Climate-driven $C_4$ plant distributions in China: divergence in $C_4$ taxa

Renzhong Wang & Linna Ma

There have been debates on the driving factors of $C_4$ plant expansion, such as $PCO_2$ decline in the late Miocene and warmer climate and precipitation at large-scale modern ecosystems. These disputes are mainly due to the lack of direct evidence and extensive data analysis. Here we use mass flora data to explore the driving factors of $C_4$ distribution and divergent patterns for different $C_4$ taxa at continental scale in China. The results display that it is mean annual climate variables driving $C_4$ distribution at present-day vegetation. Mean annual temperature is the critical restriction of total $C_4$ plants and the precipitation gradients seem to have much less impact. Grass and sedge $C_4$ plants are largely restricted to mean annual temperature and precipitation respectively, while Chenopod $C_4$ plants are strongly restricted by aridity in China. Separate regression analysis can succeed to detect divergences of climate distribution patterns of $C_4$ taxa at global scale.

Modern ecosystems, such as tropical savannas, temperate grasslands and semi-deserts, have a significant component of $C_4$ plants. At global scale, only about 3% of total plant species is characterized by $C_4$ photosynthetic pathway, $C_4$ plants, however, account for roughly 25% of global terrestrial primary production, including important crops, weed plants and potential biofuels. Understanding the occurrence and distribution of $C_4$ biota can yield important information regarding to global primary productivity and to the effects of climate changes on ecosystem structures and functions, as well as $C_4$ plant’s past, present and future.

The abundance of $C_4$ species in particular regions and their distribution in relation to climate have been well reported in North America, Africa, Europe, Australia, Middle East, but has not been studied details in China and this knowledge is essential for formulating generalization regarding to global $C_4$ occurrence and their relation with climate. The vast area and varied terrain in China with complex ecosystem components (e.g. rain forests, wet lands, temperate grasslands, deserts and tundra) and great climate changes contain more different $C_4$ information. Moreover, the deserts in China and Asia differ markedly from the arid ecosystems of North America, Australia and Europe in the taxonomic groups of $C_4$ species. In China deserts and arid regions, Chenopodiaceae is the leading $C_4$ family, but their distribution in relation to climate has not yet been addressed, this is very important for understanding the effects of climate changes on ecosystem structures and functions, particularly with the increasing of desertification in west China in recent decades.

Although the occurrence and distribution of $C_4$ plants have been documented at different scales over the past couple of decades, there have been debates on $C_4$ plant expansion at large-scale, for example, (i) what is the driving factor for $C_4$ plant expansion, decrease in atmospheric CO$_2$ concentration in the late Miocene or climate (both ancient and modern) variability? It had been hypothesized that PCO$_2$ decline caused $C_4$ plant expansion rapidly during the late Miocene (~8 to 4 Ma), but some evidences suggested that $C_4$ plant expansion was likely driven by addition factors, such as enhanced low-latitude aridity, seasonal precipitation and fire in the Miocene. The present-day global distribution of $C_4$ grasses is largely restricted to warmer climate and precipitation, for strong positive relationships between $C_4$ grass abundance and growing season temperature at continental scales. Few found that the restriction of $C_4$ grasses to warmer areas was due largely to their evolutionary history, (ii) whether the different $C_4$ taxa have similar climate distribution pattern in present-day at large-scale? Indeed, there are few large data sets with which to examine occurrence and climate distribution pattern of different $C_4$ taxa in modern vegetation at continental areas, resulting severely limits the accuracy understanding $C_4$ plant expansion and the ecological implications.

Results

Of the total vascular plants (about 30000 species) in China, 371 species are identified with $C_4$ photosynthesis in 11 families (Table 1; Supplementary Table S1), but 90.83% $C_4$ species occurring in Gramineae (53.64%), Cyperaceae...
(19.67%) and Chenopodiaceae (17.52%; Chenopod, hereafter). Relative lower C4 plant occurrence is due largely to there is no tropical savannas (with more C4 grasses) in China. In general, total C4 species abundance decreases from south to north and from east to west in China (Fig. 1a,b). The total C4 species abundance in Heilongjiang (most northern territory) is only 1/3 of that in Yunnan (most southern territory), while that in western province of Qinghai is less than 1/3 of that in Taiwan (Fig. 1b). The total C4 species abundance is strongly and positively related with mean annual temperature (Tm) ($R^2 = 0.56$, $P < 0.0001$) and mean annual precipitation ($P_m$) ($R^2 = 0.47$, $P < 0.0001$; Fig. 2a–c). Multiple regression of the total C4 species abundance ($Y_{totalC4}$) against climate variables shows that there is a strongly and positively correlation between $Y_{totalC4}$ and $T_m$, $P_m$ and aridity ($A_t$) as model:

$$Y_{totalC4} = 21.65 + 3.33T_m + 0.019P_m + 3.90A_t (F = 14.92, \ P < 0.001, \ N = 32) \tag{1}$$

