C_4 plants in the vegetation of Tibet, China: Their natural occurrence and altitude distribution pattern

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Abstract

Floristic composition, life forms for C_4 species, and the pattern of altitude distribution were studied on Tibetan Plateau. 79 species, in 7 families and 46 genera, were identified with C_4 photosynthesis. 95 % of these C_4 species belong to *Gramineae* (51 species), *Cyperaceae* (14 species), and *Chenopodiaceae* (10 species), indicating that C_4 plants mainly occur in very few families (7 of 204) on the Tibetan Plateau. High altitude distribution for all the *Chenopodiaceae* C_4 species (> 3 000 m above sea level) suggests that plants of this kind have large tolerance to cold, dryness, and strong ultraviolet radiation. Most *Gramineae* and *Cyperaceae* C_4 species occurrences are consistent with extensive distribution of steppes and meadows in the vast flat of the central Plateau (1 000-3 000 m a.s.l.). Relatively high amount of hemicryptophyte form plants (44 %) in the region indicates that the vegetation, especially grassland, meadows, and steppe, are in good condition. There is a strong relationship between numbers of C_4 species and altitude in the Tibetan Plateau. Occurrence of C_4 species is significantly less in both high and low altitude plateaux in Tibet. Altitude distribution pattern for C_4 species in the region is not only consistent with the altitude and climate, but also with the vegetation types in altitude gradient.

Additional key words: altitude distribution; geophytes; habitat types; hemicryptophytes; plant life form; precipitation; therophytes; Tibet Plateau.

Introduction

C_4 plant identification, physiology, and geographical distribution have received much attention since the work by Downton and Tregunna (1968) and Black (1971), and more than 1 700 C_4 plant species have been identified world-wide (Li 1993). Most studies focused on the classification of plant species as to their types of photosynthetic pathway (C_3, C_4, and CAM), geographic distribution, and relations with climate change (Williams and Markley 1973, Downton 1975, Teeri and Stowe 1976, Raghavendra and Das 1978, Waller and Lewis 1979, Teeri *et al.* 1980, Collins and Jones 1985, Takeda and Hakoyama 1985, Ueno and Takeda 1992, Redmann *et al.* 1995, Ehleringer *et al.* 1997, Wang *et al.* 1997, Yin and Li 1997, Collatz *et al.* 1998, Keeley 1998, Pyankov *et al.* 2000, Wang 2002b). These studies provide strong evidence that the relative abundance of different C_4 species correlates with different climatic attributes in some regions. Only few studies looked at the occurrence and response of C_4 species to altitude gradient (Sayed and Mohamed 2000).

Tibetan Plateau, with an average altitude of about 5 000 m, occupies a large area, about 1 200 000 km^2 (28°-36°N, 77°-103°E), and also is one of the important regions in the world. It is primarily a mountain plateau with forest, shrub, steppe, alpine meadow, alpine desert, and polar desert (Zhang 1978, Wu 1987a,b, Ni 2000). The relief is very complicated with both latitudinal and longitudinal climate zones, mixed with steep altitudinal gradients in the south-eastern part. The lowest elevation in the south-eastern part is no more than 100 m a.s.l., while that in the northern and western parts are as high as 4 000-5 200 m a.s.l. This steep gradient results in altitudinal vegetation distribution, varying from tropical seasonal and rain forest in the south-east to alpine steppe and desert, polar desert in the north-west, with temperate shrub, steppe, meadow in the middle (Zheng 1981, Wu 1987, Ni 2000). High-cold steppe is the major vegetation type of the Tibetan Plateau (Zhang 1978, Wu 1987). Moisture gradient is also very steep, with annual precipitation varying from 50 mm in the western desert and

