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Photosynthetic pathways, life forms, and reproductive types for forage species along the desertification gradient on Hunshandake desert, 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

Floristic compositions, life forms, reproductive types for forage species, and their responses to desertification in Hunshandake desert were studied. 164 species, in 30 families and 94 genera, were identified with C_3 (137 species), C_4 (25 species), and CAM (2 species) photosynthesis. Of the 25 C_4 species, 76 % were grasses and *Chenopodiaceae* species (hereafter chenopods). This suggests that the C_4 species mainly occurred in a few families in the desert region. The reduction of C_3 species and the increase of C_4 species with desertification indicated that C_4 species might have higher tolerance to environmental stresses (*e.g.* dry and poor soil). Relatively more hemicrytophyte and therophyte forms in the desert are related to the local temperate climate and vegetation dynamics. Relatively greater proportions of C_4/C_3 and clonal species/sexual species at mobile dune showed that the C_4 species and clonal species could make greater contribution to sand land restoration in the Hunshandake desert.

Additional key words: C_3, C_4, and CAM photosynthesis; sexual and clonal reproductions.

Introduction

C_4 biota account for approximately 18 % of the total global phyto-productivity, but it was estimated that in the world only one half of the 10 000 grass species and a thousand of the 165 000 dicotyledonous plants (hereafter dicots) have C_4 photosynthesis (Hattersley 1987, 1992, Hattersley and Watson 1992, Ehleringer *et al.* 1997). Most of the former studies on photosynthetic pathways focused on the identification of plant species as to their types of C_3, C_4, and CAM, geographic distributions, and relations with climate changes (Williams and Markley 1973, Downton 1975, Teeri and Stowe 1976, Raghavendra and Das 1978, Waller and Lewis 1979, Teeri *et al.* 1980, Collins and Jones 1985, Takeda and Hakoyama 1985, Ueno and Takeda 1992, Mateu Andrés 1993, Redmann *et al.* 1995, Ehleringer *et al.* 1997, Wang *et al.* 1997, Yin and Li 1997, Tang and Zhang 1999, Pyankov *et al.* 2000, Wang 2002b,c). Some researches tested the tolerance of C_4 species to environmental stresses (*e.g.* drought, salinity) in some regions (Redmann *et al.* 1995, Wang *et al.* 1997). These works provide strong evidence for better understanding of the occurrence of different C_4 species and their relationships with climate changes in the world. But very few have looked at the relations between C_4 species and vegetation dynamics, especially in deserts and saline grasslands (Wang 2002a).

Desertification and sand storms in the arid and semi-arid areas of China, such as those of the Hunshandake desert, and Ordos Plateau in Inner Mongolia, not only become more serious and the landscape comprises large areas of sand-covered land, but also threaten the eco-safety for North China, especially for Beijing. Most of the studies on the desertification and sandstorms were focused on the source of sandstorms and on relations to climate (Ci 1994, Gao *et al.* 1997, Sun 2001). Some authors tested the restoration of desertification lands and the characteristics of desert plants (Zhang 1994, Dong and Alaten 1999), only few identified the photosynthetic pathways for the desert species (Tang and Zhang 1999, Wang 2002b). But the relationships between photo-

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

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synthetic pathways with land desertification, as well as the role of C_4 species in the restoration of desertification lands, remain unclear. The objectives of this study were to investigate photosynthetic pathways, life forms, and reproductive types for forage plants in the Hunshandake desert and to analyse their relations with desertification. These may contribute to the restoration of desertification land and to the prevention and control of sandstorms in North China.

Materials and methods

Study site: Hunshandake desert (42°07'-43°52'N, 111°35'-117°44'E) covers an area of about 31 500 km^2 in the southern part of Xilinguole steppe, a part of Mongolian Plateau, North China, about 60 % of which is desertification land and 30 % is mobile dune. Because of serious desertification, the region has become one of the sandstorm sources in North China. Landscape comprises large areas of sand-covered land mixed with steppes, meadows and farmlands, on average 1 200 m above sea level, varying from 1 050 to 1 350 m. Because of human activities (*e.g.* overgrazing, cultivation, and road construction), desertification is becoming serious in the two recent decades. More than 60 % of the region has sandy soil with gravel, while light chestnut occurs on steppes, meadows, and farmlands. Most of the Hunshandake desert is dominated by xerophytes, *e.g.* *Stipa grandis* P. Smirn., *S. gobica* Roshev., *S. krylovii* Roshev., and *Artemisia intramongolica* H.C. Fu.