This indicates that these climate factors affect the distribution of total C4 species abundance in China. Stepwise multiple regression analysis exhibits that $T_m$ has highest contributions (61.5%) to total C4 species distribution, while the impacts of $P_m$ (2.0%) and $A_t$ (2.6%) are relative less (Table 2).

C4/C3 proportion in China flora is about 1.2%, ranging from 0.85% in Tibet to 4.77% in Shandong province (Fig. 3). Most humid southern provinces (e.g. Yunnan, Guangxi and Sichuan) have lower C4/C3, even though the occurrence of C4 species is high in these regions. There are no significant relations between C4/C3 proportions and climate variables in present-day vegetation in China ($P > 0.05$; Fig. 2d–f), indicating that C4/C3 proportion dose not exhibit certain ecological pattern, even the C4 occurrence dose significantly related with plant abundance at large-scale region.

C4 distribution patterns predicted by total C4 species abundance appear to be insensitive to climate factors known to influence C4 occurrence and expansion because of the different adaptive strategies for C4 taxa to climate variables. Both grass and sedge C4 species abundances are strongly and positively related with $P_m$ ($R^2 = 0.51$, $P < 0.001$; $R^2 = 0.58$, $P < 0.001$) and $T_m$ ($R^2 = 0.50$, $P < 0.001$; $R^2 = 0.65$, $P < 0.001$), but significantly and negatively with aridity ($R^2 = 0.23$, $P < 0.01$; $R^2 = 0.35$, $P < 0.001$) (Fig. 4a–c). Multiple regressions of grass C4 species abundance ($Y_{grassC4}$) and sedge C4 species abundance ($Y_{sedgeC4}$) against climate variables manifest that $Y_{grassC4}$ and $Y_{sedgeC4}$ are strong correlated with $T_m$, $P_m$ and $A_t$ as models:

$$Y_{grassC4} = 14.84 + 1.43T_m + 0.018P_m + 0.68A_t (F = 10.91, \ P < 0.001, \ N = 32) \tag{2}$$

$$Y_{sedgeC4} = 5.57 + 1.35T_m + 0.0025P_m - 0.91A_t (F = 19.09, \ P < 0.001, \ N = 32) \tag{3}$$

But stepwise multiple regression analysis demonstrates that grass C4 plant distribution is largely restricted to $P_m$ (50.6%), and $T_m$ and $A_t$ functions are not significant ($P > 0.05$). Sedge C4 species is mainly limited to $T_m$ (64.7%) and the impacts of $P_m$ (0.2%) and $A_t$ (2.3%) are very less and no significant ($P > 0.05$; Table 2).

On the contrary, Chenopod C4 plant abundance is strongly and positively related with $A_t$ ($R^2 = 0.88$, $P < 0.001$), and significantly and negatively with both $P_m$ ($R^2 = 0.92$, $P < 0.001$) and $T_m$ ($R^2 = 0.25$, $P < 0.001$; Fig. 4a–c). Stepwise regression of Chenopod C4 plant abundance against climate variables shows that there is a strong correlation between $Y_{ChenopodC4}$ and $P_m$, $T_m$ and $A_t$ as model:

$$Y_{ChenopodC4} = 4.48A_t - 0.014T_m + 0.0045P_m - 10.63 (F = 94.01, \ P < 0.001, \ N = 32) \tag{4}$$

Stepwise multiple regression analysis exhibits that Chenopod C4 plants is confined to arid index (88.2%) in present-day vegetation at whole China. These suggest the distributions of C4 taxa are restricted to different climate factors at present-day vegetation in China.

