

## The occurrence of C<sub>4</sub> photosynthesis in Yunnan province, a tropical region in South-western China

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### Abstract

Floristic composition, morphological functional types, and altitudinal distribution pattern for C<sub>4</sub> species were studied in Yunnan province, South-western China. 159 species, in 6 families and 60 genera, were identified with C<sub>4</sub> photosynthesis. 93 % of these C<sub>4</sub> species were found in *Monocotyledoneae*, e.g. *Cyperaceae* (18 species), *Gramineae* (129 species), and *Commelinaceae* (1 species), the other 7 % was in *Dicotyledoneae*, e.g. *Amaranthaceae* (5 species), *Portulacaceae* (4 species), and *Chenopodiaceae* (2 species). Hence C<sub>4</sub> plants mainly occurred in very few families in the tropical region. Compared with those in semi-arid grasslands and arid deserts in North China, more C<sub>4</sub> grasses and much less *Chenopodiaceae* C<sub>4</sub> species occurred in the tropical region. This indicates the physiological responses of C<sub>4</sub> plants from the two families are very different. *Chenopodiaceae* C<sub>4</sub> species may be more fit semi-arid and arid environments, while C<sub>4</sub> grasses are more fit the moist tropical conditions. There was a strong relationship between C<sub>4</sub> distribution and altitude in the tropical region. Altitudinal distribution pattern for C<sub>4</sub> species in the region was consistent with altitude, climate, and habitats.

*Additional key words:* altitudinal distribution pattern; habitats; morphological functional types.

### Introduction

Plants characterized by the C<sub>4</sub> photosynthetic pathway are generally capable of higher rates of CO<sub>2</sub> uptake than C<sub>3</sub> species, especially at low CO<sub>2</sub> concentrations (Downton and Tregunna 1968, Ehleringer *et al.* 1997), and higher tolerances to environmental stresses, e.g. drought, high temperature, and high irradiance (Ehleringer *et al.* 1997). On the global basis, only about 3 % of the total plant species can be characterized by C<sub>4</sub> photosynthetic pathway, since approximately one-half of the 10 000 grass species and fewer than a thousand of the 165 000 dicotyledons have the C<sub>4</sub> photosynthesis (Hattersley 1987, Hattersley and Watson 1992). C<sub>4</sub> biota, however, account for about 18 % of the total global productivity, including many important plants, e.g. sugarcane, maize, and sorghum, as well as serious weeds, e.g. nutsedge (*Cyperus rotundus* L.), Johnson grass (*Sorghum halepense* Pers.), and crabgrass [*Digitaria sanguinalis* (L.) Scop.]. More than 1 700 C<sub>4</sub> plant species have been identified worldwide since the work of Downton and Tregunna (1968) and Black (1971), indicating that only 1/3 of the total C<sub>4</sub> species was identified and the other 2/3 remain unclear, especially for some key ecological regions.

Yunnan province covers large continuous area, about 380 000 km<sup>2</sup> (21.1–29.3°N, 96.9–106.1°E), and also is one of the key ecological regions in China. It is primarily a mountain plateau mixed with forests, woods, rangeland, and river valleys. The relief of the region is very complicated with both latitudinal and longitudinal climate zones, mixed with steep altitudinal gradients. The eastern part belongs to the Yungui Plateau, with altitude ranging 2 000–6 000 m above sea level (a.s.l.), the western part is mountain valley (300–600 m a.s.l.). Moisture gradient varies with relief, with annual precipitation from 750 to 17 500 mm. May to October is rainy season and November to April is dry season. Mean annual air temperatures are 20–22 °C, varying within 12–15 °C in January to 16–26 °C in July. Because of the complex relief in the region, plant and vegetation diversities are highest in China. More than 300 families, 2 000 genera, and 14 000 species have been identified in the region (Institutum Botanicum Kunmingense 2000). The number of plant species in Yunnan province is a half of the total in China. Most studies on the plants in the region focused on the classification, vegetation, and biodiversity, but the

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occurrence of C<sub>4</sub> plants, their functional types and relations with habitats remain unclear. I investigated the occurrence of C<sub>4</sub> species, plant functional types, as well as their responses to habitats and altitude in the Yunnan province. This knowledge is highly relevant to a better

