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C_4 plants in the vegetation of Mongolia: their natural occurrence and geographical distribution in relation to climate

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Abstract The natural geographical occurrence, carbon assimilation, and structural and biochemical diversity of species with C_4 photosynthesis in the vegetation of Mongolia was studied. The Mongolian flora was screened for C_4 plants by using $^{13}C/^{12}C$ isotope fractionation, determining the early products of $^{14}CO_2$ fixation, microscopy of leaf mesophyll cell anatomy, and from reported literature data. Eighty C_4 species were found among eight families: Amaranthaceae, Chenopodiaceae, Euphorbiaceae, Molluginaceae, Poaceae, Polygonaceae, Portulacaceae and Zygophyllaceae. Most of the C4 species were in three families: Chenopodiceae (41 species), Poaceae (25 species) and Polygonaceae, genus *Calligonum* (6 species). Some new C_4 species in Chenopodiaceae, Poaceae and Polygonaceae were detected. C_4 Chenopodiaceae species make up 45% of the total chenopods and are very important ecologically in saline areas and in cold arid deserts. C_4 grasses make up about 10% of the total Poaceae species and these species naturally concentrate in steppe zones. Naturalized grasses with Kranz anatomy,of genera such as *Setaria, Echinochloa, Eragrostis, Panicum* and *Chloris,* were found in almost all the botanical-geographical regions of Mongolia, where they commonly occur in annually disturbed areas and desert oases. We analyzed the relationships between the occurrence of C_4 plants in 16 natural botanical-geographical regions of Mongolia and their major climatic influences. The proportion of C_4 species increases with decreasing geographical latitude and along the north-to-south temperature gradient; however grasses and chenopods differ in their responses to climate. The abundance of Chenopodiaceae species was closely correlated with aridity, but the distribution of the C_4 grasses was more dependent on temperature. Also, we found a unique distribution of different C_4 Chenopodiaceae structural and biochemical subtypes along the aridity gradient. NADP-malic enzyme (NADP-ME) tree-like species with a salsoloid type of Kranz anatomy, such as *Haloxylon ammodendron* and *Iljinia regelii*, plus shrubby *Salsola* and *Anabasis* species, were the plants most resistant to ecological stress and conditions in highly arid Gobian deserts with less than 100 mm of annual precipitation. Most of the annual C_4 chenopod species were halophytes, succulent, and occurred in saline and arid environments in steppe and desert regions. The relative abundance of C_3 succulent chenopod species also increased along the aridity gradient. Native C_4 grasses were mainly annual and perennial species from the Cynodonteae tribe with NAD-ME and PEP-carboxykinase (PEP-CK) photosynthetic types. They occurred across much of Mongolia, but were most common in steppe zones where they are often dominant in grazing ecosystems.

Key words Mongolia · Climate · Vegetation type · C_4 photosynthesis · Plant distribution

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Introduction

Mongolia occupies a large area, about 1,565,000 km^2 (52°06'–41°32'N, 87°47'–119°54'E). It is primarily a mountain country mixed with steppe, on average 1580 m above sea level, varying from 533 to 4355 m. The relief is very complicated with latitudinal climate zones mixed with altitudinal gradients, particularly in the West. Mongolia is in the center of the Asian continent which leads to an extreme continental climate and very low precipitation. The absolute temperatures vary from –50°C in win-

ter to 40°C in summer. The maximum annual precipitation is near 250–300 mm in the north, or at elevations over 3000 m; decreasing to 100–150 mm in the south, then less than 50 mm in the Transaltai Gobi deserts (Vostokova et al. 1995). Mongolia is the termination of Asia's monsoon climate zone, so about 50–70% of precipitation occurs in summer. Thus, its specific climatic features are aridity in all regions, particularly in southern and western regions, and a continental climate of extreme cold and heat.

Asian ecosystems, particularly continental deserts and mountains, have not been studied in detail for the occurrence of C_4 species and their distribution in relation to climate. The deserts of Asia differ markedly from the arid ecosystems of North America, Australia and Europe in the taxonomic groups of their C_4 species. In Asia Chenopodiaceae is the leading C_4 family and grasses with Kranz anatomy are less important, particularly in arid regions (Pyankov et al. 1986, 1992a; Pyankov and Mokronosov 1993). Several studies have identified C_4 Chenopodiaceae species from the Near East and Central Asia (Shomer-Ilan et al. 1981; Winter 1981; Ziegler et al. 1981; Zalenskii and Glagoleva 1981; Voznesenskaja and Gamaley 1986; Pyankov and Vakhrusheva 1989; Gamaley et al. 1992; Pyankov et al. 1992a, 1997; Akhani et al. 1997). The C_4 syndrome is known in about 250–300 chenopods mostly in Salsoloideae (tribes Suaedeae and Salsoleae) and Chenopodioideae (tribes Camphorosmeae and Atripliceae); but many species are unclassified. The occurrence of C_4 species has been studied mostly in west Asian deserts, e.g., the Central Karakum desert (Pyankov et al. 1986; Pyankov and Vakhrusheva 1989), in part of Mongolia (Gamaley 1985; Gamaley and Shirevdamba 1988), in South Tadjikistan (Pyankov and Molotkovskii 1992, 1993), in some regions of the former Soviet Union (Pyankov and Mokronosov 1993), the Pamir mountains (Pyankov 1993; Pyankov and Mokronosov 1993), and in northeast China (Redman et al. 1995). In large regions of Central and East Asia the plant photosynthetic types have not been studied and the climatic pattern of C_4 plant distribution is unknown.

The pioneer works of J.A. Teeri and L.G. Stowe in North America show clear relationships between climatic variables and the relative abundance of C_3 and C_4 plants within Poaceae (Teeri and Stowe 1976), in dicot plants (Stowe and Teeri 1978), and in Cyperaceae (Teeri et al. 1980). Within Poaceae and Cyperaceae the relative abundance of C_4 species in a particular region is strongly correlated with minimum daily temperatures during the growing season (r=0.97). In contrast native C_4 dicots showed strong correlations with pan evaporation during summer months (r=0.947), annual evaporation (r=0.934), and the dryness ratio (r=0.931). Their work provides strong evidence that the climatic preferences of C_4 dicots differ from those of C_4 grasses. They concluded that the photosynthetic physiology of C_4 dicots differs from that of C_4 grasses.

More recently, additional information has accumulated on the ecology of C_4 plants, mostly on their occurrence and distribution in ecosystems dominated by C_4 grasses in: Africa (Tieszen et al. 1979; Vogel et al. 1978; Batanouny et al. 1988; Schulze et al. 1996), Europe (Doliner and Jolliffe 1979; Collins and Jones 1985; Mateu Andres 1992; Kalapos et al. 1997), Australia (Hattersley 1983), and the Near East (Shomer-Ilan et al. 1981; Vogel et al. 1986). The climatic pattern of C_4 dicot and C_4 monocot distribution over the world has been summarized by Ehleringer et al. (1997).

Other studies have presented new relationships between ecological parameters, photosynthetic types, biochemical subtypes, and taxonomy in Poaceae (Hattersley and Watson 1992) and Cyperaceae (Takeda et al.1985; Ueno et al. 1986; Ueno and Takeda 1992; Li 1993). Hence "taxonomic" identification of C_4 is possible from the occurrence of species in floristic lists.

The objectives of this study in Mongolia were to identify all the plants with C_4 photosynthesis, and to analyze the geographical distribution patterns of C_4 species, with emphasis upon Poaceae and Chenopodiaceae, as a function of Mongolian climatic variables. We also studied climatic and ecological distribution of C_4 grasses and chenopods with different photosynthesis biochemistry, mesophyll structures, and life forms. Here we demonstrate that C_4 grasses and chenopods differ in their relationship to climatic variables and that morphological and anatomical features are important for survival in various habitats. Such knowledge can be useful in the evaluation and prediction of vegetation changes during global climatic changes, in the conservation and restoration of natural ecosystems, and in improving pastures for the nomadic society based on domestic livestock grazing.

Methods

Determination of photosynthetic types

Mongolian plant photosynthetic types were determined from microscopic studies of Kranz anatomy, $\delta^{13}C$ fractionation, primary $^{14}CO_2$ photosynthetic products, and ^{14}C turnover. Many experiments were conducted in 1993 during a field expedition, mainly in steppe, semidesert, and desert areas in the following places: Bulgan-Somon (44°06'N, 103°32'E), Shine-Dzhinst (44°33'N, 99°17'E), Ekhin-Gol (43°15'N, 99°00'E) and Gurvantes (43°13'N, 101°03'E).

$\delta^{13}C$ analysis was performed by standard techniques (Bender et al. 1973) with a United States National Bureau of Standards bicarbonate sample as a standard. Plant photosynthetic tissue samples were field-collected in natural habitats, sun-dried and transported to the USA for $\delta^{13}C$ analysis.

The pathway of primary $^{14}CO_2$ fixation and turnover was determined from the fixation kinetics during a $^{14}CO_2$ pulse (10-s exposure) followed by a chase exposure to $^{12}CO_2$ in air (10, 30, 60, and 120 s) with the techniques described in Pyankov et al. (1999). Species with over 50% of ^{14}C in malate or aspartate after 10 s were classified as either NADP-ME or NAD-ME, respectively.

The assignment to photosynthetic types and biochemical groups was done on the basis of data obtained from our studies, from published works, or from closely related species for grasses (Hattersley and Watson 1992) and for chenopods (Pyankov et al. 1992a, 1997; Akhani et al. 1997).

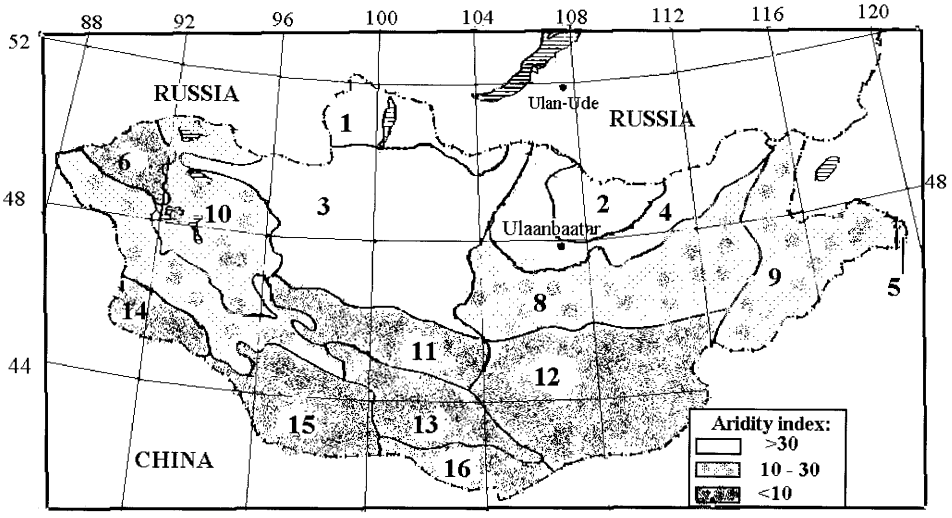

Fig. 1 Botanical-geographical regions of Mongolia (Grubov 1982) and their aridity. De Martonne aridity index, $I=P/T+10$. [P annual precipitation (mm), T average annual temperature (°C)]

Geographical distribution, climatic data and plant ecological characteristics

We used the botanical-geographical divisions of Grubov and Junatov (1952), as used in the identification of Mongolian flora (Grubov 1966, 1982; Gubanov 1996). There are 16 botanical-geographical regions in Mongolia (Fig. 1), based on similarity of climatic features (Table 1), environment, and floristic complexes. Data on climatic variables from meteorological stations were obtained from the Ministry of Nature and Environment. Actually there are few meteorological stations in these large regions; therefore the data from individual stations only give general information about the climatic features of each botanical-geographical zones. Figure 2 presents changes the main climatic variables from moist cool regions to extra arid deserts.

