PHOTOSYNTHETICA 40 (1): 97-102, 2002

The C_4 photosynthetic pathway and life forms in grassland species from North China

R.Z. WANG

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

Abstract

C_4 photosynthetic pathway and life form were determined for 159 species in 71 genera and 13 families in the grassland of North China. 45 % of the C_4 species were found in *Graminae*, 19 % in each of *Cyperaceae* and *Chenopodiaceae*. More than 51 % of these C_4 species were in therophyta and 36 % hemicryptophyta, while fewer species were in nanophanerophyta (9 %) or geophyta (5 %). The numbers of C_4 species and their life forms were closely related with grassland deterioration and succession in North China. This indicated that the C_4 species had greater capacity to tolerate environmental stress (*e.g.* drought and salinity) caused by animal grazing and cultivation.

Additional key words: C_4 species.

Introduction

The identification of plant species as to their type of photosynthesis (C_3, C_4, or CAM), and analysis of their geographic distribution and relation to climatic patterns have been reviewed by many authors (Williams and Markley 1973, Downton 1975, Teeri and Stowe 1976, Teeri *et al.* 1980, Raghavendra and Das 1978, Waller and Lewis 1979, Collins and Jones 1985, Takeda and Hakoyama 1985, Ueno and Takeda 1992, Mateu Andres 1993, Redmann *et al.* 1995, Wang *et al.* 1997, Yin and Li 1997, Tang and Zhang 1999). Some studies deal with the differences between C_3 and C_4 species in water use efficiency, drought, temperature, and salinity adaptation (Williams and Markley 1973, Redmann *et al.* 1995, Wang *et al.* 1997, Yin and Li 1997, Tang and Zhang 1999). Few researches have tested the hypothesis that C_4 species show greater tolerance to environmental stresses (Williams and Markley 1973, Wang *et al.* 1997). Approximately 1 700 C_4 species have been identified world-wide (Li 1993), but none has yet looked at the relation of the C_4 photosynthetic pathway with the life form and grassland succession.

In China, grassland covers an area of about 400 millions hectare, which is about 40 % of the whole land area of China and 12 % of the world's grasslands. Of the total grassland in China, 3/4 is distributed in North China. More than 1 322 forage species and 98 variations have been identified in 340 genera and 76 families in these areas (Zhang and Liu 1992), but the number of C_4 species and their life forms remain unclear. The objective of this study was to determine the number of C_4 species from grassland of North China and to relate C_4 photosynthetic pathway to life form and plant habitat. This information may contribute to the interpretation of the ecology of the grassland ecosystems and to grassland management decisions in North China.

Materials and methods

In North China, grassland vegetation includes meadows, steppes, deserts, and forest grasslands, extending over 6 provinces (*i.e.* Sichuan, Qinghai, Ganshu, Liaoning, Jilin and Heilongjiang) and four autonomous regions (*i.e.* Tibet, Xinjiang, Inner Mongolia, and Ningxia). The data on C_4 species and their life forms were compiled from 19 references published between 1979 and 2001 (Commissione Redactorum Flora Intramongolicae 1980, Delectis Florae Reipublicae Popularis Sinicae Agendae Academiae Sinicae Edita 1999, Jia 1989-1998, Jiang *et al.*

Received 3 January 2002, *accepted* 4 March 2002.
Fax: 0086-01-82595962; e-mail: wangrenzh@sohu.com
Acknowledgments: I am grateful for the funding provided by the National Key Basic Research Special Foundation Project (NKBRSF Project G2000018607) and in part by the Key Project of the Chinese Academy of Sciences (KSCX1-08-03).

1998, Li 1979, 1993, Redmann *et al.* 1995). More than 1 400 forage plants distributed in the grassland of North China were listed on the basis of Chinese Flora of Forage Plants, Flora Reipublicae Popularis Sinicae, Flora Intramongolica, and some local Floras. The C_4 photosynthetic pathway, plant type, life form, palatability and habitat were recorded according to the references (*e.g.* Takeda and Hakoyama 1985, Li 1993, 1979, Redmann *et al.* 1995, Yin and Li 1997, Wang *et al.* 1997, Jiang *et al.* 1998).

