Environmental Adaptations of the Gobi Desert Plants in Mongolia: An Example of C4-plants

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Abstract

This paper presents the results of our studies on the ecological adaptations and geographical distribution of plants with C4-photosynthesis in Mongolia using ^{13}C isotope discrimination.

Previous studies identified about 80 C4-species in 8 families in the Mongolian flora. Our investigations lead to the identification of four additional species, which can be regarded as C4-plants. *Orostachys spinosa* (-16.26 ‰ ^{13}C), *O. thyrsiflora* (-16.86 ‰ ^{13}C), *O. fimbriata* (-16.15 ‰ ^{13}C), and *Euphorbia humifusa* (-23.29 ‰ ^{13}C). However, as the discrimination level for *Euphorbia humifusa* is very similar to that of C3-plants it may be switching between C3 and C4 types of photosynthesis according to the environmental conditions.

C4-plants become more important in the Mongolian vegetation along a gradient of decreasing precipitation and increasing temperature from northern Mongolia to southern Mongolia. Along this gradient also soil salinity increases, vegetation cover decreases, and the relief changes from mountains to hilly steppes and finally to the relatively flat Gobi desert. The decreasing importance of C4-plants towards southern Mongolia is also reflected in the ^{13}C-levels from herbivores.

Keywords C4-photosynthesis, vegetation, Mongolia, environmental adaptations

Introduction

The main objectives of our studies in 2000–2003 were to identify plants with C4-photosynthesis in Mongolia, and to study their ecological adaptations and geographical distribution. The C3- and C4-types of photosynthesis are two of three main photosynthetic pathways found in plants (the other one is CAM, see table 1).

Further adaptations of C4-plants compared to C3-plants include:

- efficient use of enzymes
- higher leaf area
- efficient use of water and nitrogen
- adaption to higher levels of ambient CO_2

The rapid expansion of C4-plants in both the old world and the new world started 7 to 5 million years ago in the middle Miocene. Today C4-plants form a significant component of the vegetation, primarily in tropical savannas, temperate grasslands and semi desert shrub lands (Cerling et al., 1993). However, overall C4 plants are very limited in the world's flora (5 %) and were found in only 20 families of vascular plants, out of which 14 families occur in the Mongolian flora.

Methods

The mode of carbon fixation was determined using ^{13}C isotope discrimination. The atmospheric CO_2 contains the naturally occurring carbon isotopes ^{12}C (98.9 %), ^{13}C (1.1 %), and ^{14}C (10–10 %). The two carboxylating enzymes discriminate differently between the isotopes leading to different and characteristic isotope compositions in C3- and C4-plants. C3-plants have a δ^{13}C of about -28 ‰ (-23 to -35 ‰) and C4-plants have a δ^{13}C of about -13 ‰ (-10 to -14 ‰; Taiz & Zeiger, 1998).

Results & Discussion

In the Mongolian language the term 'Gobi' refers mainly to desert and desert steppe vegetation. These vegetation types are dominated by dwarf shrubs and semi-shrubs, most of which belong to the families Chenopodiaceae, Asteraceae, Polygonaceae, Zygophyllaceae, Tamaricaceae, Leguminosae, Rosaceae, and Convolvulaceae (Hilbig, 1995).

Among these dwarf shrubs and semi shrubs, C4-species were found only in the 2 families namely Chenopodiaceae and Polygonaceae. More specifically, C4-plants occurred in the following genera. *Anabasis* (7 species), *Haloxylon* (1), *Ijinia* (1), *Kochia* (5), *Nanophyton* (2), *Salsola* (3) and *Calligonum* (6).

Previous studies identified about 80 C4-species in 8 families including all the mentioned desert shrubs and semi shrubs. This has to be compared to a total of 2823 species of vascular plants in the Mongolian flora (Gubanov, 1996). Most C4-species belong to the families Chenopodiaceae, Poaceae, and Polygonaceae, which account for about 90 % of the total number of C4-species in Mongolia (Pyankov et al., 2000).

Subsequently, we performed further studies on C4-taxa in Mongolia (Black et al., 2001; Tsendeekhuu et al., 2002; Tsendeekhuu, 2003). Our investigations lead to the identification of four additional species, which could be regarded as C4-plants due to their carbon isotope discrimination levels listed in table 2.

However, as the discrimination level for *Euphorbia humifusa* is very similar to that of C3-plants ($\delta^{13}C$ -26.3, Pyankov 2000), we think that *E. humifusa* may be an intermediate species switching between C3 and C4 types of photosynthesis according to the environmental conditions. The C4 syndrome in *E. humifusa* was reported from Mongolia before by Voznesenskaja & Gamaley (1986). Currently, about 15 species with an intermediate C3–C4-type are known (Pyankov et al., 2002).

