PHOTOSYNTHETICA 42 (3): 339-344, 2004

Photosynthetic pathway types in rangeland plant species from Inner Mongolia, North China

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Abstract

Photosynthetic pathway types, based on $\delta^{13}C$ measurements, were determined for 125 species in 95 genera and 32 families growing in rangelands from Inner Mongolia. Of the total species, 4 species from 3 genera and 2 families had C_4 photosynthesis (2 species in *Gramineae* and 2 in *Chenopodiaceae*) and 118 species from 90 genera and 31 families had C_3 photosynthesis. The number of C_4 species differed significantly among four rangeland sites, 4 species in desert, 3 species in steppe, but no C_4 species were identified in meadow and dune. Six species [*e.g. Agriophyllum arenarium* Bieb., *Bassia dasyphylla* O. Kuntze, *Saussurea japonica* (Thunb.) DC.] earlier identified as C_4 species using the enzyme ratio method were found as C_3 species using the carbon isotope ratios ($\delta^{13}C$). Hence the enzyme ratio method for C_3 and C_4 identification may not always be reliable. The $\delta^{13}C$ values of 3 species of *Crassulaceae*, which had been considered as CAM species, differed remarkably [–25.79 ‰ for *Sedum aizoon* L., –24.42 ‰ for *Osostachys fimbriatus* (Turcz.) Berger, and –16.97 ‰ for *O. malacophyllus* (Pall.) Fisch], suggesting that the use of $\delta^{13}C$ method as a diagnosis for CAM photosynthetic pathway type may not always be reliable and supplementary measurements are needed.

Additional key words: C_3, C_4, and CAM plants; carbon isotope ratio; Xilingol steppe; $\delta^{13}C$.

Introduction

Photosynthetic pathway type is not only the basis for studying plant functional types, but also relates with ecological processes, *e.g.* community succession, climate changes (Collatz *et al*. 1998, Wang 2003d), as well as bridges the micro-ecology and macro-ecology. C_4 plant identification began with the works of Downton and Tregunna (1968) and Black (1971), and more than 1 700 C_4 plants have been identified worldwide (Li 1993). It is expected that approximately one-half of the 10 000 grass species and a thousand of the 165 000 *Dicotyledoneae* in the world have C_4 photosynthetic pathway (Hattersley 1987, Ehleringer *et al*. 1997) indicating that only 1/3 of the C_4 species was identified and the other 2/3 remains unclear. Various methods, *e.g.* carbon isotope ratio ($\delta^{13}C$), "Kranz" type leaf anatomy, low CO_2 compensation concentration, and photosynthetic enzyme ratio, have been used for photosynthetic pathways classification, but many studies suggested that the carbon isotope ratio method is most reliable (Redmann *et al*. 1995).

Desert and steppe are two typical rangeland vegetations in Inner Mongolia, North China. Superior both in quality and quantity of herbage production in the usual growing condition of the rangelands make them best suited for livestock grazing. Many studies of local flora, community classification, plant biomass, and photosynthetic pathways have been conducted in the region, but systematic research on identification of C_3, C_4, and CAM species by using carbon isotope ratio in the rangelands has not been done. Photosynthetic pathways are important linkages between plant species and ecosystems, and rangeland management decisions must take into account their knowledge which is closely related to seasonal development patterns (warm season *versus* cool season).

The objective of this study was to determine C_3 and C_4 photosynthetic pathways from rangelands in Inner Mongolia by using carbon isotope ratio and to uncover the relationship between pathway type and plant habitats.

Received 26 April 2004, *accepted* 2 June 2004.
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Acknowledgments: We are grateful for the fund provided by National Key Basic Research Special Foundation Project (NKBRSF project G2000018607) and in part by Key Projects of Knowledge Innovation of the Chinese Academy of Sciences (KSCX2-SW-107).

The results may help in studying the correlation of rangeland species composition with ecosystem, climate variables, and grazing management.