Generally, all botanical-geographical regions can be combined into three groups on the basis of orography, climate, soils, and vegetation plus precipitation, temperature, and aridity. The first group (regions 1–5) (Fig. 1) covers northern and western Mongolia, with forest and semisteppe vegetation, with a maximum annual precipitation of 200–350 mm, a low warm-temperature sum, and low aridity (Table 1). The second group (regions 7–10) covers mainly steppe vegetation, with an annual precipitation of 100–200 mm and medium aridity indexes from 30 to 10. The third group (regions 6, 11–16) includes those with the lowest precipitation, the highest summer temperatures, and high aridity. These are the Gobian deserts and dry mountain areas to the west and south. The areas of some botanical-geographical regions are very large, for instance, Khentei (3), Mongolian Altai (7), Middle Khalkha (8), Depression of Great Lake (10), East Gobi (12), and include areas with quite diverse altitudes, climatic subzones and vegetation types. Such data do not allow a detailed analysis of the relationship between the occurrence of different plants and climatic variables; rather we will present the main trends in plant distribution along the major climatic gradients. Region 5 was excluded from analysis, because it is not comparable with other regions in size (Fig. 1) and species number. Recently, a more detailed ecological division of Mongolia that includes 36 regions with more similar climatic and biological features has been proposed (Vostokova et al. 1995) but currently both detailed floristic and climatic data are lacking.

We used the de Martonne aridity index (Oliver and Fairbridge 1987), defined as $I=P/T+10$, where P is the average annual precipitation, and T is the average annual temperature. The minimum absolute values of this index correspond to the maximum aridity of climate.

Floristic species abundance was obtained from recent lists of Mongolian flora by Gubanov (1996). Habitats for each species were described at the time of collection, or obtained from Grubov (1982).

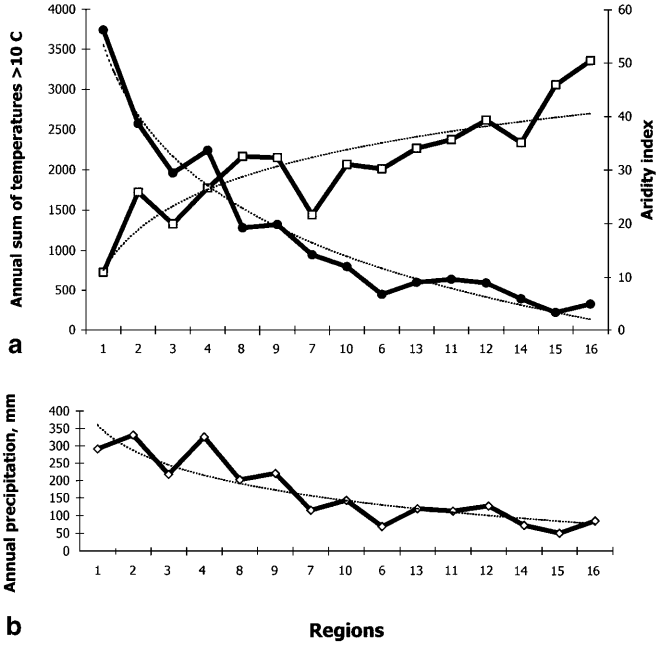

Fig. 2 Main climatic parameters for the botanical-geographical regions of Mongolia. The abscissa shows *region numbers* arranged along an aridity gradient. *Solid lines* are average annual parameters for regions; *dotted lines* are their logarithmic approximations

Pearson's correlation coefficients were calculated for the relationships between climatic variables and the occurrences of Chenopodiaceae and Poaceae species with different photosynthetic types.

Results

Taxonomic occurrence of C_4 species

There are 16 vascular plant families in which C4 photosynthesis occurs: 2 belong to Monocotyledoneae (Poaceae, Cyperaceae); and 14 to Dicotyledoneae (Acanthaceae, Aizoaceae, Amaranthaceae, Asteraceae, Boraginaceae, Caryophyllaceae, Chenopodiaceae, Euphorbiac-

Table 1 Climatic data for the botanical-geographical regions of Mongolia

Regions							
No.	Name	Place	Annual precipitation (mm)	Average annual temperature (°C)	Average aridity index[a]	Sum of temperatures >10°C	July average temperature (°C)
1	Khubsugul	Hatgal	291.7	–4.8	56.1	727	11.8
2	Khentei	Binder	331.6	–1.4	38.6	1719	17.4
3	Khangai	Ulistai	217.7	–2.6	29.4	1327	15.0
4	Mongol-Daurian	Dashbalba	326.0	–0.3	33.6	1771	18.6
5	Great Khingan	Halhgol	281.1	–0.5	29.6	2129	20.4
6	Khobdo	Hogonuur	68.6	0.2	6.7	2011	17.9
7	Mongolian Altai	Dechinzhii	115.0	–1.9	14.2	1439	15.0
8	Middle Khalka	Baruun-Urt	201.8	0.5	19.2	2166	20.2
9	East Mongolia	Matad	220.1	1.1	19.8	2150	19.8
10	Depression of Great Lake	Sain-Ust	142.8	1.9	12.0	2066	18.7
11	Valley of Lakes	Saidshan-Obo	112.1	1.7	9.6	2375	20.1
12	East Gobi	Dalanzagdad	127.1	4.3	8.9	2618	21.2
13	Gobi Altai	Bogd	119.3	3.2	9.0	2266	19.9
14	Dzungarian Gobi	Baitag	71.9	2.1	5.9	2337	20.9
15	Transaltai Gobi	Tooroi	49.5	4.9	3.3	3058	23.4
16	Alashan Gobi	Hanbogd	84.0	6.9	4.9	3360	23.8

[a] De Martonne aridity index, $I=P/T+10$, where P is annual precipitation (mm), T is average annual temperature (°C)

eae, Nyctaginaceae, Molluginaceae, Polygonaceae, Portulacaceae, Scrophyllariaceae, Zygophyllaceae). From the latest taxonomic data (Gubanov 1996) the flora of Mongolia consists of 2823 vascular species belonging to 128 families. Only representatives of Acanthaceae and Nyctaginaceae are absent in the Mongolian flora. We identified 80 species with C_4 photosynthesis occuring in eight families: Amaranthaceae, Chenopodiaceae, Euphorbiaceae, Molluginaceae, Polygonaceae, Portulacaceae, Zygophyllaceae, and Poaceae (Tables 2, 3).

Dicotyledonaeae

Chenopodiaceae

Numerous C_4 photosynthesis species in Chenopodiaceae were found in the subfamily Salsoloideae, tribes Salsoleae and Suaedeae, and in tribes Atripliceae and Camphorosmeae of the subfamily Chenopodioideae (Table 2). The Chenopodiaceae family ranks eighth amongst Mongolian flowering plants (Grubov 1996). There is a total of 91 chenopod species, and 41 of them, (*c.* 45%) exhibit C_4 photosynthesis. The largest number of species with Kranz anatomy are in the Salsoleae tribe, where 26 of 29 are C_4 photosynthesis species (Table 4). Sixteen species have a direct confirmation of C_4 photosynthesis based on anatomy and biochemical tests (Table 2). Some species that were not experimentally verified as having C_4 photosynthesis, belonging to *Anabasis*, *Climacoptera*, *Nanophyton* and *Petrosimonia*, are C_4, because these genera are derivatives of *Salsola* (Botschantzev 1969) in which all experimentally studied species demonstrate typical features of C_4 photosynthesis (see references in Table 2). There are 11 *Salsola* species in the Mongolian flora, and 9 were identified as C_4 species. *Salsola* mostly contains C_4 plants, but a few are C_3, mainly shrubby forms (Pyankov et al. 1993a, 1997; Akhani et al. 1997). The Kranz syndrome was found in seven species experimentally (Table 2). The photosynthetic type of two annual *Salsosa* species was not identified (*S. ikonnikovii* and *S. rosaceae*). They that belong to the youngest and most progressive *Salsola* section of the genus *Salsola* (Botschantzev 1969) in which all studied species are C_4 (Pyankov et al. 1992a, 1997; Akhani et al. 1997). There are two shrubby *Salsola* species, *S. abrobtanoides* and *S. laricifolia*, that are probably not C_4. *S. laricifolia* has a C_3-like $\delta^{13}C$ value of –23.1‰. *S. abrobtanoides* was not studied, but it can be included as C_3 based on it taxonomy. According Botschantzev (1976) *S. abrobtanoides* belong to section Coccosalsola, subsection Genistoides together with two others, *S. webbi* and *S. genistoides*, in which C_3 is well documented (Carolin et al. 1975; Winter 1981; Akhani et al. 1997; Pyankov et al. 1997). C_3 photosynthesis in *Sympegma regelii* is well documented. It has a C_3-like centric non-Kranz-type anatomy named "sympegmoid" by Carolin et al. (1975). The vasculature is close to the Kranz salsoloid type, therefore Carolin et al. (1975) suggested that the sympegmoid may have originated from the salsoloid type with a reversion to C_3 photosynthesis. We found high ^{14}C incorporation into C_3 primary photosynthetic products, but incorporation of label to primary C_4 acids varied from 6 to 24% during 10 s of $^{14}CO_2$ assimilation, somewhat high in comparison with typical C_3 species (Black 1973).

Some genera of Chenopodiaceae that occur in Mongolia are known to have both C_3 and C_4 photosynthetic types, such as *Suaeda*, *Kochia*, *Atriplex*, and *Bassia*. There are ten species of *Suaeda* in the Mongolian flora (Gubanov 1996). We included two species in our list of C_4 species, *S. arcuata* and *S. heterophylla*, based on previous results of early photosynthesis products and measurement of enzyme activities (Pyankov and Vakhrusheva 1989; Pyankov et al. 1992a). *S. arcuata* has C_4-like

Table 2 Occurrence, ecological distribution, and structural-biochemical features of C_4 plants of Mongolia