Results

Floristic composition: In total 159 C_4 species, about 12 % of all forage species identified in the grassland of North China, belonging to 71 genera and 13 families were identified (Table 1). Of the 159 C_4 species, 104 species were found in *Monocotyleonae*, 55 in *Dicotyleonae*. As to plant families, 72 species were in *Graminae*, 31 species in each of *Cyperaceae* and *Chenopodiaceae*, 9 species in *Amaranthaceae*, 4 in *Polygonaceae*, 2 species in each of *Portulacaceae*, *Fabaceae*, *Compositae*, and *Euphorbiaceae*, and 1 species each in *Zygophyllaceae*, *Caryophyllaceae*, *Umbelliferae*, and *Commelinaceae*, respectively. 65 % of the C_4 forage species were found in *Monocotyleonae*, *e.g. Graminae* (45 %), *Cyperaceae* (19 %); of the other 35 % in *Dicotyleonae* most were found in *Chenopodiaceae* (19 %) and *Amaranthaceae* (6 %). This indicates that the C_4 forage species in North China mostly belong to a few families.

Plant life forms and habitats: There are four life forms of the C_4 species in the grasslands of North China (Table 1). 82 species (51 %) are therophyta (Th), 55 species (36 %) are hemicryptophyta (H), 14 species (9 %) are nanophanerophyta (N), and 8 species (5 %) are geophyta (G). No C_4 forage species was identified in macrophanerophyta (M) in the grassland of North China.

Of the total C_4 species, 49 species (31 %) were distributed in disturbed lands or in old fields, 35 species (22 %) in dry steppe, 27 species (17 %) in wet habitats, 18 species (11 %) in sandy habitats, 16 species (10 %) in saline grassland, 15 species (9 %) in meadow steppe. Few species were found in forest grasslands (2 %) and in hillsides (3 %). 12 species (8 %) were cultivated.

Most of these species (86 %) were highly palatable and ideal for grazing and mowing, while 11 % of the species showed low palatability, and only 5 were poisonous species (3 %).

Discussion

The C_4 species were most common in the grassland of North China, mainly because of their greater tolerance to environmental stress and greater ability to maintain intense photosynthesis during the growing season, especially in disturbed, dry, and saline habitats (Redmann *et al.* 1995, Wang *et al.* 1997). But most of these species belonged to *Graminae*, *Cyperacae*, *Chenopodiaceae,* and *Amaranthaceae* (90 %), while the other 10 % C_4 species were in 9 families, *e.g. Fabaceae*, *Polygonaceae*, and *Portulaceae*. This mainly results from the high composition of graminaceous plants (*Graminae*, *Cyperacae*) which was about 42 % of all forage species in the grassland of North China (Zhang and Liu 1992). Most of the species in *Chenopodiaceae* and *Amaranthaceae*, and annual grasses were pioneer plants in the grassland succession caused by grazing and cultivation disturbances (Wang 1997). This supports the hypothesis that the C_4 species have greater tolerance to environmental stress, because the early succession stages may be characterised by a lower soil moisture content and higher soil pH (Wang and Ripley 1997).

The life form composition of the C_4 species was consistent with grassland succession in North China. Of the total 159 C_4 species, more than one half (51 %) were therophyta (Th); 60 % of Th plants were found in grassland disturbed by grazing and in old fields. This was primarily due to their high capacity of seed dispersal. The Th plants produce vast amounts of seeds that can be easily diffused far away (Wang 1997). This is an advantage for the recovery of deteriorated grassland and old fields. The relatively higher number of hemicryptophyta among C_4 plants (36 %) was consistent with the high forage composition of the grasslands of North China; over 60 % of the total forage were H life form in the meadows of Northeastern China (Li 1979, Wang *et al.* 2002). The proportions of nanophanerophyta (N) and geophyta (G) were lower, only 9 and 5 %, respectively, in the total C_4 species. Most of these N plants were shrubs, with smaller leaves and greater tolerance to xeric steppe environments, occurring in the dry steppe and sandy soil grassland. This has been supported by the previous research along the Transect of Northeast China (Wang *et al.* 2002).