Climate: The Hunshandake desert is near the centre of the Asian continent, which leads to a continental climate and low precipitation. In winter, the climate of the area is dominated by intense Mongolian anticyclone, which produces a strong westerly flow of cold, dry continental air, and little snowfall. As the anticyclone breaks down in spring, the region comes increasingly under the influence of moist pacific air masses, reaching a climax in the summer monsoon, which lasts two months. As the summer draws to an end, the low-pressure area over the Indo-Pakistan subcontinent disappears with the development of the Mongolian anticyclone. The mean annual air temperature ranges from –0.2 to +2.0 °C, varying from –21.6 °C in January to +19.6 °C in July. Annual precipitation varies from 100 mm in the west to 380 mm in the east. Precipitation is not distributed evenly over the growing season, of which 70 % falls between June and August (Ripley *et al.* 1996).

Methods: The desertification gradient of the region was determined using canopy cover [%] of vegetation. Canopy covers for woodland (WL), dry steppe (DS), and meadow steppe (MS) were 100-75; that for fixed dune (FD) was 75-50; 50-25 for each of semi-fixed dune (SD) and disturbed and cultivated land (DB); and less than 25 for mobile dune (MD), respectively. The desertification gradient in the region is from WL, DS, and MS to FD to SD and DB, and then to MD. Floristic species were obtained from field investigation conducted in 2001 and from 4 references published from 1980 to 1993 (Commissione Redactorum Flora Intramongolicae 1980, Shirongdaolji 1991, Zhang and Liu 1992, Liu 1993). The data on photosynthetic pathway types of species and their life forms were compiled from five references published from 1979 to 2002 (Li 1979, 1993, Redmann *et al.* 1995, Yin and Li 1997, Wang 2002b). Reproductive types were grouped into two categories to facilitate analysis: sexual species without clonal reproduction (S), and clonal species with seed production (C). More than 700 forage species distributed in the region were listed and the photosynthetic pathways, life forms, habitat, and reproductive types for each species were recorded.

Results

Floristic composition: 164 species, about 25 % of the total species in Hunshandake desert region, in 30 families and 94 genera were identified with C_3, C_4, and CAM photosynthesis (Table 1). Of the total 164 species, 118 species were found in *Dicotyledoneae, e.g. Compositae* (33 species), *Chenopodiaceae* (22 species), *Fabaceae* (12 species), *Rosaceae* (9 species), and *Ranunculaceae* (7 species). 46 species were identified in *Monocotyledoneae, e.g. Gramineae* (35 species), *Ailiaceae* (5 species), and *Cyperaceae* (4 species). As for the photosynthetic pathways, 137 C_3 species were found in 26 families and 75 genera, 25 C_4 species in 8 families and 20 genera, and 2 CAM species in 1 family and 1 genus. Of the total 25 C_4 species, about 4 % of the total identified species in the desert region, 15 were found in *Monocotyledoneae* (14 grasses and 1 sedge) and 10 in *Dicotyledoneae* (5 chenopods, 1 species in each of *Amaranthaceae, Portulacaceae, Fabaceae, Zygophyllaceae,* and *Euphorbiaceae*). This suggests that the C_4 species in this desert region occur mainly in the above families, especially in *Gramineae* and *Chenopodiaceae*, for 40 % grasses and 27 % chenopods were C_4 species (Table 1). 64 % chenopods and 46 % grasses were found in desertification stages (MD, SD, and FD), but 89 % grasses were found in meadows, woodland, and dry steppe. This indicates that chenopods are more adaptive to the dry desertification conditions in the desert region.

The occurrence of C_4 species is consistent with

Table 1. Photosynthetic pathway (C_3, C_4 and CAM) in species on Hunshandake desert, North China. Desertification gradient (DG): MD = mobile dune, SD = semi-fixed dune, FD = fixed dune, DB = disturbed and cultivated land, DS = dry steppe, WL = woodland, MS = meadow steppe (Wang 2002). Life forms: M = macrophanerophyte, N = nanophanerophyte, Ch = chamaephyte, H = hemicrryptophyte, G = geophyte, Th = therophyte. Reproductive types (RT): S = sexual species, C = clonal species with seed production.