No.	Family, tribe and species[a]	Life form[b]	Occurrence, regions[c]	Habitat[d]	Kranz anatomy[e]	Biochemical type[f]	$^{13}C/^{12}C$ value[g]	Criteria and references[h]
Chenopodiaceae Atripliceae								
1	*Atriplex cana* C. A. Mey.	SemiShrub	14	6	ATR	NAD-ME	–13.9	M [20]
2	*A. laevis* C. A. Mey.	Annual	3–4, 8–11, 13–15	6	ATR	NAD-ME	–13.0 (W)	A [8]
3	*A. sibirica* L.	Annual	2–4, 6–16	5,6	ATR	NAD-ME		A [2, 4, 13]; M [13]
4	*A. tatarica* L.	Annual	7, 10, 14	1, 6	ATR	NAD-ME	–13.6 (W)	A, E [12]
Camphorosmeae								
5	*Bassia hyssopifolia* (Pal.) O. Kuntze	Annual	6–7, 10–13	6	KOCH	NADP-ME	–13.4	A [1–2,4, 9]; M [9]; F [3]
6	*Camphorosma lessingii* Litv.	SemiShrub	6, 10, 14	5, 6	KOCH	NADP-ME	–13.1	A [1, 12]; E [12];F [3]
7	*Kochia densiflora* Tursz. ex Moq.	Annual	3–4, 6–14	5,6	KOCH	NADP-ME		A [1]
8	*K. iranica* Litv.	Annual	14, 15	6	KOCH	NADP-ME	–13.9 (W)	A [1, 9], M [9]
9	*K. krylovii* Litv.	Annual	6–7, 10–16	3, 5	KOCH	NADP-ME		[i]
10	*K. melanoptera* Bunge	Annual	3, 6–7, 10–16	6	KOCH	NADP-ME		A [4, 8]
11	*K. prostrata* (L.) Shrad.	SemiShrub	1–15	5, 6	KOCH	NADP-ME	–14.0	A [1, 7]; M [9, 17]; E [12]; F [16]
12	*K. scoparia* (L.) Schrad	Annual	3–5, 8–10	1, 2	KOCH	NADP-ME	–13.4 (A)	A [1, 2, 7]; F [3, 16]; E [20]
13	*Londesia eriantha* Fish. et Mey.	Annual	6, 10	5, 6	ATR	NADP-ME		A [4, 7]
Suaedeae								
14	*Suaeda acuminata* (C.A. Mey.) Moq.	Annual	6, 10, 14	6	ATR	NAD-ME	–12.8 (W)	A [9, 18]; F [3, 16] M [9]
15	*S. heterophylla* Kar. et Kir.) Bunge	Annual	10–13, 15	6	SUA	NAD-ME		A, E [12, 18]
Salsoleae								
16	*Anabasis aphylla* L.	SemiShrub	14	4–6	SALS	NADP-ME	–14.5 (W)	A [1]; F [4, 17]
17	*A. brevifolia* C.A. Mey.	SemiShrub	3, 6–7, 10–16	4–6	SALS	NADP-ME	–12.9	A[1, 8, 20]; M [20]; F [3, 16]
18	*A. elatior* (C.A. Mey. Schisnhk.	SemiShrub	14	5, 6	SALS	NADP-ME	–13.5 (W)	F [3, 16]
19	*A. eriopoda* (Shrenk) Benth. ex Volkens	SemiShrub	14	5	SALS	NADP-ME	–13.0 (A)	A, M [9]; F [3, 16]
20	*A. pelliotti* Danguy	SemiShrub	14	5	SALS	NADP-ME		[i]
21	*A. salsa* (C.A. Mey.) Benth. ex Volkens	SemiShrub	14	4–6	SALS	NADP-ME	–13.2	F [3,16]; E [20]
22	*A. truncata* (Shrenk) Bunge	SemiShrub	14	4–6	SALS	NADP-ME		[i]
23	*Climacoptera affinis* (C.A. Mey.) Botsch.	Annual	14	3, 6	SALS	NAD-ME		A [7, 17][i]; F [16][i]; M, E [9, 12, 17][i]
24	*C. subcrassa* (M. Pop.) Botsch	Annual	14	3, 6	SALS	NAD-ME		[i]
25	*Halogeton glomeratus* (Bieb.) C.A. Mey.	Annual	10–11, 14–15	3–6	SALS	NADP-ME	–12.8	A [1–2, 8, 13]; E, M [13, 17]
26	*Haloxylon ammodendron* (C.A. Mey.) Bunge	Shrub	10–16	3–6	SALS	NADP-ME	–13.2	A [1, 4]; F [3, 16]; M [20]
27	*Iljinia regelii* (Bunge) Korov.	Shrub	14–16	3–6	SALS	NADP-ME	–11.9	A[8]; M [20]; F [16]
28	*Micropeplis arachnoideae* (Moq.) Bunge	Annual	4, 7–16	3–6	SALS	NADP-ME	–12.6	A [4]; M [20]
29	*Nanophyton grubovii* Pratov	SemiShrub	10	3–6	SALS	NAD-ME		A [1][i]; M [17][i]; F [16][i]
30	*N. mongolicum* Pratov	SemiShrub	7, 14	3–6	SALS	NAD-ME		[i]
31	*Petrosimonia litwinovii* Korsh.	Annual	10	3, 6	SALS	NAD-ME		A [1, 11][i]; F [3, 16][i]; M [11][i]
32	*P. sibirica* (Pall.) Bunge	Annual	14	3, 6	SALS	NAD-ME		[i]
33	*Salsola arbuscula* Pall.	Shrub	13–16	3, 5	SALS	NADP-ME	–12.9	A [7, 8, 9]; F [16]; M [9, 17]; E [12]
34	*S. collina* Pall.	Annual	2–15	1, 3, 6	SALS	NADP-ME	–13.1	A [1,4, 8]; M [17]; E [20]; F [16]
35	*S. gemmascens* Pall.	SemiShrub	10	4–6	SALS	NAD-ME	–13.5	A, M [9]; E [12]; F [3, 16]
36	*S. ikonnikovii* Iljin	Annual	11–13	3	SALS	NADP-ME		[i]
37	*S. monoptera* Bunge	Annual	3, 7–13	3, 5	SALS	NADP-ME	–12.7	[i]
38	*S. passerina* Bunge	SemiShrub	8, 10–16	4–6	SALS	NAD-ME	–13.0	[i]
39	*S. paulsenii* Litv.	Annual	3, 7, 10–11, 14	3, 6	SALS	NADP-ME	–12.8	A [7, 9]; M [9, 17; F [16]; E [20]
40	*S. rosaceae* L.	Annual	7, 14	3, 5	SALS	NADP-ME		[i]
41	*S. tragus* L.	Annual	2–4, 6–16	1, 3, 6	SALS	NADP-ME	–13.0	A [1, 8, 13]; E [13]

Table 2 (continued)

No.	Family, tribe and species[a]	Life form[b]	Occurrence, regions[c]	Habitat[d]	Kranz anatomy[e]	Biochemical type[f]	$^{13}C/^{12}C$ value[g]	Criteria and references[h]
	Poaceae Andropogonae							
42	*Spodiopogon sibiricus* Trin.	Perennial	2–5, 9	2, 5	PANIC	NADP-ME	–12.3(R)	F [19]; A [10][i]
	Paniceae							
43	*Echinochloa crus-galli* (L.) Beauv.	Annual	7, 9, 11, 14–16	1, 2	PANIC	NADP-ME	–16.2 (S)	A [2, 4–7,15]; E [12]
44	*Panicum miliaceum* L.	Annual	2–4, 9–10, 12–13	1	PANIC	NAD-ME		A [2, 7]
45	*Pennisetum centralasiaticum* Tzvel.	Perennial	10, 12	1, 5	PANIC	NADP-ME		A [2, 6, 10, 15][i]; F [5, 15][i]
46	*Setaria glauca* (L.) Beauv.	Annual	2, 4, 14–15	1	PANIC	NADP-ME		A [2]; F [5]; E [12]
47	*S. pumila* (Poiret) Roem. et Schult	Annual	7	1, 2	PANIC	NADP-ME		i
48	*S. viridis* (L.) Beauv.	Annual	2–16	1, 2	PANIC	NADP-ME	–13.2	A [2, 4, 6–7, 8]; E [12]; F [5, 19]
	Aristideae							
49	*Aristida heymannii* Regel	Annual	3, 9–13, 15–16	3, 5	ARIST	NADP-ME	–14.6	A [2[i], 4, 5[i], 6[i], 8, 15[i]]; F [15][i]; M [20]
	Arundinelleae							
50	*Arundinella anomala* Steud.	Perennial	4–5, 9	1–2, 5	PANIC	NADP-ME		A [2, 10][i]; F [19][i]
	Cynodonteae							
51	*Aeluropus micranterus* Tzvel.	Perennial	10, 14–15	6	CHLOR	NAD-ME		A [4, 5[i]]; E[12][i] F [19][i]
52	*Chloris virgata* Sw.	Annual	3, 6, 8–13, 15–16	1, 4–5	CHLOR	PEP-CK	–14.6(S)	A[6, 8]; F [5, 15]
53	*Cleistogenes caespitosa* Keng	Perennial	12	5	CHLOR	NAD-ME		i
54	*C. kitagawae* Honda	Perennial	2–5, 8–9, 12	5	CHLOR	NAD-ME		i
55	*C. foliosa* Keng	Perennial	4, 12–13	2, 5	CHLOR	NAD-ME		i
56	*C. songorica* (Roshev.) Ohwi	Perennial	7–16	2, 5	CHLOR	NAD-ME	–14.7	A [4, 8]
57	*C. squarrosa* (Trin.) Keng	Perennial	2–13	1, 5	CHLOR	NAD-ME	–16.4 (R)	A [8]; F [19]
58	*Crypsis aculeata* (L.) Ait.	Annual	10–13, 15	6	CHLOR	NAD-ME or PEP-CK		F [5]; [10][i]
59	*C. schoenoides* (L.) Lam.	Annual	3, 10, 14	6	CHLOR	NAD-ME or PEP-CK		F [5]
60	*Enneapogon borealis* (Griseb.) Honda	Annual	3, 6–16	2, 5	CHLOR	NAD-ME or PEP-CK	–14.7	A [4]; F [5, 15][i]
61	*Eragrostis cilianensis* (All.) Vign.-Lut.	Annual	10	1, 3	CHLOR	NAD-ME	–15.4 (S)	A [2, 6, 15]; F [5[i], 15]
62	*E. minor* Host	Annual	1–16	1–3, 5	CHLOR	NAD-ME	–13.7	A [8]
63	*E. pilosa* (L.) Beauv.	Annual	4–5, 7–12, 16	1, 3, 5	CHLOR	NAD-ME	–15.0 (S)	A [2]
64	*Tragus mongolorum* Ohwi	Annual	12–13	3, 5	CHLOR	NAD-ME		A [2, 10][i]; F [15][i]
65	*Tripogon chinensis* (Franch.) Hack.	Annual	2, 4–5, 8–9, 12	5	CHLOR	NAD-ME		A [10][i]; F [15][i]
66	*T. purpurescens* Duthie	Annual	12–13, 16	5	CHLOR	NAD-ME		i
	Polygonaceae							
67	*Calligonum ebi-nurum* Ivanova ex Soskov	Shrub	14–15	3	SALS	NAD-ME		A [7, 8][i]; F [3][i]; M [20]
68	*C. gobicum* Bunge ex Meissn.	Shrub	14–16	3	SALS	NAD-ME		i
69	*C. junceum* (Fish. et Mey.) Litv.	Shrub	14–15	3	SALS	NAD-ME	–12.7 (W)	F [3]
70	*C. litvinovii* Drob.	Shrub	14–15	3	SALS	NAD-ME		i
71	*C. mongolicum* Turcz.	Shrub	7, 10–16	3	SALS	NAD-ME	–12.9	A [8]
72	*C. pumilum* Losinsk.	Shrub	10, 14	3	SALS	NAD-ME		i

Table 2 (continued)

No.	Family, tribe and species[a]	Life form[b]	Occurrence, regions[c]	Habitat[d]	Kranz anatomy[e]	Biochemical type[f]	$^{13}C/^{12}C$ value[g]	Criteria and references[h]
Amaranthaceae								
73	*Amaranthus albus* L.	Annual	2, 4	1	ATR	NAD-ME		A [2]
74	*A. cruentus* L.	Annual	2	1	ATR	NAD-ME		A [2]
75	*A. blitoides* S. Wats.	Annual	4, 9	1	ATR	NAD-ME		A [2}
76	*A. retroflexsus* L.	Annual	2, 4–5, 8–10, 12–13, 15	1	ATR	NAD-ME	–12.6	A [2, 8]; F [19]
Molluginaceae								
77	*Mollugo cerviana* (L.) Ser.	Annual	12, 14–15	3	ATR	NAD-ME		A [2]
Portulacaceae								
78	*Portulaca oleraceae* L.	Annual	2, 3	1	ATR	NAD-ME		A [42]
Euphorbiaceae								
79	*Euphorbia mongolicum* Prokh.	Annual	3, 7, 10–11, 13	3	ATR	NAD-ME or NADP-ME	–13.8	[8][i]
Zygophyllaceae								
80	*Tribulus terrestris* L.	Annual	3, 5–16	3–4	ATR	NADP-ME		A [4]; F [19]