Thus, adding the 4 species identified by our work, 84 C4-species among 9 families of vascular plants are presently identified in the Mongolian flora (see table 3). Within the genus *Salsola* most species show Salsoloid leaf anatomy, and the Kranz type of bundle sheath cells with C4-photosynthesis. *Salsola* is a striking example showing the evolutionary convergence of morphological and chemical traits. The large variety of *Salsola* species in Asia strongly indicates

Table 1: Distinguishing characteristics of two photosynthetic groups of higher plants (Solisbury, 1992; Black et al., 2002)

Attribute	C3 plants	C4 plants
Carboxylating enzyme	Rubisco	PEP carboxylase, rubisco
Theoretical energy requirement (CO_2, ATP, NADPH)	1:3:2	1:5:2
Kranz anatomy	No distinct bundle sheath	Well organized bundle sheath
Photosynthetic rate (mg $CO_2 \cdot dm^{-2} \cdot h^{-1}$)	15–35	40–80
Dry matter production t/ha*yr	22 ± 0.3	39 ± 17
Optimal photosynthesis temperature	15–20 °C	30–35 °C
Light saturation	40% of full sun	Full sun
Transpiration	500 g H_2O/g (dry)	200–400 g H_2O/g (dry)
CO_2 compensation point	30–70 μl/l	10 μl/l
Photorespiration	Yes	Only in bundle sheath

Table 3: Overview over the C4 plants known in Mongolia. [1)] *Euphorbia humifusa* possibly is a facultative C4 species. [2)] The Crassulaceae of the genus *Orostachys* are probably not C4-plants in the strict sense as there is strong evidence of CAM metabolism in these species (see Oyungerel & Black, 2005)

Families	Total	C4 species	Dominant genera
Amaranthaceae	4	4	–
Chenopodiaceae	91	41	*Salsola* (9 species)
Euphorbiaceae	15	2[1)]	–
Molluginaceae	1	1	–
Polygonaceae	67	6	*Calligonum* (6)
Portulaceae	2	1	–
Zygophyllaceae	13	1	–
Crassulaceae	17	3[2)]	–
Poaceae	250	25	*Cleistogenes* (5)

that the genus originated in Asia and later migrated to southern Africa (Pyankov et al., 2002). The dominance of C4 chenopods over grasses in the Central Asian continental deserts is related to their high resistance to drought.

Calligonum is the only genus in the family of Polygonaceae that contains only C4 species. These species occur mainly in the Gobi desert and are a major component of the natural vegetation in Mongolia. Together with another C4-species *Haloxylon ammodendron* they build up the most important vegetation association in the desert, the *Calligono mongolici-Haloxyletum ammodendronis* (Hilbig, 1995).

Table 2: Carbon isotope discrimination levels for four species native to Mongolia, indicating C4 photosynthetic pathway.

Species	δ^{13}C levels
Orostachys spinosa	-16.26 ‰
O. thyrsiflora	-16.86 ‰
O. fimbriata	-16.15 ‰
Euphorbia humifusa	-23.29 ‰

Species from the genera *Cleistogenes, Stipa, Koeleria, Agropyron, Elymus, Poa,* and *Festuca* dominate in the pastures of different ecological zones in Mongolia, particularly in the alpine grassland, in the central steppe, and in the desert steppes of the Gobi. Out of these, only the 5 species of *Cleistogenes* show a C4 photosynthetic pathway. These species are important forage for livestock, and proved to be more productive than other bunch grasses in an experimental study (Tsendeekhuu et al., 2003).

Following a gradient of decreasing precipitation and increasing temperature from northern Mongolia to southern Mongolia, C4-plants become more important in the vegetation. Along this gradient also soil salinity increases, vegetation cover decreases, and the relief changes from mountains to hilly steppes and finally to the relatively flat Gobi desert. Although the proportion of C4-species generally increases towards southern Mongolia, grasses and chenopods differ in their responses (see table 4).

Apart from the vegetation samples we also collected material from insects and bones of herbivorous animals because the carbon ^{13}C fractionation of their diet is reflected in the fractionation within their body tissue. Indeed, the animals' tissue also showed a trend of increasing proportions of C4-species in the vegetation towards the south (table 5).

In a global comparison, the desert vegetation of Central Asia has a unique taxonomic composition (figure 1). One unusual finding is the large diversity and the high importance of perennial species of the Chenopodiaceae family in the Central Asian vegetation (Pyankov et al., 2000;

Table 4: Proportion of C4-species in the regional vegetation along a north-south transect through Mongolia. Proportions of 15 % or higher are marked bold.