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semi-desert to 200 mm in the vast flat high-cold steppe in the central Plateau, and 600-800 mm in the forest of south-eastern part. Because of the complex relief in the region, the plant and vegetation diversities are relatively higher than on the other plateaux in China. 208 families, 1 258 genera, and more than 5 766 species have been identified in the Plateau (Wu 1978, Ni and Cheng 1992). Most studies on the plants in Tibet focused on the classification (Wu 1978, Ni and Cheng 1992), vegetation (Zheng and Chen 1981, Chang 1983, Ni and Cheng 1992), biomass, and their responses to global climate change (Ni 2000). The occurrence of C_4 plants and their responses to altitude changes remain unclear. The present study investigated the occurrence of C_4 species, distribution, and the life forms in Tibet, as well as their responses to altitudinal gradient. This study is relevant to better understanding the influences of altitude on plant photosynthetic pathways, vegetation dynamics, and ecosystem production in the Tibetan Plateau.

Methods

Plant species were obtained from 13 references about the Tibetan flora published from 1957 to 2002 (*e.g.* Delectis Florae Reipublicae Popularis Sinicae Agendae Academiae Sinicae Edita 1977-1999, Wu 1987, Ni and Cheng 1992). The data on photosynthetic pathway types were compiled from 12 references published between 1985 and 2002 (Takeda and Hakoyama 1985, Li 1993, Redmann *et al.* 1995, Yin and Li 1997, Yin and Wang 1997, Wang *et al.* 1997, Pyankov *et al.* 2000, Wang 2002a,b,c,d). C_4 photosynthetic type was determined from microscopic studies of Kranz anatomy (K), $\delta^{13}C$ fractionation (D), as well as low CO_2 compensation concentration (L) (0-10 $\mu mol\ mol^{-1}$) (Li 1993, Redmann *et al.* 1995, Yin and Wang 1997, Wang 2002a,b,c,d). Geographic data (*e.g.* elevation, physico-geographical region) were compiled from Zhang (1978), Wu (1978), and Zheng and Chen (1981). Climate data were collected from references published from 1984 to 2000 (Zhang 1978, Chinese Central Meteorological Office 1984, Ni 2000).

Results

Plant composition: There are 7 vascular plant families, about 3 % of the total plant families in Tibet, in which C_4 photosynthesis occurs (Table 1), 5 in *Dicotyledoneae* (*Amaranthaceae*, *Portulaceae*, *Chenopodiaceae*, *Zygophyllaceae,* and *Euphorbiaceae*) and 2 in *Monocotyledoneae* (*Cyperaceae* and *Gramineae*). This indicates that the C_4 species mainly occur in very few families in Tibet. For the total 79 C_4 species, about 1 % of the total plant species identified in Tibet, only 18 % (14 of 79) was found in 10 genera of *Dicotyledoneae*, while the other 82 % (65 of 79) was in 36 genera of *Monocotyledoneae,* respectively (Table 1). Of these C_4 species, *Gramineae* (51 species) was the leading C_4 family, followed by *Cyperaceae* (14 species), while *Chenopodiaceae* (10 species) are less important in Tibet. Only 1 species was identified in each of the families *Amaranthaceae*, *Portulacaceae*, *Zygophyllaceae,* and *Euphorbiaceae*. All these species are distributed extensively over China. No endemic C_4 species was found in Tibet.

Following *Compositae* (457 species in 90 genera), *Gramineae* is the second leading vascular plant family in Tibet (335 species in 104 genera). Only 51 species (15 % of the total grass species) in 27 genera (26 % of the total genera in *Gramineae*) were identified with C_4 photosynthesis, but it made up 65 % of the total C_4 species in the Tibetan region. This was much less than the estimation that one half of the 10 000 grass species in the world are C_4 species. In Tibet all the species of *Digitaria* (6 species), *Eragrostis* (4 species), and *Setaria* (4 species) have C_4 photosynthesis. Photosynthetic pathways for more than 30 species of the genus in which C_4 species occurs and other 280 grass species have not been tested in this region.