Plants with different photosynthetic pathways have different physiological and ecological responses (Williams and Markley 1973, Redmann *et al.* 1995). Grassland management decisions must take into account seasonal development patterns (warm season and cool season) and grassland succession, both of which are closely related to photosynthetic pathways. More C_4 species occur in early succession stages (*e.g.* deterioration caused by grazing and old fields) in the grassland of North China, and this can be an indication of grassland deterioration.

Table 1. The list of C_4 species and their life forms, habitats, and palatability in the grasslands of Northern China. Habitat types: DB = cultivated and disturbed land, DS = dry steppe, FG = forest grassland, MS = meadow steppe, SG = saline grassland, SS = sandy soil, WS = wet soils, HS = hillside, CP = cultivated plant. Life forms: M = macrophanerophyta, N = nanophanerophyta, Ch = chamaephyta, H = hemicryptophyta, G = geophyta, Th = therophyta. Palatability: P_1 = high, P_2 = good, P_3 = fair, P_4 = bad, P_5 = poison species, respectively.

	Species	Life form	Habitat	Palatability
Dicotyledonae				
Amaranthaceae	*Amaranthus albus* L.	Th	DB	P_2
	A. ascendens Lois.	Th	DB	P_2
	A. blitoides S. Watson	Th	DB	P_2
	A. caudatus L.	Th	CP DB	P_2
	A. lividus L.	Th	DB	P_3
	A. paniculatus L.	Th	CP	P_2
	A. retroflexus L.	Th	DB SG	P_2
	A. tricolor L.	Th	DB SG	P_1
	A. viridis L.	Th	DB	P_2
Chenopodiaceae	*Aellenia glauca* (Bieb) Aellen	N	DS	P_4
	Agriophyllum arenarium Bieb.	Th	DS SS	P_3
	A. squarrosum (L.) Moq.	Th	SS	P_3
	Anabasis aphylla L.	N	DS	P_5
	A. brevifolia C.A. Mey	N	DS	P_3
	A. salsa (C.A. Mey) Benth. *ex* Volk	N	DS SG	P_3
	Atriplex centralasiatica Iljin	Th	DS DB	P_3
	A. dimorphostegia Kar. *et* Kir.	Th	DS	P_2
	A. laevis C.A. Mey	Th	MS	P_3
	A. sibirica L.	Th	DB SG	P_2
	A. tatarica L.	Th	DS SG	P_3
	Bassia dasyphylla (Fisch. *et* Mey) D. Kuntze, *revis.*	Th	DS SS	P_2
	B. hyssopifolia (Pall.) O. Kuntze, *revis. gen.*	Th	DS	P_3
	Camphorosma monspeliaca L.	N	DS SS	P_2
	Halogeton glomeratus (Bieb.) C.A. Mey	Th	DS	P_4
	H. tibeticus (Bunge.) Grub.	Th	DS	P_4
	Haloxylon ammodendron (C.A. Mey) Bunge.	N	DS	P_2
	H. persicum Bunge. *ex* Boiss *et* Buhse	N	DS	P_2
	Kochia prostrata (L.) Schrad.	N	DS	P_2
	K. scoparii (L.) Schrad.	Th	SG	P_3
	K. sieversiana (Pall.) C.A.M.	Th	SG	P_3
	Salsola brachiata Pall.	Th	DS	P_4
	S. collina Pall.	Th	DB SG	P_4
	S. foliosa (L.) Schrad.	Th	DB SG	P_4
	S. lanata Pall.	Th	SG	P_4
	S. laricifolia Turcz. *ex* Litv.	N	SS	P_3
	S. orientalis S.G. Gmel.	N	DS	P_4
	S. paulsenii Litv.	Th	DS	P_4
	S. pellucida Litv.	Th	DS	P_4
	S. pestifer Litv.	Th	DS	P_4
	S. praecor Litv.	Th	DS	P_4
Polygonaceae	*Calligonum arborescens* Litv.	N	CP	P_3
	C. caput-medusae Schren.	N	CP	P_3
	C. junceum Fisch. *et* Ney	N	DS	P_3
	C. leucocladum (Schrenk) Bge.	N	DS	P_3
Portulacaceae	*Portulaca grandiflora* Hook.	Th	CP	P_3
	P. oleracea L.	Th	DB	P_2
Caryophyllaceae	*Dianthus amurensis* Jacq.	H	SS	P_4
Fabaceae	*Oxytropis filiformis* D.C.	H	DS	P_4
	Thermopsis lanceolata R.Br.	H	DS SG	P_5
Euphorbiaceae	*Euphorbia maculata* L.	Th	DB	P_5
	E. thymifolia L.	Th	DB	P_5

