

## C<sub>4</sub> plant species and geographical distribution in relation to climate in the desert vegetation of China

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### ABSTRACT

Water use efficiency of C<sub>4</sub> plants is higher than that of C<sub>3</sub> plants, and CAM (Crassulaceae Acid Metabolism) plants have the highest water use efficiency. In the desert regions of China, CAM plants are scarce, and C<sub>4</sub> plants, especially C<sub>4</sub> woody plants, have an important position and role in the desert ecosystem. There are 45 species of C<sub>4</sub> woody plants in the desert regions of China, including semi-woody plants, accounting for 6% of the total desert plant species in China, and most of them are concentrated in the families of Chenopodiaceae and Polygonaceae, which are 19 species and 26 species, respectively. The number of C<sub>4</sub> herbaceous plants is 107 species, including 48 monocot species and 59 dicot species. C<sub>4</sub> woody plants mainly inhabit the northwestern arid desert regions of China west of the Helan Mountains. The drought-resistance and drought-tolerance of C<sub>4</sub> herbaceous plants are worse than C<sub>4</sub> woody plants, and C<sub>4</sub> herbaceous plants mainly inhabit areas with shallow groundwater depth and better water conditions in the desert regions, and are widely distributed along the margins of oases. The abundance of C<sub>4</sub> woody plants is closely correlated with drought, but the abundance of C<sub>4</sub> herbaceous plants increases with wet conditions.

**Keywords:** desert plant; C<sub>4</sub> photosynthesis; woody plant; geographical distribution

### 1. Introduction

Most plants are characterized by C<sub>3</sub> photosynthesis, but the evolution of C<sub>4</sub> and CAM pathways exceeds the ancestral C<sub>3</sub> pathway, resulting in superior carbon-gain capacities in particular environmental conditions (Ehleringer *et al.*, 1997). Terrestrial vegetation is composed of about 95% C<sub>3</sub> plants and 5% C<sub>4</sub> plants (Warrick *et al.*, 1986), but primary productivity of C<sub>4</sub> plants accounts for only 20% of the total primary productivity (Ward *et al.*, 1999). C<sub>4</sub> plants are widely distributed in tropical and subtropical savannas, temperate grassland and shrub lands of semi-arid regions (Cerling *et al.*, 1993).

C<sub>3</sub> and C<sub>4</sub> plants have different adaptation strategies to the environment; C<sub>4</sub> plants show a lower transpiration rate than C<sub>3</sub> plants when water conditions are restricted, but the biological characteristic performance of C<sub>4</sub> plants is inhib-

ed in adverse environmental conditions (Ehleringer *et al.*, 1997). In northern Canada, green leaves per plant of C<sub>3</sub> grasses reach their maximum in spring and autumn, while C<sub>4</sub> grasses reach their maximum in mid-summer (Schwarz *et al.*, 1990). This indicates that plants with C<sub>3</sub> photosynthetic pathways grow rapidly in a cool and humid climate, but plants with C<sub>4</sub> photosynthetic pathways are more suitable to warm and dry environments relatively. In Mongolia, C<sub>4</sub> plant species increases with the decrease of geographical latitude and temperature variations, where most of the annual Chenopodiaceae C<sub>4</sub> plants are halophytes and succulents, distributed in saline, arid grassland and desert regions (Pyankov *et al.*, 2000). In northeastern China, the habitat of C<sub>4</sub> plants in grasslands are mostly arid and alkaline grasslands (Yin and Wang, 1997), and the drought-resistance and salt-tolerance of C<sub>4</sub> plants are stronger than C<sub>3</sub> plants. C<sub>4</sub> plants are mainly concentrated in Chenopodiaceae and

Gramineae in the Alashan Plateau desert regions of China, with annual and biennial herbaceous plants, the vertical zone distribution is positively correlated with temperature, and horizontal distribution is positively correlated with precipitation (He *et al.*, 2010).

The major climate characteristics in arid and semi-arid deserts are drought and minimal precipitation (Su *et al.*, 2006), where desert plants adapt to the harsh environment by various means and strategies (Zhang *et al.*, 2005), such as changes in leaf traits and structures (Li *et al.*, 2010; Zhao *et al.*, 2010), but changes in the photosynthetic pathway is the fundamental variation in which plants adapt to adversity. These traits are very important in determining the diversity of C<sub>4</sub> plants in the vast desert regions of China, and the relationship between C<sub>4</sub> woody and C<sub>4</sub> herbaceous plants. This study is the basis for the conservation of desert ecosystems, which can provide important information for changes of vegetation patterns of desert ecosystems to environmental variation, and characteristics of desert ecosystem evolution in response to global climate change.

## 2. Study methods

### 2.1. Determination of C<sub>4</sub> plant

Identifying the plant photosynthetic pathway by the following methods and sequence: (1) Analysis of  $\delta^{13}\text{C}$  values for photosynthetic organs. The collected plant leaves or assimilating shoots were taken to the laboratory and dried at 80 °C for 24 h, then subjected to analysis. Stable carbon isotope ratio was analyzed by a MAT-252 mass spectrometer, with the plant material measured 2–3 times, having high or controversial  $\delta^{13}\text{C}$  values. The  $\delta^{13}\text{C}$  values of C<sub>4</sub> plants range from –6‰ to –19‰, while that of C<sub>3</sub> plants are from –23‰ to –32‰ (Bender, 1971; Smith and Epstein, 1971), while CAM plants have  $\delta^{13}\text{C}$  values from –10‰ to –22‰ (Smith and Epstein, 1971). The significantly higher  $\delta^{13}\text{C}$  value is the necessary condition for C<sub>4</sub> plants. (2) Observing anatomical structure of photosynthetic organs. Field collected leaves or assimilating shoots were fixed with FAA fixative, then sliced by using paraffin microtome, and photographed with a Nikon 1671-CHR optical microscope. While C<sub>4</sub> plants may or may not have Kranz anatomy, it is sufficient but not a necessary condition for C<sub>4</sub> plant photosynthesis (Voznesenskaya *et al.*, 2001). (3) Measurement of CO<sub>2</sub> compensation point. The CO<sub>2</sub> response curve was determined under low CO<sub>2</sub> concentration ( $\leq 70 \mu\text{mol/mol}$ ) by using the LI-6400 portable photosynthesis system and CO<sub>2</sub> steel bottles, and then CO<sub>2</sub> compensation point was obtained according to the linear regression of low CO<sub>2</sub> concentration corresponding to net photosynthetic rate (Nijs *et al.*, 1997). CO<sub>2</sub> concentration of C<sub>4</sub> plants is less than 10  $\mu\text{mol/mol}$ , while CO<sub>2</sub> concentration of C<sub>3</sub> plants is between 30–70  $\mu\text{mol/mol}$ . (4) Measuring photosynthetic enzyme activity. Phosphoenolpyruvate carboxylase (PEPC) and ribulose 1,5-bisphosphate carboxylase (RuBPC) are key enzymes of photosynthesis, with enzyme extraction and

activity determination using tissue triturator and Liquid Scintillation analyzer (Institute of Shanghai Plant Physiology, 1999). PEPC/RuBPC ratio greater than 1 indicates C<sub>4</sub> plants while less than 1 indicates C<sub>3</sub> plants (Yin and Wang, 1997). (5) Gas exchange measurement. The photosynthetic rate ( $P_n$ ) and transpiration rate ( $T_r$ ) were measured by a LI-6400 Photosynthesis System, and calculated water use efficiency (WUE) ( $WUE=P_n/T_r$ ). WUE of C<sub>4</sub> plants is higher than C<sub>3</sub> plants; net photosynthetic rate was measured under different light intensities, and light saturation point was obtained according to light response curves. C<sub>4</sub> plants have no or significantly high light saturation point. (6) C<sub>4</sub> plants were judged according to the same plant characteristics in the same genus and combined with other researches (Winter, 1981).