Materials and methods

The study was conducted in typical desert and steppe vegetations in Xilingol rangelands (41°35′–46°46′N, 111°09′–119°58′E), which is part of Mongolian plateau, and covers about 200 000 km^2 area, with average 1 200 m above sea level, varying from 900 m in the north-east to 1 300 m in the south-west. Most of the rangelands have chestnut, chernozem, and sandy soils. Located in semi-arid area of mid-temperate zone, the rangelands have the characteristics of temperate steppe climate, with air temperature and precipitation varying sharply all round the year. Mongolia anticyclone and moist Pacific air mass are the two major factors determining the climate type in this region. The sharp gradient between the high-pressure and Aleutian low-pressure system bring a strong westerly flow of cold, dry continental air at the surface. As the anticyclone breaks down in spring, the rangeland region comes increasingly under the influence of moist Pacific air mass, reaching a climax in the summer monsoon, which lasts 2–3 months. The typical climate characteristics of the region are: cold dry and frequently windy spring; warm and wet summer, but with possible seasonal droughts, early autumn frosts, and long cold winter with less snowfall. The mean annual air temperature ranges from 0 to 3 °C, varying from –21 °C in January to 21 °C in July. Moisture gradient is very steep, with annual precipitation varying from 100 mm in the western desert to 400 mm in the eastern meadow. Precipitation mainly falls between June and August over the growing season.

Four types of sites, *e.g.* meadow, steppe, desert, and dune, were selected for the plant sampling. Shoot tissue was collected from field-grown plants, dried at 80 °C for 48 h, and ground. Stable carbon isotope ratio ($\delta^{13}C$) in the plant tissue was determined by using *Delta^{plus} XP* mass spectrograph. Plants with $\delta^{13}C$ values above –19 ‰ were considered to have C_4 photosynthetic pathway, and with $\delta^{13}C$ values less than –21 ‰ to have C_3 photosynthesis (Smith and Brown 1973) (Table 1).

Table 1. Photosynthetic pathway types (C_3, C_4) in species from rangelands of Inner Mongolia, North China. Nomenclature follows Redmann *et al.* (1995). Habitats; ME = meadow, TS = typical steppe, DS = desert and DU = dune.

	Species	$\delta^{13}C$ [‰]	C_3/C_4	Habitat
Gymnospermae				
Ephedraceae	*Ephedra sinica* Stapf	–24.449	C_3	DS
Angiospermae				
Dicotyledoneae				
Asclepiadaceae	*Cynanchum thesioides* (Freyn) K. Schum.	–25.167	C_3	DS
Boraginaceae	*Lappula redowskii* (Horn) Green	–28.594	C_3	TS
Campanulaceae	*Adenophora stenanthina* (Ledeb.) Kitag.	–26.560	C_3	ME
Caryophyllaceae	*Dianthus chinensis* L.	–25.734	C_3	ME
	Silene repens Patr.	–25.765	C_3	ME
Chenopodiaceae	*Agriophyllum arenarium* Bieb.	–25.340	C_3	DU
	Axyris amarantoides L.	–26.691	C_3	TS
	Bassia dasyphylla O. Kuntze	–25.113	C_3	DS
	Chenopodium aristatum L.	–26.148	C_3	TS
	Ch. glaucum L.	–27.213	C_3	TS
	Corispermum declinatum Steph. *ex* Stev.	–26.841	C_3	DU
	Kochia prostrata (L.) Schrad.	–14.036	C_4	TS DS
	Salsola collina Pall.	–11.400	C_4	TS DS
Compositeae	*Artemisia annua* L.	–27.306	C_3	ME
	A. dracunculus L.	–26.941	C_3	ME
	A. eriopoda Bunge	–27.669	C_3	ME
	A. frigida Willd.	–28.125	C_3	TS DS ME
	A. intramongolica H.C. Fu.	–25.840	C_3	DU
	A. oxycephala Kitag.	–25.783	C_3	DU
	A. pectinata Pall. [*Neopallasia pectinata* (Pall.) Polsak.]	–24.204	C_3	DS
	A. scoparia Waldst *et* Kit	–27.869	C_3	DS
	Aster alpinus L.	–28.003	C_3	ME

