C_4 species and their response to large-scale longitudinal climate variables along the Northeast China Transect (NECT)

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Abstract

Natural occurrence of C_4 species, life forms, and their longitudinal distribution patterns along the Northeast China Transect (NECT) were studied. Six vegetation regions experiencing similar irradiation regimes, but differing in longitude, precipitation, and altitude were selected along the NECT from 108 to 131 °E, around altitude of 43.5 °N. Seventy C_4 species were identified in 41 genera and 13 families. 84 % of the total C_4 species were found in four families: *Gramineae* (38 species), *Chenopodiaceae* (11 species), *Cyperaceae* (5 species), and *Amaranthaceae* (5 species). C_4 grasses make up 54 % of the total identified C_4 species along the NECT and form the leading C_4 family in meadow, steppe, and desert along the NECT. C_4 *Chenopodiaceae* species make up about 16 % of the C_4 species and become less important, particularly in the meadow and the eastern end of the NECT. 57 % of the total C_4 species are therophytes and 37 % are hemicryptophytes, which is consistent with floristic composition and land utilization. In general, the number of C_4 species decreased significantly from the west to the east or from dry to moist areas along the NECT, and was remarkably correlated with annual precipitation (r^2 = 0.677) and aridity (r^2 = 0.912), except for salinized meadow region. The proportion of C_4 species from all the six vegetation regions was considerably correlated with these two climatic parameters (r^2 = 0.626 or 0.706, respectively). These findings suggest that the natural occurrence of C_4 species varies significantly along the large-scale longitudinal gradient of the NECT. The notable relationship of C_4 species number and proportion in the flora with variations in annual precipitation and aridity suggest that these two climatic parameters are the main factors controlling the longitudinal distribution patterns of C_4 species along the NECT.

Additional key words: C_4 plants; climatic pattern; large-scale longitudinal gradient; life form.

Introduction

More than 1 700 C_4 plant species have been identified (Li 1993) since the work of Downton and Tregunna (1968) and Black (1971). Most of the former studies focused on the classification of plant species as to their photosynthetic pathway (C_3, C_4, and CAM) (Williams and Markley 1973, Downton 1975, Waller and Lewis 1979, Redmann *et al*. 1995, Tang and Zhang 1999, Wang 2002b). The geographic distribution of C_4 species and their climatic patterns have also been well documented (Teeri and Stowe 1976, Teeri *et al*. 1980, Collins and Jones 1985, Takeda and Hakoyama 1985, Ueno and Takeda 1992, Ehleringer *et al*. 1997, Wang *et al*. 1997, Yin and Li 1997, Collatz *et al*. 1998, Keeley 1998, Pyankov *et al*. 2000). Some studies have illuminated relations between climate change and the occurrence of C_4 species in *Poaceae* (Teeri and Stowe 1976), *Dicotyledoneae*, and *Cyperaceae* (Teeri *et al*. 1980). These reports provide strong evidence that the occurrence of C_4 species is correlated with climatic variables in some regions. The knowledge on C_4 species is important for the evaluation and prediction of vegetation change during global climatic change and for the restoration and conservation of natural ecosystems (Pyankov *et al*. 2000, Wang 2002a). But nobody has yet looked at the occurrence of C_4 species and their life forms based on large-scale longitude climatic and topographic variations over large-scale terrestrial transect.

The Northeast China Transect (NECT), identified as a mid-latitude semi-arid terrestrial transect by the Global Change and Terrestrial Ecosystems (GCTE), runs in

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parallel to 43°30'N, ranging from 42 to 46 °N and from 108 to 131 °E (Zhang *et al.* 1997). Most studies on the NECT have focused on the effect of climatic and geographic variability on ecosystem production and vegetation distribution (Zhang *et al.* 1997, Ni and Zhang 2000, Wang and Gao 2003, Wang *et al.* 2003). Some authors tested photosynthesis of plant functional types with climatic changes along the NECT (Tang and Zhang 1999, Wang 2003). Few authors identified C_4 species by discrimination analysis (Tang and Zhang 1999). However, the natural occurrence of C_4 species, life form composition, and their response to the large-scale longitude climatic variables along the NECT remain unclear. The objective of the present study was to investigate the natural occurrence of C_4 species, life form variations, and their response to large-scale climatic and geographic changes along the NECT. This study is highly relevant to better understanding the effects of global change on photosynthetic pathways, vegetation dynamics, and ecosystem production.