## Materials and methods

Floristic species were obtained from references about the local flora published from 1980 to 2003 (e.g. Yunnan Institute of Tropical Botany 1980, Institutum Botanicum Kunmingense 2000-2003) and some local flora. The data on photosynthetic pathway types were compiled from papers published between 1968 and 2004 (Downton and Tregunna 1968, Downton 1975, Raghavendra and Das

## Results

**C<sub>4</sub> plant composition:** 159 species, about 1.1 % of the total species in Yunnan province, in 60 genera and 6 families were identified with C<sub>4</sub> photosynthesis (Table 1). Of the total C<sub>4</sub> species, 7 % (11 of 159) was found in *Dicotyledoneae*, e.g. *Amaranthaceae* (5 species), *Portulacaceae* (4 species), and *Chenopodiaceae* (2 species). 93 % was found in *Monocotyledoneae*, e.g. *Cyperaceae* (18 species), *Gramineae* (129 species), and *Commelinaceae* (1 species). About 3 % genera and 2 % families were found with the occurrence of C<sub>4</sub> species in the region. Of these C<sub>4</sub> species, *Gramineae* was the leading C<sub>4</sub> family with 129 C<sub>4</sub> species (81 % of the total C<sub>4</sub> species), about 14 % of the total grasses identified in Yunnan province. *Cyperaceae* (11 % of the total C<sub>4</sub> species and 12 % of the total sedges occurring in the region) and *Amaranthaceae* (3 % of the total C<sub>4</sub> species) followed. The C<sub>4</sub> species of other families were only 4 % of the total C<sub>4</sub> species. *Eragrostis* was the leading C<sub>4</sub> genus with 15 C<sub>4</sub> species, followed by *Setaria* (10 C<sub>4</sub> species), *Fimbristylis* (8 species), and *Cymbopogon*, *Digitaria*, and *Sorghum* (7 species for each). However, more than 400 species in the genera with C<sub>4</sub> plants have not been determined, including 109 species in *Panicum*, 80 species in *Andropogon*, 27 species in *Digitaria*, 26 species in *Cymbopogon*, and 25 species in *Arundinella*. This suggested that the C<sub>4</sub> abundance may be much greater in this tropical region. Unlike that, in northeast China grasslands and Mongolian deserts only 2 C<sub>4</sub> species in *Chenopodiaceae* were identified with C<sub>4</sub> photosynthesis and the abundance of *Chenopodiaceae* plants was no more than 0.1 % in the local flora. No endemic C<sub>4</sub> species has been found in the region.

**Morphological functional types:** Within the tropical region, all C<sub>4</sub> plants fall within 7 morphological functional types (Table 1). Of the total 159 C<sub>4</sub> species in Table 1, all 11 C<sub>4</sub> dicots and 1 C<sub>4</sub> species in *Commelinaceae* fall into annual forbs, ANF (7.5 % of the total). For C<sub>4</sub> grasses and sedges, 56 % (83 of 147) was perennial

understanding of the responses of photosynthetic pathways to climate changes and land-use, the theory and modelling of community successions, as well as vegetation changes under global changes.

1978, Mateu Andrès 1993, Redmann *et al.* 1995, Pyankov *et al.* 2000, Wang 2002a, 2004). C<sub>4</sub> photosynthetic types were determined from microscopic studies of Kranz anatomy (K),  $\delta^{13}\text{C}$  fractionation (D), as well as low CO<sub>2</sub> compensation concentration (L) (0–10  $\mu\text{mol mol}^{-1}$ ) (Redmann *et al.* 1995, Wang 2002a, 2004).

species, including 54 high perennials, HPG (34 % of the total), 24 mediate perennials, MPG (15 %), and 5 short perennials, SPG (3 %). This suggested that perennial grasses and sedges are the main functional type of the C<sub>4</sub> species occurring in the region. 44 % C<sub>4</sub> grasses and sedges was annual species, 15 % of the total C<sub>4</sub> species (23 of 159) was high annuals, HAG, 19 % was mediate annuals, MAG (31 of 159), and 6 % was short annuals, SAG. Relatively less annual C<sub>4</sub> species in the region indicated that the ecosystems are stable in the tropical region, for stable ecosystems may reduce the introduction of weeds and annual species.

