF, ANG, and SPG types suggested these three functional types were more fit for the dry steppe conditions, because C₄ species have greater ability to tolerate the drought and to maintain high water use efficiency and intense photosynthesis. The occurrence of C₄ species in PEF, HPG,

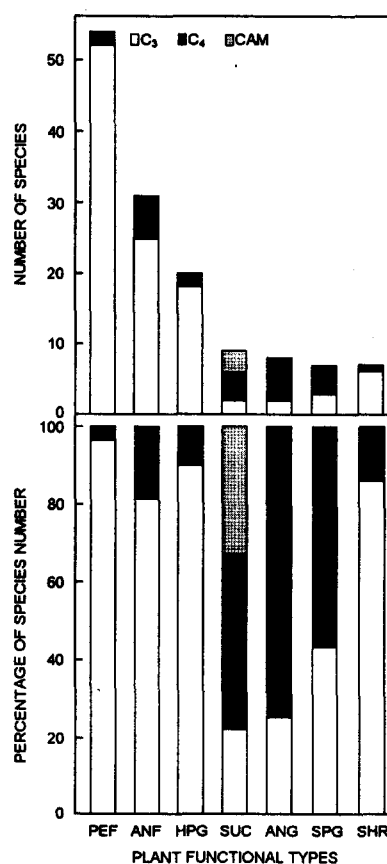


Fig. 3. The morphological functional types for the species from Inner Mongolian steppe (top) and their photosynthetic pathway compositions (bottom). Plant functional types: SHR = shrubs, HPG = high perennial grasses, SPG = short perennial grasses, ANG = annual grasses, ANF = annual forbs, PEF = perennial forbs, SUC = succulents.

and SHR was not as common as that in ANF, ANG, and SPG, and percentages of C₄ species in these types varied from 4 to 15 %. In succulent type, 4 C₄ species, 2 C₃ species, and 3 CAM species were identified. Relatively more C₄ species, succulents and annuals occurred in sandy soil and dry steppe in the region indicated that the moisture stress, especially seasonal dry, in the steppe region was relative severe.

Discussion

Photosynthetic pathway and morphological types were the common means for plant functional type classification. The occurrence of C_4 species was most common in the Xilingol steppe, North China, likely due to their greater tolerance to environmental stresses (drought, salinity, desertification) and capacities to maintain higher water use efficiency and intense photosynthesis (Wang 2002a,d). But the number of families (9 families) with C_4 photosynthesis in the steppe region was much less than that in Mongolia (16 families), where there are more types of large landscapes, e.g. forests, steppes, and gobi deserts (Pyankov *et al.* 2000). Of the total 27 C_4 species identified in the steppe region, 70 % were found in *Chenopodiaceae* (7 species) and *Gramineae* (12 species), indicating that C_4 species occurred mainly in these two families. 39 % of grasses and 54 % of *Chenopodiaceae* species identified in the steppe were found with C_4 photosynthesis. Few species were found with CAM photosynthesis (Table 1). The plants with C_3 photosynthesis, however, were the dominants [e.g. *Stipa grandis* P. Smirn., *S. gobica* Roshev., *S. krylovii* Roshev., *Leymus chinensis* (Trin.) Tzvel.], about 80 % of the total identified species and 90 % of the total herbage production in the steppe. Classification for plant functional types by photosynthetic attributes (C_3 , C_4 , and CAM) was coarse. It may not fit for the studies (e.g. community classification and community structure analysis) and land management (e.g. grazing and mowing) in plant community, landscape, and local scales in the steppe region, because of the high C_3 photosynthesis composition and the few families in which C_4 species occur.

Morphological functional types, however, did not only bring more details for studying the linkage between species, communities, and ecosystems (Smith *et al.* 1993, Aguiar *et al.* 1996, Diaz and Cabido 1997), but also for steppe management decisions (warm season and cool

season). Relative complex geo-relief and landscape in Xilingol steppe resulted in vegetation complexes, e.g. dry steppes, shrubwoods, meadows, saline meadows, wetlands, and forests (Li *et al.* 1988, Zhao *et al.* 1988, Xiao *et al.* 1995). Morphological functional types may more fit for depicting the differences between these vegetations (Li *et al.* 1988, Zhao *et al.* 1988), and reflect their seasonal dynamics in the steppe. These may be supported by the previous observations that species number and biomass in both PEF and HPG types dropped significantly in the dry seasons and dry years, while that for SPG and SUC types remarkably increased (Li *et al.* 1988, Bai and Chen 2000). Species in ANF, ANG, and SUC types were the main plant components in the dry steppes and sandylands, likely because these types of species can use the limited water resource in rainy seasons and survive the dry seasons in the form of dormant seeds (Wang 2002d). This suggests that morphological functional types in the steppe region can indicate both spatial and temporal changes in steppe ecosystems in local and region scales.

