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C_4 plants in the deserts of China: occurrence of C_4 photosynthesis and its morphological functional types

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Abstract

C_4 photosynthetic pathway and morphological functional types were determined for 104 species in 45 genera and 10 families from the deserts of China. 67 C_4 species (64.4 %) were found in *Dicotyledoneae* (*e.g*. *Chenopodiaceae*, *Polygonaceae*, and *Amaranthaceae*), the other 37 species were in *Monocotyledoneae* (*e.g*. *Gramineae*, *Cyperaceae*, and *Commelinaceae*). 36.5 % of the *Chenopodiaceae* species (predominantly members of the genera *Anabasis*, *Atriplex*, *Kochia*, *Salsola*, and *Suaeda*) identified in the desert regions were found with C_4 photosynthesis, which was about 48 % of the total C_4 species. Many C_4 species (58.7 %) were annuals (*e.g*. *Amaranthus*, *Atriplex*, *Digitaria*, *Eragrostis*, *Kochia*, and *Salsola*) and experienced long-term droughts, high temperature, and high irradiance. Relatively more shrub C_4 species (28 species of 104) were found in *Chenopodiaceae* (*e.g*. *Anabasis*, *Camphorosma*, *Haloxylon*, and *Salsola*) and *Polygonaceae* (*e.g*. *Calligonum*) in the desert regions. Most of shrub C_4 species with small leaf area were no more than 1 m in height and distributed in sandy soils. Composition of relatively more annual species, shrubs, and *Chenopodiaceae* C_4 species was the primary characteristic for the C_4 species occurrence in deserts, and this was remarkably related with the arid environmental conditions.

Additional key words: annual plants; *Chenopodiaceae*; forbs; grasses; shrubs.

Introduction

The total amount of C_4 plant species is rather small, having been estimated as 6 000 plant species, approximately one-half of the 10 000 grass species and fewer than a thousand of the 165 000 dicots can be characterized by C_4 photosynthetic pathway (Hattersley 1987, Hattersley and Watson 1992). But there were only less than 1 800 identified C_4 species worldwide; even though this number has increased since this date, it is still very low when compared with about 220 000 known species of angiosperms (Kennedy *et al.* 1980, Mateu Andrés 1993). C_4 biota, however, account for about 18 % of the total global productivity, especially high productivity of C_4 monocots in grasslands and deserts. Plants characterized by C_4 photosynthetic pathway are generally capable of higher rates of CO_2 uptake than C_3 species, especially at low CO_2 concentrations (Downton and Tregunna 1968, Ehleringer *et al*. 1997), and higher tolerances to drought, high temperature, and high irradiance (Ehleringer *et al*. 1997). The knowledge of C_4 plant occurrence, geographic distribution, and climatic patterns have been used as a basis for works dealing with global climate changes, land-uses, and modelling of community successions, as well as vegetation changes under global changes (Teeri and Stowe 1976, Raghavendra and Das 1978, Teeri *et al*. 1980, Redmann *et al*. 1995, Pyankov *et al*. 2000, Wang 2002a). However, C_4 occurrence in many key ecological regions remains unclear.

Deserts in China, located in 37–45°N, 75–125°E, extend over 9 provinces (*e.g*. Xinjiang, Inner Mongolia, Qinghai, Ganshu, Ningxia, Shanxin, Liaoning, Hebei, and Jilin) and cover an area of 2 670 000 km^2, about 28 % of the total land area of China. Large expanse deserts are primarily low mountain-plateau-basin regions. Geolocation and complex geo-relief of the deserts lead to extreme continental climate and very low precipitation. Main climatic characteristics are long cold winter, dry and windy spring, short warm summer with high irradiance, and cool autumn with early frosts. Mean annual air temperature ranges from 2–5 °C in the north to 10–11 °C in the south. Moisture gradient varies with relief changes, with annual precipitation varying from 200–250 mm in the north to 9–250 mm in the south. Annual precipitation

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in some regions (*e.g*. Tieqianlike and Nuoqiang) is even less than 10 mm. Because of climate changes (*e.g.* droughts, high temperature, and big winds) and human activities (*e.g.* overgrazing and cultivation), land desertification is becoming serious in the last two decades. Most of the desert regions have sandy soils, chestnut, chernozem, and lithosol. Typical vegetation types include desert rangelands, shrubs, steppes, and oasis. More than 1 770 vascular plant species and subspecies in 568 genera from 96 families have been identified in the regions, but the occurrence of C_4 species and their morphological functional types in the regions have not been studied in detail. The objective of this study was to investigate C_4 occurrence and their morphological functional types in deserts of China. This study may contribute new information for better understanding the responses of C_4 plants to global climatic changes and land use.