Materials and methods

Study sites: The NECT runs parallel to 43°30'N, ranging from 42 to 46 °N and 108 to 131 °E in Northeast China, about 1 600 km in length and 300 km in width (Zhang *et al.* 1997). Due to the steep gradient of precipitation and elevation from the west to the east, vegetation varies gradually from desert, desert steppe, and typical steppe in the west to woodland, temperate conifer-broadleaf mixed forests, and deciduous broadleaf forests in the east, with meadow grasslands in the middle (Fig. 1) (Zhang *et al.* 1997, Ni and Zhang 2000). The temperate conifer-broadleaf mixed forests, deciduous broadleaf forests, and woodland have mountain dark brown forest soils and brown soils (Table 1). Most of the meadows have dark meadow soils, while those of typical steppe and desert steppe in the west have chestnut and sandy chestnut soils. The elevation gradient along the NECT is also steep, ranging from 140 m in the middle to 1 000 m in the east and 1 700 m in the west (Ni and Zhang 2000).

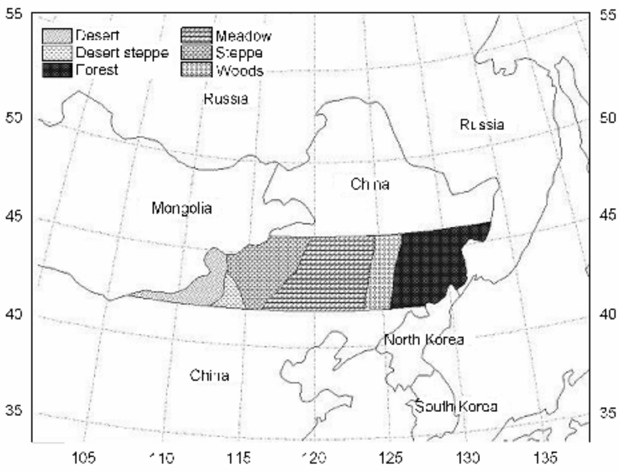

Fig. 1. Location of the Northeast China Transect (NECT) and vegetation division.

Climate: The main determinants of the climate in Northeast China are the Mongolian anticyclone and the moist Pacific air mass. In winter, Northeast China is dominated by an intense Mongolian anticyclone (Domros and Peng 1988). The steep pressure gradient between this high and the Aleutian low-pressure system produces a strong westerly flow of cold, dry continental air at the surface over Northeast China. As the anticyclone breaks down in spring, the region increasingly comes under the influence of the moist Pacific air mass, reaching a climax in two months as summer monsoon. As the summer draws to end, the low pressure area over the Indo-Pakistan subcontinent disappears with the development of the Mongolian anticyclone. The mean annual air temperature ranges from 0.7 to 6.0 °C, varying from –21 °C in January to 23 °C in July. Moisture gradient is very steep, with annual precipitation varying from 100–300 mm in the west to 600–1 000 mm in the east (Table 1). Precipitation is not distributed evenly over the growing season, with 70 % falling between June and August in this region. The aridity indexes vary from 0.7 in the eastern forest to 6.0 in the western desert. A more detailed description of the climate of northeast China and the NECT can be found in Ripley *et al.* (1996) and Ni and Zhang (2000).

Methods: The experiment was conducted from 1997 to 2000 along the NECT. Floristic composition was obtained from references published from 1957 to 2002 (Qian 1957, China Vegetation Committee 1980, Commissione Redactorum Florae Intramongolicae 1980, Shirongdaolji 1991, Liu 1993, Shai and Li 1994, Chen and Jia 2002), as well as from sampling data (*e.g.* species number, distribution, and vegetation type) conducted from 1997 to 2000 (Wang 2002a, Wang *et al.* 2002). Data on photosynthetic pathways were compiled from references published between 1985 and 2002 (Takeda and Hakoyama 1985, Li 1993, Redmann *et al.* 1995, Wang *et al.* 1997, Yin and Li 1997, Tang and Zhang 1999, Pyankov *et al.* 2000, Wang 2002a,b). Plant life form was classed into macrophanerophyte (M), nanophanerophyte (N), chamaephyte (Ch), hemicryptophyte (H), geophyte (G), and therophyte (Th), based on the Raunkiaer system (Li 1979, Wang *et al.* 2002).