Table 1 (continued)

	Species	$\delta^{13}C$ [‰]	C_3/C_4	Habitat
Compositeae	*Filifolium sibiricum* (L.) Kitam.	–26.835	C_3	ME
	Heteropappus altaicus (Willd.) Novopokr.	–26.895	C_3	DS
	Hieracium umbellatum L.	–27.424	C3	ME
	Ixeris chinensis (Thunb.) *Nakaisubsp graminifolia* (Ledeb.) Kitag.	–26.835	C_3	DU
	Ligularia mongolica (Turcz) DC.	–26.900	C_3	ME
	Olgaea leucophylla (Turcz.) Iijin	–27.205	C_3	TS ME
	Saussurea japonica (Thunb.) DC.	–27.258	C_3	TS ME
	Scorzonera austriaca Willd.	–25.373	C_3	ME
	Serratula coronata L.	–28.079	C_3	TS ME
	Stemmacantha uniflora (L.) Dittrich	–27.720	C_3	ME
	Youngia tenuifolia (Willd.) Babc.	–23.829	C_3	DS
Convolvulaceae	*Convolvulus ammannii* Desr.	–25.271	C_3	DS
	C. arvensis L.	–25.271	C_3	DS
Crassulaceae	*Osostachys fimbriatus* (Turcz.) Berger	–24.420	C_3	ME
	O. alacophyllus (Pall.) Fisch	–16.965	C_4	TS DU
	Sedum aizoon L.	–25.788	C_3	ME
Cruciferae	*Dontostemon micranthus* C.A. Mey.	–25.534	C_3	TS
	Lepidium apetalum Willd.	–25.478	C_3	TS
	Ptilotrichum tenuifolium (Steoh) C.A. Mey.	–26.524	C_3	TS
Dipsacaceae	*Scabiosa comosa* Fisch. *ex* Roemer Schult	–26.600	C_3	DU
	S. tschiliensis Crrunning	–27.039	C_3	ME
Labiatae	*Lagochilus ilicifolius* Bungein	–25.895	C_3	DS
	Phlomis tuberosa L.	–25.942	C_3	TS
	Schizonepeta multifida (L.) Briq.	–27.520	C_3	TS ME
	Scutellaria baicalensis Georgi	–26.989	C_3	ME
	S. scordifolia Fisch. *ex* Schrank	–27.544	C_3	DU
Leguminosae	*Astragalus melilotoides* Pall.	–26.466	C_3	ME
	Caragana microphylla Lam.	–24.483	C_3	TS
	C. stenophylla Pojark.	–24.572	C_3	DS
	Hedysarum fruticosum Pall. var. *lignosum* (Trautv.) Kitag.	–27.416	C_3	DU
	Medicago falcate L.	–27.096	C_3	ME
	Melilotoides ruthenia (L.) Sojak	–26.956	C_3	DU
	Oxytropis myriophylla (Pall.) DC.	–27.481	C_3	ME
	Thermopsis lanceolata R. Br.	–25.873	C_3	TS ME
	Trifolium lupinaster L.	–25.314	C_3	ME
	Vicia multicaulis Ldb.	–25.629	C_3	ME
	V. unijuga R. Br.	–24.735	C_3	ME
Linaceae	*Linum perenne* L.	–25.604	C_3	TS
Urticaceae	*Urtica cannabina* L.	–26.725	C_3	DU
Papaveraceae	*Papaver nudicaule* L.	–28.050	C_3	DU
Plumbaginaceae	*Limonium bicolor* (Bunge) Q. Kuntze	–30.125	C_3	TS
Polygonaceae	*Polygonum divaricatum* L.	–26.855	C_3	TS ME DU
	Polygonum viviparum L.	–27.345	C_3	SS
	Rheum undulatum L.	–28.628	C_3	ME
Ranunculaceae	*Clematis hexapetala* Pall.	–24.343	C_3	ME
	Pulsatilla turczaninovii Kryl. *et* Serg.	–26.770	C_3	ME
	Thalictrum petaloideum L.	–27.685	C_3	TS ME
	Th. squarrosum Steh. *ex* Willd.	–26.134	C_3	ME
	Delphinium grandiflorum L.	25.878	C_3	ME
Rosaceae	*Prunus sibirica* L.	–25.360	C_3	DU
	Potentilla acaulis L.	–27.263	C_3	TS ME
	P. betonicaefolia Poir	–25.330	C_3	ME
	P. bifurca L.	–25.565	C_3	ME TS