The total number of genera and species in the desert vegetation were counted according to "Flora in Deserti Reipublicae Populorum Sinarum" (Institute of Lanzhou Desert Research, 1985, 1987, 1992) and Flora's of Xinjiang (Editorial Committee of Flora of Xinjiang, 1992), Gansu (Editorial Committee of Flora of Gansu, 2005), Qinghai (Editorial Committee of Woody Flora of Qinghai, 1987), Inner Mongolia (Commissione Redactorum Florae Intramongolicae, 1990), and Ningxia (Ma and Liu, 1986). C<sub>4</sub> plant lists and characteristics were consulted from published accounts of above different areas, and compared with "Flora in Deserti Reipublicae Populorum Sinarum" (Institute of Lanzhou Desert Research, 1985, 1987, 1992) and the aforementioned local floras. Meanwhile, according to our results, the list, characteristics and distribution of C<sub>4</sub> woody and C<sub>4</sub> herbaceous plants of the desert regions of China were arranged. Botanical nomenclature is according to "New Latin-Chinese-English Names of Plants" (Institute of Botany, 1996).

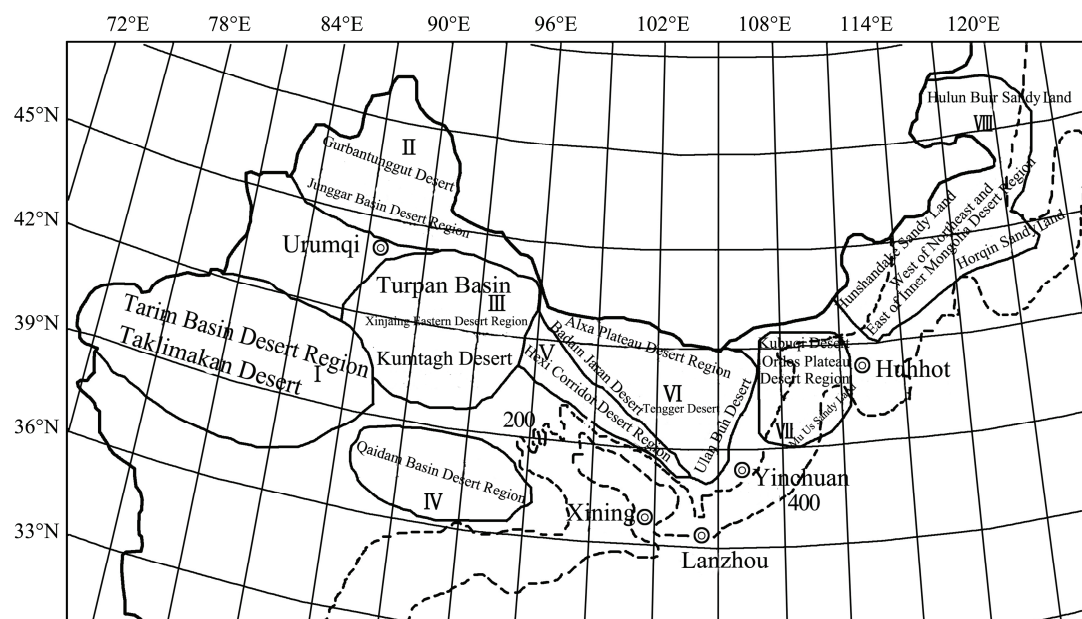
### 2.2. Desert climate data analysis

The geomorphic types of desert regions in China are desert, Gobi, wind erosion yardang, hilly, piedmont and flat soils. The area of Chinese deserts is 1.427 million km<sup>2</sup>, distributed in eight deserts which are Taklimakan, Gurbantunggut, Kumtagh, Qaidam Basin, Badan Jaran, Tengger, Ulan Buh, and Kubuqi, and four Sandy lands, which are Mu Us, Hunshandake, Horqin, and Hulun Buir (Zhu *et al.*, 1980). According to natural characteristics and desert distribution, the aforementioned deserts have been divided into eight desert regions, which are Tarim Basin (I), Junggar Basin (II), Xinjiang Eastern (III), Qaidam Basin (IV), Hexi Corridor (V), Alxa Plateau (VI), Ordos Plateau (VII), and West of Northeast and East of Inner Mongolia (VIII) (Zhu *et al.*, 1980) (Figure 1).

Climate data was analyzed by partitioning, the meteorological raw data derived from the National Natural Science Foundation of China "Environmental and Ecological Science Data Center for West China", and meteorological element data from the northern weather stations of China from 1951 to 2008. The weather stations corresponding to the eight desert regions respectively are: Area I (Aksu, Baicheng,

Luntai, Kuqa, Korla, Tuergate, Wuqia, Kashgar, Aheqi, Patrul, Kelpin, Arael, Tazhong, Tieganlike, Ruqiang, Yarkand, Pishan, Hetian, Minfeng, Andehe, Qiemo, Yutian), Area II (Habahe, Jimunai, Fuhai, Altay, Fuyun, Tacheng, Hebukesai, Qinghe, Alataw Shankou, Tuoli, Karamay, North Tashan, Jinghe, Wusu, Shihezi, Caijiahu, Qitai), Area III (Daban city, Qijiaoqing, Kumux, Yanqi, Turpan, Balitang, Yiwu, Hami, Hongliuhe), Area IV (Mangnai, Cold Lake, Xiaozaohuo, Da Qaidam, Delhi, Golmud, Nomhon), Area V

(Mazongshan, Dunhuang, Anxi, Yumen town, Wutonggou, Dingxin, Jinta, Jiuquan, Gaotai, Zhangye, Shandan, Yongchang, Wuwei, Minqin), Area VI (Ejin Qi, Jihede, Guaizihu, Bayan Mod, Alxa Youqi, Hailisu, Jilantai, Alxa Zuoqi, Zhongwei), Area VII (Mandalt, Darhan Lianheqi, Hanggin Houqi, Baotou, Linhe, Otag Qi, Dongsheng, Ejin Horo Qi), and Area VIII (Ulanhot, Erenhot, Naran Bulag, Abag Qi, Sonid Zuoqi, Jurh, Xi Ujimqin Qi, Jarud Qi, Bairin Zuoqi, Xilinhaote, Linxi).