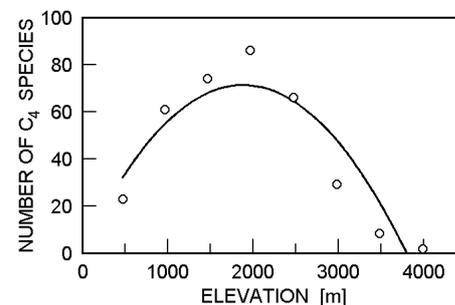


Fig. 1. Relationship between C<sub>4</sub> plant distribution and altitudinal gradient in Yunnan province, South-western China.

Of the total 159 C<sub>4</sub> species, more than half (51 %) was found distributed in disturbed and cultivated lands (DB) [e.g. *Amaranthus caudatus* L., *A. lividus* L., *Portulaca grandiflora* Hook., *Cynodon dactylon* (L.) Pers.], 25 % in river valley, RV [e.g. *Kyllinga brevifolia* Rottb., *Rhynchospora rubra* (Lour.) Makino, *Dinebra retroflexa* (Vahl) Panzer], 23 % in rangeland, RL [e.g. *Eremochloa bimaculata* Kack., *Ophiuros exaltatus* (L.) Ktze], 18 % in each of wet land, WL and hillside, HS [e.g. *Cyperus iria* L., *Mariscus sumatrensis* (Retz.) T., *Axonopus compressus*. Beauv., *Achnatherum chingii* (Hitc.) Keng], 19 % in frost region, FO (e.g. *Alloteropsis semialata* Hitc., *Hyparrhenia filipendula* Stapf), 13 % in cultivated region

Table 1. The occurrence, plant functional types, and ecological distribution of C<sub>4</sub> species in Yunnan, South-western China. C<sub>4</sub> feature: D = <sup>13</sup>C/<sup>12</sup>C, K = Kranz anatomy, L = low CO<sub>2</sub> compensation concentration. Plant functional types: HPG = high perennial grass and sedge (> 80 cm), MPG = mediate perennial grass and sedge (30–80 cm), SPG = short perennial grass and sedge (<30 cm), HAG = high annual grass and sedge (>80 cm), MAG = mediate annual grass and sedge (30–80 cm), SAG = short annual grass and sedge (<30 cm), ANF = annual forbs, Habitat types: FO = frost, RL = rangeland, DB = disturbed and cultivated land, WL = wet land, HS = hillside, RV = river valley, SS = sandy soil, CU = cultivation.