[a] List of species, names of species, and families by Gubanov (1996), division of Chenopodiaceae by Iljin (1936) and Botschantzev (1969, 1976); division of Poaceae by Tsvelev (1987)
[b] Life forms according to Grubov (1982)
[c] Species occurrence after Grubov (1982)and Gubanov (1996)
[d] Habitat: *1* moist, meadows or banks of rivers and lakes, oases, *2* dry and non-saline, dry meadow and steppe, *3* sandy and semi-sandy deserts, *4* takyrs, weakly saline clay deserts, *5* rocky surfaces, *6* salt-marshes
[e] Kranz anatomy types after Carolin et al. (1975, 1978) (*ATR* atriplecoid, *KOCH* kochioid, *SUE* suaedoid, *SALS* salsoloid, *PANIC* panicoid, *ARIST* aristidoid, *CHLOR* chloridoid)
[f] Biochemical types were determined on preferential (>50% of total) incorporation of $^{14}CO_2$ after 10 s to malate or aspartate
[g] Carbon isotope fractionation: *W* Winter (1981), *R* Redman et al. (1995), *A* Akhani et al. (1997), *S* Schulze et al. (1996)
[h] Criteria: *A* Kranz anatomy, *M* photosynthesic carbon metabolism, *E* enzyme activity of C_4 cycle, *F* carbon isotope fractionation. References: *1* Carolin et al. 1975, *2* Downton 1975, *3* Winter 1981, *4* Gamaley 1985, *5* Batanouny et al. 1986, *6* Vogel et al. 1986, *7* Voznesenskaja and Gamaley 1986, *8* Gamaley and Shirevdamba 1988, *9* Pyankov and Vakhrusheva 1989, *10* Hattersley and Watson 1992, *11* Glagoleva et al. 1992, *12* Pyankov et al. 1992a, *13* Pyankov et al. 1992b, *15* Schulze et al. 1996, *16* Akhani et al. 1997, *17* Pyankov et al. 1997, *18* Fisher et al. 1997, 19 Redman et al. 1995, *20* authors' unpublished work
[i] C_4 traits found in another species of the same genus

Table 3 The occurrence of C_4 photosynthesis in different plant families in Mongolia[a]

Family	Genus numbers		Species numbers	
	Total	C_4 number	Total	C_4 number
Dicotyledonae				
Amaranthaceae	1	1	4	4
Chenopodiaceae	**25**	**14**	**91**	**41**
Euphorbiaceae	2	1	15	1
Molluginaceae	1	1	1	1
Polygonaceae	**14**	**1**	**67**	**6**
Portulacaceae	2	1	2	1
Zygophyllaceae	2	1	13	1
Total Dicots	**47**	**20**	**193**	**55**
Monocotyledonae				
Poaceae	**60**	**15**	**250**	**25**
Total	**107**	**35**	**443**	**80**

[a] Total genera and species statistics according to Gubanov (1996)

Table 4 Occurrence of C_3 and C_4 species in Mongolian taxa of Chenopodiaceae

Taxon	Number of species		
	Total	C_3	C_4
Chenopodieae	**16**	**16**	**0**
Chenopodoium	16	16	0
Corispermae	8	8	0
Agriophyllum	1	1	0
Corispermum	7	7	0
Salicornieae	6	6	0
Halocnemum	1	1	0
Kalidium	4	4	0
Salicornia	1	1	0
Atripliceae	**12**	**8**	**4**
Atriplex	5	1	4
Axyris	3	3	0
Ceratocarpus	2	2	0
Krasheninnikovia	2	2	0
Capmphorosmeae	**10**	**1**	**9**
Bassia	2	1	1
Camphorosma	1	0	1
Kochia	6	0	6
Londesia	1	0	1
Suaedeae	**10**	**8**	**2**
Suaeda	10	8	2
Salsoleae	**29**	**3**	**26**
Anabasis	7	0	7
Climacoptera	2	0	2
Halogeton	1	0	1
Iljinia	1	0	1
Londesia	1	0	1
Micropeplis	1	0	1
Nanophyton	2	0	2
Petrosimonia	2	0	2
Salsola	11	2	9
Sympegma	1	1	0
Total	**91**	**50**	**41**

values of $^{13}C/^{12}C$ fractionation (Winter 1981; Akhani et al. 1997), which confirms the recent review of photosynthetic types in *Suaeda* (Fisher et al. 1997). It seens likely that eight other species, *S. corniculata, S. foliosa, S. glauca, S. kossinskyi, S. linifolia, S. prostrata, S. prezhewalskii*, and *S. salsa* are C_3. Some of them, *S. corniculata, S. glauca, S. linifolia* and *S. salsa*, show C_3-like carbon fractionation values (Winter 1981; Akhani et al. 1997). In addition, taxonomic analysis of photosynthesis amongst *Suaeda* species show C_3 $^{14}CO_2$ fixation for species belonging to the most primitive sections *Chenopodina* (syn. *Heterospermae*) (*S. corniculata, S. kossinskyi, S. prostrata, S. salsa*), and *Schanginia* (*S. glauca, S. linifolia*). There is some disagreement in identification of photosynthetic types; for instance, Gamaley (1985) included *S. corniculata* as a C_4 plant, but this may be an incorrect species identification. Experimental data are completely absent for *S. foliosa* and *S. przhevalskii*, so we have not included them in our list of C_4 species.

In the Camphorosmeae tribe C_4 species occur in *Camphorosma*, *Bassia*, *Kochia* and *Londesia*. *C. lessingi*, *L. eriantha* and almost all *Kochia* species have direct evidences of C_4 photosynthesis (Table 1). *K. krylovii* has no experimental data, but was included as a C_4 plant. All studied Asian species of *Kochia* demonstrate C_4 photosynthesis (Pyankov and Mokronosov 1993); and we agree with Carolin et al. (1975) that Eurasian *Kochia* species commonly have the Kranz syndrome.

For the two Mongolian *Bassia* species, one, *B. hyssopifolia*, is a typical C_4 plant with kochioid Kranz anatomy (Carolin et al. 1975; Gamaley 1985), C_4-like $\delta^{13}C$ values (Table 1) and primary C_4 carbon metabolism (Pyankov and Vakhrusheva 1989). *B. dasyphylla* is a C_3 succulent with centric mesophyll structure (Gamaley and Shirevdamba 1988; Pyankov 1993) and a $\delta^{13}C$ value of –24.8‰.

Four of five *Atriplex* species were classified in the Kranz anatomy group. Mesophyll structure and photosynthesis enzyme activities were studied in *A. tatarica* and *A. sibirica* (syn. *A. centralasiatica*) (Pyankov et al. 1992a, 1992b). *A. cana* is included based on leaf anatomy, $\delta^{13}C$ value, and primary photosynthetic products (Table 2). There is evidence of Kranz anatomy (Gamaley and Shirevdamba 1988) and a C_4-like $\delta^{13}C$ value (Winter 1981) in *A. laevis*; but Akhani et al. (1997) found a C_3-like $\delta^{13}C$ value, and it is a C_3 species according to Carolin et al. (1975). *A. fera* was not included in our C_4 list, because of lack of information about its type of carbon metabolism.

Akhani et al. (1997) reported a C_4-like $\delta^{13}C$ value in *Axyris amarantoides*, which habitats in Mongolia (Gubanov 1996). However it seems likely, that this species is C_3. Carolin et al. (1975) did not find Kranz anatomy in *A. amaranthoides*, and *Axyris* is systematically very close to *Krashennikovia*, all representatives of which are typical xerophytes with a C_3 isopalisade leaf structure (Gamaley and Shirevdamba 1988).

The relationships between systematic groups of C_4 Chenopodiaceae and their Kranz anatomy and biochemical types now seem clear (Carolin et al. 1975; Voznesenskaja and Gamaley 1986; Glagoleva et al. 1992; Pyankov and Vakhrusheva 1989; Pyankov et al. 1992a, 1997). All species of *Atriplex* and *Suaeda* are NAD-ME. The species of Camphorosmeae (*Camphorosma, Kochia, Bassia*) are NADP-ME. But there are

different biochemical pathways for CO_2 metabolism among representatives of Salsoloideae. Annual plants belonging to section *Salsola* and derivative (*Halogeton, Micropeplis*), *Anabasis* and shrubs from section *Coccosalsola* (*S. arbuscula*) and its derivative (*Haloxylon, Ijinia*) have the NADP-ME biochemical type. *Salsola* species of section *Malpigipila* (*S. gemmascens, S. passerina*), derivative species of sections *Belantera* (*Climacoptera*), *Caroxylon* (*Nanophyton*), and species of *Petrosimonia* genus are probably all NAD-ME photosynthetic types.

Polygonaceae

Calligonum is a single genus in Polygonaceae that contains only C_4 species (Winter 1981; Voznesenskaja and Gamaley 1986; Pyankov et al. 1994). There are six *Calligonum* species found in Mongolia (Table 2). All species have a centric type of Kranz anatomy, similar in appearance to the salsoloid type (Voznesenskaja and Gamaley 1986). These species occur mainly in Gobian deserts; only *C. mongolicum* has a broader geographical distribution (Table 2).

Other dicots

C_4 species were identified in five others dicotyledonous families (Table 2). There are mainly well-known naturalized species, e.g., *Amaranthus* (*Amaranthaceae*), *Portulaca oleraceae* (*Portulacaceae*), and the cosmopolitian species *Mollugo cerviana* (*Molluginaceae*) and *Tribulus terrestris* (*Zygophyllaceae*). We found a C_4-like $\delta^{13}C$ value in *Euphorbia mongolicum* (*Euphorbiaceae*). Voznesenskaja and Gamaley (1986) reported the C_4 syndrome in *E. humifusa* from Mongolia; but our $\delta^{13}C$ determination of –26.3, is a C_3-like value.

Monocotyledoneae

Poaceae

Grasses include 250 species and the *Poaceae* family is third in abundance in the Mongolian flora (Gubanov 1996). Identification of C_4 grass species was on the basis of experimental studies of Kranz anatomy and $\delta^{13}C$ values plus published data (Table 2), and there are strong taxonomic relationships in grasses (Hattersley and Watson 1992). Based on these characters we identified 25 grasses with the Kranz syndrome, i.e., 10% of total Poaceae. We found species with the C_4 syndrome in five tribes Andropogoneae, Paniceae, Aristideae, Arundinelleae, and Cynodonteae. A majority of C_4 grasses, 16 species, belong to Cynodonteae and have NAD-ME or PEP-CK metabolism. Species with NADP-ME are comparatively few, and tribes Andropogoneae, Aristideae, and Arundinelleae consist of only single species. The representatives of Paniceae (*Ehinochloa, Panicum*, and *Setaria*) are naturalized species and occur mainly in annually disturbed regions and oases. Other C_4 annuals with an aspartate-forming type of metabolism, NAD-ME or PEP-CK, i.e., *Chloris virgata*, *Enneapogon*, and *Eragrostis* species are cosmopolitan, and their apperance in natural ecosystems very strongly depends on precipitation. Thus, only a few C_4 grasses, such as species of *Cleistogenes, Aristida, Aeluropus, Tragus*, and *Eragrostis*, are important in natural ecosystems.

Cyperaceae

In the Mongolian flora, the *Cyperaceae* family includes 127 species belonging to 27 genera (Gubanov 1996); but no C_4 species were identified in Mongolia.