The location and elevation of each sampling area were measured using GPS. Climate data, including annual and monthly precipitation, annual and monthly mean temperature and aridity, were taken from the Climate Database of Laboratory of Quantitative Vegetation Ecology, Institute of Botany, Chinese Academy of Sciences, and from forty local weather stations throughout the NECT.

Regressions of C_4 species number and C_4 species proportion against climate parameters were performed using *Excel for Windows 98*.

Table 1. The topographic, edaphic and climatic characteristics of the vegetation regions along the Northeast China Transect (NECT). Aridity index = 0.16 ΣT/P, where T is the sum of daily mean temperatures (≥10 °C) and P is the sum of precipitation [mm] of the same period.

	Desert	Desert steppe	Steppe	Meadow	Woodland	Forest
Longitude location (E)	108–113	113–115	114–117	118–123	123–126	126–131
Annual precipitation [mm]	100–300	266–387	200–350	300–400	500–700	800–1000
Soil type	Sandy brown	Chestnut	Chestnut	Dark meadow	Brown	Mountain dark brown
Elevation [m]	900–1500	1400–1600	900–1300	130–240	290–360	380–800
Annual mean temperature [°C]	2.0–5.0	–0.2–2.0	0–3.0	2.7–4.7	3.7–4.4	1.8–3.4
Aridity index	2.3 – 6.0	2.3–4.2	1.8–2.2	1.4–2.5	1.4–1.5	0.7–1.2
Area size (10 000 km^2)	> 7	> 4	> 13	> 15	> 6	> 13

Results

Floristic composition: There were 13 vascular plant families, about 11 % of the total plant families of the flora along the NECT, in which C_4 photosynthesis occurs (Table 2), 3 in *Monocotyledoneae* (*e.g. Cyperaceae*, *Gramineae,* and *Commelinaceae*), and 10 in *Dicotyledoneae* (*e.g.* *Amaranthaceae*, *Portulacaceae*, *Chenopodiaceae*, *Caryophyllaceae*, *Fabaceae*, *Zygophyllaceae*, *Euphorbiaceae*, *Compositae*, *Solanaceae,* and *Umbelliferae*). Of the total 1 754 plant species identified along the NECT, 70 species are C_4 species, with 37 % (26 of 70) in *Dicotyledoneae* and 63 % (44 of 70) in *Monocotyledoneae* (Table 2). *Gramineae* is the leading C_4 family in the whole area of the NECT, followed by *Chenopodiaceae*, *Amaranthaceae,* and *Cyperaceae* (Table 3). This indicates that the C_4 plants along the NECT mostly belong to these few families.

Gramineae is the most abundant family in the flora along the NECT with 121 species in 53 genera (Table 2). 38 species of the total 121 grass species, in 22 genera, were identified as having C_4 photosynthetic pathway, and the genera with C_4 grass species made up 42 % of the total *Gramineae* genera. All the species of *Aristida*, *Arundinella*, *Chloris*, *Digitaria*, *Echinochloa*, *Enneapogon*, *Eragrostis*, *Eriochloa*, *Imperata*, *Miscanthus*, *Panicum*, *Setaria*, *Spodiopogon,* and *Tripogon* were identified as having C_4 photosynthetic pathway (Table 4). A majority of C_4 grasses (36 of 38) can be found from the middle meadow to the western steppe, desert steppe, and desert along the NECT, and only a few species (*e.g.* *Eragrostis ferruginea* Beauv. and *Miscanthus sinensis* Anderss.) are distributed in the eastern woodland and forests.