Table 1 (continued).

	Species	Life form	Habitat	Palatability
Umbelliferae	*Sanicula rubriflora* Fr. Schmidt	G	FG	P_2
Zygophyllaceae	*Tribulus terrestris* L.	Th	SS DB	P_5
Compositae	*Hypochoeris grandiflora* Ledeb.	H	MS	P_4
	Saussurea japonica (Thunb.) D.C.	G	MS	P_4
Monocotyledonae				
Graminae	*Achnatherum avinoides* (Honda) Chang	H	DS MS	P_2
	A. chingii (Hitchc.) Keng *ex* Kuo	H	SG	P_2
	A. splendens (Trin.) Nevski	H	SG	P_2
	Aeluropus littoralis (Gouan) Parl.	H	SG	P_2
	Aristida pennata Trin.	H	SS	P_2
	Arundinella hirta (Thunb.) F. Tanaka	H	MS	P_2
	A. setosa Trin.	H	MS	P_2
	Arthraxon hispidius (Thunb.) Makino	Th	WS DB	P_1
	Bothriochloa punctata (Roxb.) L.	H	DB	P_2
	B. ischaemum (L.) Keng	H	DS	P_3
	Bouteloua curtipendula (Michx.) Torr.	H	CP	P_2
	Buchloa dactyloides (Nutt.) Engelm.	H	DS CP	P_3
	Capillipedium parviflorum (R. Br) Stapf	H	MG	P_2
	Chloris gayaana Kunth	Th	DB	P_1
	C. virgata Sw.	Th	DB SG	P_1
	Cleistogenes hackeli (Honda) Honda Var.	H	FG	P_2
	C. squarrossa (Trin.) Keng	H	MS DS	P_2
	Coix lacryma-jobi L.	Th	MS	P_2
	Crypsis aculeata (L.) Ait.	Th	SS	P_2
	Cymbopogon jwarancusa (Jones) Schult.	H	MG	P_4
	Cynodon dactylon (L.) Pers.	H	DB	P_3
	Digitaria ciliaris (Retz.) Koel	Th	DB	P_2
	D. cruciata (Nees) A. Camus	Th	DB	P_2
	D. ischaemus (Schreb.) Schreb.	Th	DB	P_2
	D. sanguinalis (L.) Scop	Th	DB	P_2
	D. violascens Link	Th	DB	P_2
	Echinochloa caudata Roshev	Th	DB WS	P_1
	E. colonum (L.) Link	Th	CP	P_1
	E. crusgalli (L.) Beauv.	Th	DB WS	P_1
	E. frumentacea (Roxb.) Link	Th	CP	P_1
	E. hispidula (Retz.) Nees	Th	DB	P_1
	E. oryzoides (Ard.) Fritsch.	Th	WG	P_1
	Eleusine coracana (L.) Gaertn.	Th	CP	P_2
	E. indica (L.) Gaertn.	Th	DB	P_2
	Enneapogon borealis (Griseb.) Honda	Th	DS	P_1
	Eragrostis cilianensis (All.) Link	Th	DB WS	P_1
	E. ferruginea (Thunb.) Beauv.	H	MG	P_2
	E. pilosa (L.) Beauv.	Th	DB WS	P_1
	E. poaeoides Beauv.	Th	DB	P_1
	Eriochloa villosa (Thunb.) Kunth	Th	DB	P_1
	Eulalia speciosa (Debeaux) Ktze	H	FG	P_2
	Hemarthria sibirica (Gand.) Ohwi	G	MS WS	P_2
	Heteropogon contorus (L.) Beauv.	H	MS	P_2
	Hierochloe glabra Trin.	H	MS	P_2
	Imperata cylindrica (L.) Beauv.	G	DS	P_3
	Ischaemum aristatum L.	H	DB	P_3
	Miscanthus sacchariflorus (Maxim.) Hack	H	MS	P_2
	M. sinensis Anderss	H	DB	P_2
	Orinus kokonorica (Hao) Keng	G	SS	P_2
	O. thoroldii (Stapf *ex* Hemsl.) Bor.	G	SS	P_2
	Panicum miliaceum L.	Th	CP	P_1