Table 5 Distribution of Chenopodiaceae species with different types of photosynthesis and life forms in botanical-geographical regions of Mongolia

Regions						
No.	Name	Total number C_3+C_4	C_4 number	C_4+C_3, succulent species	C_4 salsoloid type species	C_4 salsoloid NADP-ME shrub species
1	Khubsugul	10	1	1	0	0
2	Khentey	10	4	4	2	0
3	Khangai	34	11	15	5	0
4	Mongol – Daurian	29	8	11	3	0
5	Great Khingan	13	3	3	1	0
6	Khobdo	31	12	18	4	1
7	Mongolian Altay	35	15	20	9	2
8	Middle Khalkha	34	10	17	6	0
9	East Mongolia	34	9	18	5	0
10	Depression of the Great Lakes	61	25	37	13	5
11	Valley of Lakes	37	18	26	11	2
12	East Gobi	38	15	25	8	2
13	Gobi Altai	44	17	28	10	3
14	Dzhungarian Gobi	61	31	40	21	14
15	Transaltai Gobi	36	16	23	9	4
16	Alashan Gobi	31	10	21	7	4

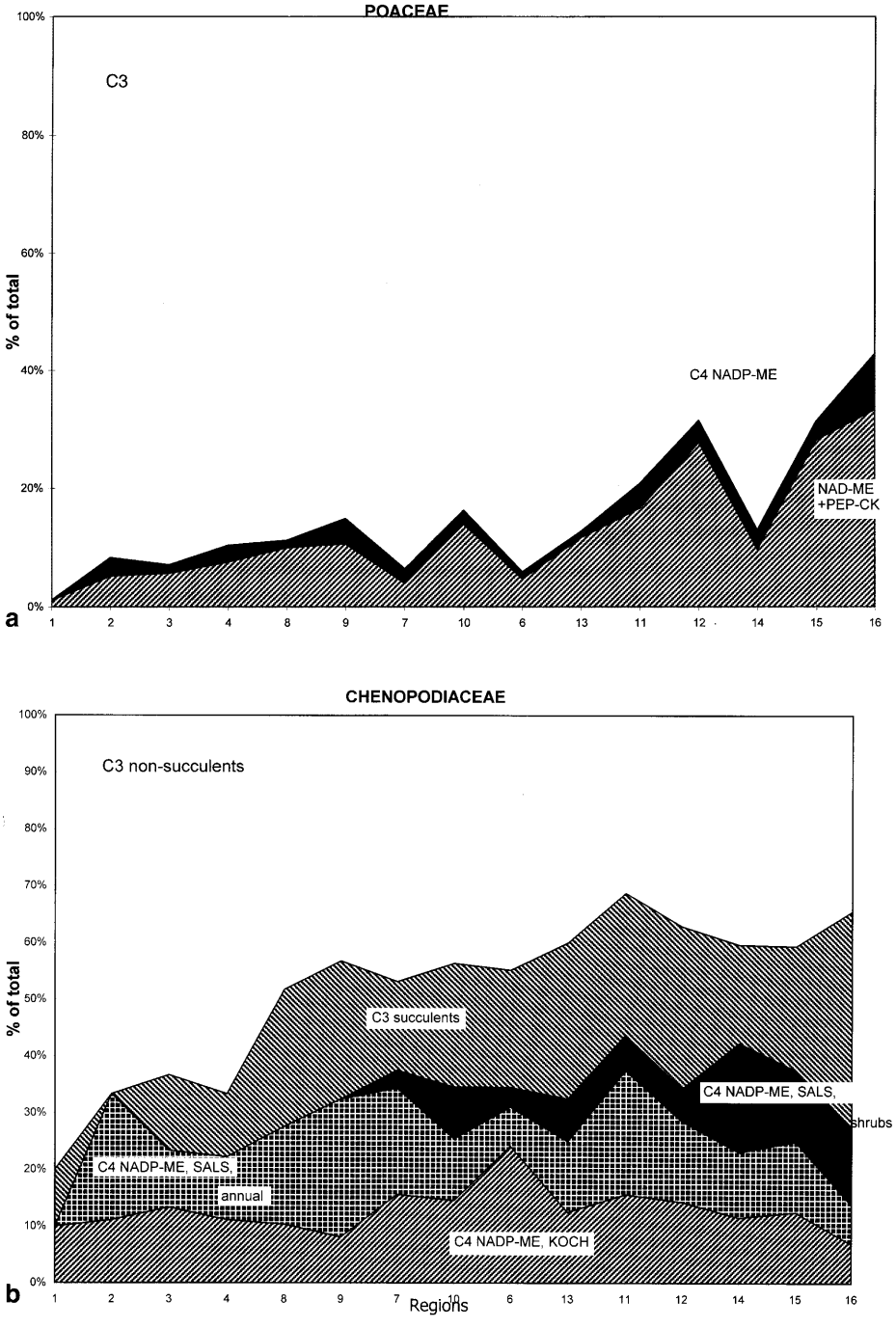

Fig. 3 Proportions of **a** Poaceae and **b** Chenopodiaceae families with different types of photosynthesis, structural and biochemical features of C_4 syndrome, and life forms, along the aridity gradient in botanical-geographical regions of Mongolia (*SALS* and *KOCH* are salsoloid and kochioid types of Kranz anatomy, respectively). Region 5 was excluded

Patterns of climatic distribution for C_4 Chenopodiaceae and Poaceae

Chenopodiaceae

Table 5 summarizes our data on the distribution and relative abundance of Chenopodiaceae species with different photosynthetic types in the botanical-geographical regions of Mongolia. In general, we found increasing numbers and percentage of C_3 and C_4 chenopods along an increasing warm and aridity gradient. The number of C_4 species varied from 1 (Khubsugul) to 31 (Dzungarian Gobi). The C_4 percentage increased along an aridity and temperature gradient, but the highest absolute and relative abundance of the C_4 chenopods, 31 (50.8%) was found in Dzhungarian Gobi. In other southern hot and arid deserts, Transaltai and Alashan Gobi, chenopod numbers were lower, and consisted of only 10 C_4 species (32.3% of Chenopodiaceae) in Alashan Gobi.

The proportions of chenopods with different types of CO_2 fixation and structural and biochemical subtypes of C_4 also changed along the temperature and aridity gradient (Fig. 3). The relative abundance of non-succulent C_3 chenopod species decreased from cool moist to warm de-

Table 6 Correlation coefficients of s betweeen occurrence of C_4 species in Chenopodiaceae (*CH*) and Poaceae (*POA*) and climatic variables in Mongolia. Correlations >0.50 are significant at $P<0.05$

Plant group	Aridity index (de Martonne)	Sum of temperatures >10°C	Annual precipitation (mm)	Annual average temperature (°C)	July average temperature (°C)
POA+CH, total species	0.21	–0.63	0.26	–0.57	–0.57
%C_4 POA+CH, of total POA+CH species	–0.80	0.92	–0.72	0.92	0.88
% all C_4 POA of POA total	–0.60	0.90	–0.50	0.90	0.83
% C4 native POA of POA total	–0.59	0.87	–0.48	0.89	0.80
% NAD-ME+PEP-CK species of POA total	–0.62	0.89	–0.53	0.91	0.83
% NADP-ME species number of POA total	–0.44	0.72	–0.31	0.69	0.65
CH, C_3+C_4 species	–0.70	0.40	–0.62	0.47	0.43
CH, C3 succulent species	–0.80	0.70	–0.70	0.79	0.68
CH, % C3 succulent species of CH total	–0.68	0.72	–0.63	0.76	0.65
CH, C_4 species	–0.71	0.39	–0.68	0.44	0.41
%C_4 of CH total	–0.74	0.49	–0.64	0.46	0.48
CH, C_4+C_3 succulent species	–0.81	0.54	–0.74	0.60	0.55
% C_4+C_3 succulents of CH total	–0.97	0.80	–0.82	0.80	0.77
% C4 shrubby NADP-ME salsoloid type of CH total	–0.69	0.69	–0.75	0.72	0.64
%of C4 annual NADP-ME salsoloid type of CH total	–0.16	0.15	0.11	0.07	0.22
%, NADP-ME shrubby Kochioid type of CH total	–0.57	0.17	–0.47	0.15	0.15

sert regions. In general, the percentage of C_4 species of Chenopodiaceae positively correlated with increasing of aridity (or negative with aridity index) in each district (Table 6), r=–0.74, $P<0.05$. Temperature parameters, i.e., the sum of effective temperatures or average annual or July temperatures were positively, but not significantly, correlated with the relative abundance of C_4 Chenopodiaceae (Table 6).

The chenopods with C_4 CO_2-fixation have different types of Kranz anatomy, biochemical subtypes, and life forms (Table 2). There are four types of Kranz anatomy: atriplecoid, suaedoid, kochioid, and salsoloid, and two biochemical subtypes, NAD-ME and NADP-ME. Plants with salsoloid Kranz anatomy included both biochemical variants plus two contrasting groups with different life forms – shrubs and annuals. We hypothesized that various groups of C_4 Chenopodiaceae responded differently to environmental variables. This hypothesis could be tested by analyzing each group of Chenopodiaceae in relation to climatic variables, but there were not enough C_4 *Atriplex* and *Suaeda* species for this analysis. We therefore studied the climatic patterns in Camphorosmeae and the main groups of Salsoleae, which contain the largest number of C_4 chenopods. We found a different composition of groups along the aridity gradient (Fig. 3, Table 5). Large shrubs with a salsoloid type of assimilation organs and NADP-ME biochemical subtypes, such as *Haloxylon, Iljinia, Salsola arbuscula*, and semishrubs of genus *Anabasis*, appeared only in dry and hot regions with an aridity index near 10 or less, and occurred mainly in Gobian deserts. Their relative abundance was significantly and positively correlated with aridity (r=69) and the average annual temperature (r=0.69), and negatively with annual precipitation (r=–75).

The annuals, *Salsola* NADP-ME species, are common in all regions (Fig. 3), but their percentages show no correlation with the main climatic variables in Mongolia (Table 6). Species with a kochioid type of Kranz anatomy, which include semishrub and annual species, occur over a broad climatic range, and their relative abundance is maximum in dry, but not very hot areas (Fig. 3). The percentage of C_4 species of this group was positively and significantly correlated with aridity (r=0.57), but not with temperature parameters. The correlation coefficient between aridity and precentage of C_4 speciesin this group is significantly lower than in the group of NADP-ME shrubs and semishrubs with a salsoloid type of mesophyll structure. The highest coefficient between aridity and percentage of C_4 species was found for a group, of C4 NADP-ME shrubs with a salsoloid anatomy and C_3 succulents combined, that consisted of *Halocnemum, Kalidium, Salicornia, Salsola, Suaeda, Sympegma*. The relative abundance for this group of combined C_3 and C_4 succulents correlated best with aridity (r=0.97) (Table 6, Fig. 4). The correlation with temperature was also high (r=0.80), but lower than that for aridity. Thus chenopods with C_4 photosynthesis and C_3 succulents are favored in areas with a hot, dry climate.

Poaceae

There is considerable variation in the frequency of C_3 and C_4 grasses in different Mongolian regions (Table 7). We found different patterns of distribution for grasses with C_3 versus C_4 types of photosynthesis. The highest absolute number of C_3 grasses, 80–140 species per district, was detected in areas with cool and moist climates in northern and central mountain regions (Khangai, Khentei, Mongolian Altai, Depression of the Great Lakes), and in drier and warmer eastern regions (Middle Khalkha, East Mongolia, Gobi Altai). The highest total number of C_4 grasses and percentages were in southern districts – Valley of Lakes, Transaltai, Alashan and East Gobi (Table 7). In semiarid steppe and semidesert areas the percentage of C_4 grasses was between 10 and 20%.