Family	Species	C <sub>4</sub> feature	PFTs	Habitats	Elevation	
<i>Dicotyledoneae</i>						
<i>Amaranthaceae</i>	<i>Amaranthus caudatus</i> L.	K	ANF	DB	500–2 100	
	<i>A. lividus</i> L.	K	ANF	DB	800–1 500	
	<i>A. spinosus</i> L.	K L	ANF	DB	1 000–2 000	
	<i>A. retroflexus</i> L.	D	ANF	DB	500–3 000	
	<i>A. viridis</i> L.	K	ANF	DB	800–2 500	
<i>Chenopodiaceae</i>	<i>Kochia scoparia</i> (L.) Schrad.	D K	ANF	DB HS	600–2 100	
	<i>Salsola collina</i> Pall.	D	ANF	DB HS	800–1 800	
<i>Portulacaceae</i>	<i>Portulaca grandiflora</i> Hook.	D K	ANF	DB	200–1 000	
	<i>P. oleracea</i> L.	K	ANF	DB RL	100–2 000	
	<i>P. pilosa</i> L.	D	ANF	DB	500–700	
	<i>P. quadrifida</i> L.	D K	ANF	DB	380–700	
<i>Monocotyledoneae</i>						
<i>Cyperaceae</i>	<i>Bulbostylis densa</i> (Wall.) Hand.- Mazz	D	MAG	WL DB	1 200–4 300	
	<i>Cyperus iria</i> L.	D K	SAG	WL RV DB	500–2 500	
	<i>C. pilosus</i> Vahl.	K	MPG	WL RV	1 300–2 100	
	<i>C. rotundus</i> L.	C D K	HPG	DB FO	220–2 600	
	<i>Fimbristylis aestivalis</i> (Retz.) Vahl.	D K	SAG	DB RL	120–2 000	
	<i>F. bisumbellate</i> (Forsk.) Bub.	D K	SAG	DB RV WL	600–2 400	
	<i>F. complanata</i> (Retz.) Link.	D K	MPG	RL	1 800–3 000	
	<i>F. dichotoma</i> (L.) Vahl.	D K	MPG	DB	500–3 000	
	<i>F. miliacea</i> (L.) Vahl.	D K	MAG	WL DB	500–2 100	
	<i>F. ovata</i> (Burm. F.) Kern	D	SPG	FO DB	1 000–2 000	
	<i>F. squarrosa</i> Vahl.	K	MAG	RV WL DB	400–2 400	
	<i>F. stauntonii</i> Vahl.		MAG	WL DB	500–1 700	
	<i>Kyllinga brevifolia</i> Rottb.	K	SPG	RV DB	1 500–3 000	
	<i>K. nemoralis</i> (Vahl.) Spreng.	K L	SPG	WL HS DB	380–1 570	
	<i>Lipocarpa microcephala</i> Kunth	D	SAG	DB WL	500–750	
	<i>Mariscus sumatrensis</i> (Retz.) T. Koyama	K	MPG	WL FO DB	500	
	<i>Pycreus sanguinolentus</i> (Vahl.) Nees	K	SAG	RV DB	1 200–3 400	
	<i>Rhynchospora rubra</i> (Lour.) Makino	K	MPG	RV	1 500–2 000	
	<i>Gramineae</i>	<i>Achnatherum chingii</i> (Hitche.) Keng	D	MPG	HS FO	3 400–4 000
		<i>A. splendens</i> (Trin.) Nevski	K	MPG	HS FO RV	1 800
<i>Alloteropsis semialata</i> Hitche.		D K	HPG	FO HS	1 000–2 300	
<i>Andropogon brevifolius</i> SW.		K	MAG	HS WL	500	
<i>A. mutica</i> L.		K	HPG	HS DB	300–2 100	
<i>Aristida adscensionis</i> L.		D K L	MAG	FO DB	400–1 800	
<i>Arthraxon hispidus</i> (Thunb.) Makino		D	MAG	HS RL WL	1 300–1 800	
<i>A. hispidus</i> var. <i>junnarensis</i> P. C.		D	MAG	RV WL	1 100	
<i>Arundinella anomala</i> Steud.		K	HPG	HS FO RV	2 000	
<i>A. hirta</i> Thunb.		D K	HPG	HS FO RV	2 000	
<i>A. nepalensis</i> Trin.		K	HPG	HS RL	1 200–2 400	
<i>A. setosa</i> Trin.		D K	HPG	FO RL HS	1 500–2 600	
<i>Axonopus compressus</i> Beauv.		D K	MPG	DB WL	700–1 400	
<i>Bothriochloa glabra</i> (Roxb.) A. Camus		L	HPG	HS GV FO	1200	
<i>B. gracilis</i> W. Z. Fang		D L	MPG	RL		
<i>B. intermedia</i> var. <i>punctata</i> Keng		L	HPG	FO RV	1 000–1 900	
<i>B. ischaemum</i> (L.) Keng		L	HPG	HS RL FO	600–2 400	
<i>B. pertusa</i> (L.) A. Camus		L	HPG	RV GL	600–2 000	
<i>Brachiaria eruciformis</i> Griseb.		D L	MAG	DB HS	1 050–1 850	
<i>B. ramosa</i> (L.) Stapf in Prain		L	MAG	RV DB WL	100–800	

Table 1 (continued)