Of the total 7 families with C_4 photosynthetic pathway, *Cyperaceae* was the sixteenth in abundance in the local flora, but it was the second leading C_4 family in Tibet. 117 species in 14 genus were identified, and 12 % of them (14 of 117) was found with C_4 photosynthesis. 18 % (14 of 79) of the total C_4 species was found in *Cyperaceae*, even if the *Cyperaceae* species form only 2 % (117 of 5766) of the total vascular plants in Tibet. This suggests that precipitation in some Tibetan regions is sufficient, because the abundance of C_4 *Cyperaceae* species was strongly related with local rainfall (Yin and Li 1997).

For the 14 *Dicotyledoneae* C_4 species, 10 were found in *Chenopodiaceae* (13 % of the total C_4 species), the other 4 species in the *Amaranthaceae*, *Portulaceae*, *Zygophyllaceae,* and *Euphorbiaceae*. The abundance of *Chenopodiaceae* plants in the local flora was 0.6 % (33 of 5 766), but 30 % of the *Chenopodiaceae* plants exhibit C_4 photosynthesis. This is much less than in Mongolia (41 %) (Pyankov *et al.* 2000), but more than in Northeast China (22 %) (Wang 2002b). The relatively less *Chenopodiaceae* C_4 species indicated that precipitation was not a critical factor for plant distribution in the whole area of Tibet, because the abundance of *Chenopodiaceae* C_4 species is strongly related with precipitation or aridity (Pyankov *et al.* 2000).

Life form of C_4 species: There were 3 life forms of C_4

species in Tibet. Of the total 79 species, 36 species (46 %) were therophytes (Th), 35 species (44 %) were hemicryptophytes (H), and 8 species (10 %) were geophytes (G). No C_4 species in Tibet was identified as belonging to macrophanerophytes and nanophanerophytes. All dicotyledons were found in the Th form. For *Gramineae*, 35 % (18 of 51) was in Th form, 49 % (25 of 51) in H form, and 16 % (8 of 51) in G form. Nanophanerophytes can be found in dry desert regions of North China and Mongolia. Of the 36 Th-form C_4 species, 47 % were distributed in mountains higher than 3 500 m or high Plateau, while the distribution for 35 H-form C_4 species was only 14 %. This suggests that the Th form C_4 species are more tolerant to environmental stress and have greater ability to maintain intense photosynthesis in the high altitude Tibetan Plateau.

Pattern of altitude distribution: Table 1 and Fig. 1 summarise the botanical-altitude distribution of the C_4 species in Tibet and the relative abundance of these C_4 species with altitude gradient. Most of C_4 species (85 %) can be found from 1 000 to 3 000 m a.s.l., the vast flat of the central Plateau, where the annual precipitation varies from 200 to 300 mm. 42 % C_4 species can be found on the mid-altitude Plateau (2 000-2 500 m a.s.l.). Only 10 and 5 % of the total C_4 species can be found in the high-altitude (> 3 500 m, high-cold steppe or desert with less annual precipitation (50-100 mm), and low-altitude (< 1 000 m), forest vegetation with higher annual precipitation (600 mm). This suggests that the occurrence of C_4 species was significantly less in both high and low altitude Plateau in Tibet (Fig. 1).

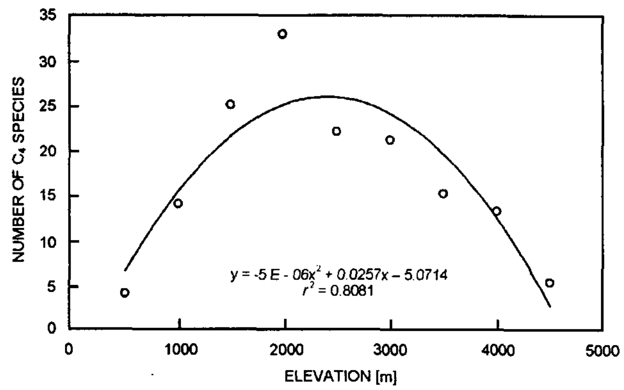

Fig. 1. The relationship between numbers of C_4 species and altitude in Tibetan Plateau.