Region	% of C4 species from total	
	Chenopodiaceae	Poaceae
Khövsgöl	1.3 %	1.2 %
Khentiy	5.0 %	8.3 %
Khangay	13.8 %	7.1 %
Mongol Daurian	10.0 %	10.4 %
Great Hinggan	3.8 %	9.6 %
Khovd	**15.0** %	5.8 %
Mongolian Altay	**18.8** %	6.4 %
Middle Khalkha	12.5 %	11.3 %
East Mongolia	11.3 %	14.9 %
Depression of the Great Lakes	**31.3** %	**16.3** %
Valley of Lakes	**22.5** %	**20.8** %
East Gobi	**18.8** %	**31.5** %
Gobi Altay	**21.8** %	12.8 %
Dzungarian Gobi	**38.8** %	12.9 %
Trans-Altay Gobi	**20.0** %	**31.3** %
Alashan Gobi	12.2 %	**42.9** %

Table 5: $\delta^{13}C$ values for different material from insects and large herbivores in different ecological zones: a) Ulaanbaatar site, b) Bulgan sum mountain steppe, c) dry steppe site.

site	material	$\delta^{13}C$	material	$\delta^{13}C$
a	grasshopper	25.1 ‰	cattle jaw bone	20.7 ‰
a	grasshopper	25.7 ‰	cattle rib bone	22.5 ‰
b	grasshopper	22.2 ‰	sheep jaw bone	18.4 ‰
b	grasshopper	22.2 ‰	sheep teeth	18.7 ‰
b	grasshopper	24.7 ‰		
c	grasshopper	19.4 ‰	cattle tooth	19.4 ‰
c	grasshopper	19.5 ‰	sheep rib	18.2 ‰
c	grasshopper	23.3 ‰	unknown rib	19.1 ‰

Gunin et al., 1999; Black et al., 2001, 2003). In contrast to this, grass species (Poaceae) dominate in North America, Australia, and Europe. Thus, C4 grasses and C4 chenopods appear to have a different origin and global distribution.

Conclusion

- The proportion of C4 species in the total Mongolian flora is about 3.6 %, reaching a maximum in the Gobi deserts with 14.4 % of C4-species, which is comparable to Turanian deserts where about 15–17 % of the species are C4-plants (Pyankov et al., 1993). At present, 84 species within 9 families of the vascular plants have been found to show C4-photosynthesis. However, three of these species belong to the genus *Orostachys* and are most probably CAM plants rather than true C4-plants (see Oyungerel & Black, 2005).

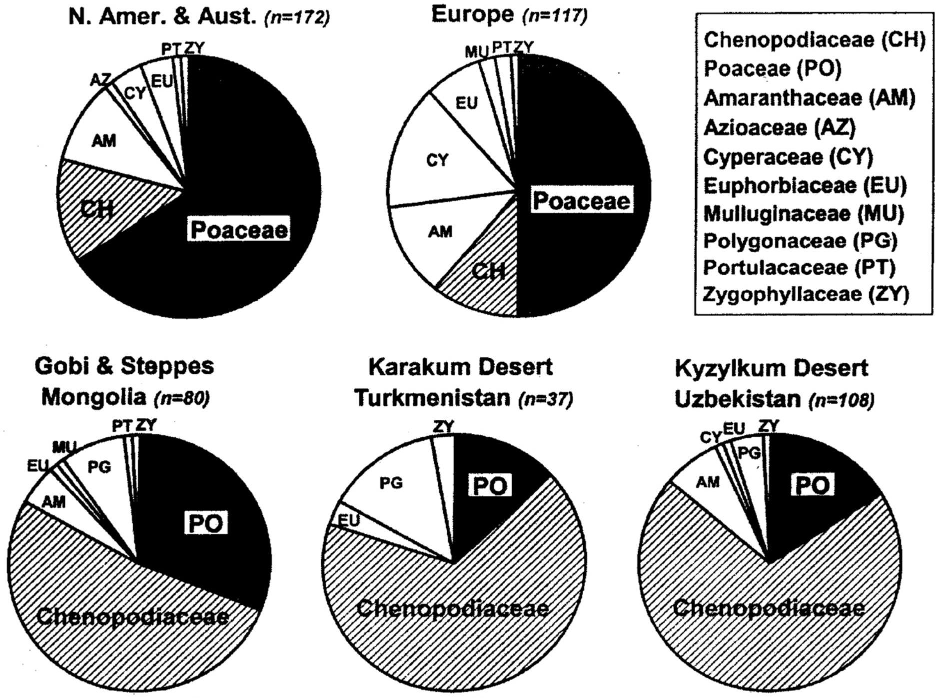

Figure 1: A global comparison of C4-photosynthesis taxonomic diversity versus C4 plant diversity in Central Asian deserts.

- It is speculated that changes in the Mongolian vegetation could be an important early indicator of global changes in the 3rd millennium (Smith et al., 1997). However, this seems unlikely for the following reasons: C4 plants are known to respond to increased levels of CO_2 and use water more efficiently at higher temperatures. Nonetheless, they are not likely to increase their growth under increasing CO_2-levels because this is not the limiting factor, given that Mongolia is a semi-arid environment with water being the most strongly limited resource for vegetation growth. Therefore, the predicted increases in CO_2 and temperature will have little effect on the growth of Mongolia's vegetation.
- In order to assess the relative importance of C4-plants for the ecosystem we clearly need further studies on δ^{13}C signatures at various trophic levels and under various ecological conditions including healthy and presumably degraded or even deserted sites.

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