**Figure 1** The distribution map of deserts in China

The aridity index is indicated by  $K$  ( $K=(0.16\Sigma t)/r$ ), where  $\Sigma t$  is the active accumulated daily average temperature of  $\geq 10^\circ\text{C}$ , and  $r$  is precipitation when daily average temperature is  $\geq 10^\circ\text{C}$  (College of Forestry of Beijing Forestry University, 1983). The humidity index is indicated by  $I$  ( $I=P/(T+10)$ ), where  $P$  (mm) is annual precipitation, and  $T$  ( $^\circ\text{C}$ ) is average

annual temperature (Pyankov *et al.*, 2000). From the drought-wet intensity which was reflected in our desert areas, humidity index is rough, aridity index is more accurate, but the calculation of humid index is simple and aridity index is relatively cumbersome. The climate characteristics of eight desert regions are shown in Table 1.

**Table 1** Climatic data in desert regions of China

No.	Name	$P$ (mm)	AAT ( $^\circ\text{C}$ )	AI	HI	ST $\geq 10^\circ\text{C}$	Jan. AT ( $^\circ\text{C}$ )	Jul. AT ( $^\circ\text{C}$ )	ST $\geq 10^\circ\text{C}$ days	ASH (hr)
I	Tarim Basin desert region	73.7	10.1	15.8	3.7	3,944	-7.8	24.1	196	2,826
II	Junggar Basin desert region	173.7	5.2	5.9	11.6	3,167	-15.8	22.7	165	2,862
III	Eastern of Xinjiang desert region	68.9	7.8	13.6	3.9	3,591	-11.5	23.7	178	3,180
IV	Qaidam Basin desert region	61.4	3.4	9.8	4.6	1,900	-11.5	16.7	128	3,215
V	Hexi Corridor desert region	104.0	7.4	6.7	5.9	3,144	-9.4	22.1	172	3,131
VI	Alashan Plateau desert region	117.0	8.1	6.4	6.4	3,509	-10.2	24.5	178	3,221
VII	Ordos Plateau desert region	251.8	6.3	2.5	15.2	3,013	-11.4	22.0	165	3,081
VIII	Northeast west and east of Inner Mongolia desert region	290.3	3.4	1.9	21.9	2,717	-17.2	21.7	150	3,017

$P$ : Annual precipitation; AAT: Average annual temperature; AI: Aridity index; HI: Humidity index; ST: Sum of temperatures; Jan. AT: January Average temperature; Jul. AT: July Average temperature; ASH: Annual sunshine hours

The relationship between climatic factors and number of  $C_4$  woody and herbaceous species in different desert regions were analyzed by linear regression.

### 3. Results and analysis

#### 3.1. Occurrence quantity of $C_4$ species in our desert regions

$C_4$  plants are only found in Angiosperms, about 20 families, but mainly exists in 16 vascular families, the Dicotyledonae have 14 families, which are Acanthaceae, Aizoaceae, Amaranthaceae, Boraginaceae, Caryophyllaceae, Chenopodiaceae, Compositae, Convolvulaceae, Euphorbiaceae, Nyctaginaceae, Polygonaceae, Portulacaceae, Scrophulariaceae and Zygophyllaceae; the Monocotyledonae have two families, which are Cyperaceae and Gramineae (Ehleringer *et al.*, 1997). There are nine types of Dicotyledonae and three types of Monocotyledonae in our desert regions that have been found to be  $C_4$  plants, which are Amaranthaceae, Chenopodiaceae, Compositae, Convolvulaceae, Polygalaceae, Polygonaceae, Portulacaceae, Ranunculaceae, Zygophyllaceae and Cyperaceae, Gramineae, and Potamogetonaceae (Table 2), in which Chenopodiaceae, Polygonaceae, Cyperaceae, and Gramineae are rich in  $C_4$  plants. The number of

$C_4$  species in our desert regions is shown in Table 3.

It can be seen that 12 families contain  $C_4$  plants in our desert regions (Tables 2 and 3). Besides Chenopodiaceae, Cyperaceae and Gramineae, other families contain only one genus that is  $C_4$  plants. In Dicotyledonae, Chenopodiaceae has the most  $C_4$  plants with 19 genera and 62 species, in which *Salsola*, *Suaeda*, *Atriplex* and *Camphorosma* contain the most  $C_4$  plants. In Monocotyledonae, Gramineae contain the most  $C_4$  plants with 21 genera and 36 species, and Cyperaceae have five genera and 10 species, which are called  $C_4$  grasses and  $C_4$  sedges, respectively.

In the northern desert regions of China, there are 27 dicotyledonous genera of  $C_4$  plants which account for 18.2% of the total genera; there are 104 species of  $C_4$  plants which account for 18.3% of the total species; the genera of  $C_4$  plants account for 40.3% of the total genera in Monocotyledonae, and the species of  $C_4$  plants account for 26.8% of the total species. For the total numbers of species,  $C_4$  plants in Dicotyledonae are 2.2 times higher than Monocotyledonae, but in terms of occurrence proportion  $C_4$  plants of Monocotyledonae are 46% higher than Dicotyledonae. On the whole, the genera of  $C_4$  plants account for 25.1% of the total genera, and the species accounted for 20.3% of the total species in the desert regions of China.

**Table 2** Families and genera known to contain  $C_4$  species in desert regions of China

Family	Genus
<b>Dicotyledonae</b>	
Amaranthaceae	<i>Amaranthus</i>
Chenopodiaceae	<i>Aellenia</i> , <i>Anabasis</i> , <i>Atriplex</i> , <i>Axyris</i> , <i>Bassia</i> , <i>Borsszczowia</i> , <i>Camphorosma</i> , <i>Chenopodium</i> , <i>Comulaca</i> , <i>Girgensohnia</i> , <i>Halimocnemis</i> , <i>Halogeton</i> , <i>Haloxydon</i> , <i>Iljinia</i> , <i>Kochia</i> , <i>Londesia</i> , <i>Petrosimonia</i> , <i>Salsola</i> , <i>Suaeda</i>
Compositae	<i>Artemisia</i>
Convolvulaceae	<i>Cuscuta</i>
Polygalaceae	<i>Polygala</i>
Polygonaceae	<i>Calligonum</i>
Portulacaceae	<i>Portulaca</i>
Ranunculaceae	<i>Thalictrum</i>
Zygophyllaceae	<i>Tribulus</i>
<b>Monocotyledonae</b>	
Cyperaceae	<i>Blysmus</i> , <i>Cyperus</i> , <i>Fimbristylis</i> , <i>Juncellus</i> , <i>Pycneus</i>
Gramineae	<i>Aeluropus</i> , <i>Aristida</i> , <i>Arthraxon</i> , <i>Arundinella</i> , <i>Bothriochloa</i> , <i>Chloris</i> , <i>Cleistogenes</i> , <i>Crypsis</i> , <i>Cynodon</i> , <i>Digitaria</i> , <i>Echinochloa</i> , <i>Eragrostis</i> , <i>Erianthus</i> , <i>Hemarthria</i> , <i>Hierochloa</i> , <i>Imperata</i> , <i>Miscanthus</i> , <i>Pennisetum</i> , <i>Setaria</i> , <i>Spodiopogon</i> , <i>Tragus</i>
Potamogetonaceae	<i>Potamogeton</i>

#### 3.2. Species and distribution of $C_4$ woody plants in desert regions of China

The species and distribution of  $C_4$  woody plants in Chinese deserts is shown in Appendix table 1. Chenopodiaceae and Polygonaceae (Dicotyledonae) are  $C_4$  woody and semi-woody plants, with a total number of 45 species, with 19 species in Chenopodiaceae and 26 species in Polygonaceae. There are 568 species of desert plants in nine dicoty-

ledonous families of  $C_4$  plants in desert regions of China,  $C_4$  woody plants account for 7.9% of the total number of dicotyledonous desert plants, and accounting for 6.0% of the total number of desert plants.