Family	Species	C <sub>4</sub> feature	PFTs	Habitats	Elevation
Gramineae (cont.)	<i>Bothriochloa semiundulata</i> Stapf in Prain	K L	SAG	DB HS	1 000–1 900
	<i>B. subquadripa</i> Trin.	D K	SAG	RL RV FO	500–800
	<i>B. villosa</i> Lam.	D	SAG	DB RL	500–2 500
	<i>B. urochloaoides</i> S. L. Chen	D K	MAG	DB RL	500–900
	<i>Capillipedium parviflorum</i> Stapf.	L	HPG	HS FO RV	1 350–2 800
	<i>Cenchrus calyculatus</i> L.	D	MAG	SS DB	90–120
	<i>C. setigerus</i> Vahl.	D L	HPG	DB	
	<i>Chloris anomala</i> B. S. Sun et Z. H. Hu	D	MPG	SS RV	200–1 500
	<i>C. gayana</i> Kunth	D K	HPG	RL	200–1 000
	<i>C. virgata</i> Sw.	D	MAG	DB RV SS	100–3 000
	<i>Coix aquatica</i> Roxb.	K L	HPG	WL	
	<i>C. lachryma-jobi</i> L.	K	HAG	RV WL	500–1800
	<i>Cymbopogon citrates</i> Stapf	D K	HPG	CU	
	<i>C. flexuosus</i> Wats.	L	HPG	FO RL	
	<i>C. jwarancusa</i> (Jones) Schult	D K	HPG	RV WL	1 000
	<i>C. martini</i> (Roxb.) Wats.	D K	HPG	HS	500–800
	<i>C. nardus</i> (L.) Rendle	K L	HPG	CU	
	<i>C. tortilis</i> A. Camus	K	HPG	RL HS FO	300–600
	<i>C. winterianus</i> Jowitt	K L	HPG	CU	
	<i>Cynodon dactylon</i> (L.) Pers.	D K	MPG	DB RV RL	2 800
	<i>C. dactylon</i> var. <i>biflorus</i> Merino	D K	MPG	DB RV RL	2800
	<i>Dactyloctenium aegyptium</i> Willd.	D K	MAG	DB RV	1 100–1 600
	<i>Desmostachya bipinnata</i> (L.) Stapf	D	HPG	RL HS	800–1 500
	<i>Dichanthium annulatum</i> Stapf	D	HPG	HS RL DB	100–2 200
	<i>D. aristatum</i> C. E. Hubb.	K	MPG	RV DB	700–1 200
	<i>Digitaria bicornis</i> Roem. et Schult.	K	MAG	HS	2 000
	<i>D. ciliaris</i> (Rotz.) Koel	L	HAG	RL FO DB	2 200
	<i>D. crucita</i> (Nees ex Steud.) A. Camus	L	MAG	HS RL	1 700–2 500
	<i>D. ischaemum</i> (Schreb.).	L	MAG	SS	1 700–2 400
	<i>D. sanguinalis</i> (L.) Scop.	D K	MAG	HS RL	1 300–2 900
	<i>D. violascens</i> Link	D	MAG	HS FO DB	1 800–3 200
	<i>D. yunnanensis</i> Henr.	L	MPG	RL FO	1 550–2 500
	<i>Dinebra retroflexa</i> (Vahl) Panzer	K	MAG	RV SS DB	1 000–1 200
	<i>Echinochloa colonum</i> Link	K L	MAG	DB	600–2 500
	<i>E. colonum</i> var. <i>frumentacea</i> Trimen	K L	HAG	CU	
	<i>E. crusgalii</i> (L.) Beauv.	D	HAG	WL RV	2 500
	<i>E. hispidula</i> Nees ex Royle	L	HAG	RV DB	800–2 000
	<i>E. utilis</i> Ohwi	D	HAG	CU	
	<i>Eleusine coracana</i> (L.) Gaertn.	D K	HAG	CU DB	
	<i>E. indica</i> (L.) Gaertn.	K L	HAG	DB	200–2 500
	<i>Eragrostis autumnalis</i> Steud.	L	MPG	DB	1 600–2 400
	<i>E. bulbifera</i> Steud.	L	MPG	DB	1 600–2 400
	<i>E. chariis</i> (Schult.) Hitchc.	L	MAG	DB	1 000–1 350
	<i>E. cilianensis</i> F. T. Hubbard	D K	MAG	DB	400–2 200
	<i>E. curvula</i> Nees	D K	HPG	CU	
	<i>E. ferruginea</i> Beauv.	L	MPG		3 000
	<i>E. elongata</i> Jacq.	K	MAG	RL FO	1 000
	<i>E. japonica</i> Trin.	L	HAG	DB	1 500–1 800
	<i>E. mairei</i> Hack.	L	HPG	FO RL DB	1 600–2 800
	<i>E. minor</i> Host	D	MAG	RL DB	1 700–2 400
	<i>E. nevinii</i> Nees ex Steud.	L	MPG	RL DB	1 500–1 800
	<i>E. nigra</i> Nees ex Steud.	D	MPG	DB RL	1 400–2 700
	<i>E. pilosa</i> (L.) Beauv.	K L	MAG	RL DB	1 600–2 400
	<i>E. tenella</i> (L.) Beauv. ex Roem.	D	HAG	RL DB	800
	<i>E. unioloides</i> Nees ex Steud.	D L	MAG	HS RL DB	500–1 800
	<i>Eremochloa bimaculata</i> Kack.	K	MPG	RL	1 200–2 200
	<i>Hackelochloa granularis</i> (L.) O. Ktze.	D K	MAG	DB	800–1 400
	<i>Heteropogon contortus</i> (L.) Beauv.	K L	HPG	RL	100–2 300
	<i>Hyparrhenia filipendula</i> Stapf	K	HPG	FO	800–1 300