	Species	C_3/C_4	DG	Life form	RT
Dicotyledoneae					
Polygonaceae	*Polygonum aviculare* L.	C_3	DB MS	Th	S
	P. sibiricum Laxm.	C_3	MS	G	S
Chenopodiaceae	*Agriophyllum pungens* (Vahl) Link A. Dietr.	C_4	MD SD FD	Th	S
	Atriplex sibirica L.	C_4	MS SD FD	Th	S
	Axyris amaranthoides L.	C_3	DB MD SD	Th	S
	A. hybrida L.	C_3	DB SD FD	Th	S
	Ceratoides latens (J.F.) Reveal.	C_3	FD SD MS	Ch	S
	C. arborescens (Losinsk.) Tsien *et* C.G. Ma	C_3	FD SD MS	Ch	S
	Chenopodium acuminatum Willd.	C_3	MD SD DB	Th	S
	Ch. album L.	C_3	DB MS	Th	S
	Ch. aristatum L.	C_3	MD SD DB	Th	S
	Ch. foetidum Schrad.	C_3	DB MS	Th	S
	Ch. glaucum L.	C_3	DB MS	Th	S
	Ch. hybridum L.	C_3	DB WL	Th	S
	Corispermum candelabrum Iljin	C_3	MD SD FD DS	Th	S
	C. chinganicum Iljin	C_3	MD SD FD DS	Th	S
	C. declinatum Steph. *ex* Stev.	C_3	MD SD FD DB	Th	S
	C. stenolepis Kitag.	C_3	SD FD	Th	S
	Kochia prostrata Schrad.	C_4	DB SD MS	Ch	S
	K. scoparia (L.) Schrad.	C_4	DB DS	Th	S
	Salsola collina Pall.	C_4	MD SD FD DB	Th	S
	Suaeda corniculata (C.A. Mey.) Bunge	C_3	MS	Th	S
	S. glauca Bunge	C_3	MS	Th	S
	S. liaotungensis Kitag.	C_3	MS	Th	S
Amaranthaceae	*Amaranthus retroflexus* L.	C_4	DB	Th	S
Portulacaceae	*Portulaca oleracea* L.	C_4	DB	Th	S
Ranunculaceae	*Clematis hexapetala* Pall.	C_3	DS MS FD	G	S
	Delphinium grandiflorum L.	C_3	FD DS MS	G	S
	Paeonia lactiflora Pall.	C_3	WL SD	G	C
	Ranunculus japonicus Thumb.	C_3	WL MS	G	S
	Thalictrum petaloedeum L. var. *supr.* (Nakai) Kitag.	C_3	DS MS FD	G	S
	Th. simplex L.	C_3	WL MS	G	S
	Th. squarrosum Steph.	C_3	DS FD SD	G	S
Cruciferae	*Dontostemon micranthus* C.A. Mey.	C_3	WL MS DS	Th	S
	Lepidium apetalum Willd.	C_3	DB MS WL	H	S
Crassulaceae	*Orostachys fimbriatus* (Turcz.) Berger	CAM	FD SD	Th	S
	O. malacophyllum (Pall.) Fisch.	CAM	FD SD	Th	S
Rosaceae	*Geum aleppicum* Jacq.	C_3	WL MS	H	S
	Potentilla acaulis L.	C_3	DS SD FD	H	C
	P. anserina L.	C_3	MS	H	C
	P. bifurca L.	C_3	DS WL	H	C
	P. bifurca L. var. *major* Ledb.	C_3	DS WL	H	C
	P. chinensis Seringe	C_3	DS WL	H	C
	P. flagellaris Willd.	C_3	MS WL	H	C
	P. fragaricides L.	C_3	DS	H	C
	Sanguisorba officinalis L.	C_3	MS WL SD FD	H	S
Fabaceae	*Astragalus scaberrimus* Bunge	C_3	MS SD FD	H	S
	Caragana intermedia Kuang *et* H.C. Fu	C_3	SD FD	N	C
	C. microphylla Lam.	C_3	DS SD FD	N	C
	C. stenophylla Pojark.	C_3	DS SD FD	N	C

Table 1 (continued)