*Calligonum* species (Polygonaceae) are  $C_4$  plants and is the main component of woody plants in our desert natural ecosystem,  $\delta^{13}C$  values are from  $-16\text{‰}$  to  $-13\text{‰}$ , the habit is shrublet or shrub, ecotypes are xerophytic or extreme xerophytes, and is distributed mainly in the northwest desert

regions, including 22 species in Xinjiang. Xinjiang lacks *Calligonum alaschanicum* A. Los, but it is distributed in the Tengger and Kubuqi deserts. *Calligonum kozlovi* is a peculiar species in the Qaidam Basin of Qinghai, *C. potaninii* is distributed in the Anxi and Linze of Hexi Corridor, and *C. zaidamense* is distributed in the Gel mud of Chaidamu Basin of Qinghai.

*Aellenia*, *Anabasis*, *Atriplex*, *Camphorosma*, *Iljinia*, *Kochia* and *Suaeda* (Chenopodiaceae) are C<sub>4</sub> subshrubs; the two species of *Haloxylon* are C<sub>4</sub> shrubs or dungarunga. *Salsola* are C<sub>4</sub> subshrubs and shrubs such as *S. arbuscula*. Subshrubs of *Kochia prostrata* and *Camphorosma lessingii* have higher productivity in semi-deserts and mountainous areas.

**Table 3** The occurrence of C<sub>4</sub> species in different plant families in desert regions of China

Family	Genus numbers		Species numbers	
	Total	C <sub>4</sub> number	Total	C <sub>4</sub> number
<b>Dicotyledonae</b>				
Amaranthaceae	1	1	5	5
Chenopodiaceae	34	19	137	62
Compositae	83	1	281	3
Convolvulaceae	3	1	17	4
Polygalaceae	1	1	1	1
Polygonaceae	5	1	59	26
Portulacaceae	1	1	1	1
Ranunculaceae	15	1	39	1
Zygophyllaceae	5	1	28	1
Total Dicots	148	27	568	104
<b>Monocotyledonae</b>				
Cyperaceae	11	5	53	10
Gramineae	54	21	120	36
Potamogetonaceae	2	1	6	2
Total Monocots	67	27	179	48
<b>Total</b>	<b>215</b>	<b>54</b>	<b>747</b>	<b>152</b>

### 3.3. The species and distribution of C<sub>4</sub> herbaceous plants in desert regions of China

The species and distribution of C<sub>4</sub> herbaceous plants in desert regions of China are shown in Table 2. There are 107 species, including 48 monocot species and 59 dicot species. In the Monocotyledonae, C<sub>4</sub> sedges have 10 species, C<sub>4</sub> grasses have 36 species, and Potamogetonaceae two species. In the Dicotyledonae, Chenopodiaceae has 43 species, Amaranthaceae five species, Convolvulaceae four species, Compositae three species, and Polygalaceae, Portulacaceae, Ranunculaceae and Zygophyllaceae one species, respectively. The drought-resistance and drought-tolerance in C<sub>4</sub> herbaceous plants are worse than C<sub>4</sub> woody plants, and C<sub>4</sub> herbaceous plants mainly inhabit areas with shallow ground-water depth and better water conditions in desert regions, and are also widely distributed along the margins of oases.

*Tragus racemosus* is thought of *Tragus mongolorum* (Tang and Liu, 2001), it is an annual C<sub>4</sub> herbaceous plant, distributed in the Horqin and Alxa regions. *Tragus racemosus* (L.) Scop. is also thought of *Tragus mongolorum* (Institute of Botany, 1996). *Tragus mongolorum* Ohwi is thought of *Tragus mongolorum* (Institute of Lanzhou Desert Research, 1985), it is an annual herbaceous plant found along the sides of roads and fields, river banks, lithic hillsides and sandy lands of Horqin, Mu Us and Hexi Corridor, plus the Kubuqi and Tengger deserts. Pyankov *et al.* (2000) noted that *T. mongolorum* is a C<sub>4</sub> plant. *Tragus mongolorum* may consist of 1–2 species, which needs to be sorted out by phytotaxonomist.

A large number of plant species were judged as C<sub>4</sub> plants, such as *Bolboschoenus maritimus* (L.) Palla (Cyperaceae) with a PEPC/RuBPC ratio of 1.520, and *Erodium stephanianum* Willd. (Geraniaceae) with a PEPC/RuBPC ratio of 1.129 (Yin and Wang, 1997). We measured  $\delta^{13}\text{C}$  of *Achnatherum splendens* (Trin.) Nevski (Gramineae) as  $-26.1\%$  while Wang *et al.* (2005) recorded a value of  $-11.8\%$ . *Carex pediformis*, *Digitaria lineis*, *Setaria arenaria*, *Agriophyllum pungens* and *Thermopsis lanceolata* R. Br. are perennial herbaceous C<sub>4</sub> plant of the Hunshandake desert (Wang *et al.*, 2005). *Agriophyllum pungens* (Vahl) Link ex A. Dietr. is an annual xerophilous herbaceous C<sub>4</sub> plant (Tang and Liu, 2001), *Potentilla anserine* L. is a rosaceous perennial creeping C<sub>4</sub> herb (Yin *et al.*, 1989), and *Saussurea japonica* (Thunb.) D. C. (Compositae) is a C<sub>4</sub> plant (Yin and Li, 1997).

*Tragus racemosus* is thought of *Tragus mongolorum* (Tang and Liu, 2001), it is an annual C<sub>4</sub> herbaceous plant, distributed in the Horqin and Alxa regions. *Tragus racemosus* (L.) Scop. is also thought of *Tragus mongolorum* (Institute of Botany, 1996). *Tragus mongolorum* Ohwi is thought of *Tragus mongolorum* (Institute of Lanzhou Desert Research, 1985), it is an annual herbaceous plant found along the sides of roads and fields, river banks, lithic hillsides and sandy lands of Horqin, Mu Us and Hexi Corridor, plus the Kubuqi and Tengger deserts. Pyankov *et al.* (2000) noted that *T. mongolorum* is a C<sub>4</sub> plant. *Tragus mongolorum* may consist of 1–2 species, which needs to be sorted out by phytotaxonomist.