Materials and methods

Floristic species were obtained from references about desert flora published from 1977 to 1999 (*e.g*. Delectis Florae Reipublicae Popularis Sinicae Agendae Academiae Sinicae Edita 1977–1999, Institute of Botany 1978, Liu 1985–1992, Commissione Redactorum Florae Xinjiangensis 1996) and some local flora, as well as from field surveys (1999–2005). Photosynthetic pathways data were compiled from references published between 1968 and 2004 (Black 1971, Downton 1975, Raghavendra and Das 1978, Stowe and Teeri 1978, Waller 1979, Winter 1981, Ziegler *et al*. 1981, Mateu Andrés 1993, Redmann *et al*. 1995, Pyankov *et al.* 2000, Wang 2002a, 2004), and from the stable carbon isotope ratio ($\delta^{13}C$) of the plant tissue measured by using *Delta*^{plus}*XP* mass spectrograph. C_4 photosynthetic types were determined from microscopic studies of Kranz anatomy, $\delta^{13}C$ fractionation, and low CO_2 compensation concentration (Γ 0–10 μmol mol^{-1}) (Redmann *et al*. 1995, Wang 2002a, 2004). C_4 species identified in the desert regions were grouped into 5 categories, *e.g.* shrub (SHR), high perennial grass (HPG), short perennial grass (SPG), annual grass (ANG), and annual forb (ANF) by morphological attributes.

Results

C_4 taxa in the deserts: 104 vascular plant species, in 45 genera and 10 families, were characterized by C_4 photosynthetic pathway that was about 5.9 % (104 of 1 771 species) of the total vascular plant species identified in these deserts. About 7.9 % genera and 10.4 % families were found with the occurrence of C_4 species in these regions, and these parameters were much higher than those from grasslands, steppes, and dry regions (*e.g.* Xinjiang, Tibet, and Inner Mongolia). Of the total 104 C_4 species, 64.4 % (67 of 104) was found in *Dicotyledoneae*, including *Chenopodiaceae* [50 species, *e.g*. *Aellenia glauca* (M.B.) Fisch. (*Salsola glauca* M.B.), *Bassia hyssopifolia* (Pall.) O. Kuntze (*Echinopsilon hyssopifolium* (Pall.) Moq.), *Camphorosma lessingii* Litv., *C. monspeliaca* L., *Girgensohnia oppositiflora* (Pall.) Fenzl (*Salsola oppositiflora* Pall.), *Halogeton glomeratus* (Bieb.) C.A. Mey., *Haloxylon ammodendron* (C.A. Mey.) Bge., *H. persicum* Bge. *ex* Boiss. (*H. aphyllum* (Minkw.) Iljin), *Iljinia regelii* (Bge.) Korov, *Londesia eriantha* Fisch. *et* Mey., *Petrosimonia sibirica* (Pall.) Bge., *P. litwinowii* Korsh.], *Polygonaceae* [8 species**,** *Calligonum arborescens* Litv., *C. caput-medusae* Schrenk, *C. ebi-nuricum* Ivanova, *C. gobicum* (Bge.) A. Los., *C. junceum* (Fisch. *et* Mey.) Litv., *C. leucocladum* (Schrenk) Bge., *C. mongolicum* Turcz., *C. pumilum* A. Los.], *Amaranthaceae* (4 species, *Amaranthus albus* L., *A. blitoides* S. Watson, *A. lividus* L., *A. retroflexus* L.), *Euphorbiaceae* (2 species, *Euphorbia mongolicum* Prokh. and *E. humifusa* Will.), 1 species in each of *Crassulaceae* [*Orostachys malacophyllus* (Pall.) Fisch], *Portulacaceae* (*Portulaca oleracea* L.), and *Zygophyllaceae* (*Tribulus terrestris* L.), respectively. The other 35.6 % was found in *Monocotyledoneae*, including *Gramineae* [31 species, *e.g. Achnatherum splendens* (Trin.) Nevski, *Aeluropus litteralis* (Willd.) Parl., *Aristida adscensionis* L. (*A. heymannii* Regel), *Arthraxon hispidus* (Thunb.) Makino, *Arundinella hirta* (Thunb.) C. Tanaka, *Bothriochloa ischaemum* (L.) Keng, *Chloris virgata* Sw., *Cynodon dactylon* (L.) Pers., *Erianthus ravennae* (L.) Beauv., *Hemarthria sibirica* (Gand.) Ohwi., *Imperata cylindrica* (L.) Beauv., *Miscanthus sinensis* Anderss., *Panicum miliaceum* L., *Pennisetum centrasiaticum* Tzvel., *Spodiopogon sibiricus* Trin., *Tragus mongolorum* Ohwi], *Cyperaceae* [5 species, *Cyperus esculentus* L. var. *sativus* Boeck., *C. globosus* auct. (*Pycreus globosus* Rei.), *C. glomeratus* L., *C. serotinus* Rottb., *Fimbristylis dichotoma* (L.) Vahl.], and *Commelinaceae* (1 species, *Commelina communis* L.). Like in Mongolia, *Chenopodiaceae* was the leading C_4 family, 48 % of the total C_4 species and 36.5 % of the total *Chenopodiaceae* species identified in the desert regions were C_4 *Chenopodiaceae*. They were followed by *Gramineae* (29.8 % of the total C_4 species and 25.8 % of the total grasses) and *Polygonaceae* (7.7 % of the total C_4 species and 14.3 % of the total *Polygonaceae* species). The C_4 species occurring in the other families were only 8.6 % of the total C_4 species.