Photosynthetic pathway type compositions in each morphological type differed significantly in Xilingol steppe (Fig. 3B). More than a half of the total species in each of SUC, ANG, and SPG types was C_4 species, while that in the other types was less than 25 %. Relatively more C_4 species in SUC, ANG, and SPG suggested these types are more fit the dry steppe conditions, because these C_4 species have great capacity to tolerate dry stress and maintain higher water use efficiency and intense photosynthesis. Pyankov *et al.* (2000) proved that the combination of C_4 species with succulence allows plants to occupy very arid conditions (Pyankov *et al.* 2000). This and previous studies (Box 1996, McIntyre *et al.* 1999, Pillar 1999) suggest that the identification of optimal plant functional types depends on the selection of plant attributes and study scales.

References

- Aguiar, M.R., Paruelo, J.M., Sala, O.E., Lauenroth, W.K.: Ecosystem responses to changes in plant functional type composition: an example from the Patagonian steppe. – *J. Veget. Sci.* 7: 381-390, 1996.
- Bai, Y.F., Chen, Z.Z.: Effects of long-term variability of plant species and functional groups on stability of a *Leymus chinensis* community in the Xilin river basin, Inner Mongolia. – *Acta phytocol. sin.* 24: 641-647, 2000.
- Box, E.O.: Plant functional types and climate at the global scale. – *J. Veget. Sci.* 7: 309-320, 1996.
- Chapin, P.S.: Functional role of growth forms in ecosystem and global processes. – In: Ehleringer, J.R., Field, C.B. (ed.): *Scaling Physiological Processes: Leaf to Globe*. Pp. 287-312. Academic Press, San Diego 1993.
- Collatz, G.J., Berry, J.A., Clark, J.S.: Effects of climate and atmospheric CO_2 partial pressure on the global distribution of C_4 grasses: present, past, and further. – *Oecologia* 114: 441-454, 1998.
- Collins, R.P., Jones, M.B.: The influence of climatic factors on the distribution of C_4 species in Europe. – *Vegetatio* 64: 121-129, 1985.
- Commissione Redactorum Flora Intramongolicae: *Flora Intramongolica*. Vol. 1-5. – Inner Mongolian Press, Huhehaote 1980.
- Cramer, W.: Using plant functional types in a global vegetation model. – In: Smith, T.M., Shugart, H.H., Woodward, F.I. (ed.): *Plant Functional Types: Their Relevance to Ecosystem Properties and Global Change*. Pp. 271-288. Cambridge University Press, Cambridge 1997.
- Diaz, S., Cabido, M.: Plant functional types and ecosystem function in relation to global change. – *J. Veget. Sci.* 8: 463-474, 1997.