### 3.4. The relationship between the distribution of C<sub>4</sub> plants and climate in desert regions of China

The majority of C<sub>4</sub> species are in the Junggar Basin, with 92 species accounting for 61% of the total C<sub>4</sub> species in the

desert regions of China (Table 4). The mean annual precipitation since 1951 is 174 mm in this region, the active accumulated annual temperature ( $\geq 10^\circ\text{C}$ ) is above  $3,100^\circ\text{C}$  (Table 1), and the average sea level is 739 m. The number of  $\text{C}_4$  species is minimal in the Qaidam Basin which accounts for 26% of the total  $\text{C}_4$  species in the desert regions. The mean annual precipitation is minimal with 61 mm, the active accumulated annual temperature ( $\geq 10^\circ\text{C}$ ) is the lowest with  $1,900^\circ\text{C}$ , the average sea level is 2,914 m, and belongs to the cold and arid desert regions. In the Tarim Basin, the active accumulated annual temperature ( $\geq 10^\circ\text{C}$ ) is above  $3,900^\circ\text{C}$ , there are 200 days with temperatures  $\geq 10^\circ\text{C}$ , the annual average temperature is above  $10^\circ\text{C}$ , it has the longest frost-free period and maximum temperature, and belongs to the temperate arid desert region. There are 72  $\text{C}_4$  species in this region.

The correlation between the number of  $\text{C}_4$  species and climatic factors in different desert regions are shown in

Table 5. It can be seen that a negative correlation exists between the distribution of  $\text{C}_4$  woody plants and annual precipitation, the number of  $\text{C}_4$  woody plants in the north-western arid desert region west of the Helan Mountains were more than in the semi-arid desert region east of the Helan Mountains, and  $\text{C}_4$  woody plants have important ecological position and function in this region.  $\text{C}_4$  herbaceous plants have a positive correlation with annual precipitation reaching to the significant level ( $p < 0.05$ ), while showing a negative correlation with aridity index. There is a dominance of  $\text{C}_4$  herbaceous plants in wet conditions, mainly inhabiting areas of shallow groundwater depth and better water conditions in desert regions, and are widely distributed along the margins of oases. The abundance of  $\text{C}_4$  woody plants is closely related with aridity, and the abundance of  $\text{C}_4$  herbaceous plants increases with wet conditions.  $\text{C}_4$  woody plants have an important role in indicating arid environments.

**Table 4** The number of  $\text{C}_4$  species in desert regions of China

No.	Regions	Woody plants				Herbaceous plants				TN
		Che.	Pol.	SubT	Cyp.	Gra.	Che.	Oth.	SubT	
1	Tarim Basin desert region	8	6	14	5	22	18	13	58	72
2	Junggar Basin desert region	17	5	22	4	21	32	13	70	92
3	Xinjiang eastern desert region	7	10	17	1	19	15	8	43	60
4	Qaidam Basin desert region	2	3	5	0	14	14	7	35	40
5	Hexi Corridor desert region	6	9	15	2	22	23	8	55	70
6	Alxa Plateau desert region	6	2	8	4	28	22	9	63	71
7	Ordos Plateau desert region	4	2	6	6	29	15	14	64	70
8	West of northeast and East of Inner Mongolia desert region	2	1	3	8	29	14	16	67	70

Che.: Chenopodiaceae; Pol.: Polygonaceae; SubT: Subtotal; Cyp.: Cyperaceae; Gra.: Gramineae; Oth.: Others; TN: Total number

**Table 5** Relationship between the occurrences of  $\text{C}_4$  species and climatic factors in desert regions of China

Climatic factor	The number of $\text{C}_4$ woody plants		The number of $\text{C}_4$ herbaceous plants	
	<i>R</i>	<i>p</i>	<i>R</i>	<i>p</i>
Annual precipitation	-0.3950	0.3328	0.7126	0.0473*
Annual mean temperature	0.4291	0.2887	0.0600	0.8879
Aridity index	0.4270	0.2910	-0.5788	0.1328
Humidity index	-0.4236	0.2956	0.6432	0.0853
The active accumulated annual temperature of $\geq 10^\circ\text{C}$	0.5402	0.1669	0.3612	0.3793
Average temperature of January	0.0950	0.8229	-0.3909	0.3384
Mean temperature of July	0.4427	0.2721	0.5556	0.1528
The number of days of temperature of $\geq 10^\circ\text{C}$	0.5195	0.1870	0.3319	0.4219

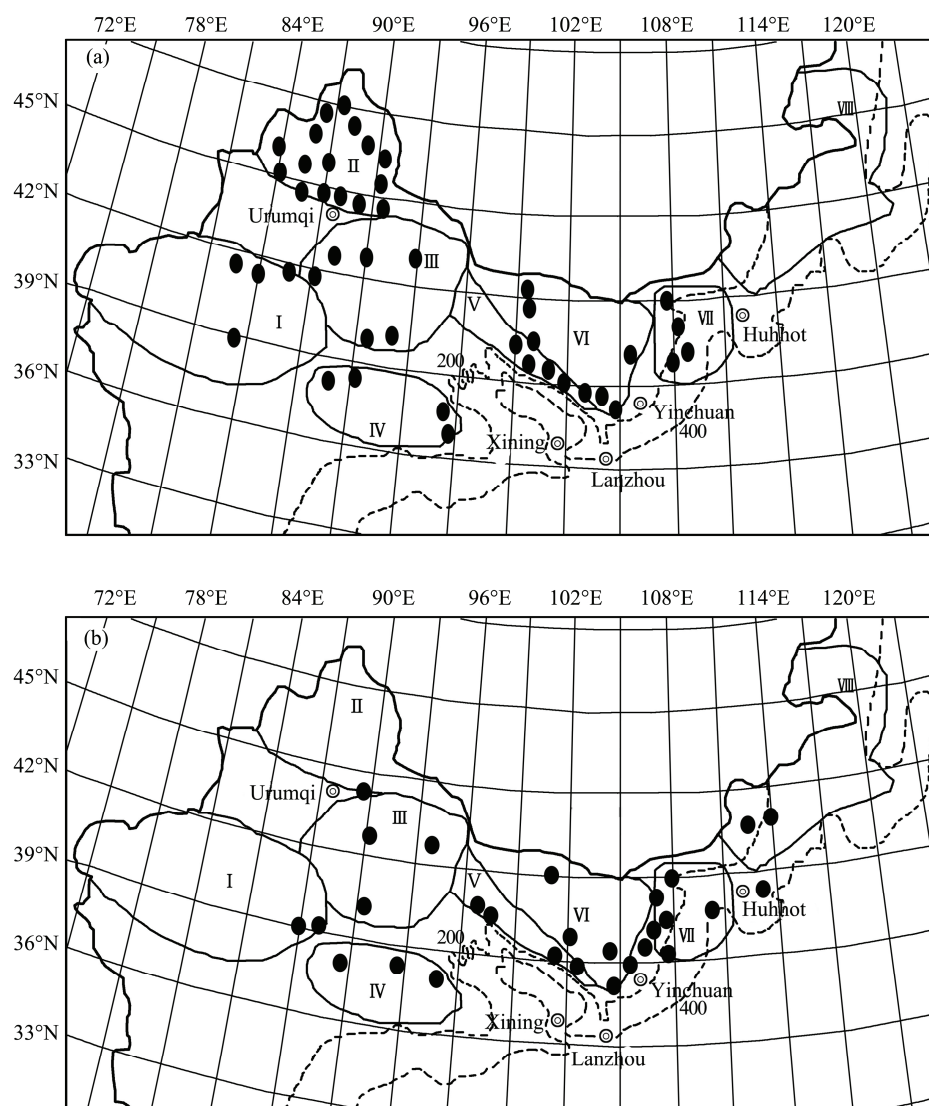
*R* stands for correlation coefficient, *p* stands for significant level at 0.05.