Table 1 (continued)

	Species	$\delta^{13}C$ [‰]	C_3/C_4	Habitat
Rosaceae	*P. nudicaulis* Willd.	–26.201	C_3	ME
	P. tanacetifolia Willd. *ex* Schlecht	–26.852	C_3	ME TS
	P. verticillaris Steph. *ex* Willd.	–26.609	C3	ME
	Sanguisorba officinalis L.	–26.758	C_3	ME
	Spiraea aquilegifolia Pall.	–27.571	C_3	TS ME ME
Rubiaceae	*Galium verum* L.	–25.810	C_3	TS ME
Rutaceae	*Haplophyllum dauricum* (L.) Juss.	–27.040	C_3	TS DS
Saxifragaceae	*Ribes diacanthum* Pall.	–27.934	C_3	DU
Scrophulariaceae	*Cymbarria dahurica* L.	–27.768	C_3	TS ME
	Linaria vulgaris Mill.	–27.748	C_3	ME
	Pedicularis striata Pall.	–27.771	C_3	ME
	Veronica linariifolia Pall. *ex* Link	–27.124	C_3	ME
Thymelaceae	*Stellera chamaejasme* L.	–25.780	C_3	ME
Umbelliferae	*Bupleurum scorzonerifolium* Willd.	–25.800	C_3	ME TS
	Peucedanum rigidium Bunge	–24.595	C_3	DS DU
	Siler divaricatum Benth. *et* Hook.	–26.620	C_3	DS ME
	Sphallerocarpus gracilis (Bess.) K. Pol.	–23.913	C_3	ME
Valerianaceae	*Patrinia rupestris* Juss.	–26.144	C_3	ME
Zygophyllaceae	*Peganum harmala* L.	–23.361	C_3	DS
Monocotyledoneae				
Cyperaceae	*Carex duriuscula* C.A. Mey.	–24.354	C_3	TS
	C. pediformis C.A. Mey.	–25.257	C_3	ME
	C. korshinskyi Kom.	–25.831	C_3	TS
Gramineae	*Achnatherum sibiricum* (L.) Keng	–25.731	C_3	ME
	Agropyron cristatum (L.) Gaertn.	–27.157	C_3	TS DS ME
	Bromus inermis Leyss.	–24.882	C_3	ME
	Cleistogenes squarrosa (Trin.) Keng	–14.639	C_4	TS
	C. songorica (Roshev.) Ohwi	–14.757	C_4	DS
	Elymus dahuricus Turcz.	–25.145	C_3	ME
	Festuca rubra L.	–27.089	C_3	ME
	Koeleria cristata (L.) Pers.	–26.347	C3	ME
	Leymus chinensis (Trin.) Tzvel.	–26.008	C_3	TS ME
	Poa pratensis L.	–24.635	C_3	ME
	Psammochloa villosa (Trin.) Bor	–28.118	C_3	DU
	Stipa baicalensis Roshev.	–25.920	C_3	ME
	S. grandis P. Smirn.	–26.541	C_3	TS
	S. krylovii Roshev.	–25.285	C_3	DS
*Iridacea*e	*Iris dichotoma* Pall.	–24.938	C_3	ME
	I. lacteal Pall. var. *chinensis* (Fisch) Koidz.	–25.844	C_3	DS
	I. tenuifolia Pall.	–26.233	C_3	DU
	I. ventricosa Pall.	–26.078	C_3	ME
Liliaceae	*Allium bidentatum* Fisch. *ex* Prokh.	–25.140	C_3	DS
	A. polyrhizum Turcz.	–25.805	C_3	DS
	A. ramosum L.	–25.562	C_3	DS TS
	A. senescens L.	–25.179	C_3	DU
	A. tenuissimum L.	–26.089	C_3	DS
	Anemarrhena asphodeloides Bunge	–24.620	C_3	TS
	Asparagus dauricus Fisch. *ex* Link	–24.719	C_3	DS
	Hemerocallis minor Mill.	–25.811	C_3	ME
	Veratrum nigrum L.	–23.762	C_3	ME