Table 1 (continued).

	Species	Life form	Habitat	Palatability
Graminae	*Panicum ruderale* (Kitag.) Cheng	Th	DB	P_1
	Pennisetum alopecuroides (L.) Spreng	H	DB	P_3
	P. centrasiaticum Tzvel.	G	FG DG	P_2
	P. flaecidum Griseb.	G	SS	P_2
	Phacelurus latifolius (Steud.) Ohwi.	H	SG	P_3
	Roegneria kokonorica Keng	H	SS	P_2
	Saccharum sinense Roxb.	H	CP	P_2
	Sacciolepis indica (L.) Chase.	Th	WS	P_3
	S. sibiricus Trin.	H	SS MS	P_3
	Setaria arenaria Kitag.	Th	SS	P_1
	S. glauca (L.) Beauv.	Th	DB	P_1
	S. italica (L.) Beauv.	Th	DB	P_1
	S. lutescens (Weigel) F.T. Hubb.	Th.	DB SS	P_1
	S. viridis (L.) Beauv.	Th	DB SS	P_1
	Sorghum sudanense (Piper) Stapf	Th	DB	P_3
	Spodiopogon sibiricus Trin.	H	SS MS	P_3
	Themeda triandra Forssk.	H	DS	P_3
	Tragus berteronianus Schult.	Th	DB	P_2
	Tripogon filiformis Nees *ex* Steud.	H	DS	P_3
	Zoysia japonica Steud.	H	SS	P_1
	Z. sinica Hance	H	SS	P_1
Cyperaceae	*Carex leiohyncha* C.A. Mey	H	DS	P_2
	C. pediformis C.A. Mey	H	WS	P_2
	Cyperus amuricus Steud.	Th	DB HS	P_3
	C. brevifolius (Rottb.) Hassk.	H	SS WS	P_3
	C. compressus L.	Th	DB	P_3
	C. esculentus Vahl.	H	CP	P_2
	C. flabelliformis Rottb.	H	CP	P_2
	C. globosus Auct.	Th	WS	P_2
	C. glomeratus L.	Th	MS	P_3
	C. iria L.	Th	DB WS	P_2
	C. micoiria Steud.	Th	DB WS	P_2
	C. pannonicus Jacq.	H	WS	P_3
	C. rotundus L.	H	MS WS	P_3
	C. serotinus Rottb.	H	WS	P_3
	Fimbristylis dichotoma (L.) Vahl.	Th	WS	P_4
	F. bisumbellata (Forsk.) Bub.	Th	WS	P_3
	F. complanata (Retz.) Link	H	WS HS	P_3
	F. dichotoma (L.) Vahl.	H	HS	P_3
	F. miliacea (L.) Vahl.	Th	WS	P_2
	F. quinquangularis (Vahl.) Kunth	H	WS HS	P_3
	F. squarrosa Vahl.	Th	WS	P_3
	F. stauntonii Deb. *et* Fr.	Th	DB WS	P_2
	Kyllinga brevifolia Rottb.	H	WS	P_3
	K. monocephala Rottb.	H	DB WS	P_2
	Lipocarpha chinensis (Osbeck) Kern	H	HS	P_3
	L. microcephala (R.Br.) Kunth	H	DS MS	P_3
	Mariscus sumatrensis (Retz.) Koyama	H	WS	P_3
	Pycreus flavidus (Retz.) Koyama	H	HS	P_3
	P. globosus (All.) Reicht.	Th	WS DB	P_3
	P. polystachyos (Rottb.) Beauv.	Th	WS	P_3
	P. sanguinolentus (Vahl.) Nees	H	WS	P_3
Commelinaceae	*Commelina communis* L.	Th	DB WS	P_1

References

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.