	Species	C_3/C_4	DG	Life form	RT
Fabaceae (cont.)	*Gueldensfaedtia stenophylla* Bunge	C_3	MS DS	H	S
	Lespedeza davurica Schindler	C_3	DS SD FD	Ch	C
	Melilotus suaveolens Ledeb.	C_3	MS SD FD WL	H	S
	Melilotoides ruthenica (L.) Sojak	C_3	DS SD FD	G	S
	Oxytropis hirta Bunge	C_3	DS	H	S
	O. filiformis D.C.	C_3	DS SD FD	H	S
	O. myriophylla D.C.	C_3	MS DS SD FD	H	S
	Thermopsis lanceolata R.Br.	C_4	MS DS WL	H	S
Geraniaceae	*Erodium stephanianum* Willd.	C_3	DS SDFD	G	S
Zygophyllaceae	*Tribulus terrestris* L.	C_4	SD FD	Th	S
Rutaceae	*Haphophyllum dauricum* Juss	C_3	DS SD FD	H	C
Polygalaceae	*Polygala tenuifolia* Willd.	C_3	DS MS WL	H	S
Euphorbiaceae	*Euphorbia esula* L.	C_3	DS SD FD	G	S
	E. humifusa Willd.	C_4	SD DB FD	Th	S
Violaceae	*Viola dissecta* Ledeb.	C_3	SD DB DS WL	H	S
Thymelaeaceae	*Diarthron linifolium* Turcz.	C_3	SD FD	Th	S
	Stellera chamaijasme L.	C_3	FD SD	H	S
Umbelliferae	*Bupleurum scorzonerifolium* Willd.	C_3	DS WL	H	S
	Siler divaricatum Benth. *et* Hook	C_3	FD DS	G	S
Primulaceae	*Glaux maritima* L.	C_3	MS	Th	S
Plumbaginaceae	*Limonium bicolor* O. Kuntze	C_3	MS DS	H	S
Asclepiadaceae	*Cynanchum amplexicaule* Hemsl.	C_3	MS SD FD	G	S
	Pycnostelma paniculatum K. Schum.	C_3	DS	G	S
Boraginaceae	*Cynoglossum divaricatum* Steph.	C_3	SD DB	G	S
Labiatae	*Phlomis tuberosa* L.	C_3	MS WL SD FD	H	S
	P. umbrosa Turcz.	C_3	WL MS	H	S
	Schizonepeta multifida (L.) Brig.	C_3	DS MS	H	S
	Scutellaria baicalensis Georgi	C_3	MS SD FD	H	S
	S. ikonnikovii Juz.	C_3	MS WL	H	S
	Thymus serphyllum L.	C_3	DS FD SD	Ch	C
Solanaceae	*Datura stramonium* L.	C_3	DB	Th	S
	Solanum nigrum L.	C_3	DB	Th	S
Plantaginaceae	*Plantago asiatica* L.	C_3	DB MS	H	S
	P. depressa Willd.	C_3	DB MS	H	S
Rubiaceae	*Galium verum* L.	C_3	MS WL	H	S
Compositae	*Artemisia anethifolia* Weber	C_3	DB MS	H	S
	A. anethoides Mattf.	C_3	MS	H	S
	A. annua L.	C_3	FD SD	H	S
	A. argyi Levl. *et* Vant.	C_3	MS WL DB	H	S
	A. desertorum Spreng.	C_3	MD FD SD	H	S
	A. dracunculus L.	C_3	DB DS WL	H	S
	A. frigida Willd.	C_3	DS SD FD WL	H	S
	A. integrifolia L.	C_3	MS WL	H	S
	A. intramongolica H.C. Fu	C_3	MD SD FD DS	H	S
	A. japonica Thunb. var. *manshurica* Kom.	C_3	MS SD FD	H	S
	A. pectinata Pall. (*Neopallasia pectinata*) Polsak.	C_3	DS SD FD	H	S
	A. pubescens Ledeb.	C_3	SD FD	H	S
	A. scoparia Waldst. *et* Kit.	C_3	DB DS	H	S
	A. selengensis Turcz. *ex* Bess.	C_3	MS	H	S
	A. sieversiana Willd.	C_3	DB	H	S
	A. sphaerocephala Krasch	C_3	FD SD MD	Ch	S
	Aster alpinus L.	C_3	DS WL	H	S

Table 1 (continued)