- Diaz, S., Cabido, M., Casanoves, F.: Plant functional traits and environmental filters at a regional scale. – *J. Veget. Sci.* **9**: 113-122, 1998.
- Downton, W.J.S.: The occurrence of C₄ photosynthesis among plants. – *Photosynthetica* **9**: 96-105, 1975.
- Duckworth, J.C., Kent, M., Ramsay, P.M.: Plant functional types: an alternative to taxonomic plant community description in biogeography? – *Progr. phys. Geography* **24**: 515-542, 2000.
- Ehleringer, J.R., Cerling, T.E., Helliker, B.R.: C₄ photosynthesis, atmospheric CO₂, and climate. – *Oecologia* **112**: 285-299, 1997.
- Jiang, S., Qi, Q.H., Kong, D.Z.: A comparative study on the biomass between *Aneurolepidium chinense* and *Stipa grandis* communities. – In: Jiang, S. (ed.): *Research on Grassland Ecosystems*. Vol. 1. Pp. 12-23. Science Press of China, Beijing 1985.
- Keeley, J.E.: C₄ photosynthetic modifications in the evolutionary transition from land to water in aquatic grasses. – *Oecologia* **116**: 85-97, 1998.
- Kitagawa, M.: *Neo-Lineamenta Floreae Manshuricae*. – J. Cramer, Vaduz 1979.
- Leemans, R.: The use of plant functional type classifications to model the global land cover and simulate the interactions between the terrestrial biosphere and the atmosphere. – In: Smith, T.M., Shugart, H.H., Woodward, F.I. (ed.): *Plant Functional Types: Their Relevance to Ecosystem Properties and Global Change*. Pp. 271-288. Cambridge University Press, Cambridge 1997.
- Li, B., Yong, S.P., Lui, Z.H.: The vegetation of the Xilin river basin and its utilization. – In: Inner Mongolia Grassland Ecosystem Research Station, Academia Sinica (ed.): *Research On Grassland Ecosystem*. Vol. 3. Pp. 84-183. Science Press, Beijing 1988.
- Li, M.: List of plants with C₄ photosynthesis. – *Plant Physiol. Commun.* **29**: 148-159, 221-240, 1993.
- Liu, S.R. (ed.): *Flora of Xilinguole River Region*. – Inner Mongolian Press, Huhehaote 1993.
- McIntyre, S., Diaz, S., Lavorel, S., Cramer, W.: Plant functional types and disturbance dynamics: introduction. – *J. Veget. Sci.* **10**: 603-608, 1999.
- Paruelo, J.M., Lauenroth, W.K.: Relative abundance of plant functional types in grassland and shrublands of North American. – *Ecol. Applic.* **6**: 1212-1224, 1996.
- Pillar, V.D.: On the identification of optimal plant functional types. – *J. Veget. Sci.* **10**: 631-640, 1999.
- Pyankov, V.I., Gunin, P.D., Tsoog, S., Black, C.C.: C₄ plants in the vegetation of Mongolia: their natural occurrence and geographical distribution in relation to climate. – *Oecologia* **123**: 15-31, 2000.
- Raghavendra, A.S., Das, V.S.R.: The occurrence of C₄-photosynthesis: A supplementary list of C₄ plants reported during late 1974-mid 1977. – *Photosynthetica* **12**: 200-208, 1978.
- Redmann, R.E., Yin, L., Wang, P.: Photosynthetic pathway types in grassland plant species from Northeast China. – *Photosynthetica* **31**: 251-255, 1995.
- Scholes, R.J., Pickett, G., Ellery, W.N., Blackmore, A.C.: Plant functional types in African savannas and grasslands. – In: Smith, T.M., Shugart, H.H., Woodward, F.I. (ed.): *Plant Functional Types: Their Relevance to Ecosystem Properties and Global Change*. Pp. 255-270. Cambridge University Press, Cambridge 1997.
- Smith, T.M., Shugart, H.H., Woodward, F.I., Burton, P.J.: Plant functional types. – In: Solomon, A.M., Shugart, H.H. (ed.): *Vegetation Dynamics and Global Change*. Pp. 272-292. Chapman and Hall, New York 1993.
- Takeda, T., Hakoyama, S.: Studies on the ecology and geographical distribution of C₃ and C₄ grasses. 2. Geographical distribution of C₃ and C₄ grasses in far east and south east Asia. – *Jap. J. Crop Sci.* **54**: 65-71, 1985.
- Teeri, J.A., Stowe, L.G.: Climatic patterns and the distribution of C₄ grasses in North America. – *Oecologia* **23**: 1-12, 1976.
- Teeri, J.A., Stowe, L.G., Livingstone, D.A.: The distribution of C₄ species of the *Cyperaceae* in North America in relation to climate. – *Oecologia* **47**: 307-310, 1980.
- Ueno, O., Takeda, T.: Photosynthetic pathways, ecological characteristics, and the geographical distribution of the *Cyperaceae* in Japan. – *Oecologia* **89**: 195-203, 1992.
- Waller, S.S., Lewis, J.K.: Occurrence of C₃ and C₄ photosynthetic pathways in North American grasses. – *J. Range Manage.* **32**: 12-28, 1979.
- Wang, R.Z.: Photosynthetic pathway types of forage species along grazing gradient from the Songnen grassland, North-eastern China. – *Photosynthetica* **40**: 57-61, 2002a.
- Wang, R.Z.: The C₄ photosynthetic pathway and life forms in grassland species from North China. – *Photosynthetica* **40**: 97-102, 2002b.
- Wang, R.Z.: Photosynthetic pathways and life forms in different grassland types from North China. – *Photosynthetica* **40**: 243-250, 2002c.
- Wang, R.Z.: Photosynthetic pathways, life forms, and reproductive types for forage species along desertification gradient on Hunshandake desert, North China. – *Photosynthetica* **40**: 321-329, 2002d.
- Williams, G.J., III, Markley, J.L.: The photosynthetic pathway type of North American shortgrass prairie species and some ecological implications. – *Photosynthetica* **7**: 262-270, 1973.
- Xiao, X., Wang, Y., Jiang, S., Ojima, D.S., Bonham, C.D.: Interannual variation in the climate and above-ground biomass of *Leymus chinensis* steppe and *Stipa grandis* steppe in the Xilin river basin, Inner Mongolia, China. – *J. Arid Environ.* **31**: 283-299, 1995.
- Yin, L., Li, M.: A study on the geographic distribution and ecology of C₄ plants in China. C₄ plant distribution in China and their relation with regional climatic condition. – *Acta ecol. sin.* **17**: 350-363, 1997.
- Yin, L., Wang, P.: [Distribution of C₃ and C₄ photosynthetic pathways of plants on the steppe of Northeastern China.] – *Acta ecol. sin.* **17**: 113-122, 1997. [In Chin.]
- Zhang, Z.T., Liu, Q.: [Rangeland Resources of the Main Pasture Area in China and Their Development and Utilization.] – Science and Technology Press of China, Beijing 1992. [In Chin.]
- Zhao, X.Y., Yao, Y.C., Yang, R.R.: Ecological geographic characteristics and outlook of natural grasslands resources in Xilin river basin. – In: Inner Mongolia Grassland Ecosystem Research Station, Academia Sinica (ed.): *Research On Grassland Ecosystem*. Vol. 3. Pp. 182-226. Science Press, Beijing 1988.