Table 1 (continued)

Family	Species	C <sub>4</sub> feature	PFTs	Habitats	Elevation
Gramineae (cont.)	<i>Hyparrhenia rufa</i> (Nees) Stapf	L	HPG	FO	
	<i>Imperata arundinacea</i> Cyr.	D	HPG	DB HS	
	<i>I. cylindrica</i> (L.) P. B.	D	HPG	DB HS	
	<i>Isachne dispar</i> Trin.	K L	SAG	WL RV FO	1 500
	<i>Manisuris altissima</i> Hitchc.	K	HPG	DB WL	700–1 900
	<i>Melinis minutiflora</i> Beauv.	K	HPG	CU	
	<i>Miscanthus sinensis</i> Anders.	K	HPG	HS RL DB	1 900
	<i>Muhlenbergia huegelii</i> Trin.	K	MPG	RL SS	2 000–2 600
	<i>Ophiuros exaltatus</i> (L.) Ktze	K	HPG	RL	150–850
	<i>Panicum colonum</i> Link.	L	HAG	DB	600–2 400
	<i>P. crusgalli</i> Beauv.	D	HAG	WL RV	2 500
	<i>P. decompositum</i> Tindle	D K	MPG	WL SS	2 000
	<i>P. indicum</i> L.	K L	HAG	WL FO	100–2 400
	<i>P. maximum</i> Jacq.	D	HPG	CU	400–1 000
	<i>P. miliaceum</i> L.	D K	HAG	CU	1 500–2 000
	<i>P. repens</i> L.	K L	HPG	DB	1 500
	<i>P. reptans</i> Stapf	D K	MAG	RV DB	100–1 000
	<i>Paspalum commersonii</i> Lam.	K L	HPG	RV DB	500
	<i>P. dilatatum</i> Poir.	K L	HPG	RV DB	1 500–2 400
	<i>P. distichum</i> Sw	K	MPG	WL RV	200–2 000
	<i>P. notatum</i> Flugge	K	HPG	CU	
	<i>P. scrobiculatum</i> L.	L	HPG	DB WL	1 000–2 400
	<i>Pennisetum alopecuroides</i> Spreng.	K	HPG	DB WL	1 400–2 100
	<i>P. purpureum</i> Schum.	K L	HPG	CU	500
	<i>Rottboellia exaltata</i> L.	K	HAG	SS DB	500–1 700
	<i>Saccharum officinarum</i> L.	D K	HPG	CU	
	<i>S. sinense</i> Roxb.	K	HPG	CU	
	<i>S. spontaneum</i> L.	K	HPG	RV WL	1 400–2 000
	<i>Sehima nervosum</i> Stapf	D	HPG	RL RV FO	500–1 500
	<i>Setaria faberi</i> Herrm.	L	HAG	DB	1 100–1 700
	<i>S. forbesiana</i> Hook.	L	HPG	RL DB FO	800–2 600
	<i>S. geniculata</i> Beauv.	K	HAG	DB FO	2 800
	<i>S. glauca</i> (L.) Beauv.	K	HAG	MAG	700–2 600
	<i>S. italica</i> (L.) Beauv.	D	HAG	CU	1 000–2 400
	<i>S. plicata</i> T. Cooke	L	HPG	DB	1 000–2 360
	<i>S. palmifolia</i> (Koenig) Stapf.	K L	HPG	DB FO RV	1 500
	<i>S. verticillata</i> Beauv.	L	HAG	RL RV	400–1 600
	<i>S. viridis</i> (L.) Beauv.	D K	HAG	DB	2 400
	<i>Sorghum bicolor</i> Moench	D	HAG	CU	
	<i>S. dochna</i> Forssk.	L	HAG	CU	
	<i>S. halepense</i> Pers.	K	HPG	CU	
	<i>S. propinquum</i> Hitchc.	K	HPG	WL	
	<i>S. sudanense</i> Stapf	K L	HAG	CU	
	<i>Sporobolus elongatus</i> Hitchc.	KL	MPG	HS DB FO	2 600
	<i>Themeda triandra</i> Forssk.	D K	HPG	RV FO	1 700–1 800
	<i>Tragus berteroninus</i> Schult.	K	MAG	SS	1 400–2 500
	<i>T. biflorus</i> Schult.	D K	SAG	RV	200–1 770
<i>Vetiveria zizanioides</i> Nash	L	HPG	CU		
<i>Zoysia matrella</i> var. <i>japonica</i> Sasaki	K	SPG	CU		
<i>Z. tenuifolia</i> Willd. ex Trin.	K	SPG	CU		
Commelinaceae	<i>Commelina communis</i> L.	L	ANF	DB	1 200–1 800