Table 7 Distribution of Poaceae species with different types of photosynthesis in botanical-geographical regions of Mongolia

Regions					
No.	Name	Total number, C_3+C_4	C_4 number	C_4 number, NAD-ME+PEP-CK	C_4 number, NADP-ME
1	Khyhubsugul	88	1	1	0
2	Khentey	96	8	5	3
3	Khangai	141	10	8	2
4	Mongol-Daurian	106	11	8	3
5	Great Khingan	73	7	4	3
6	Khobdo	86	5	4	1
7	Mongolian Altay	125	8	5	3
8	Middle Khalkha	80	9	8	1
9	East Mongolia	94	14	10	4
10	Depression of the Great Lakes	86	14	12	2
11	Valley of Lakes	48	10	8	2
12	East Gobi	54	17	15	2
13	Gobi Altai	94	12	11	1
14	Dzhungarian Gobi	62	8	6	2
15	Transaltai Gobi	32	10	9	1
16	Alashan Gobi	21	9	7	2

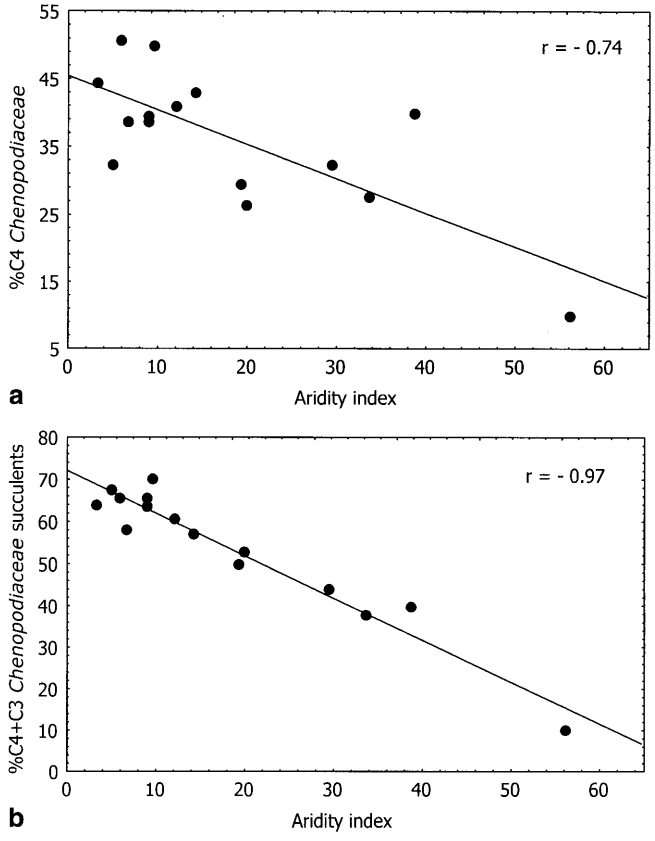

Fig. 4 Relationship between the occurrence of **a** C_4 Chenopodiaceae species, and **b** C_3+C_4 succulent Chenopodiaceae species, and aridity index in Mongolia

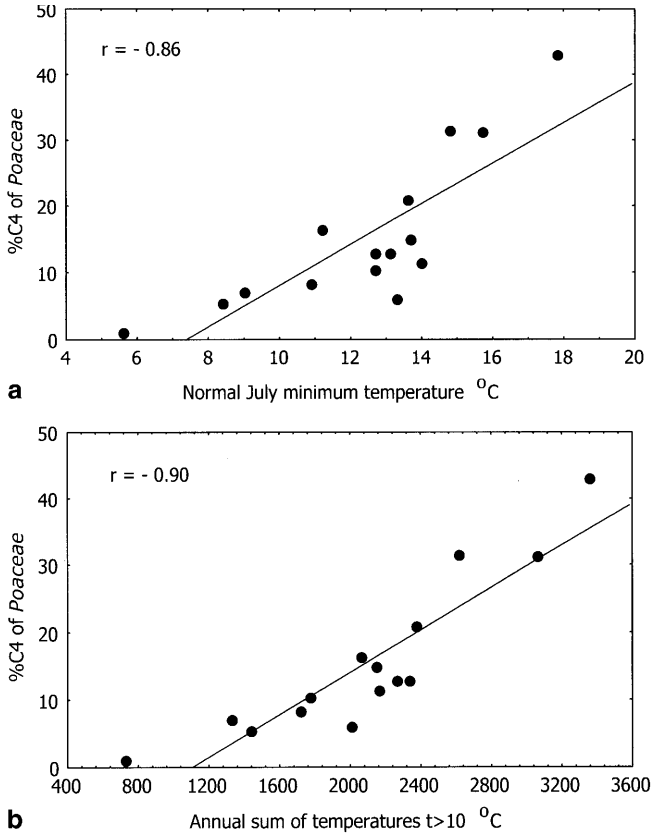

Fig. 5 Relationship between the abundance of C_4 Poaceae and **a** normal July minimum temperature and **b** the annual sum of temperatures over 10°C in Mongolia

Temperature was the climatic variable which showed the strongest correlation with the percent of C_4 grasses (r=0.90) (Table 6, Fig. 5). Only one C_4 cosmopolitan grass species, *Eragrostis minor*, occured in the northern district (Khubsugul), where the July average mininmum temperature is 5.6°C. In the Khangai region, where the average July minimum temperature was 9°C, we identified four grasses with Kranz anatomy. The regression line of percentage C_4 Poaceae versus temperature (Fig. 5) shows a decrease in the relative abundance C_4 grasses to zero when the July normal minimum temperature is about 7.5°C. The distribution of C_4 grass species was

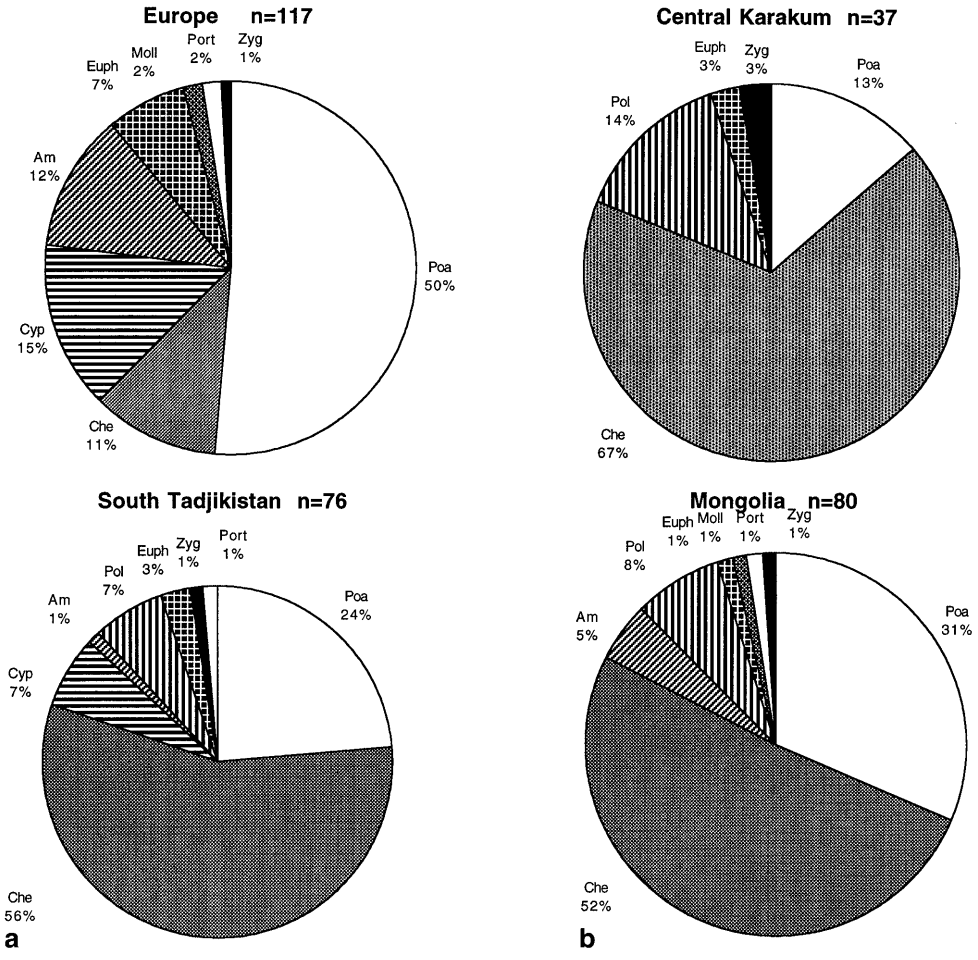

Fig. 6 Taxonomic spectrums of C_4 taxa in different Eurasian regions: Europe (Mateu-Andres 1992); Central Karakum desert, Turkmenistan (Pyankov et al. 1986); South Tadjikistan (Pyankov and Molotkovskii 1992, 1993); and Mongolia (families: *Che* Chenopodiaceae, *Poa* Poaceae, *Pol* Polygonaceae, *Euph* Euphorbiaceae, *Port* Portulacaceae, *Zyg* Zygophyllaceae, *Am* Amarantaceae; *n* total C_4 species number, *%* percent of C_4 taxa out of total C_4 species)

highly and positively correlated with all temperature parameters. The highest correlation (r=0.90) was with the sum of temperatures over 10°C, i.e., with the total amount of warmth in a region. Grasses with C_4 photosynthesis normally habitats in regions with a sum of temperatures over 10°C that exceeds 1200°C.

The correlation analysis shows some differences in the climatic preferences of C_4 grasses of different biochemical groups. Species belonging to aspartate-forming types of C_4 photosynthesis (NAD-ME and PEP-CK), mainly native grasses, are more closely correlated with temperature than NADP-ME species, which belong to the weedy naturalized flora (*Echinochloa* and *Setaria*) (Table 6).

Patterns of climatic distribution for C_4 plants in other families

The plants of genus *Calligonum*, Polygonaceae, are the most interesting of the other families. All six species of this genus occur in very arid deserts (Dzhungarian, Transaltai, and Alashan Gobi). Only *C. mongolicum* has a broad distribution in the Gobian deserts that occur in more northern regions, including eastern Mongolia and the Depression of the Great Lakes. The climatic range of *Calligonum* species is similar to that of C_4 shrubby Chenopodiaceae species, and depends upon aridity and warm temperatures.

Other C_4 dicotyledonous species, excluding *Euphorbia mongolicum*, are weedy or cosmopolitan species that occur in many botanical-geographical districts; but their habitat is connected with annually disturbed areas and oases, i.e., with human activities (Table 2).

Discussion

Our studies show a "Turanian" type of C_4 species composition in Mongolia with a strong dominance by Chenopodiaceae, which make up over 50% of the total C_4 species. Turanian deserts are arid places with hot continental climates that occupy the region of Turanian lowland, limited by the Caspian sea to the west, and the Pamirs and Tien-Shan mountains to the south and south-sast (Lavrenko and Nikolskaja 1963). Turanian type deserts, such as the Karakum and Kyzylkum, are characterized by a strongly continental climate with hot dry summers and cold winters. These deserts contain different kinds of soil substrates (sand, clay, rocky surfaces, salt-marshes) with a very strong dominance of C_4 plants in the Chenopodiaceae family (Pyankov et al. 1986; Pyankov and Mokronosov 1993).

The relative abundance of C_4 grasses and chenopod species in Mongolia is close to the taxonomic composition of C_4 plants found previously in Central Karakum deserts (Pyankov et al. 1986) and South Tadjikistan (Pyankov and Molotkovskii 1992, 1993) (Fig. 6). Monocots with Kranz anatomy are very few in Mongolia. Only 25 species are present, including about 10 naturalized and cosmopolitian species in *Chloris, Ehinochloa, Eragrostis, Panicum,* and *Setaria.* There are no C_4 Cypereaceae. This composition is very different from the desert and semidesert regions in Australia (Hattersley 1983), South Africa (Vogel et al. 1978; Schulze et al. 1996), North Africa (Batanouny et al. 1988), and North America (Ehleringer et al. 1997) where C_4 grasses are dominants, and chenopods with C_4 photosynthesis are not abundant. Even in Europe, about 50% of total C_4 species are Poaceae, while Chenopodiaceae make up only 11% (Mateu Andres 1992). The total numbers of C_4 families in Mongolia is also low, and four of the eight families (Amaranthaceae, Molluginaceae, Portulacaceae, and Zygophyllaceae) contain only weedy and cosmopolitian species. Thus, the native Mongolian C_4 flora presumably formed from representatives of three main families: Chenopodiaceae, Poaceae, and Polygonaceae, which together make up about 90% of the total number of C_4 photosynthesis species (Fig. 6).