Fifty-seven *Cyperaceae* species in 8 genera were identified along the NECT (Table 2). However, only 5 species in 3 genera had C_4 photosynthetic pathway (1 in *Bolboschoenus*, 3 in *Carex,* and 1 in *Cyperus*) (Tables 3 and 4). The number of sedge C_4 species found along the NECT was less than that from Northeast China grasslands (12 species in 6 genera) (Yin and Li (1997).

Of the 13 plant families with C_4 photosynthesis along the NECT, *Chenopodiaceae* was the forth in abundance. Eleven chenopods (22 % of total chenopods) in 5 genera were C_4 plants (Table 2), which was less than that found in *Gramineae* of this study and in the vegetation from Mongolia (Pyankov *et al*. 2000). Most of these species are distributed in the meadow, steppe, and desert, and few are found in the woodland and forests along the NECT. *Amaranthaceae* is the second leading dicotyledonous family with high number of C_4 species in this large transect. *Amaranthaceae*, *Portulacaceae,* and *Commelinaceae* were the only three families in which all the species in a particular genus were identified as having C_4 photosynthetic pathway along the NECT (Table 2).

Life form for C_4 species: There were four life forms for C_4 species along the NECT (Table 5). Of the total 70 C_4 species, 57 % was therophyte (Th), 37 % was hemicophyte (H), 4 % was geophyte (G), and only 1 species was chamaephyte (Ch). One half of the Th life form was *Dicotyledoneae* plants and the other half was *Monocotyledoneae* species. 19 % (5 of 26) of the H life form were in *Dicotyledoneae* with the other 81 % (21 of 26) in *Monocotyledoneae* (Table 4). Of the C_4 species identified in steppe, desert steppe, and desert, 65 % had the Th life form, 30 % had the H life form, while those in G and Ch life forms formed only 5 %. This indicates that the Th life form is fit for the drought conditions along the NECT.

Patterns of climatic distribution: The number of C_4 species and their proportion varied considerably with climatic variables along the NECT. The saline meadow in the middle of the NECT had the highest number of C_4 species (45 of 70), mainly due to the increase of halophytes (*e.g.* *Achnatherum avinoides* (Honda) Chang, *Aeluropus littoralis* (Gouan) Parlat., *Hemarthria sibirica*

Table 2. The occurrence of C_4 species in different plant families and genera along the Northeast China Transect (NECT).

	Family	Genus numbers		Species numbers	
		Total	C_4 species	Total	C_4 species
Dicotyledoneae	*Amaranthaceae*	1	1	5	5
	Portulacaceae	1	1	1	1
	Chenopodiaceae	16	5	49	11
	Caryophyllaceae	11	1	30	2
	Fabacea	17	1	69	1
	Zygophyllaceae	4	1	5	1
	Euphorbiaceae	4	1	8	1
	Compositae	49	2	91	2
	Solanaceae	6	1	8	1
	Umbelliferae	16	1	28	1
Monocotyledoneae	*Cyperaceae*	8	3	57	5
	Gramineae	53	22	121	38
	Commelinaceae	1	1	1	1
Total		187	41	473	70

Table 3. The list of C_4 species and their life forms along the Northeast China Transect (42–46°N, 106–131°E). Nomenclature follows Yin and Wang (1997). Habitat types: FO = forest, WO = wood, ME = meadow, ST = steppe, DS = desert steppe, DE = desert. Life forms: M = macrophanerophyte, N = nanophanerophyte, Ch = chamaephyte, H = hemicryptophyte, G = geophyte, Th = therophyte.