Results

125 vascular plant species in 95 genera and 32 families, about 20 % of the total species in Xilingol rangelands, were examined for photosynthetic pathway types. Carbon isotope ratios indicative of C_4 photosynthesis were found in 4 species from 3 genera and 2 families, 2 were found in *Gramineae* [*Cleistogenes squarrosa* (Trin.) Keng and *C. songorica* (Roshev.) Ohwi] and the other two in *Chenopodiaceae* [*Kochia prostrata* (L.) Schrad. and *Salsola collina* Pall.]. 118 species from 90 genera and 31 families had C_3 photosynthesis. This suggested that the abundance of C_4 plants in these sample sites was very low, even the occurrence of C_4 species in the desert and steppe was common. Three species, *i.e. Osostachys fimbriatus* (Turcz.) Berger, *O. malacophyllus* (Pall.) Fisch, and *Sedum aizoon* L. in *Crassulaceae* had been considered as CAM photosynthesis, but their $\delta^{13}C$ values varied remarkably: –25.79 ‰ for *Sedum aizoon* L. and –24.42 ‰ for *O. fimbriatus* (Turcz.) Berger, while that for *O. malacophyllus* (Pall.) Fisch was –16.97 ‰. Thus the identification of CAM photosynthetic pathway may need other supplementary measurements.

According to the literature, the photosynthetic pathways of more than 50 % of the total 125 species in Table 1, *e.g. Ephedra sinica* Stapf., *Corispermum declinatum* Steph. *ex* Stev., *Stemmacantha uniflora* (L.) Dittrich, *Scabiosa comosa* Fisch. *ex* Roemer Schult, were identified for the first time (Table 1). The following species, with C_3 carbon isotope ratios, had earlier been identified as C_4 based on phosphoenolpyruvate carboxylase : ribulose-1,5-bisphosphate carboxylase ratios (Yin and Li 1997, Wang 2002a,c): *Agriophyllum arenarium* Bieb., *Bassia dasyphylla* O. Kuntze, *Saussurea japonica* (Thunb.) DC., *Thalictrum squarrosum* Steh. *ex* Willd., *Thermopsis lanceolata* R.Br., and *Carex pediformis* C.A. Mey. This suggests that the use of the enzyme ratio method as diagnosis for photosynthetic pathway type may not always be reliable and some previous results need to be corrected.

As for floristic composition of the total 125 species, 1 C_3 species was found in *Gymnospermae*, 124 species in *Angiospermae*, 94 species (about 25 % of the total *Dicotyledoneae* species in Xilingol rangelands) in 74 genera and 27 families were found in *Dicotyledoneae*, *e.g. Compostitae* (20 species) *Leguminosae* (11 species), *Rosaceae* (9 species), and *Chenopodiaceae* (8 species), and they were the leading families with 48 species identified (about 51 % of the total 94 species in *Dicotyledoneae*). The other 23 families had a total of 46 species, less than 50 % of the total *Dicotyledoneae* species. 30 species in 19 genera and 4 families were identified in *Monocotyledoneae*, *e.g. Gramineae* (14 species), *Liliaceae* (9 species), *Iridaceae* (4 species), and *Cyperaceae* (3 species). These 30 species make up 16 % of the total *Monocotyledoneae* species in this region, indicating that the species abundance of *Monocotyledoneae* was smaller than that of *Dicotyledoneae*.