	Species	C_3/C_4	DG	Life form	RT
Compositae (cont.)	*Echinops gmelini* Turcz.	C_3	MS	G	S
	Filifolium sibiricum Kitam.	C_3	DS FD WL	H	S
	Heteropappus altaicus (Willd.) Novopokr.	C_3	DS SD FD	H	S
	H. altaicus (Willd.) Novopokr. var. *millefolium* (Vant.) Wang	C_3	DS FD	H	S
	Inula britanica L. var. *sublanata* Kom.	C_3	MS	H	S
	I. japonica Thunb.	C_3	MS	H	S
	Ixeris chinensis Nakai subsp. *graminifolia* Kitag.	C_3	DB MS	H	S
	I. sonchifolia Hance	C_3	DB SD	H	S
	Leontopodium leontopodioides Reauv.	C_3	MS DS SD FD	H	S
	Ligularia mongolica (Turcz.) D.C.	C_3	MS WL	H	S
	Picris japonica Thunb.	C_3	MS DS DB	H	S
	Saussurea japonica (Thunb.) D.C.	C_3	MS	G	S
	S. runcinata D.C.	C_3	MS	G	S
	Taraxacum mongolicum Hand.	C_3	MS DB	H	S
	T. ohwianum Kitam.	C_3	MS DB	H	S
	Xanthium strumarium L.	C_3	DB	Th	S
Monocotyledoneae					
Cyperaceae	*Carex dahurica* Kukenth.	C_3	DS SD FD MS	H	C
	C. duriuscula C.A.M.	C_3	SD FD DS MS	H	C
	C. lanceolata Boott.	C_3	WL DS MS	H	C
	C. pediformis C.A.M.	C_4	WL DS	H	C
Gramineae	*Achnatherum splendens* (Trin.) Nevski	C_4	MS	H	C
	Agropyron cristatum (L.) Gaertner	C_3	DS MD SD FD	H	C
	A. desertorum (Fisch.) Schult.	C_3	FD SD MD DS	H	C
	Aristida adscenionis L.	C_4	DS	H	C
	Avena fatua L.	C_3	MS DB DS	Th	S
	Beckmannia syzigachne (Steud.) Fernald	C_3	MS	Th	C
	Bromus inermis Leyss.	C_3	MS WL MD DS	H	C
	Calamagrostis epigeios (L.) Roth	C_3	MS	H	C
	Chloris virgata Sw.	C_4	MS DS	Th	C
	Cleistogenes squarrosa (Trin.) Keng	C_4	MD SD FD MS	H	C
	Digitaria ischaemum (Schreb.) Schreb. *ex* Muhl.	C_4	DB	Th	C
	Echinochles crusgalli (L.) Beauv.	C_4	MS	Th	C
	Elymus dahuricus Turcz.	C_3	MS DS WL	H	C
	Eragrostis cilianensis (All.) Link.	C_4	DB DS	Th	C
	E. pilosa (L.) P.B.	C_4	MS FD	Th	C
	E. poaeoides Beauv.	C_4	MS SD FD	Th	C
	Festuca ovina L.	C_3	DS FD	H	C
	F. rubra L.	C_3	DS WL	H	C
	Hordeum brevisubulatum (Trin.) Link	C_3	MS	H	C
	Koeleria cristata (L.) Pers.	C_3	DS MS FD SD	H	C
	Leymus chinensis (Trin.) Tzvel.	C_3	MS DS FD	H	C
	Pennisetum flaecidum Griseb.	C_4	SD FD	G	C
	Phragmites australis (Cav.) Trin. *ex* Steudel	C_3	MS	H	C
	Poa annua L.	C_3	MS DB DS	Th	C
	P. pratensis L.	C_3	MS SD FD	H	C
	P. tenuiflora (Turcz.) Scrib. *et* Merr.	C_3	MS	H	C
	Setaria glauca (L.) Beauv.	C_4	DB	Th	C
	S. lutescens Weig F.T. Hubb.	C_4	DB	Th	C
	S. viridis (L.) Beauv.	C_4	DB	Th	C
	Spodiopogon sibiricus Trin.	C_4	MS DS WL	H	C
	Stipa baicalensis Roshev.	C_3	DS SD FD	H	C
	S. *breviflora* Griseb.	C_3	FD SD	H	C
	S. gobica Roshev.	C_3	DS MD SD FD	H	C
	S. grandis P. Smirn.	C_3	DS	H	C
	S. krylovii Roshev.	C_3	DS MD SD FD	H	C

Table 1 (continued)

	Species	C_3/C_4	DG	Life form	RT
Liliaceae	*Allium macrostemon* Bunge	C_3	DB WL MS	G	S
	A. polyrrhizum Turcz.	C_3	MS SD FD	G	S
	A. senescens L.	C_3	DS MS	G	S
	A. tenuissimum L.	C_3	DS SD FD	G	S
	Asparagus dauricus Fisch. *ex* Link	C_3	SD FD	G	S
Iridaceae	*Iris dichotoma* Pall.	C_3	DB DS	G	C
	I. ruthenica Ker-Gawl.	C_3	DB	G	C

desertification in the Hunshandake desert (Fig. 1). MS had the highest numbers of both C_3 and C_4 species, likely due to its moist condition. WL had less numbers of both C_3 and C_4 species, though it was relatively moist, but the higher canopy and height for tree species may enhance their competition exclusion and reduce the other competitors. The C_3 numbers did not differ between DS and each of FD and SD, but those for DB and MD dropped remarkably with desertification. Those for C_4 species, however, increased from WL to DB, and then dropped in MD. Unlike that for C_3 and C_4 species, the proportions of C_4/C_3 for the desertification sites (MD, DB, SD, and FD) were relative greater than proportions for the MS, WL, and DS, indicating that C_4/C_3 proportions increased with land desertification in this region.