Delectis Florae Reipublicae Popularis Sinicae Agendae Academiae Sinicae Edita: Flora Reipublicae Popularis Sinicae. Vol. 9. – Pp. 25, 26, 41, 74. Academy Press, Beijing 1999.

Downton, W.J.S.: The occurrence of C_4 photosynthesis among plants. – Photosynthetica **9**: 96-105, 1975.

Jia, S.X. (ed.): Chinese Flora of Forage Plants. Vol. 1-6. – Chinese Agriculture Press, Beijing 1989-1998.

Jiang, Y.X., Guo, Q.S., Ma, J.: The Community Classification and Community Characteristics in China. – Pp. 179-215. Academy Press, Beijing 1998.

Li, J.D.: Basic plant life form in the northeastern grasslands in China. – J. Jilin normal Univ. **2**: 143-155, 1979.

Li, M.: List of plants with C_4 photosynthesis. – Plant physiol. Commun. **29**: 148-159, 221-240, 1993.

Mateu Andres, I.: A revised list of European C_4 plants. – Photosynthetica **26**: 323-331, 1993.

Raghavendra, A.S., Das, V.S.R.: The occurrence of C_4-photosynthesis: A supplementary list of C_4 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.

Takeda, T., Hakoyama, S.: Studies on the ecology and geographical distribution of C_3 and C_4 grasses. 2. Geographical distribution of C_3 and C_4 grasses in far east and south east Asia. – Jap. J. Crop Sci. **54**: 65-71,1985.

Tang, H.P., Zhang, X.S.: A new approach to distinguishing photosynthetic types of plants. A case study in Northeast China Transect (NECT) platfform. – Photosynthetica **37**: 97-106, 1999.

Teeri, J.A., Stowe, L.G.: Climatic patterns and the distribution of C_4 grasses in North America. – Oecologia **23**: 1-12, 1976.

Teeri, J.A., Stowe, L.G., Livingstone, D.A.: The distribution of C_4 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 C_3 and C_4 photosynthetic pathways in North American grasses. – J. Range Manage. **32**: 12-28, 1979.

Wang, P., Yin, L., Li, J.: Ecological distribution and physiological adaptation to saline-alkali environment of C_3 and C_4 plants in Northeastern China prairie area. – Chinese J. appl. Ecol. **8**: 407-411, 1997.

Wang, R.Z.: The niche breadths and niche overlaps of main plant populations in *Leymus chinensis* grassland for grazing. – Acta phytoecol. sin. **21**: 304-311, 1997.

Wang, R.Z.: Photosynthetic pathway types of forage species along grazing gradient from the Songnen grassland, Northeastern China. – Photosynthetica **39**: 569-573, 2001.

Wang, R.Z., Gao, Q., Tang, H.P.: Variations of plant life form diversity along Northeast China Transect and its direct gradient analysis. – J. environ. Sci. (China) **14**: in press. 2002.

Wang, R.Z., Ripley, E.A.: Effects of grazing on a *Leymus chinensis* grassland on the Songnen plain of northeastern China. – J. Arid Environ. **36**: 307-318, 1997.

Williams, G.J., III, Markley, J.L.: The photosynthetic pathway type of North America shortgrass prairie species and some ecological implications. – Photosynthetica **7**: 262-270, 1973.

Yin, L., Li, M.: A study on the geographic distribution and ecology of C_4 plants in China. I. C_4 plant distribution in China and their relation with regional climatic condition. – Acta ecol. sin. **17**: 350-363, 1997.

Zhang, Z.T., Liu, Q.: Rangeland Resources of the Main Pasture Areas in China and Their Development and Utilization. – Science and Technology Press of China, Beijing 1992.