Four C_4 species were found in desert site and 3 in steppe site, but no C_4 species was identified in meadow and dune sites. The value of C_4/C_3 in desert site was two times that in the steppe site. This suggests that the occurrence of C_4 species was common in the more arid region. Meadow site had most species abundance, with 67 species (about 54 % of the total 125), in, *e.g.*, *Compositeae* (12 species), *Gramineae* (8 species), *Legaminosae* (7 species), and *Rosaceae* (6 species). However, only 36 species (about 29 %) and 26 species (21 %) were found in steppe and desert sites, respectively.

Discussion

The identification of photosynthetic pathway types is the basic knowledge for studying the logical linkages between physiological and life-history strategies at plant level, and ecological process at ecosystem and global levels. The $\delta^{13}C$ value of plant tissue is diagnostic for photosynthetic pathways (Smith and Brown 1973) and is widely used as a criterion for C_3 and C_4 classification (Downton 1975, Li 1993, Redmann *et al*. 1995, Pyankov *et al*. 2000). 125 species from four sites were classified to their types of photosynthesis (Table 1): only 4 species were found with C_4 photosynthesis, while most species had C_3 photosynthesis. Relatively low amount of C_4 species identified in this study was mainly due to the small scale of sampling area (about 1 km^2) and species abundance in the four sites, as well as the reduction of C_4 species which had earlier been identified as C_4 species, *e.g. Agriophyllum arenarium* Bieb., *Bassia dasyphylla* O. Kuntze, *Saussurea japonica* (Thunb.) DC., *Thalictrum squarrosum* Steh. *ex* Willd., *Thermopsis lanceolata* R.Br., and *Carex pediformis* C.A. Mey. This suggests that the use of stable carbon isotope ratio ($\delta^{13}C$) was more reliable for C_3 and C_4 identification and some of the previous classifications by using the enzyme, "Kranz" type leaf anatomy, and low CO_2 compensation concentration need to be modified.

Of the total 125 species, $\delta^{13}C$ values of 3 *Crassulaceae* species, which had been classified as CAM species (Wang 2002a), were remarkably different (Table 1). The $\delta^{13}C$ values for *Osostachys fimbriatus* (Turcz.) Berger and *Sedum aizoon* L. were less than –24.42 ‰, while that for *O. malacophyllus* (Pall.) Fisch was 16.97 ‰. We can not classify the 3 species into their photosynthetic pathway types by using the $\delta^{13}C$ values, and supplementary measurements, *e.g.* leaf acidometric titration in the morning and in the dusk (Lin *et al*. 1988) should be taken. This suggests that the use of carbon isotope ratio ($\delta^{13}C$)

method as diagnosis for CAM photosynthetic pathway type may not always be reliable and supplementary measurements are needed.

The changes of plant photosynthetic pathway composition are consistent with vegetation dynamics caused by nature and human activities, especially in grassland and deserts (Wang 2002a). Four C_4 species were found in desert site, 3 in steppe site, and no C_4 species was identified in meadow and dune sites. Of the 4 C_4 species identified in Table 1, two were xerophytic grass species [*Cleistogenes squarrosa* (Trin.) Keng and *C. songorica* (Roshev.) Ohwi] and the other two belonged to annual *Chenopodiaceae* [*Kochia prostrata* (L.) Schrad. and *Salsola collina* Pall.]; this suggests that these species had greater tolerance to drought. Previous studies (Williams and Markley 1973, Wang 2002a,b,c) also clearly documented the importance of photosynthetic pathway types in predicting vegetation dynamics and the occurrence of C_4 species could be an indicator for both diagnosis of grassland conditions and management decisions. Future studies in North China could evaluate the responses of photosynthetic pathways to land use managements.

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