| Family | Genera | Species number | % of total C4 |
|--------|--------|----------------|--------------|
| Dicotyledoneae | | | |
| Aizoaceae | 3 | 3 | 0.80 |
| Amaranthaceae | 3 | 18 | 4.85 |
| Chenopodiaceae | 17 | 65 | 17.52 |
| Grassulaceae | 1 | 1 | 0.27 |
| Euphorbiaceae | 1 | 2 | 0.54 |
| Nyctaginaceae | 1 | 2 | 0.54 |
| Polygonaceae | 1 | 5 | 1.35 |
| Portulaceae | 1 | 2 | 0.54 |
| Zygophyllaceae | 1 | 1 | 0.27 |
| Monocotyledoneae | | | |
| Cyperaceae | 12 | 73 | 19.67 |
| Gramineae | 72 | 199 | 53.64 |
| Total | 113 | 371 | 99.99 |

Table 1. The occurrence of C4 species in plant families and genera in China.
Discussion

There were many studies on the C₄ plant expansion and distribution in relation to climate over the past couple of decades¹⁻⁻¹⁹, but only few manifested the detail floristic data of C₄ occurrence in large regional scale (e.g. ...
Europe9,10, Middle East13, Central Asia14). 371 identified C4 species within China account for roughly 20% of known C4 plants (about 1800 species global) and that is much greater than the percentage (~13%) of China vascular species to worldwide angiosperms, even though China is not a hot spot for C4 photosynthesis (Fig. 1; Supplementary Table S1). The total number of C4 species in China (Table 1), mainly grasses (53.64%), sedges (19.67%) and Chenopods (17.52%), is much greater than that in Europe9 and Middle East13. However, the number

|          | Pm   | Probability | Tm   | Probability | A1   | Probability |
|----------|------|-------------|------|-------------|------|-------------|
| Total C4 | 0.020| 0.243       | 0.615| 0.000       | 0.265| 0.180       |
| Grass C4 | 0.506| 0.000       | 0.031| 0.176       | 0.002| 0.710       |
| Sedge C4 | 0.002| 0.703       | 0.647| 0.000       | 0.023| 0.170       |
| Chenop C4| 0.027| 0.006       | 0.000| 0.945       | 0.882| 0.000       |

Table 2. Results of stepwise multiple regression analyses. Dependent variables: total C4, grass C4, sedge C4 and Chenop C4; Independent variables: mean annual precipitation (Pm), mean annual temperature (Tm) and arid index (A1). The values of parameter estimate refer positive/ negative relationships between the examined dependent variable and the independent variables.

Figure 2. Regression of the total C4 species numbers and C4/C3 versus mean annual precipitation (Pm), mean annual temperature (Tm) and arid index (Ai) in China.

Figure 3. The C4/C3 fractions in 32 provinces and municipalities of China.
of Chenopod C₄ species is only 1/3 of that in Middle East and 1.5 times of that in Mongolia, probably because China arid regions is smaller than Middle East, but larger than Mongolia. This knowledge is essential for building global C₄ plant database and formulating generalization regarding their relation to global climate.

What is the driving factor for C₄ plant expansion and distribution remains controversial. The evidences of palaeo-vegetation and fossil tooth enamel indicated the global expansion of C₄ plants may be related to lower PCO₂ in the Miocene, but some evidences suggested that C₄ plant expansion was likely driven by climate variables and fire in both old world and present-day vegetation. Our data clearly demonstrate that C₄ plant distributions are restricted to mean annual climate variables (e.g., Tm, Pm and Ai) in the present-day vegetation in China (Fig. 2). From the south to the north, Tm governs the vegetation changes, while from the east to the west moisture gradient (Pm) drives plant distributions. Within China, the total C₄ species abundance is strongly and positively related with Tm and Pm, this suggests that there is remarkably strong tendency for C₄ species to grow in hot and wet conditions, even though the stepwise multiple regression analysis exhibits that the impact of Pm is relative less (Table 2). This is much different with previous observations, their evidences manifest that July average daily temperature is a critical factor for C₄ distribution and the precipitation gradients seem to have much less impacts. Such significant difference is probably because almost 2/3 identified C₄ species are perennial grasses, sedges and some Polygonaceae species, relative higher Pm and Tm are not only favor for their growth in growing seasons, but also for their survival in winters. This is also partly supported by the observation of soil organic carbon and present vegetation which indicates that C₄ fraction of Inner Mongolia grassland has increased by approximately 10% in the past decades because of increasing of temperature.