	Species	Sites	Life form
Dicotyledoneae			
Amaranthaceae	*Amaranthus ascendens* Lois.	FO WO ME	Th
	A. blitoides S. Watson	ME	Th
	A.livdis L.	FO	Th
	A. retroflexus L.	FO WO ME ST DE	Th
	A. viridis L.	FO	Th
Portulacaceae	*Portulaca oleracea* L.	FO WO ME ST DS	Th
Chenopodiaceae	*Agriophyllum pungens* (Vahl) Link A. Dietr.	ME ST DS DE	Th
	Atriplex centralasiatica Iljin	DE	Th
	A. sibirica L.	ST DS DE	Th
	Bassia dasyphylla O. Kuntze	ME ST DE	Th
	Kochia prostrata Schrad.	ME ST DS DE	Ch
	K. scoparia (L.) Schrad.	FO WO ME DS DE	Th
	K. sieversiana (Pall.) C. A. Mey.	ME ST DE	Th
	Salsola collina Pall.	FO WO ME ST DS DE	Th
	S. foliosa (L.) Schrad.	ME	Th
	S. laricifolia Turcz.	DE	Th
	S. pestifer Litv.	ST DS DE	Th
Caryophyllaceae	*Dianthus amurensis* Jacq.	ME	H
	D. chinensis L.	FO WO DE	H
Fabaceae	*Thermopsis lanceolata* R. Br.	ME ST DS DE	H
Zygophyllaceae	*Tribulus terrestris* L.	FO WO ME ST DS DE	Th
Euphorbiaceae	*Euphorbia humifusa* Willd.	FO WO ME ST DS DE	Th
Compositae	*Hypochaeris grandiflora* Ledeb.	ME	H
	Senecio cannabifolius Less. var. *integrifolius* (Koidz.) Kitam.	FO	H
Solanaceae	*Siphonostegia chinensis* Benth.	FO	Th
Umbelliferae	*Sanicula rubriflora* Fr. Schm.	WO	G
Monocotyledoneae			
Cyperaceae	*Bolboschoenus maritimus* (L.) Pall.	FO WO ME	H

Table 3 (continued)

	Species	Sites	Life form
Cyperaceae	*Carex enervis* C. A. M.	ST	H
	C. leiorhyncha C. A. M.	FO	H
	C. pediformis C. A. M.	ST DS	H
	Cyperus orthostachys Fr. et Sav.	FO	H
Gramineae	*Achnatherum avinoides* (Honda) Chang	ME	H
	A. splendens (Trin.) Nevski	ST DS DE	H
	Aeluropus littoralis (Gouan) Parlat	ME DE	H
	Aristida adscensionis L.	DS DE	H
	Arthraxon hispidus (Thunb.) Makino	FO ME	H
	Arundinella hirta (Thunb.) Tanaka	ME	H
	Chloris virgata Sw.	WO ME ST DS DE	Th
	Cleistogenes chinensis (Maxim.) Keng	ME	H
	C. squarrosa (Trin.) Keng	WO ME ST DS DE	H
	Crypsis schoenoides (L.) Lam.	DE	Th
	Digitaria ciliaris (Rotz.) Koel	ME	Th
	D. ischaemum (Schreb.) *Schreb. ex* Muhl.	WO ME ST DS DE	Th
	D. lineis (Krock.) Crep	ME	Th
	D. sanguinalis Scop.	WO ME	Th
	Echinochloa candata Roshev.	ME	Th
	E. crus galli (L.) Beauv.	FO WO ME ST DS DE	Th
	Enneapogon borealis (Griseb.) Honda	ST DE	Th
	Eragrostis cilianensis (All.) Link.	FO ME DS	Th
	E. ferruginea Beauv.	WO	H
	E. filiformis Link.	ME	Th
	E. minor Host	ST	Th
	E. pilosa (L.) P. B.	WO ME DS	Th
	E. poaeoides Beauv.	DS DE	Th
	Eriochloa villosa (Thunb.) Kunth L.	ME	Th
	Hemarthria sibirica (Gand.) Ohwi.	ME	H
	Hierochloe glabra Trin.	ME DE	H
	Imperata cylindrica (L.) P. B.	ME	G
	Miscanthus sacchariflorus (Maxim.) Hack.	ME	H
	M. sinensis Anderss.	WO	H
	Panicum ruderale (Kitag.) Cheng	ME	Th
	Pennisetum centrasiaticum Tzvel.	ST	H
	P. flaecidum Griseb.	ME DS DE	G
	Setaria arenaria Kitag.	ME ST	Th
	S. glauca (L.) Beauv.	FO ST DS	Th
	S. lutescens Weigel. F. T. Hubb.	FO WO DS DE	Th
	S. viridis (L.) Beauv.	FO WO ME ST DS DE	Th
	Spodiopogon sibiricus Trin.	WO ME DS	H
	Tripogon chinensis (Franch.) Hack.	DE	H
Commelinaceae	*Commelina communis* L.	FO WO ME	Th