Table 1. Occurrence, ecological distribution, and life form of C_4 species in Tibet, China. Nomenclature follows Kitagawa (1979) and Yin and Wang (1997). Habitat types: FO = frost, RL = range land, DB = disturbed and cultivated land, SS = sandy soil, WL = wet land, HS = hillside, RV = river valley, GL = gravel land. Life forms: H = hemicryptophyte, G = geophyte, Th = therophyte.

	Species	Habitat type	Life form	C_4 feature	Elevation
Dicotyledoneae					
Amaranthaceae	*Amaranthus paniculatus* L.	FO RL	Th	K	2 200
Portulacaceae	*Portulaca oleracea* L.	DB	Th	D K	2 000
Chenopodiaceae	*Agriophyllum squarrosum* (L.) Moq.	SS RV	Th	K	4 000-4 500
	Atriplex centralasiatica Iljin	SS GL	Th	K	3 300-3 600
	Bassia dasyphylla O. Kuntze	SS GL	Th	D	4 200-4 350
	Halogeton glomeratus C.A. Mey	SS	Th	K	4 250
	H. glomeratus var. *tibeticus* Bunge.	SS	Th	K	4 200
	Kochia scoparia (L.) Schrad.	RL	Th	D	3 000
	Salsola collina Pall.	DE	Th	D	3 000-4 000
	S. kali auct. non L.	RV GL	Th	D K	3 500
	S. monoptera Bunge.	RV GL	Th	D	4 000-4 800
	S. nepalensis Grab.	SS GL	Th	K	3 500-4 000
Zygophyllaceae	*Tribulus terrestris* L.	RV SS	Th	D	2 900-3 800
Euphorbiaceae	*Euphorbia humifusa* Willd.	DB HS	Th	K	3 000-3 800
Monocotyledoneae					
Cyperaceae	*Bulbostylis densa* (Wall.) Hand - Mazz	RV HS	Th	D	1 200-4 300
	Cyperus amuricus Maxim.	HS RL	H	K	2 000
	C. cuspidatus Kunth	HS RV WL	Th	D K	2 100- 4 000
	C. iria L.	FO DB	Th	D K	1 000
	C. pilosus Vahl.	HS FO	H	K	1 000-1 300
	Fimbristylis complanata (Retz.) Link.	RV HS	H	D K	2 000-3 100
	F. dichotoma (L.) Vahl	RL FO	H	D K	1 100-1 300

Table 1 (continued)