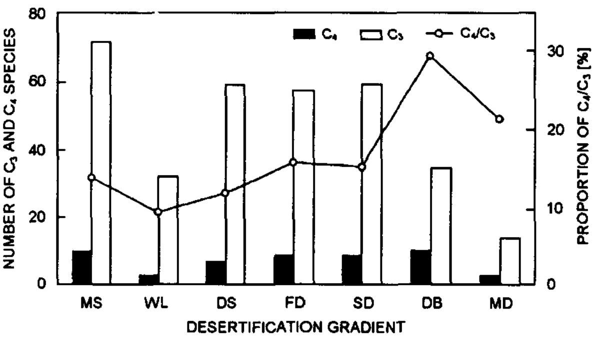

Fig. 1. The occurrence of C_3 and C_4 species and variations of C_4/C_3 proportions along the desertification gradient in Hunshandake desert, North China.

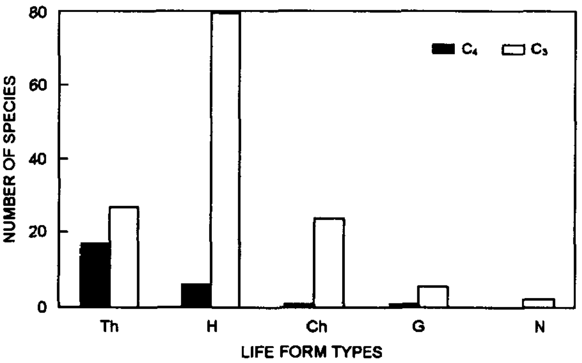

Fig. 2. The life forms for C_3 and C_4 species in Hunshandake desert, North China.

Life forms: There were five life form types for the identified species in the Hunshandake desert (Table 1). 27 % species (44 of 164) were found in therophyte (Th) form, 52 % species (85 of 164) in hemicryptophyte (H), 15 % species (25 of 164) in geophyte (G), 4 % species (7 of 164) in chamaephyte (Ch), and 2 % species (3 of 164) in nanophanerophyte (N) form, respectively. Most C_4 species were in Th form (68 %) and H form (24 %), but only 4 % in each of Ch and G forms (Fig. 2). No C_4 forage species was identified in N and macrophanerophyte (M) forms in this desert region. The numbers for C_3 species in each life form were significantly greater than those found for C_4 species in the desert region (Fig. 2). Unlike those for C_4 species, 57 % (79 of 139) C_3 species were found in H form, 19 % (27 of 139) in Th form, 17 % (24 of 139) in Ch form, 4 % (6 of 139) in G form, and merely 2 % (3 of 139) in N form, respectively. As for the leading families, 86 % chenopods and 67 % *Graminaceae* (grasses and sedge) were in Th form, 31 % *Graminaceae* in Th form, and all the species in *Ranunculaceae* were in G form.

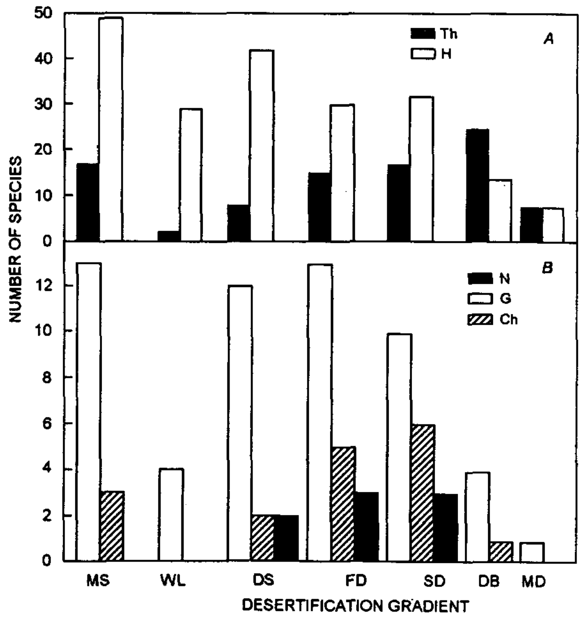

Fig. 3. The variations of life forms along the desertification gradient in Hunshandake desert, North China.

In general, life forms of plants were related with desertification in the Hunshandake desert (Fig. 3). The numbers of species in each life form for good condition sites (MS, WL, and DS) were relatively larger, except those in WL. Those of H and G forms dropped with the desertification process (from MS and DS to FD, SD, DB, and MD). While those of Th and Ch forms at first increased, peaking at DB or SD, respectively, they dropped with further desertification. This indicates that the role of each life form in vegetation dynamics is different.

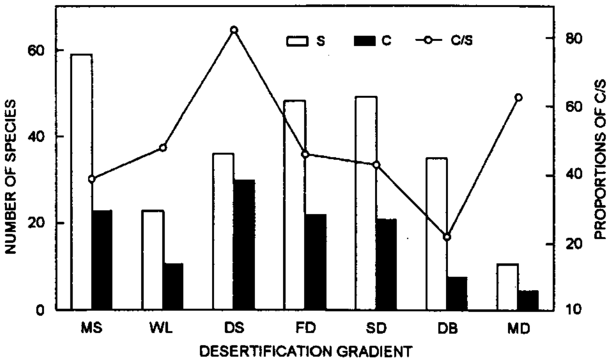

Fig. 4. The numbers of reproductive types (S = sexual species, C = clonal species) and the C/S proportions along the desertification gradient in Hunshandake desert, North China.