(Gand) Ohwi., and *Kochia scoparia* (L.) Schrad.), and invaders caused by overgrazing [*e.g. Amaranthus blitoides* S. Watson, *Salsola foliosa* (L.) Schrad., *Digitaria ciliaris* (Rotz.) Koel, and *D. lineis* (Krock.) Crep.]. C_4 species numbers in the other 5 vegetation regions dropped from the western desert (30 species) to the eastern forests (22 species). In general, numbers of C_4 species in both *Gramineae* and *Chenopodiaceae* increased from the moist eastern forests to the dry western desert. The climatic distribution patterns for C_4 species along the NECT appear to be mainly related to annual precipitation and aridity, likely due to the significant moisture gradient along the NECT. The numbers of C_4 species pooled over all the 6 vegetation regions were not significantly correlated with annual precipitation (r^2 = 0.075; Fig. 2*A*) or aridity (r^2 = 0.063; Fig. 2*C*). Those from the desert, desert steppe, steppe, woodland, and forests were, however, significantly correlated with annual precipitation (r^2 = 0.677; Fig. 2*B*) or aridity (r^2 = 0.912; Fig. 2*D*). The proportion of C_4 species in the flora dropped linearly with the increase of annual precipitation from the west to the east along the NECT (r^2 = 0.626; Fig. 3*A*), and increased significantly with aridity from the east to the west (r^2 = 0.706; Fig. 3*B*). This suggests that the relative abundance of C_4 species in the flora clearly correlates with the variations of moisture along the NECT.

Discussion

C_4 species are most common in the grasslands of Northeast China (Redmann *et al*. 1995, Wang 2002a), but less common in the woodland and forests of the region. C_4 species composition along the NECT was strongly dominated by *Gramineae*, which makes up 54 % of the total C_4 species. This was mainly due to the high graminaceous plant (grasses and sedges) composition, which made up to 42 % of the total forage (Li 1979) and 64 % of C_4 species in the North China grasslands (Wang 2002b). These findings are much different from the work conducted in Asian deserts and steppes by Pyankov *et al*. (2000). They found that the *Chenopodiaceae* was the leading C_4 family and grasses were less important because of the dry climate in the Asian deserts in Mongolia. The NECT, however, is relatively moist compared to these regions and this may result in the relatively higher abundance of C_4 grasses and sedges. Relatively more C_4 chenopods occurred in the NECT