The C₄/C₃ proportion in China flora is about 1.2% and much lower than 3% estimated at global scale. This is mainly due to complex relief in China, 2/3 of the total area is mountains and plateaus. More mountains and high moisture in southern provinces lead to vast forest vegetation with relative more tree species and lower fractions of grasses and Chenopod species, even the species abundances for both C₃ and C₄ plants are much high in the southern regions. In addition, lower C₄ plant occurrence in China is for the absence of tropical savannas, which is estimated with more C₄ grasses, but large area of temperate grasslands and deserts (40% of China land) devotes considerable C₄ plant resources. There are no significant relations between C₄/C₃ proportions and climate variables in present-day vegetation in China (Fig. 2d–f), indicating that C₄/C₃ proportions do not show significant difference is probably because almost 2/3 identified C₄ species are perennial grasses, sedges and some Polygonaceae species, relative higher Pm and Tm are not only favor for their growth in growing seasons, but also for their survival in winters. This is also partly supported by the observation of soil organic carbon and present vegetation which indicates that C₄ fraction of Inner Mongolia grassland has increased by approximately 10% in the past decades because of increasing of temperature.

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Separate analysis for different C₄ taxa succeed in detecting C₄ distribution patterns accurately at continental scale, for the separate analysis can eliminate the noise signal from the C₄ taxon with different responses to climate variables and adaptive strategies. Previous studies had found that grass and sedge C₄ plants were largely restricted to July average daily temperature. However, it is different in China, separate multiple regression analyses display that the grass and sedge C₄ plant abundances are mainly restricted to Pm and Tm respectively (Table 2). Most grass C₄ species are terrarium plants and their distributions are mainly restricted to Pm, while almost all sedge C₄ species are aquatic plants and the distribution of sedge C₄ taxa is governed by Tm in China. This explanation is also supported by the relative higher proportions of perennial C₄ grasses and sedges in the floristic data (Supplementary Table S1). Unlike the grass and sedge C₄ plants, the distribution of Chenopod C₄ taxon is driven by aridity (Table 2; Fig. 4). Chenopod C₄ plants are favored arid regions with hot summer and sufficient summer precipitation, because most of Chenopod C₄ plants are annual plant species, they can use seasonal precipitation efficiently in dry and hot conditions where the precipitation mainly falls in growing season, and these species can withstand severe droughts as seeds. Even though there are a few studies on the occurrence of C₄ Chenopods in particular regions, but C₄ Chenopod distribution in relation to large-scale climate change has remain largely unexplored and this is important for understanding the effects of climate changes on arid ecosystems with the increase of desertification in west China. In the dry west China (e.g., Xinjiang, Qinghai and Inner Mongolia), 30–45% of the total C₄ species is Chenopod plants, while that in the east and south China is less than 1%. Predominant C₄ Chenopods in hot and arid ecosystems, as well as strong relations with aridity (Fig. 4), imply that the expansion of C₄ Chenopods may be enhanced in China with an increase in hot and aridity worldwide as some climate-change scenarios suggested. Moreover, previous studies proved that the advantage of C₄ plants in water-limited deserts are not considered critical for establishing C₄ grass distribution pattern, and are commonly

![Figure 4. Relations of grass, sedge and Chenopod C₄ plant abundances with mean annual precipitation (Pm), mean annual temperature (Tm) and arid index (Ai) in China.](image-url)
invoked to explain the dominance of C₄ dicots²¹–²⁷, even though they did not separate Chenopod C₄ species from dicots.

Driving factor for C₄ plant expansion at spatial and temporal large-scale is controversial. The palaeosol carbonate and fossil tooth enamel data implicated that the C₄ plant expansion may have been due to decreasing of PCO₂ in late Miocene¹, but other evidences suggested that the development of low-latitude season aridity and changes in growing conditions led to the expansion of C₄ plants at ~7 Ma¹⁹. These different explanations are mainly due to the lack of direct evidences and extensive data analysis. Our mass flora data analysis partly supports Pagani’s perspective¹⁹, but their evidences also can not explain the divergence distribution pattern of different C₄ taxa. The divergence in C₄ climate pattern implicates these C₄ taxa may be with different area of origins, evolutionary histories²¹–²³, expansion mechanism and adaptive strategies, because the Chenopod C₄ taxon has a diametrically opposed distribution pattern with grass and sedge C₄ taxa (Fig. 4). In the previous studies²⁶–²⁸–³³, it had been found that grass and sedge C₄ plants are governed by July average daily temperature, but the distribution of grass, sedge and Chenopod C₄ species in China are largely restricted to Pₘ, Tₘ and Aₙ respectively, for the mean annual climate variables (especially Pₘ and Tₘ) can accurately describe the climate restrictions of plant distributions in China²³–²⁴. Edwards and Still also proved that the restriction of C₄ grasses to warmer areas was due largely to their evolutionary history².