For the genera with C_4 photosynthesis, *Salsola* was the leading C_4 genus with 14 C_4 species [*e.g*. *Salsola arbuscula* Pall., *S. brachiata* Pall., *S. collina* Pall., *S. ikonnikovii* Iljin, *S. lanata* Pall., *S. orientalis* S.G. Gmel. (*S. rigida* Pall.), *S. paletzkiana* Litv., *S. paulsenii* Litv., *S. pellucida* Litv., *S. pestifer* auct. (*S. kali* auct.),

S. praecox Litv., *S. richteri* Kar. *et* Kir., *S. rosacea* L., *S. soda* L.], followed by *Calligonum* (8 species), *Anabasis* [7 species, *e.g. Anabasis aphylla* L., *A. brevifolia* C.A. Mey., *A. elatior* (C.A. Mey.) Schischk., *A. eriopoda* (Schrenk) Benth *ex* Volkens, *A. pelliotii* Danguy, *A. salsa* (C.A. Mey.) Benth., *A. truncata* (Schrenk) Bge.], *Kochia* [7 species, *e.g. Kochia dasyphylla* Fisch. *et* Mey. (*Bassia dasyphylla* Kuntze), *K. iranica* Litv. *ex* Bornm., *K. krylovii* Litv., *K. melanoptera* Bge., *K. prostrata* (L.) Schrad., *K. scoparia* (L.) Schrad., *K. sieversiana* (Pall.) Graebn.], *Atriplex* [6 species, *e.g. Atriplex cana* C.A. Mey., *A. centralasiatica* Iljin, *A. dimorphostegia* Kar. *et* Kir., *A. laevis* C.A. Mey., *A. sibirica* L., *A. tatarica* L.], *Suaeda* [4 species, *e.g. Suaeda acuminata* (C.A. Mey.) Moq., *S. altissima* (L.) Pall., *S. dendroides* (C.A. Mey.) Moq., *S. heterophylla* Bge], *Cyperus* (4 species), and *Amaranthus* (4 species). C_4 species in five *Chenopodiaceae* genera (*e.g. Anabasis*, *Atriplex*, *Kochia*, *Salsola*, and *Suaeda*) made up of 36.5 % of the total C_4 species in the deserts. For the C_4 grass genera, 3 species were identified each of *Digitaria* [*Digitaria ciliaris* (Rotz.) Koel, *D. ischaemum* Schreb. *ex* Mnchl., *D. sanguinalis* (L.) Scop.], *Eragrostis* [*Eragrostis cilianensis* Link. *ex* Vignolo, *E. minor* Host, *E. pilosa* (L.) Beauv.], *Setaria* [*Setaria glauca* (L.) Beauv., *S. lutescens* (Weigel) F.T. Hubb., *S. viridis* (L.) Beauv.], and 2 species in each of *Cleistogenes* [*Cleistogenes songorica* (Rashev.) Ohwi. and *C. squarrosa* (Trin.) Keng], *Crypsis* [*Crypsis aculeata* (L.) Engelm. and *C. schoenoides* (L.) Lam.], *Echinochloa* [*Echinochloa crusgalli* (L.) Beauv. and *E. crusgalii* var. *mitis* (Pursh) Peterm.]. More than 80 species in the genera with C_4 plants have not been determined, including 47 species in *Chenopodiaceae*, 10 species in *Calligonum* of *Polygonaceae*, 15 species in *Gramineae*. This indicated a few more C_4 species may be identified in the regions. No endemic C_4 species has been found in the region.