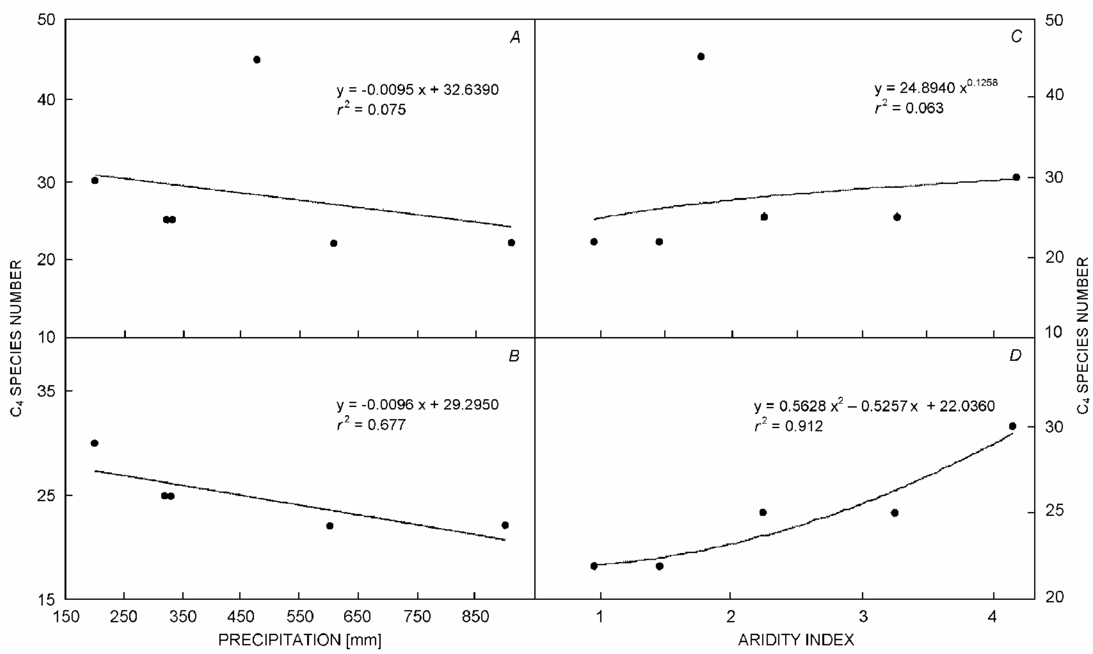

Fig. 2. Relationships between the occurrence of C_4 species and annual precipitation (*A* and *B*) and aridity (*C* and *D*) along the Northeast China Transect (NECT).

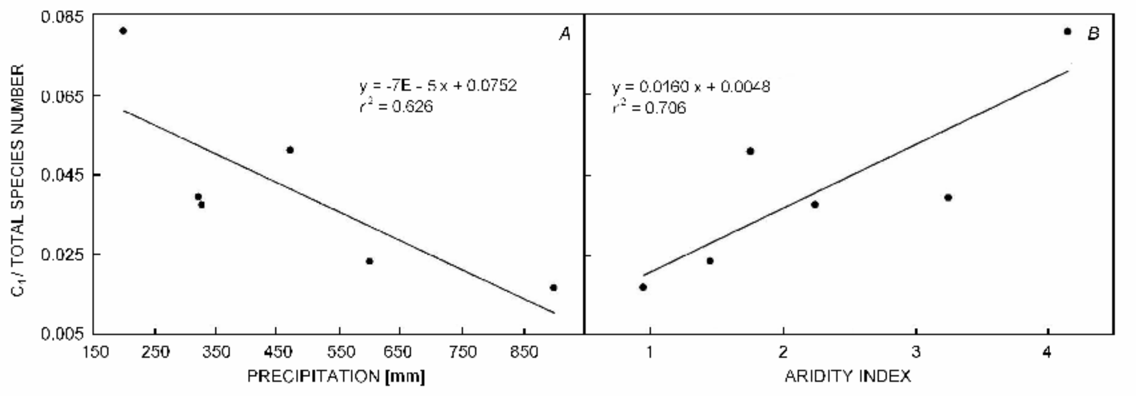

Fig. 3. Relationships between the proportion of C_4 species and annual precipitation (*A*) and aridity (*B*) along the Northeast China Transect (NECT).

Table 4. Total identified species and C_4 species in the genera in which C_4 species occurred in *Gramineae*, *Chenopodiaceae*, *Cyperaceae*, and *Amaranthaceae* along the Northeast China Transect (NECT).

	Taxon	Total	C_4
Gramineae	*Achnatherum*	6	2
	Aeluropus	2	1
	Aristida	1	1
	Arthraxon	2	1
	Arundinella	1	1
	Chloris	1	1
	Cleistogenes	5	2
	Crypsis	3	1
	Digitaria	4	4
	Echinochloa	2	2
	Enneapogon	1	1
	Eragrostis	6	6
	Eriochloa	1	1
	Hemarthria	1	1
	Hierochloe	3	1
	Imperata	1	1
	Miscanthus	2	2
	Panicum	1	1
	Pennisetum	2	2
	Setaria	4	4
	Spodiopogon	1	1
	Tripogon	1	1
	Total	53	38
Chenopodiaceae	*Agriophyllum*	1	1
	Atriplex	7	2
	Bassia	2	1
	Kochia	3	3
	Salsola	7	4
	Total	20	11
Amaranthaceae	*Amaranthus*	5	5
	Total	5	5
Cyperaceae	*Bolboschenus*	2	1
	Carex	36	3
	Cyperus	5	1
	Total	43	5

Table 5. Life forms of C_4 species in each family identified along the Northeast China Transect (NECT). Life forms: M = macrophanerophyte, N = nanophanerophyte, Ch = chamaephyte, H = hemicryptophyte, G = geophyte, and Th = therophyte.