Comparing with most previous researches¹–¹⁹ this work provides detail floristic data of C₄ occurrence in large regional scale based on China flora sources, which is essential for building worldwide C₄ plant database, and also contributes direct evidence formulating generalization regarding the driving factors of C₄ plant expansion. We suggest that the restriction of C₄ distributions at continental scale is due to largely the annual climate variables (e.g. Pₘ, Tₘ and Aₙ) in present-day ecosystems in China. Different C₄ taxa may exhibit diametrically opposite pattern in relation to climate at large-scale likely due to their differences in adaptations, area of origins and evolutionary histories²¹–²³. Our findings suggest that the expansion of Chenopods will increase with the increasing of aridity in western and central China as climate- change scenarios expected, on the contrary, that for grass and sedge C₄ species may decrease in the future. This may have huge impacts on vegetation dynamics and primary plant production for the C₄ plants accounts for roughly 1/4 of global terrestrial primary production²³–²⁴.

Methods

China topography and climate. China, occupied a large area, about 9.6 million km² (3°51′−53°33.5′ N; 73°33′−135°05′ E), stretches 5,026 km across the East Asian landmass. It is primarily mountains, plateaus and plains country, 2/3 of the total area is mountains and plateaus²³. Land elevation in the east plains is about 100–200 m above sea level (as l), while that in the southwest mountains and plateaus are as high as 4000–8000 m as l. The relief is very complicated with both latitudinal and longitudinal climate zones, mixed with steep altitudinal gradients in the northwest and southwest parts, leading great changes in climate.

The climate in China is extremely diverse due to its wide coverage, assortment of terrains and distances to the sea for different locations. Most of China lies in the temperate belt, with its south in subtropical belt and north in subarctic belt. In general, the average temperature in China is 11.8 °C, varying from 31 °C in July to −10 °C in January. Because of the Influences of both latitude and monsoon activities, temperatures vary a great deal, low temperature in winter is −40 °C in Mohe, the northernmost of China, while in hot summer temperature can be as high as 50 °C in Turpan basin, Xinjiang. The average annual precipitation is about 620 mm, ranging from 800–1000 mm in the eastern and coastal areas. Most of China lies in the temperate belt, with its south in subtropical belt and north in subarctic belt. In general, the average temperature in China is 11.8 °C, varying from 31 °C in July to −10 °C in January. Because of the Influences of both latitude and monsoon activities, temperatures vary a great deal, low temperature in winter is −40 °C in Mohe, the northernmost of China, while in hot summer temperature can be as high as 50 °C in Turpan basin, Xinjiang. The average annual precipitation is about 620 mm, ranging from 800–1000 mm in the eastern and coastal areas. The main nature vegetation types include tropical rain forest, wet land, grassland, desert and tundra²³.

Obtaining C₄ taxon data and analysis. Local C₄ taxon data of 32 provinces and municipalities (Fig. 1a) were collected from the C₄ plant database of Plant Adaptation Strategy and Mechanism Group, Institute of Botany, CAS, Republicale Popularis Sinicae²³. Catalogue of Life China and local flora sources²⁸–³³. Long-term (1950–2010) climate data were provided by the National Meteorological Information Center of China Meteorological Administration. C₄/C₃ proportion refers to the ratio of C₄ species number to C₃ species number in local flora. Regressions of C₄ taxon (e.g. total C₄ species abundance, grass and sedge C₄ species abundances) against climate variables (e.g. temperature, precipitation and aridity) were performed using SPSS 17.0 in order to explain the distribution patterns of C₄ taxa accurately at global scale. Stepwise multiple regression analyses between C₄ taxon data and analysis.

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R.Z.W. conceived and designed the experiments and wrote the main manuscript text; L.N.M. analyzed the data; R.Z.W. and L.N.M. prepared Figures 1–4, tables and supporting information; all authors reviewed the manuscript.

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