Morphological functional types and habitats: In the desert regions, C_4 species fall within 5 morphological functional types. 39.4 % C_4 species was in ANF, followed by SHR (26.9 %), ANG (19.2 %), HPG (9.6 %), and SPG (5.8 %). More than 58.7 % of the total C_4 species was annual species (*e.g.* species from *Amaranthus*, *Atriplex*, *Digitaria* and *Eragrostis*, *Kochia*, *Salsola*), suggesting that annual C_4 species fit the desert environments. Grass and sedge C_4 species (including ANG, HPG, and SPG) was the second big morphological functional type, it was about 34.6 % of the total C_4 species. All of the SHR C_4 species were found in *Chenopodiaceae* (*e.g.* species from *Anabasis*, *Camphorosma*, *Haloxylon*, and *Salsola*) and *Polygonaceae* (*e.g. Calligonum*). Some C_4 SHR species are as high as 3–5 m (*e.g. Calligonum arborescens* Litv., *C. caput-medusae* Schrenk, *Haloxylon persicum* Bge. *ex* Boiss.), but most of the SHR were no more than 1 m high [*e.g. Anabasis aphylla* L., *A. brevifolia* C.A. Mey., *Iljinia regelii* (Bge.) Korov].

C_4 species occurrence was consistent with habitats and land uses. 55.8 % of the total C_4 species was found in sandy lands (*e.g.* species in *Calligonum*, *Kochia,* and *Salsola*), 26 % C_4 species in disturbed and cultivated lands (*e.g.* species in *Amaranthus*, *Digitaria*, *Portulaca*, and *Setaria*), 22.1 % in saline soils [*e.g. Atriplex cana* C.A. Mey., *Suaeda acuminata* (C.A. Mey.) Moq., *S. heterophylla* (Kar. *et* Kir.) Bge], 21.2 % in wet lands (*e.g.* species from *Cyperaceae* and *Gramineae*), 18.3 % in rangelands (*e.g.* species from *Gramineae* and *Chenopodiaceae*), 16.3 and 10.6 % in hillside and river valley, respectively. Relative high C_4 abundance in sandy lands suggested that most of these species have higher tolerance to environmental stresses in dry deserts (*e.g.* droughts, high temperature, and high irradiance).

Discussion

Many studies have proved that the occurrence of C_4 species is common in grasslands (Teeri and Stowe 1976, Waller *et al*. 1979, Teeri *et al*. 1980, Redmann *et al*. 1995, Wang 2002a, 2004) and some studies suggested that the deserts (particularly the deserts of the Middle East and the Middle Asia) represent centres for the evolution of *Dicotyledoneae* C_4 flora (Winter 1981, Pyankov *et al*. 2000 – see Table 1). The deserts in China are the eastern parts of the Middle Asia deserts, and experiencing similar environmental regimes (*e.g.* droughts, high temperature, and high irradiance), but differed in longitude and precipitation, as well as vegetation types. However, C_4 species occurrence and their morphological functional types in the desert regions remain unclear. In deserts of China, 10 of 96 vascular plant families (10.4 %) were identified with C_4 species occurrence, which was much more than those found in grassland regions and agro-forestry ecotones (Wang 2002b, 2003a, 2004), but similar to that in Mongolia (Pyankov *et al*. 2000). 5.9 % of the total vascular species and 7.9 % genera found with the plants characterized by C_4 photosynthetic pathway suggest that C_4 species were more common in the desert regions, especially in *Chenopodiaceae* (36.5 %), *Gramineae* (25.8 %), and *Polygonaceae* (14.3 %). Of the total 96 vascular plant families, *Chenopodiaceae* ranks the third leading in abundance, *Gramineae* ranks the fourth in the deserts, while these two families rank the first and second leading in C_4 abundance with 50 and 31 C_4 species in each family. In the local flora, *Compositae* and *Leguminosae* are the two leading families in species abundance, but no C_4 species was identified in the two families, indicating C_4 species mainly occurred in a few families.