The percentage of C_4 species in the total Mongolian flora is only about 3.5%. However if we calculate the percentage of species that occur in Gobian deserts (about 550 species) (Vostokova et al. 1995), there are nearly 14.5% C_4 species, quite comparable with the figures for hot Turanian deserts, where about 15–17% of total species are C_4 (Pyankov et al. 1986; Pyankov and Molotkovskii 1993). Hot Turanian deserts are very rich in absolute numbers of C_4 Chenopodiaceae species. There are over 200 chenopods with C_4 photosynthesis (not including *Atriplex*) in the arid regions of the former Soviet Union (Pyankov and Mokronosov 1993). They also are broadly distributed in desert regions of the Near and Middle East, the Arabian peninsula and in northern Africa (Shomer-Ilan et al. 1981; Ziegler et al. 1981; Winter 1981; Akhani et al. 1997). Similar proportions of C_4 plants and patterns of climatic distribution in those regions is likely connected with the common origin of the flora in these regions. According to Lavrenko (1962) these areas all belong to an Afro-Asian or Saharo-Gobian desert region characterized by common features of their desert flora, the first of which is a high abundance of Chenopodiaceae species.

The physiological background for the broad species distribution of Salsoleae in Afro-Asian desert regions is connected with their C_4 type of photosynthesis. Over 300 species of Salsoleae have been studied in those regions, but a C_3 type of photosynthesis was found only in about 6 *Salsola* species and *Sympegma regelii* (Winter 1981; Pyankov et al. 1993a, 1993b, 1997; Akhani et al. 1997). Probably this abundance of C_4 is related to known traits such as a high water use efficiency, higher photosynthesic temperature optimum, and a stable quantum yield at high temperatures (Black 1971, 1973; Ehleringer 1978; Ehleringer and Monson 1993; Ehleringer et al. 1997).

The preponderance of C_4 chenopods over grasses in Asian continental deserts is connected with a high resistance to drought. All C_4 chenopods of tribes Salsoleae, Suaedeae, and Camphorosmeae are succulents with water-storage tissue occupying the central part of cylindrical leaves, and in many species there is an additional layer of hypodermal cells under the epidermis to lower H_2O loss (Carolin et al. 1975; Shomer-Ilan et al. 1981; Gamaley 1985; Voznesenskaja and Gamaley 1986). Usually the rate of transpiration in C_4 chenopods is significantly lower than in C_4 grasses. For instance, the average transpiration rates of *Salsola passerina*, *Haloxylon ammodendron* and *Anabasis brevifolia* in Gobian deserts were in the range 150–350 mg H_20 g fresh mass^{-1} h^{-1}; but in a C_4 grass, *Cleistogenes songorica*, the range was 200–800 mg H_20 g fresh mass^{-1} h^{-1} (Bobrowskaja 1991). In the Karakum desert, the maximum values of transpiration recorded were about 200–700 mg H_20 g fresh mass^{-1} h^{-1} in *Haloxylon aphyllum* and *Salsola richterii*; but 590–1100 mg H_20 g fresh mass^{-1} h^{-1} in the Kranz grass *Stipagrostis karelinii*. The transpiration rates of *Haloxylon aphyllum* and *Salsola richterii* were 4–18 times lower than evaporation from a water surface, while the rate for *Stipagrostis karelinii* was only 3–9 times lower (Sveshnikova 1972). C_4 chenopod succulents are also characterized by high osmotic pressures and leaf suction forces that were about twice those in desert C_4 grasses (Sveshnikova 1972; Bobrowskaja 1991). In general these traits provide stable water regimes and little water deficit in assimilation organs of succulent chenopods, particularly shrubs as from *Haloxylon, Salsola,* and *Iljinia* that never decrease their water contents to lethal levels (Sveshnikova 1972; Bobrowskaja 1985, 1991). Many chenopods are also halophytes, particularly species with NAD-ME biochemistry (Pyankov and Vakhrusheva 1989; Glagoleva et al. 1992; Pyankov et al. 1992a; Fisher et al. 1997), and can grow on soils with salinity up to 2–3.5% and accumulate up to 30–47% mineral content (Kolchevskii et al. 1995). Therefore the combination of C_4 photosynthesis with succulence, water relations, and salt resistance in Chenopodiaceae allow these plants to occupy a broad range of ecological conditions in very arid environments.

Some succulent Chenopodiaceae species with C3 photosynthetic type, for instance *Sympegma regelii*, are dominants of true deserts and are broadly distributed in all desert regions, particularly western Mongolia (Vostokova et al. 1995). Two C_3 *Salsola* species, *S. laricifolia* and *S. abrotanoides,* occur in arid regions, *and S. laricifolia* occurs in all Gobian deserts (Gubanov 1996). Other C_3 succulents, such as species of *Kalidium, Salicornia, Suaeda, Halocnemum,* occur preferentially in moist saline soils, where high aridity and water evaporation are common, in southern Mongolia. Hence the abundance of succulent chenopods increases with aridity in Mongolia, where C_4 species preferentially occupy dry habitats and C_3 species are commoner in moist saline habitats. Leaf succulence is

an effective mechanism in desert sites with limited water supply both for C_4 and C_3 plants. Chenopodiaceae as a whole is the principal family in desert regions of Asia and North Africa (Lavrenko 1962). We speculate that the broad distribution of chenopods in these desert regions and their adaptations to arid conditions were the physiological basis for the origin of C_4 photosynthesis.

We also found that the proportion of C_4 chenopods changed with different Kranz anatomy, biochemical types, and life forms along the aridity gradient (Fig. 3). Perennial shrubs with a salsoloid type of mesophyll and NADP-ME biochemistry, such as *Anabasis brevifolia, Iljinia regelii, Salsola arbuscula, Haloxylon ammodendron,* mainly occur in Gobian deserts and dominate the plant cover (Vostokova et al. 1995). *S. arbuscula* and *I. regelii* occur only in deserts with extra arid climate with annual precipitation about 50–70 mm, and less than 10 mm in some years (Vostokova et al. 1995). Those plants are characterized by low transpiration rate, with a range of 100–400 mg H_20 g fresh mass^{-1} h^{-1}. The variation in water content of assimilation organs in *H. ammodendron* and *I. regelii* during the hot days of summer is no more than 5–7%, which is very far from the lethal water deficit for these species of 43.8 and 38.6% respectively (Bobrowskaja 1991). These plants are large, even tree-like, shrubs with a deep root system that reaches underground water supplies. Once again the combination of a water-use efficient type of CO_2 fixation (C_4 type) with water storage (succulence) and effective collection of ground water with the shrub or tree life form allows these plants to grow and survive in very arid deserts. Despite a relatively low species number, their contribution to the productivity of Gobian deserts is very high, 30–90% of total ecosystem plant biomass (Vostokova et al. 1995).

Amongst other C_4 dicots only the Polygonaceae representative *Calligonum* is a major component of natural ecosystems in Mongolia. The climatic distribution pattern of *Calligonum* is similar to that of shrubs with NADP-ME metabolism and salsoloid assimilation organ anatomy. All *Calligonum* species, besides *C. mongolicum* and *C. pumilum*, occur only in the arid desert regions of southern Mongolia (Table 2). The assimilation organs in *Calligonum* are the green shoots, which have a centric mesophyll structure similar in appearance to the salsoloid Kranz type (Voznesnskaja and Gamaley 1986). All species of *Calligonum* studied have NAD-ME biochemistry (Pyankov et al. 1994). *Calligonum* species in the hot deserts of Mongolia make up only about 20% of the total species number (Soskov 1989). Transpiration rate in *Calligonum* species is low and similar to that of desert C_4 large chenopod shrubs, such as *Haloxylon* and *Salsola richteri* (Sveshnikova 1972). Hence it is clear that C_4 dicots with similar anatomy and life form, even though they belong to different taxa, have similar climatic distribution patterns.

Plants with a kochioid type of Kranz anatomy, e.g., *Bassia, Camphorosma, Kochia,* and *Londesia,* grow over a broad climatic range with a maximum abundance in steppe and semidesert regions (Fig. 3). This group shows little correlation with aridity index (r=–0.57) or temperature sum (r=0.17). Only two semishrub species, *Kochia prostrata* and *Camphorosma lessingii*, make significant contributions to productivity in a limited number of semi-desert and arid mountain areas. These annual species have little ecological importance in Mongolian ecosystems. Thus, plants with kochioid type anatomy are not part of the typical desert vegetation; rather they are adapted to drought and to a broad range of temperature conditions, particularly to cold.

Temperature is the main factor that controls the abundance of C_4 grasses in Mongolia, r=0.90, P<0.01 (Table 6, Fig. 5). The spread of grasses with Kranz anatomy to the north iss limited by the normal average July minimum temperature of 7.5°C or a 1200°C sum of temperatures over 10°C (Fig 5, Table 7). Geographically this limit is close to 50°N. Plants with NADP-ME biochemistry are mainly weedy naturalised species, whose habitats are mainly associated with disturbed areas, agricultural fields, and oases in desert regions. The absolute number and percentage of NADP-ME grasses are similar in steppe and desert regions in Mongolia (Table 7) and correlate poorly with climatic parameters in comparison with the percentage of C_4 in Poaceae (Table 6). The relative abundance of aspartate-forming grasses of NAD-ME and PEP-CK biochemical subtypes, belonging to the Cynodonteae tribe, was highly and positively (r=0.89, P<0.01) correlated with temperature. The absolute number of aspartate-type grasses is highest in steppe regions of East Gobi, the Depression of the Great Lakes, and in mountain regions of southern Mongolia, as in Gobi Altai. Some species of that group, such as *Cleistogenes songorica*, are co-dominant in desert steppes with annual precipitation about 100 mm (Vostokova et al. 1995). In true deserts, where average annual precipitation is 50–70 mm, and sometimes less than 10 mm, e.g., in Gobian deserts, grasses occur mainly in oases and make no regular contribution to the natural vegetation. Large perennial thermophilic grasses, like *Stipagrostis karelinii* and *S. pennata,* that have NADP-ME and are summer dominants in the hot, sandy Karakum and Kyzylkum deserts (Voznesensky 1977), are absent in Mongolia.

The C_4 flora of Mongolia is the most cold-resistant variant of Turanian desert vegetation, indeed it forms part of the northern boundary of C_4 plant distribution. In Mongolia 13 Chenopodiaceae species with C_4 photosynthesis, from the genera *Atriplex, Halogeton, Kochia,*and *Suaeda*, are common, with C_4 plants occurring in the Pamir mountains at elevations from 1700 to 4500 m (Pyankov 1993; Pyankov and Mokronosov 1993). These make up about 70% of the Pamirian mountain flora with C_4 photosynthesis. Eight species with C_4 photosynthesis occur in the dry and cool mountain desert of the East Pamirs around 3600–4500 m, and four of those species in the genera *Atriplex, Halogeton, Salsola,* and *Kochia* (Pyankov 1993) are common among Mongolian plants. These species occur near the summer snow line (4600–4800 m) and at the limit of everyday night frost (4100–4200 m); therefore they are amongst the most cold-resistant plants with C_4 photosynthesis known.