	Species	Habitat type	Life form	C_4 feature	Elevation
Cyperaceae (cont.)	*F. quinquangularis* (Vahl.) Kunth	HS WL	H	D	1 100
	F. squarrosa Vahl	RV	Th	K	1 000-1 300
	Kyllinga brevifolia Rottb.	WL HS	H	K	900-2 600
	Lipocarpha chinensis (Osbeck) Kern	HS	H	D	1 100
	Mariscus sumatrensis (Retz.) T. Koyama	HS FO	H	K	1 900-2 600
	Pycreus flavidus (Retz.) T. Koyama	HS FO	H	K	800-2 200
	P. sanguinolentus (Vahl.) Nees	WL	H	K	2 400
Gramineae	*Achnatherum chingii* (Hitchc.) Keng	FO	H	D	4 000
	A. splendens (Trin.) Nevski	RL GL	H	K	3 400-4 250
	Andropogon brevifolius SW.	HS	Th	K	2 000
	Apluda mutica L.	FO HS	G	K	1 800-2 300
	Arundinella bengalensis (Spreng.) Druce	HS	H	D	1 000-1 300
	A. nepalensis Trin.	FO	H	K	2 300-2 500
	A. setosa Trin.	HS	H	D K	1 000-1 200
	Bothriochloa ischaemum (L.) Keng	HS RV	G	L	2200-3500
	Capillipedium parviflorum (R.Br.) Stapf.	DB	H	L	2 650
	Chloris virgata Sw.	DB	Th	D	2 300-3 900
	Cymbopogon jwarancusa (Jones) Schult	DB RV	H	D K	1 900
	Cynodon dactylon (L.) Pers.	DB	H	D K	1 900
	Digitaria ciliaris (Rotz.) Koel	RL	Th	L	1 000
	D. crucita (Nees *ex* Steud.) A. Camus	FO	Th	L	2 400
	D. crucita var. *esculenta* Bor.	RV GL	Th	L	3 700
	D. denudata Link	HS RL	Th	L	1 800
	D. *ischaemum* (Schreb.) Schreb. *ex* Muhl.	DB RL	Th	L	3 700
	D. violascens Link	RL FO	Th	D	2 000-2 300
	Echinochloa crus galli (L.) Beauv.	DB	Th	D	3 000
	Eleusine coracana (L.) Gaertn.	HS	Th	D K	800-2 000
	E. indica (L.) Gaertn.	DB	Th	K L	1 000
	Eragrostis ferruginea Beauv.	WL	H	L	2 100-3 300
	E. minor Host	HS RL	Th	D	2 000
	E. nigra Nees *ex* Steud.	HS	H	D	3 600-4 000
	E. pilosa (L.) Beeauv.	FO	Th	K L	2 000
	Eulalia phaeothrix (Hack) Kuntge	HS RL	H	K	2 000
	Helictotrichon tibeticum (Roshev.) Holub.	SS RV	H		3 800-4 600
	Heteropogon contortus (L.) Beauv.	HS	H		1 800-2 300
	Hierochloë odorata (L.) Beauv.	RL WL	H		3 500
	Imperata cylindrica (L.) P. B.	HS	G	D	2 100
	Muehlenbergia huegelii Trin.	WL	H		2 000
	Orinus thoroldii (Stapf) Bor.	RV GL	G		4 000-5 200
	Panicum miliaceum L.	DB	Th	D K	2 000
	Paspalum orbiculare G. Forst.	DB	H	D K	2 200
	Pennisetum alopecuroides (L.) Spreng	DB	H	K	2 000
	P. flaccidum Griseb.	DB FO	G	L	2 900-4 500
	P. lanatum Klotztch.	HS	H	L	1 800
	Phaenosperma globosa Munro	FO	H	K	2 500
	Saccharum officinarum L.	FC	G	D K	2 000
	S. sinensis Roxb.	FC	G	K	1 800
	S. spontaneum L.	SS RV	G	K	2 000
	Setaria glauca (L.) Beauv.	RS	Th	K	2 500
	S.italica (L.) Beauv.	DB	Th	D	650-1 800
	S. lutescens (Weigel) F.T. Hubb.	DB	Th	L	650-2 000
	S. palmifolia (Koenig) Stapf.	FO	H	K L	650-2 200
	S. viridis (L.) Beauv.	RS	Th	K L	1 700-3 700
	Sporobolus fertilis (Steud.) W.D. Clayton	HS	H	KL	2 500
	Themeda triandra Forssk.	FO	H	D K	2 000-2 500
	Tripogon bromoides Roem *ex* Schult.	HS RL	H	K	1 800-3 200
	T. chinensis (Franch.) Hack.	HS DB	H	K	2 800-3 200
	T. filiformis Nees *ex* Steud.	HS GL	H	K	2 200-3 200