Reproductive types: The number of reproductive types for the identified species in the Hunshandake desert varied significantly along the desertification gradient (Fig. 4). Of the total 164 species, 33 % (54 of 164) was identified as clonal species with seed production, while that for C_4 species was as high as 60 %. 88 % dicotyledons were sexual species, the percent for monocotyledons, however, was only 13. The numbers for both sexual and clonal species were relative higher at MS, but those for WL were relative lower than the numbers for FD and SD. The numbers of sexual species increased from WL and DS, peaking at FD and SD, than dropped to the lowest at MD. That for clonal species, however, dropped remarkably from DS to MD. Unlike that for sexual and clonal species, C/S proportions increased from 39 % at MS to 83 % at DS, then decreased to 22 % at DB, but showed partial recovery at MD, increasing by 186 % as compared with DB. C/S proportions were reduced by 45 % at FD, by 48 % and 74 % at SD and DB, respectively, compared with DS.

Discussion

The changes of plant photosynthetic pathway composition were consistent with vegetation dynamics caused by nature and human activities, especially in grasslands and desert (Wang 2002a). In general, the C_4 species were most common in the Hunshandake desert. Of the total 164 identified species, 15 % were identified as C_4 species, which is 20 % more than in North China grassland (12 %) as reported by Wang (2002b). 76 % C_4 species in the region were grasses (14 species) and chenopods (5 species), indicating that C_4 species occurred mainly in these few families. More grasses were identified as C_4 species in this desert region; this suggests that *Gramineae* is the leading family with C_4 photosynthesis (Table 1). This was much different from the previous work conducted by Pyankov *et al.* (2000) in Asian deserts and steppes. Their results showed that *Chenopodiaceae* was the leading C_4 family and grasses were less important in the dry climate of the Asian deserts in Mongolia and some regions of the former Soviet Union. The Hunshandake desert, however, is relatively moist, although it is on the east of the Mongolian Steppe, and this may result in the relatively larger abundance of C_4 grasses in the region. More C_4 grass species in the region may also result from high presence of grasses, which make up 16 % of the total identified species in the Hunshandake desert (Shirongdaolji 1991). Relatively more chenopods (64 %) in the desertification sites support the result of Pyankov *et al.* (2000) that the abundance of chenopods is closely correlated with aridity. This also suggests that chenopod C_4 species may be more tolerant to dry stress.

The occurrence of C_3 and C_4 species is related with desertification in the desert region (Fig. 1). The reduction of C_3 species and increase of C_4 species and C_4/C_3 proportions from DS to MD indicate that the C_4 species have larger tolerance to environmental stresses, especially to dry and poor soil. Both soil moisture and organic matter dropped with desertification in the desert regions. This also suggests that the C_4 species are efficient plants for the restoration of desertification lands in the Hunshandake desert.

More than one half (53 %) of the identified species in the Hunshandake desert were in hemicryptophyte form (Fig. 2). This was mainly due to local temperate climate and high presence of forage plants, because over 60 % of the total forage plants were in the H form in temperate grasslands of North China (Li 1979, Wang 2002b). Relatively high amount of Th form was found in the desert region; this is consistent with land use and desertification. Th species are more adaptive to dryness and salinity, because they can use the limited water resource in growing season and survive the dry season in the form of dormant seeds. This probably explains the fact that the numbers of H form species decreased with desertification gradient, while that of Th species increased (Fig. 3). This explanation can also be supported by the observation that 68 % of C_4 species was found in Th form in this study and previous researches (Wang 2002b).

The response of sexual production and clonal growth to resource supply, *e.g.* water and nutrients, have received much attention in the past decades. In contrast to sexual species, clone species tend to occur in more disturbed sites, *e.g.* more xeric, poor soil, higher altitudes and latitudes, for they can survive as independent units (Michaels and Bazzaz 1986, Dong and Alaten 1999). In this study, the proportion of sexual species for total identified species was about 70 %, and that for dicotyleds was as high as 90 %. This showed that the seed production was the main means for vegetation renewal in this desert region. Relatively more sexual species at FD, SD, and DB indicated that seed dispersal was important for the desertification land restoration. The reduction in number of clonal species and C/S proportions from DS to DB (Fig. 4) suggests that the role of clonal species in protecting lands from desertification was getting less. But the higher C/S proportion at MD indicates that the capacities of dispersal and colonisation for clonal plants is greater than that for sexual species in the dry and poor soil conditions in this desert region. This supports the previous results that clone species tend to occur in more disturbed sites (Michaels and Bazzaz 1986, Dong and Alaten 1999). The results of the present and previous studies (Redmann *et al.* 1995, Yin and Wang 1997, Dong and Alaten 1999, Pyankov *et al.* 2000, Wang 2002a,b) suggest that C_4 species and clonal plants contribute much to sandy land restoration in desert regions. Hence different management decisions for these species must be taken into account in arid and semi-arid regions.