*Haloxylon ammodendron* and *Calligonum mongolicum* are widely distributed in the desert regions of China as shown in Figure 2. *Haloxylon ammodendron* is a xerophyte and halophyte shrub or subshrub, distributed in eight desert regions except for the west of northeastern and eastern Inner Mongolia desert region (Figure 2a). It is widely distributed in the Junggar Basin and easily regenerates. It can be found in fixed and semi-fixed sand dunes of lake basin margins in

desert regions of Inner Mongolia, gravel sandy lands, flat gravel gobi and dry beds. It is an indicator of ground water in the Alashan region, and is an important dominant species in saline-wet deserts. In the flat gravel gobi west of Ejina, *H. ammodendron* forms a zonal community mostly as a dwarf shrub, with a height of about 1 m; it also grows in other desert communities with companion species. *Haloxylon ammodendron* inhabits semi-desert and desert regions where

the sea level is lower than 3,000 m in Qinghai, where the habitat is mainly lowlands of shallow groundwater depth, dry beds, basin margins, piedmont plains, and gravel lands. The community coverage of *H. ammodendron* is less than 20% when dependent on precipitation for growth. With groundwater supply, *H. ammodendron* forms small arbors with coverage reaching 30%–40%, and eventually develop into a forest. *Haloxylon ammodendron* is also distributed in desert regions where precipitation is 60–250 mm, and active accumulated annual temperature of  $\geq 10^{\circ}\text{C}$  is above

3,000  $^{\circ}\text{C}$ . In the Tarim Basin, *H. ammodendron* is distributed only along the margins of the Taklimakan Desert, where the annual precipitation is less than 100 mm and the active accumulated annual temperature of  $\geq 10^{\circ}\text{C}$  is about 4,000  $^{\circ}\text{C}$ . In the Qaidam Basin, *H. ammodendron* is a small shrub, where precipitation is rare, the active accumulated annual temperature of  $\geq 10^{\circ}\text{C}$  is less than 2,000  $^{\circ}\text{C}$ , and the annual average temperature is also low. *Haloxylon ammodendron* grows well in the Junggar Basin and the Hexi Corridor desert regions.



**Figure 2** Distribution of (a) *Haloxylon ammodendron* (b) *Calligonum mongolicum* in desert regions of China

*Calligonum* is mainly distributed in Asia, southern Europe and northern Africa. There are 26 species in China, including Inner Mongolia, Gansu, Ningxia, Qinghai and Xinjiang. Xinjiang contains the most species with 22 (Editorial Committee of Flora of Xinjiang, 1992). Gansu has 11 species, six of which are introduced and cultivated. In the Hexi Corridor (Editorial Committee of flora of Gansu, 2005),

there are three species in Inner Mongolia and Qinghai, respectively. *Calligonum* is an important dominant species in deserts, especially for windbreaks and sand-fixation. *Calligonum mongolicum* Turcz is distributed in eight desert regions of China and is the most widely distributed  $\text{C}_4$  woody species in China. The climatic characteristics within the distributed regions include precipitation of 60–300 mm, aver-



age temperature is 3–10 °C, aridity index is 2–16, active accumulated annual temperature of  $\geq 10$  °C is 2,000–3,900 °C, average temperature for January is from –17 °C to –8 °C while in July it is 17–25 °C, and the sunshine hour is 2,800–3,200 hr.

*Calligonum mongolicum* is a strong drought tolerant shrub, widely distributed in shifting and semi-shifting sandy land of desert regions and desert grassland regions, the gobi with sand, sandy or gravel sloping lands and dry beds. It is a dominant species for sandy desert, and is also an accompanying species which scattered or clustered in *Artemisia* communities and *H. ammodendron* desert communities. *Calligonum mongolicum* forms sparse single populations in gravel sand and sand dunes where the sea level is about 3,000 m in Qinghai, and has a small distribution in the mild salinization loam of alluvial fan margins. Seed propagation and root tilling capacity of *C. mongolicum* is the strongest, and can cluster more new branches in sandy lands. The ecotype of *C. mongolicum* is different for each desert region because of a large difference of habit; it is a small shrub of 0.3 m in a low water condition; it is a larger shrub in wetter conditions, sometimes reaching up to or above 3 m thus forming a shrub forest.

#### 4. Discussion and conclusion

There are more than 1,700 kinds of plants that have been identified utilizing the  $C_4$  photosynthesis pathway, but they only account for 1/3 of the total number of  $C_4$  plants. There are about 5,000–6,000  $C_4$  plants in the world (Ehleringer *et al.*, 1997; Wang, 2002), and 5,000 kinds of grasses with  $C_4$  photosynthesis (Hattersley and Watson, 1992). On the contrary, only 1,000 species in 165,000 kinds of dicots may be with  $C_4$  photosynthesis (Ehleringer *et al.*, 1997).

Plants which are widely distributed in tropical and subtropical regions tend to be  $C_4$  photosynthetic, and plants which originate from the arctic and temperate regions tend to be  $C_3$  photosynthetic (Ehleringer *et al.*, 1997). All Asian species of *Kochia scoparia* (Chenopodiaceae) are  $C_4$  photosynthetic, and Eurasian species also have a Kranz anatomy (Pyankov and Mokronosov, 1993). It is reported that *Artemisia vestita* (Asteraceae) is a subshrub with  $C_4$  photosynthesis (Yin and Wang, 1997). Our research proved that *Salsola laricifolia* Turcz has no Kranz anatomy, and the  $\delta^{13}C$  value is –23.1‰ (Pyankov *et al.*, 2000), and is not a  $C_4$  plant. The  $\delta^{13}C$  value of *Salsola abrotanoides* Bge. is –11.36‰, and is a  $C_4$  plant (Tang and Liu, 2001), but Pyankov *et al.* (2000) thought it may be a  $C_3$  plant. *Bassia dasyphylla* (Fisch. et Mey.) O. Kuntze is a typical  $C_4$  plant (Tang and Liu, 2001), but Pyankov *et al.* (2000) proved it to be a  $C_3$  plant with the  $\delta^{13}C$  value of –24.8‰, and we measured the  $\delta^{13}C$  value of –27.6‰. *Euphorbia humifusa* Willd. is a  $C_4$  plant with the  $\delta^{13}C$  value of –12.76‰ (Tang and Liu, 2001), Voznesenskaya and Gamaley (1986) reported *Euphorbia humifusa* Willd. in Mongolia with a  $C_4$ -like syndrome, but Pyankov *et al.* (2000) measured the  $\delta^{13}C$  value of *Euphorbia*

*humifusa* Willd. as –26.3‰, proving that *Euphorbia humifusa* Willd. is a  $C_3$  plant. Some plants, from one or two results, proved to be  $C_4$  plants, but without stable carbon isotope analysis and anatomical structure observation, further research is needed.