CU, and only 4 % in sandy soil, SS. Relative high C<sub>4</sub> abundance in disturbed and cultivated land (DB) suggested that most of these species have higher tolerance to environmental stresses caused by land uses (e.g. cultivation, forest felling, and grazing) and become

the pioneer species in community succession. Even though tropical forests were the dominant vegetation in Yunnan province, the occurrence of C<sub>4</sub> species in forests was less than 19 %, mainly due to their higher tolerances to high temperature and high irradiance.

Table 1 and Fig. 1 summarize the data on the botanical-altitude distribution of the C<sub>4</sub> species in Yunnan province and the relative abundance of these C<sub>4</sub> species with altitude gradient (Fig. 1). Most of C<sub>4</sub> species (90 %) was found from 500 to 3 000 m a.s.l., with annual precipitation varying from 1 000 to 1 500 mm. 43 % C<sub>4</sub>

## Discussion

The occurrence of C<sub>4</sub> species and their relations with climate, geography, and land use have been well documented in many vegetation types (Teeri and Stowe 1976, Stowe and Teeri 1978, Waller and Lewis 1979, Teeri *et al.* 1980, Collins and Jones 1985, Collatz *et al.* 1998, Pyankov *et al.* 2000, Wang 2002a,b,c), especially in grasslands. C<sub>4</sub> monocots account for about 20 % of the total productivity in grassland ecosystems. These studies provide strong evidence that the occurrence of C<sub>4</sub> species is most common and significantly correlated with climate attributes and land use in semi-arid and arid ecosystems. But few researchers have looked at C<sub>4</sub> occurrence in tropical ecosystems. The total area of Yunnan province is no more than 4 % of the total China, but the flora includes more than 50 % of the total China (Yunnan Institute of Tropical Botany 1980). This indicates that plant abundance in the region (more than 14 000 vascular plant species) is highest in China. High species diversity and moist tropical environments lead to more occurrences of C<sub>4</sub> species, especially C<sub>4</sub> grasses and sedges. In the region, about 2 % families, 3 % genera, and 1 % of the total species were found with C<sub>4</sub> metabolism. Six vascular families, *e.g.* *Amaranthaceae*, *Chenopodiaceae*, *Portulacaceae*, *Cyperaceae*, *Gramineae*, and *Commelinaceae*, included C<sub>4</sub> species, which was much less than found in semi-arid grasslands and arid deserts in North China (10–11 families). This indicated that the families with C<sub>4</sub> species occurrence in tropical region were not as common as in the dry regions (Pyankov *et al.* 2000, Wang 2002b,c). The total family number in Yunnan province was more than 300, while that in North China grasslands was only 89. C<sub>4</sub> proportion (C<sub>4</sub>/total species) in moist tropical region (1.1 %) was also less than that in North China grasslands (2–5 %), even if the total species number was about 4 times as high as the latter (Wang 2002c,d, Wang 2004). According to the published data (Yunnan Institute of Tropical Botany 1980, Institutum Botanicum Kunmingense 2000-2003) and rough estimation (Teeri and Stowe 1976, Wang 2004), there should be more than 250 C<sub>4</sub> species in the Yunnan province, for more than 400 species in the genera with C<sub>4</sub> plants have not been determined, including species from *Panicum*, *Andropogon*, *Digitaria*, *Cymbopogon*, and *Arundinella*. Further studies on C<sub>3</sub> and C<sub>4</sub> plant identification are needed to explore the C<sub>4</sub> plant occurrence and their relations with climate changes.