Discussion

The common occurrence of C_4 species and the relations with climate and geography have been well documented in the grasslands in China (Redmann *et al.* 1995, Yin and Li 1997, Wang 2002a,b,c). But no one has looked at the occurrence of C_4 species and their relation with altitude. In Tibet Plateau, 7 of 208 vascular plant families were found with C_4 species occurrence, which was much less than that found in North China grasslands (Wang 2002c). Of the total 79 C_4 species (about 1 % of the identified plants), 95 % (75 of 79) belong to *Gramineae*, *Cyperaceae,* and *Chenopodiaceae*, but only few (4 species) were found in *Amaranthaceae*, *Portulaceae*, *Zygophyllaceae,* and *Euphorbiaceae*. This suggests that the occurrence of C_4 species in Tibetian Plateau is not as common as in other regions (Pyankov *et al.* 2000, Wang 2002b,c). Tibetan Plateau has a complex geo-relief and climatic zones, as well as diverse vegetation, but the high elevation and cold climate may reduce C_4 species occurrence, which may be supported by relatively less vascular plant families with C_4 species in the region. More than 80 % C_4 species were found in *Gramineae* and *Cyperaceae*, mainly due to high presence of graminaceous plants (*Gramineae* and *Cyperaceae*). Of the total 208 vascular plant families, *Gramineae* ranks the second leading in abundance, and *Cyperaceae* rank sixteenth in Tibet (Wu 1987, Ni and Cheng 1992). Relatively more precipitation (> 600 mm) in the southern part of the region may also result in the greater occurrence of graminaceous C_4 plants. Unlike in Mongolia (Pyankov *et al.* 2000) and Hunshandake desert (Wang 2002d), the proportion of *Chenopodiaceae* plants was less (0.6 %) in Tibetan flora, even if the numbers for both total species and C_4 species in this family were relatively greater in the northern part of the region. All of the 10 identified C_4 *Chenopodiaceae* species can be distributed on high altitude of the North-western Tibetan Plateau (from 3 000 to 4 800 m), with cold and dry climate. This indicates that plants of this type have greater tolerance to environmental stress, *e.g.* drought, cold, and strong ultraviolet radiation, and greater ability to maintain intense photosynthesis. Further experiments should be conducted to test the morphological, genetic, or physiological bases of tolerance abilities for these species. No endemic C_4 species was identified in Tibet, but more than 50 species in the genus with C_4 plants have not been determined, including some endemic species, *e.g. Arundinella hookeri* Munrc *ex* Keng. and *Hierochloë tibetica* Bor.

Plant life form composition represents the climate changes and land use (Wang 2002c,d). Unlike in the northeastern grasslands in China and in Hunshandake desert, more than 40 % of the identified C_4 species were found in each of Th (46 %) and H (44 %) forms and only few species in G form (Table 1). Relatively more H-form plants in the region indicate that the vegetation, *e.g.* grasslands, meadows, or steppes, are in good condition, because the increase of Th form proportion is consistent with grassland deterioration and desertification (Wang 2002c,d). Relatively larger precipitation in the southern Tibet and greater graminaceous plant composition may in part explain the fact of higher presence of H-form in the region. More Th-form C_4 species found in the high altitude suggest that the Th-form species are adaptive to extreme environmental stress, *e.g.* dryness, salinity, and cold climate, because they can survive the extreme environments in the form of dormant seeds (Wang 2002d).

Patterns of climate distribution for C_4 species, especially in precipitation and temperature, have been well documented for many regions (Teeri and Stowe 1976, 1980, Collins and Jones 1985, Takeda and Hakoyama 1985, Ehleringer *et al.* 1997, Pyankov *et al.* 2000). But no one has tested the pattern of altitude distribution for C_4 species in Tibetan Plateau. Fig. 1 and Table 1 summarise the altitude distribution pattern for C_4 species from low to high altitude in the region. The numbers of C_4 species were relatively less in both low and high altitude in Tibetan Plateau, most of these species (85 %) were present between 1 000 and 3 000 m a.s.l. The lowest elevation in the south-eastern Tibet is no more than 100 m a.s.l., and typical vegetation is forest with relatively less C_4 species. But the north-western Tibet is as high as 4 000-5 200 m a.s.l., with alpine steppe and polar desert with relatively less C_4 species. Extensive steppes and meadows are the typical vegetation for the vast flat of the central Plateau (1 000-3 000 m a.s.l.), and most C_4 species occur in these vegetation types, especially C_4 species of *Gramineae* and *Cyperaceae*. This suggests that the occurrence for C_4 species is consistent with climate and geography, as well as with vegetation (Williams and Markley 1973, Wang 2002d). Therefore the vegetation management in the region must take into account C_4 species occurrence and its composition, which are closely related to land conditions and climate.

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