*Orostachys malacophyllus*, *O. fimbriatus*, and *Sedum aizoon* (Crassulaceae), located in the west of northeast and east of Inner Mongolia desert region, have a CAM photosynthetic pathway. In eight desert regions of China, CAM plants are rare, while  $C_4$  plants, especially  $C_4$  woody plants have an important ecological function and indicate the type of environment in the desert ecosystem (Su, 2010). There are 45 species of  $C_4$  woody plants in the desert regions of China, including dungarunga, shrub, undershrub and semi-shrub, accounting for 6% of the total number of desert species in China, of which most are Chenopodiaceae and Polygonaceae with 19 species and 26 species, respectively. The number of  $C_4$  herbaceous plants including annual, biennial and perennials are 107 species, including 48 monocot species and 59 dicot species.

$C_4$  woody plants mainly inhabit the northwestern arid desert regions west of the Helan Mountains. The drought-resistance and drought-tolerance in  $C_4$  herbaceous plants are worse than  $C_4$  woody plants. The abundance of  $C_4$  woody plants is closely related with aridity, and has an important role in indicating the type of arid environments.  $C_4$  woody plant abundance are closely linked to aridity, and have an important constructive role in arid environments.  $C_4$  herbaceous plants are more indicative of wet conditions; they have a positive correlation with annual precipitation and a negative correlation with the aridity index.  $C_4$  herbaceous plants mainly inhabit areas with shallow groundwater depth and better water conditions in the desert regions, and are widely distributed along the margins of oases.

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**Appendix table 1** The list of C<sub>4</sub> woody species and distribution in desert regions of China

Name	Place*	Name	Place*
<b>Chenopodiaceae</b>			
<i>Aellenia glauca</i> (M. Bieb.) Aellen	2	<i>Anabasis aphylla</i> L.	1–3
<i>A. brevifolia</i> C. A. Mey.	1–3,5,6	<i>A. elatior</i> (C. A. Mey.) Schischk.	2
<i>A. eriopoda</i> (Schenk) Benth. ex Volken	2	<i>A. pelliottii</i> Danguy	1
<i>A. salsa</i> (C. A. Mey.) Benth. ex Volken	1–3	<i>A. truncate</i> (Shrenk) Bunge	2
<i>Atriplex cana</i> C. A. Mey.	2	<i>Camphorosma lessingii</i> Litv.	2
<i>C. monspeliaca</i> L.	2	<i>Haloxylon ammodendron</i> (C. A. Mey) Bge.	1–7
<i>H. persicum</i> Bge.	2,5	<i>Iljinia regelii</i> (Bge) Korov.	1–3
<i>Kochia prostrata</i> (L.) Schrad.	1–3,5–8	<i>Salsola arbuscula</i> Pall.	1–3,5–7
<i>S. orientalis</i> S. G. Gmel.	2	<i>S. passerina</i> Bge.	4–8
<i>Suaeda dendroides</i> (C. A. Mey.) Moq.	2,6		
<b>Polygonaceae</b>			
<i>Calligonum alaschanicum</i> A. Los.	6,7	<i>C. arborescens</i> Litv.	3,5
<i>C. aphyllum</i> (Pall.) Gürke	2	<i>C. caput-medusae</i> Schrenk	5
<i>C. chinense</i> A. Los.	5	<i>C. colubrinum</i> Borszcz.	1
<i>C. cordatum</i> Korov. Ex Pavl.	3	<i>C. densum</i> Borszcz.	3
<i>C. ebi-nuricum</i> Ivanova ex Soskov	3	<i>C. gobicum</i> (Bge.) A.Los.	5
<i>C. jimunaium</i> Z. M. Mao.	1	<i>C. junceum</i> (Fisch. et Mey.) Litv.	3
<i>C. juochiangense</i> Liou f.	1	<i>C. klementzii</i> A. Los.	2,5
<i>C. kozlovi</i> A. Los.	4	<i>C. kuerlese</i> Z. M. Mao.	1
<i>C. leucocladum</i> (Schrenk) Bge.	2	<i>C. mongolicum</i> Turcz.	1–8
<i>C. potaninii</i> A. Los.	5	<i>C. pumilum</i> A. Los.	3
<i>C. roborowskii</i> A. Los.	1,5	<i>C. rubicundum</i> Bge.	2
<i>C. Squarrosus</i> N. Pavl.	3	<i>C. trifaricum</i> Z. M. Mao.	3
<i>C. yingisaricum</i> Z. M. Mao.	3	<i>C. zaidamense</i> A. Los.	4,5

\*1: Tarim Basin desert region; 2: Junggar Basin desert region; 3: Eastern of Xinjiang desert region; 4: Qaidam Basin desert region; 5: Hexi Corridor desert region; 6: Alashan Plateau desert region; 7: Ordos Plateau desert region; 8: West of Northeast and East of Inner Mongolia desert region.