References

Ci, L.J.: The impact of global change on the desertification in China. – J. nat. Res. **9**: 289-303, 1994.

Collins, R.P., Jones, M.B.: The influence of climate 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.

Dong, M., Alaten, B.: Clonal plasticity in response to rhizome severing and heterogeneous resource supply in the rhizomatous grass *Psammochloa villosa* in an Inner Mongolian dune, China. – Plant Ecol. **141**: 53-58, 1999.

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

Ehleringer, J.R., Cerling, T.E., Helliker, B.R.: C_4 photosynthesis, atmospheric CO_2, and climate. – Oecologia **112**: 285-299, 1997.

Gao, Q., Liang, N., Dong, X.: A modeling analysis on dynamics of hilly sandy grassland landscapes using spatial simulation. – Ecol. Model. **98**: 163-172, 1997.

Hattersley, P.W.: Variations in photosynthetic pathway. – In: Soderstrom, T.R. *et al.* (ed.): Grass Systematics and Evolution. Pp. 49-64. Smithsonian Institution Press, Washington 1987.

Hattersley, P.W.: C_4 photosynthetic pathway variation in grasses (*Poaceae*): its significance for arid and semi-arid lands. – In: Desertifed Grasslands: Their Biology and Management. Pp. 181-212. Linnean Society, London 1992.

Hattersley, P.W., Watson, L.: Diversification of photosynthesis. – In: Chapman, C.P. (ed.): Grass Evolution and Domestication. Pp. 38-116. Cambridge University Press, Cambridge 1992.

Li, J.D.: Basic plant life from 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.

Liu, S.R. (ed.): Flora of Xilinguole River Region. – Inner Mongolian Press, Huhehaote 1993.

Mateu Andrés, A.T.: A revised list of the European C_4 plants. – Photosynthetica **26**: 323-331, 1993.

Michaels, H.J., Bazzaz, F.A.: Resource allocation and demography of sexual and apomictic *Antennaria parlinii*. – Ecology **67**: 27-36, 1986.

Pyankov, V.I., Gunin, P.D, Tsoog, S., Black, C.C.: C_4 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 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.

Ripley, E.A., Wang, R.Z., Zhu, T.C.: The climate of the Songnen plain, Northeast China. – Int. J. ecol. environ. Sci. **22**: 1-22, 1996.

Shirongdaolji (ed.): Seed Plant Resources in Zhenglanqi. – Inner Mongolian University Press, Huhehaote 1991.

Sun, J.: Spatial and temporal characteristics of dust storms in China and its surrounding regions, 1960-1999: relations to source area and climate. – J. geophys. Res. **106**: 10325-10333, 2001.

Takeda, T., Hakoyama, S.: Studies on the ecology and geographical distribution of C_3 and C_4 grasses. 2. Geographi-cal 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) platform. – 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, J.A., Takeda, T.: Photosynthetic pathway, 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 pathway 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. – Chin. J. appl. Ecol. **8**: 407-411, 1997.

Wang, R.Z.: Photosynthetic pathway types of forage species along grazing gradient from the Songnen grassland, Northeastern China. – Photosynthetica **40**: 57-61, 2002a.

Wang, R.Z.: The C_4 photosynthetic pathway and life forms in grassland species from North China. – Photosynthetica **40**: 97-102, 2002b.

Wang, R.Z.: Photosynthetic pathway and life forms in different grassland types from North China. – Photosynthetica **40**: 243-250, 2002c.

Williams, G.J., Markley, J.L.: The photosynthetic pathway type of North American 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. C_4 plant distribution in China and their relation with regional climate condition. – Acta ecol. sin. **17**: 350-363, 1997.

Yin, L., Wang, P.: Distribution of C_3 and C_4 photosynthetic pathways of plants on the steppe of Northeastern China. – Acta ecol. sin. **17**: 113-122, 1997.

Zhang, X.S.: The ecological background of the MuUs sandland and the principles and optimal models for grassland management. – Acta phytoecol. sin. **18**: 1-16, 1994.

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.