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References

Akhani H, Trimborn P, Ziegler H (1997) Photosynthetic pathways in *Chenopodiaceae* from Africa, Asia and Europe with their ecological, phytogeographical and taxonomical importance. Plant Syst Evol 206:187–221

Batanouny KH, Stichler W, Ziegler H (1988) Photosynthetic pathways, distribution, and ecological characteristics of grass species of Egypt. Oecologia 75:539–548

Bender MM, Rouhani I, Vines HM, Black CC Jr (1973) $^{13}C/^{12}C$ ratio changes in Crassulaceae acid metabolism. Plant Physiol 52:427–430

Black CC (1971) Ecological implications of dividing plants into groups with distinct photosynthetic production capacity. Adv Ecol Res 7:87–114

Black CC (1973) Photosynthetic carbon fixation in relation to net CO_2 uptake. Annu Rev Plant Physiol 24:253–286

Bobrowskaja NI (1985) Water regime of trees and shrubs of deserts (in Russian). Nauka, Leningrad

Bobrowskaja NI (1991) Water relations of steppe and desert plants of Mongolia (in Russian). Komarov Botanical Institute, St Petersburg

Botschantzev VP (1969) The genus *Salsola*: a concise history ot its development and dispersal. Bot Zh 54:989–1001 (in Russian)

Botschantzev VP (1976) Conspectus specierum sectionis *Coccosalsola* Fenzl generis *Salsola* L. (in Russian). Novit Syst Plant Vasc 13:74–102

Carolin RC, Jacobs SWL, Vesk M (1975) Leaf structure in *Chenopodiaceae*. Bot Jahrb Syst Pflanzengesch Pflanzengeogr 95:226–255

Carolin RC, Jacobs SWL, Vesk M (1978) Kranz cells and mesophyll in *Chenopodiaceae*. Aust J Plant Physiol 26:683–698

Collins RP, Jones MB (1985) The influence of climate factors on the distribution of C_4 species in Europe. Vegetatio 64:121–129

Doliner LH, Jolliffe PA (1979) Ecological evidence concerning the adaptive significance of the C_4 dicarboxylic acid pathway of photosynthesis. Oecologia 38:23–34

Downton WJS (1975) The occurence of C_4 photosynthesis among plants. Photosynthetica 9:96–105

Ehleringer JR (1978) Implications of quantum yield differences to the distributions of C_3 and C_4 grasses. Oecologia 31: 255–267

Ehleringer JR, Monson RK (1993) Evolutionary and ecological aspects of photosynthetic pathway variation. Annu Rev Ecol Syst 24:411–439

Ehleringer JR, Cerling TE, Helliker BR (1997) C4 photosynthesis, atmospheric CO_2, and climate. Oecologia 112:285–299

Fisher DD, Schenk HJ, Thorson JA, Ferren WR Jr (1997) Leaf anatomy and subgeneric affiliations of C_3 and C_4 species of *Suaeda (Chenopodiaceae)* in North America. Am J Bot 84:1198–1210

Gamaley YV (1985) The variations of the Kranz anatomy in Gobi and Karakum desert plants (in Russian). Bot Zh 70:1302–1314

Gamaley YV, Shirevdamba T (1988) The structure of plants of Trans-Altai Gobi. In: Gamaley YV, Gunin PD, Kamelin RV, Slemnev NN (eds) Deserts of Trans-Altai Gobi. Characteristics of dominant plants (in Russian). Nauka, Leningrad, pp 44–106

Gamaley YV, Glagoleva TA, Kolchesvski KG, Chlanovskaja MV (1992) Ecology and evolution of C_4-syndrome types in relation with phylogeny of families *Chenopodiaceae* and *Poaceae* (in Russian). Bot Zh 77:2–12

Glagoleva TA, Chulanovskaya AM, Pakhomova MV, Voznesenskaja EV, Gamaley YV (1992) Effect of salinity on structure of assimilating organs and ^{14}C labeling patterns in C_3 and C_4 plants of the Ararat plain. Photosynthetica 26:363–269

Grubov VI (1966) Plants of Central Asia (in Russian). Nauka, Leningrad

Grubov VI (1982) Key to the vascular plants of Mongolia (in Russian). Nauka, Leningrad

Grubov VI, Junatov AA (1952) Characteristic features of the flora of Mongolian People's Republic in relation to its zonation. (in Russian). Bot Zh 37:45–64

Gubanov IA (1996) Conspectus of flora of Outer Mongolia (vascular plants) (in Russian). Valang, Moscow

Hattersley PW (1983)The distribution of C_3 and C_4 grasses in Australia in relation to climate. Oecologia 57:113–128

Hattersley HA, Watson L (1992) Diversification of photosynthesis. In: Chapman GP (ed) Grass evolution and domestication. Cambridge University Press, Cambridge, pp 38–116

Iljin MM (1936) Chenopodiaceae Less. In: Komarov VL, Shishkin BK (eds) Flora of the USSR, vol VI, Centrospermae (English translation, 1970, by N. Landau). Israel Program for Scientific Translation, Jerusalem, pp 4–272

Kalapos T, Baloghne-Nyakas, Csontos P (1997) Occurrence and ecological characteristics of C_4 dicot and *Cyperaceae* species in the Hungarian flora. Photosynthetica 33:227–240

Kolchevskii KG, Kocharyan NI, Koroleva O (1995) Effect of salinity on photosynthetic characteristics and ion accumulation in C_3 and C_4 plants of Ararat plain. Photosynthetica 31: 277–282

Lavrenko EM (1962) The main features of botanical geography of deserts of Euroasia and North Africa (in Russian). Academy of Sciences of the USSR, Moscow Leningrad

Lavrenko EM, Nikolskaja NI (1963) Areas of some Central Asian and North Turanian desert plant species and questions about botanical-geographical frontier between Middle and Central Asia (in Russian). Bot Zh 48:1744–1761

Li M (1993) Distribution of C_3 and C_4 species of *Cyperus* in Europe. Photosynthetica 28:119–126

Mateu Andres I (1992) A revised list of the European C_4 plants. Photosynthetica 26:323–311

Oliver JE, Fairbridge RW (eds) (1987) The encyclopedia of climatology, vol XI. Van Nostrand Reinold, New York, NY

Pyankov VI (1993) C_4 species of high mountain desert of the Eastern Pamirs. Russ J Ecol 24:156–160

Pyankov VI, Mokronosov AT (1993) Basic tendencies in changes of the Earth's vegetation in relation to global warming of the climnate. Russ J Plant Physiol 40:443–458

Pyankov VI, Molotkovskii YI (1992) Species composition and ecological role of C_4 grasses in the arid zone of Central Asia. Sov J Ecol 23:144–151

Pyankov VI, Molotkovskii YI (1993) C_4 flora of Tiger Valley reserve, South Tadjikistan (in Russian). Proc Acad Sci Tadjikistan 35:38–43

Pyankov VI, Vakhrusheva DV (1989) The pathways of primary CO_2 fixation in *Chenopodiaceae* C_4-plants of Central Asian arid zone. Sov Plant Physiol 36:178–187

Pyankov VI, Vakhrusheva DV, Burundukova OL (1986) The photosynthetic pathway types in the hot desert of Central Karakum and its ecological importance (in Russian). Probl Desert Dev 2:45–54

Pyankov VI, Kuzmin AN, Demidov ED, Maslov AI (1992a) Diversity of biochemical pathways of CO_2 fixation in plants of the families *Poaceae* and *Chenopodiaceae* from arid zone of Central Asia. Sov Plant Physiol 39:411–420

Pyankov VI, Voznesenskaja EV, Kuzmin AN, Demidov ED, Vasiljev AA, Dzubenko OA (1992b) C_4-photosynthesis in alpine species of the Pamirs. Sov Plant Physiol 39:421–430

Pyankov VI, Voznesenskaja EV, Kondratschuk AV (1993a) Mountain saltwort *Salsola oreophila* (Chenopodiaceae) – a possible stage between C_4 and C_3 species. Dokl Bot Sci 332:71–75

Pyankov VI, Voznesenskaja EV, Kondratschuk AV (1993b) Structural and biochemical features of the photosynthetic

apparatus in the Pamir high mountain succulent species of the family Chenopodiaceae with different types of CO_2 fixation (in Russian). Tsitologia 39:30–38

Pyankov VI, Vakhrusheva DV, Seidova RD (1994) Structure of the assimilation apparatus of plants of the genus *Calligonum* in relation to ecological conditions and uses for phytoamelioration in the arid zone (in Russian). Probl Desert Dev 1:41–49

Pyankov VI, Voznesenskaja EV, Kondratschuk AV, Black CC (1997) A comparative anatomical and biochemical analysis in *Salsola* (Chenopodiaceae) species with and without a Kranz-type leaf anatomy: a possible reversion of C_3 to C_4 photosynthesis. Am J Bot 84:597–606

Pyankov VI, Black CC, Artusheva EG, Voznesenskaja EV, Ku MSB, Edwards GE (1999) Features of photosynthesis in *Haloxylon* species of Chenopodiaceae that are dominant plants in Central Asian deserts. Plan Cell Physiol 40:125–134

Redman RE, Yin L, Wang P (1995) Photosynthetic pathway types in grassland plant species from Northern China. Photosynthetica 31:251–255

Schulze E-D, Ellis R, Schulze W, Trimborn P (1996) Diversity, metabolic types and $\delta^{13}C$ carbon isotope ratios in the grass flora of Namibia in relation to growth form, precipitation and habitat conditions. Oecologia 106:352–369

Shomer-Ilan AS, Nissenbaum A, Waisel Y (1981) Photosynthetic pathways and the ecological distribution of the Chenopodiaceae in Israel. Oecologia 48:244–248

Soskov YD (1989) Genus *Calligonum* L. (systematics, geography and evolution) (in Russian). Doctor of biological sciences thesis dissertation. All-Union Institute of Plant Industry of N.I. Vavilov, Leningrad

Stowe LG, Teeri J (1978) The geographical distributionof C_4 species of the Dicotyledonae in relation to climate. Am Nat 112:609–623

Sveshnikova VM (1972) New approach on water regime of the Karakum desert plants. In: Rodin LE (ed) Eco-physiological foundation of ecosystems productivity in arid zone. Nauka, Leningrad, pp 53–57

Takeda T, Ueno O, Samejima M, Ontani T (1985) An investigation for the occurence of C_4 photosynthesis in the Cyperaceae from Australia. Bot Mag (Tokyo) 98:393–411

Teeri JA, Stowe LG (1976) Climatic patterns and the distribution of C_4 grasses in North America. Oecologia 23:1–12

Teeri JA, Stowe LG, Livingstone DA (1980) The distribution of C_4-species of Cyperaceae in North America. Oecologia 47: 307–310

Tieszen LL, Senyimba MM, Imbamba SK, Troughton JH (1979) The distribution of C_4 grasses and carbon isotope discrimination along an altitudinal and moisture gradient in Kenya. Oecologia 37:338–350

Tsvelev NN (1987) The system of grasses (Poaceae) and their evolution (37th Komarov lecture) (in Russian). Nauka, Leningrad

Ueno O, Takeda T (1992) Photosynthetic pathways, ecological characteristics, and the geographical distribution of the Cyperaceae in Japan. Oecologia 89:195–3

Ueno O, Takeda T, Murata T (1986) C_4 acid decarboxylating enzyme activities of C4 species possesing different Kranz anatomical types in the Cyperaceae. Photosynthetica 20:111–116

Vogel JC, Fuls A, Ellis RP (1978) The geographical distribution of Kranz-grasses in South Africa. S Afr J Sci 74:209–215

Vogel JC, Fuls A, Danin A (1986) Geographical and environmental distribution of C_3 and C_4 grasses in the Sinai, Negev, and Judean deserts. Oecologia 70:258–265

Vostokova EA, Gunin PD, Rachkovskaja EI, et al. (1995) Ecosystems of Mongolia (in Russian). Nauka, Moscow

Voznesenskaja EV, Gamaley YV (1986) The ultrastuctural characteristics of leaf types with Kranz anatomy (in Russian). Bot Zh 71:1291–1307

Voznesensky VL (1977) Photosynthesis of desert plants of Karakum desert (in Russian). Nauka, Leningrad

Winter K (1981) C4 plants of high biomass in arid regions of Asia: occurrence of C_4 photosynthesis in Chenopodiaceae and Polygonaceae from the Middle East and USSR. Oecologia 48: 100–106

Zalenskii OV, Glagoleva TA (1981) Pathway of carbon metabolism in halophytic desert species from Chenopodiaceae. Photosynthetica 15:244–255

Ziegler H, Batanouny KH, Sankhla N, Vyas OP, Stichler W (1981) The photosynthetic pathway types of some desert plants from India, Saudi Arabia, Egypt, and Iraq. Oecologia 48:93–99