Table 1. Occurrence of C_4 genera and species numbers in *Chenopodiaceae* from deserts of China, Mongolia (Pyankov *et al*. 2002), and Middle East and USSR (Winter 1981).

Genera	China	Mongolia	Middle East and USSR
Aellenia	1	0	10
Anabasis	7	7	10
Arthrophytum	0	0	1
Atriplex	6	4	17
Bassia	1	1	4
Camphorosma	2	1	3
Climacoptera	0	1	0
Cornulaca	0	0	3
Cytobasis	0	0	1
Gamanthus	0	0	1
Girgensohnia	1	0	1
Halanthium	0	0	3
Halimocnemis	0	0	3
Halocharis	0	0	5
Halostigmaria	0	0	1
Halotis	0	0	3
Halogeton	1	1	1
Haloxylon	2	1	5
Hammada	0	0	3
Horaninovia	0	0	1
Hypocyclix	0	0	1
Iljinia	1	1	0
Kochia	7	6	5
Londesia	1	1	0
Micropeplis	0	1	0
Nanophyton	0	2	0
Noaea	0	0	4
Panderia	0	0	1
Petrosimonia	2	2	2
Salsola	14	9	50
Suaeda	4	2	11
Traganum	0	0	1
Total species	50	41	151

The occurrence of C_4 species is common in *Chenopodiaceae* in most desert regions (Table 1). 137 *Chenopodiaceae* species were identified in the deserts of China, 50 species (36.5 %) were found with C_4 photosynthesis, which was more than that from Mongolia (41 species) (Pyankov *et al*. 2000), but much less than that from the Middle East (151 species) (Winter 1981). The percent of C_4 *Chenopodiaceae* species in the total of *Chenopodiaceae* species from the deserts of China was also less than those from Mongolia (50 %) and Middle East (86.3 %). There were 14–15 genera with the occurrence of C_4 photosynthesis in both deserts in China and Mongolia, while that in Middle East was 27 genera. The percent of coexisting C_4 *Chenopodiaceae* species between deserts from China and Mongolia was about 70.6 %, but those between China and Middle East, and between Mongolia and Middle East were 41.4 and 31.3 %, respectively. This suggests that there are significant differences in C_4 flora from the deserts worldwide. This also proves that the Middle East deserts represent centres for the evolution of *Chenopodiaceae* C_4 flora. Compared with northeast China grasslands and tropical region, more *Chenopodiaceae* C_4 species were identified in the deserts, indicating that *Chenopodiaceae* C_4 species may have higher tolerances to drought, high temperature, and high irradiance than the other types of plants. Pyankov *et al*. (2000) also proved that the occurrence of *Chenopodiaceae* C_4 species was strongly related with aridity in Mongolia (Pyankov *et al*. 2000).

Morphological functional type compositions can well represent the regional climate and land use patterns (Ziegler *et al*. 1981, Wang 2004). Like those in semi-arid grasslands and steppes of China, more than 55.8 % of the identified C_4 species was annual species (*e.g*. 39.4 % ANF and 19.2 % ANG). Annual species can use seasonal precipitation efficiently in the arid regions where the precipitation mainly falls between June and August (70–90 % of total rain fall), and these species can withstand the severe dry seasons as form of seeds (Wang 2004). 62 % (31 of 50) *Chenopodiaceae* C_4 species was annual species; this may in part explain the facts that more *Chenopodiaceae* species with C_4 photosynthesis were found in the dry deserts worldwide. Relatively more C_4 shrub species (26.9 %) in the deserts is another typical trait in arid regions. Even though some C_4 SHR species can be as high as 3–5 m (*e.g*. *Calligonum arborescens* Litv., *C. caput-medusae* Schrenk, *Haloxylon persicum* Bge. *ex* Boiss.), most of the SHR were no more than 1 m high [*e.g*. *Anabasis aphylla* L., *A. brevifolia* C.A. Mey., *Iljinia regelii* (Bge.) Korov]. Generally, short shoots associated with small leaf area are the main characteristics of high water use efficiency for these C_4 shrub species, for both short shoots and small leaf area can reduce water consumption by transpiration. Relative abundance of annual and shrub C_4 species in sandy land (SL) and saline soil (SS) habitats also confirms that these two types of plants have great capacity to tolerate environmental stresses in dry deserts. Relatively greater percentage of C_4 species in deserts of China consists with previous conclusion that the C_4 species favour the higher temperature and dryer conditions (Ehleringer *et al*. 1997).

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