**Appendix table 2** The list of C<sub>4</sub> herbaceous species and distribution in desert regions of China

Name	Place*	Name	Place*
<b>Monocots</b>			
<b>Cyperaceae</b>			
<i>Blysmus sinocompressus</i> Tang et Wang	1,5–8	<i>Cyperus esculentus</i> L.	6–8
<i>C. glomeratus</i> L.	2,8	<i>C. orthostachyus</i> Franch. et Savat.	8
<i>Fimbristylis dichotoma</i> (L.) Vahl	1	<i>Juncellus pannonicus</i> (Jacq.) C. B. Clarke	1,2,5–8
<i>J. serotinus</i> (Rottb.) C. B. Clarke	1,2,6–8	<i>Pycreus globosus</i> (All.) Reichb.	7,8
<i>P. korshinskyi</i> (Meinsh.) V. Krecz.	1–3,7	<i>P. polystachyus</i> (Rottb.) P. Beauv.	8
<b>Gramineae</b>			
<i>Aeluropus littoralis</i> (Willd.) Parl.	1,2,5,6	<i>A. littoralis</i> var. <i>micrantherus</i> (Tzvel.) K. L. Chang	1,6
<i>A. littoralis</i> var. <i>sinensis</i> Debeaux	1–3,5,6	<i>Aristida adscensionis</i> L.	1–3,6–8
<i>Arthraxon hispidus</i> (Thunb.) Makino	1–8	<i>Arundinella hirta</i> (Thunb.) C. Tataka	7,8
<i>Bothriochloa ischaemum</i> (L.) Keng	1–3,5–7	<i>Chloris virgata</i> Swartz	1–8
<i>Cleistogenes caespitosa</i> Keng	6–8	<i>C. songorica</i> (Roshev.) Ohwi	1,2,4,5–7
<i>C. squarrosa</i> (Trin.) Keng	2,7,8	<i>Crypsis aculeata</i> (L.) Ait.	6–8
<i>C. schoenoides</i> (L.) Lam.	2,3,5–7	<i>Cynodon dactylon</i> (L.) Pers.	1–8
<i>Digitaria ciliaris</i> (Retz.) Koel.	1,3,8	<i>D. ischaemum</i> Schreb. ex Muhl.	1–8
<i>D. sanguinalis</i> (L.) Scop.	1–8	<i>Echinochloa caudata</i> Roshev.	6–8
<i>E. crusgalli</i> (L.) Beauv.	1–3,5–8	<i>E. crusgalli</i> var. <i>hispidula</i> (Retz.) Honda	8
<i>E. crusgalli</i> var. <i>mitis</i> (Pursh) Peterm.	1–3,5–8	<i>Eragrostis cilianensis</i> (All.) Vign.-Lut.	1–8

(to be continued)

(continuation)  
**Appendix table 2** The list of C<sub>4</sub> herbaceous species and distribution in desert regions of China

<i>E. pilosa</i> (L.) Beauv.	1–8	<i>E. pilosa</i> var. <i>imberbis</i> Franch.	1–8
<i>E. poaeoides</i> Beauv.	1–8	<i>Erianthus ravennae</i> (L.) Beauv.	1
<i>Hemarthria sibirica</i> (Gand.) Ohwi	7,8	<i>Hierochloe glabra</i> Trin.	6–8
<i>Imperata cylindrica</i> (L.) Beauv.	6–8	<i>Miscanthus sacchariflorus</i> (Maxim.) Hack	8
<i>Pennisetum centrasiaticum</i> Tzvel.	1–8	<i>Setaria glauca</i> (L.) Beauv.	1–8
<i>S. viridis</i> (L.) Beauv.	1–8	<i>Spodiopogon sibiricus</i> Trin.	1–8
<i>Tragus berteronianus</i> Schult.	6–8	<i>Tragus mongolorum</i> Ohwi	5–8
<b>Potamogetonaceae</b>			
<i>Potamogeton lucens</i> L.	1,7	<i>P. perfoliatus</i> L.	1,4,7
<b>Dicots</b>			
<b>Amaranthaceae</b>			
<i>Amaranthus albus</i> L.	2	<i>A. blitoides</i> S. Wats.	7,8
<i>A. lividus</i> L.	1	<i>A. retroflexus</i> L.	2,6–8
<i>A. roxburghianus</i> Kung	2,6,7		
<b>Chenopodiaceae</b>			
<i>Atriplex centralasiatica</i> Iljin	6–8	<i>A. dimorphostegia</i> Kar. et Kir.	2
<i>A. laevis</i> C. A. Mey.	2,6–8	<i>A. sibirica</i> L.	1–8
<i>A. tatarica</i> L.	1–8	<i>Axyris amaranthoides</i> L.	1–8
<i>Bassia hyssopifolia</i> (Pall.) O. Kuntze	2,3,5–7	<i>Borsszczowia aralocaspica</i> Bge.	2
<i>Chenopodium acuminatum</i> Willd.	1–8	<i>C. album</i> L.	1–8
<i>C. aristatum</i> L.	1–8	<i>C. glaucum</i> L.	1–8
<i>C. hybridum</i> L.	1–8	<i>C. serotinum</i> L.	1–8
<i>Cornulaca alaschanica</i> Tsien et G. L. Chu	6	<i>Girgensohnia oppositiflora</i> (Pall.) Fenzl.	2
<i>Halimocnemis villosa</i> Kar. et Kir.	2	<i>Halogeton arachnoides</i> Moq.	1–8
<i>H. glomeratus</i> (Bieb.) C. A. Mey.	1–3,5	<i>H. glomeratus</i> var. <i>tibeticus</i> (Bge.) Grub.	1,4,5
<i>Kochia iranica</i> Litv.	1–3,5	<i>K. krylovii</i> Litv.	2,6
<i>K. laniflora</i> (S. G. Gmel.) Borb.	2	<i>K. melanoptera</i> Bunge	2,4–6
<i>K. scoparia</i> (L.) Schrad	1–8	<i>K. scoparia</i> var. <i>sieversiana</i> (Pall.) Ulbr. ex Asche	1–8
<i>Londesia eriantha</i> Fish. et Mey.	2	<i>Petrosimonia litwinovii</i> Korsh.	2
<i>P. sibirica</i> (Pall.) Bunge	2	<i>Salsola beticolor</i> Iljin	5,6
<i>S. brachiata</i> Pall.	2	<i>S. collina</i> Pall.	1–8
<i>S. ikonnikovii</i> Iljin	2,5,6	<i>S. lanata</i> Pall.	2
<i>S. paulsenii</i> Litv.	1,2,5	<i>S. pellucida</i> Litw.	5,6
<i>S. praecox</i> Litw.	1	<i>S. rosacea</i> L.	2
<i>S. ruthenica</i> Iljin	1–8	<i>Suaeda acuminata</i> (C. A. Mey.) Moq.	2
<i>S. altissima</i> Pall.	1	<i>S. przewalskii</i> Bge.	5,6
<i>S. pterantha</i> (Kar. et Kir.) Bunge	6		
<b>Compositae</b>			
<i>Artemisia anethifolia</i> Web. ex Stechm.	1–8	<i>A. dracunculus</i> L.	1,2,6,8
<i>A. sieversiana</i> Willd.	1–8		
<b>Convolvulaceae</b>			
<i>Cuscuta australis</i> R. Br.	1	<i>C. chinensis</i> Lam.	1–3,5,7,8
<i>C. europaea</i> Lam.	1–5	<i>C. japonica</i> Choisy	1–3,7,8
<b>Polygalaceae</b>			
<i>Polygala tenuifolia</i> Willd.	5–8		
<b>Portulacaceae</b>			
<i>Portulaca oleracea</i> L.	1–8		
<b>Ranunculaceae</b>			
<i>Thalictrum squarrosum</i> Steph. ex Willd.	7,8		
<b>Zygophyllaceae</b>			
<i>Tribulus terrestris</i> L.	1–8		

\*1: Tarim Basin desert region; 2: Junggar Basin desert region; 3: Eastern of Xinjiang desert region; 4: Qaidam Basin desert region; 5: Hexi Corridor desert region; 6: Alashan Plateau desert region; 7: Ordos Plateau desert region; 8: West of Northeast and East of Inner Mongolia desert region.