Family	Th	H	G	Ch
Dicotyledoneae				
Amaranthaceae	5	0	0	0
Portulacaceae	1	0	0	0
Chenopodiaceae	10	0	0	1
Caryophyllaceae	0	2	0	0
Fabaceae	0	1	0	0
Zygophyllaceae	1	0	0	0
Euphorbiaceae	1	0	0	0
Compositae	0	2	0	0
Solanaceae	1	0	0	0
Umbelliferae	0	0	1	0
Monocotyledoneae				
Cyperaceae	0	5	0	0
Gramineae	20	16	2	0
Commelinaceae	1	0	0	0
Total	40	26	3	1

steppe and desert steppe than in its woodland and forests, which agrees with the findings of Pyankov *et al*. (2000) that the abundance of chenopods is closely correlated with aridity. This suggests that C_4 chenopods may have greater tolerance to drought stress than grasses.

Life form composition for C_4 species was consistent with grassland succession and floral composition along the NECT (Wang 2002b, Wang *et al*. 2002). More than one half (57 %) of the C_4 species identified along the NECT was therophyte (Th), and most of these species (60 %) were found in the grasslands disturbed by grazing and in the old fields (Wang 2002b). These Th life form species were mainly annual grasses, invaders, and halophytes. The relatively high number of Th plants in meadow, steppe, desert steppe, and desert along the NECT is primarily due to their high capacity of seed productions and seed dispersal, which are advantages for the recovery of deteriorated grasslands and old fields (Wang 2002a). Having high number of Th plants is also an adaptation for the highly climatic variable in the NECT, where 70 % of the total annual rainfall occurs between June and August in the growing season. Th life from plants can use seasonal precipitation efficiently (Wang 2002a). The relative abundance of halophyte C_4 species with Th life form (*e.g. Chloris virgata* Sw. and *Kochia sieversiana* Pall.) in the meadow is likely due to their higher tolerance to salt and seasonal drought (Redmann *et al*. 1995, Wang 2002a). The relatively high numbers of H life form C_4 species along the NECT are consistent with the climatic attributes of the north, temperate zone (Li 1979, Wang 2002a,b).

The relationships between the occurrence of C_4 species and climatic variables have been well documented in many regions (Teeri and Stowe 1976, Teeri *et al*. 1980, Pyankov *et al*. 2000). In general, the number and proportion of C_4 species in the flora increased with increasing aridity along the NECT (Fig. 2). This reflects the greater tolerance of C_4 species to drought. The increase in number of C_4 chenopods from the eastern end to the western end of the NECT is consistent with the results from Mongolia of Pyankov *et al*. (2000). The number of graminaceous plants also increased from the east to the west along the NECT. But the highest abundance of C_4 species found in the meadow may result from the integration of moisture and salinity in the meadow region (Wang 2002a,b). Previous studies show that 20 % C_4 species and 18 % C_3 species identified in China were found in the salinized meadow of Northeast China (Wang *et al.* 1997, Wang 2002a). C_4 species number from the salinized meadow was about 1.5–2.0 times of the other five vegetation regions. This may in part explain the fact that the correlation between C_4 species number from all the 6 vegetation regions and precipitation (Fig. 2*A*) or aridity (Fig. 2*C*) was not significant, but the correlation was significant when the meadow was not included. Hence particular soil conditions may alter C_4 species distribution pattern along large-scale climatic gradient. The significant correlation between number of C_4 species and precipitation or aridity along the NECT indicates that these two climatic parameters are the main controlling factors for C_4 species distribution. This and other previous studies (Redmann *et al.* 1995, Yin and Li 1997, Wang 2002a,b) have clearly documented the distribution of C_4 species, their relationships with large-scale climate change, and the impact of grassland utilization in Northeast China. Because of the confounding factors of climate, soil fertility, and plant water use efficiency, further studies, *e.g.* reciprocal transplanting, manipulation of water, and greenhouse cultivation, are needed to explore the fundamental bases of relationships between C_4 plant distribution and climate change.

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