C<sub>4</sub> species in the tropical region mostly belong to few families, *e.g.* *Gramineae* and *Cyperaceae* (Table 1). Of

species was found on the mid-altitude Plateau (2 000–2 500 m a.s.l.). Only 3 % of the total C<sub>4</sub> species can be found in the high altitude (>3 500 m, high-cold mountain plateau) and 7 % in the low altitude (<500 m). This suggests that the occurrence of C<sub>4</sub> species is significantly less in both high and low altitudes in the tropical region.

the total 159 identified C<sub>4</sub> species, 129 species were C<sub>4</sub> grasses, about 81 % of the total C<sub>4</sub> species and about 14 % of the total grasses identified in Yunnan province. 18 sedge species were identified with C<sub>4</sub> photosynthesis, which was about 11 % of the total C<sub>4</sub> species and 12 % of the total sedges identified in the region. Only two *Chenopodiaceae* species were identified with C<sub>4</sub> photosynthetic pathway. This was much different from North China grasslands (Wang 2002a, 2003a) and Mongolian deserts (Pyankov *et al.* 2000). These studies found that *Chenopodiaceae* C<sub>4</sub> species was about 18–19 % of total identified C<sub>4</sub> species in semi-arid and arid regions, but in the tropical region it was less than 1.3 %. This may indicate *Chenopodiaceae* C<sub>4</sub> species may be more fit for semi-arid and arid environments, *e.g.* grasslands and deserts, while C<sub>4</sub> grasses and sedges more fit the moist conditions. This suggested that the climatic pattern for *Chenopodiaceae* C<sub>4</sub> species was different from that for grass and sedge C<sub>4</sub> plants.

Steep gradient of moisture and complex geo-relief in the Yunnan province resulted in high abundance of morphological functional types (Table 1). Of the total 159 C<sub>4</sub> species, 49 % fall into HPG (34 %) and HAG (15 %), mainly due to sufficient moisture in the tropical region (750 to 17 500 mm). Some species are as high as 2–4 m, *e.g.* *Pennisetum purpureum* Schum., *Rottboellia exaltata* L., *Saccharum spontaneum* L. 34 % species belonged to MPG (15 %) and MAG (19 %), 9 % was in SPG and SAG. In general, the amount of C<sub>4</sub> species is much higher in the tropical region than in the semi-arid grasslands and arid deserts in North China (Wang 2002b,c). Relatively higher HPG and HAG proportion may lead to higher C<sub>4</sub> productivity in the moist tropical region, and this information may contribute to the interpretation of C<sub>4</sub> biota productivity in tropical regions.

Similar to other regions in China, C<sub>4</sub> plant distribution is consistent with habitats, altitude, climate, and geography in the Yunnan province (Table 1). Even though forests and woods are the dominant vegetation in the tropical region, the occurrence of C<sub>4</sub> species in these two vegetation types is much less (19 %), while more than half (51 %) of them is found in disturbed and cultivated land (DB). More C<sub>4</sub> species in early succession stages (DB, RL) suggested plants of this type have higher tolerance to high temperature and high irradiance and can be pioneer species in community restoration in tropical regions. Similar to that in Tibetan Plateau (Wang 2003b), C<sub>4</sub> plant distribution is a significant response to altitude in

the region (Fig. 1). The numbers of  $C_4$  species were relative less in both low and high altitudes, most of these species (90 %) can be found from 500 to 3 000 m a.s.l., where annual precipitation varies from 1 000 to 1 500 mm. The finding suggests that the occurrence of  $C_4$  species in tropical region is consistent with climate and

geography, as well as with community succession (Table 1 and Fig. 1). Therefore land managements in the tropical region must take into account  $C_4$  species occurrence and its composition, which are closely related to climate changes, land use, and vegetation dynamics.

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