SCIENTIFIC REPORTS

OPEN

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

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Received: 20 January 2016
Accepted: 27 May 2016
Published: 15 June 2016

There have been debates on the driving factors of C_4 plant expansion, such as PCO_2 decline in the late Micocene 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[1]. 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[2,3]. 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[2,4,5], 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[6], Africa[7,8], Europe[9,10], Australia[11], Middle East[12,13], 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[5,14]. 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[15].

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[1,16–19], 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[19−21]? It had been hypothesized that PCO_2 decline caused C_4 plant expansion rapidly during the late Micocene (~8 to 4 Ma)[1,16,17], but some evidences suggested that C_4 plant expansion was likely driven by addition factors, such as enhanced low-latitude aridity, seasonal precipitation[19] and fire[20] 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[5,18]. Few found that the restriction of C_4 grasses to warmer areas was due largely to their evolutionary history[2]. (ii) whether the different C_4 taxa have similar climate distribution pattern in present-day at large-scale[21,22]? 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*

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Family	Genera	Species number	% of total C_4
Dicotyledoneae			
Aizoaceae	3	3	0.80
Amaranthaceae	3	18	4.85
Chenopodiaceae	17	65	17.52
Crassulaceae	1	1	0.27
Euphorbiaceae	1	2	0.54
Nyetaginaceae	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 C_4 species in plant families and genera in China.

(19.67%) and *Chenopodiaceae* (17.52%; Chenopod, hereafter). Relative lower C_4 plant occurrence is due largely to there is no tropical savannas (with more C_4 grasses) in China. In general, total C_4 species abundance decreases from south to north and from east to west in China (Fig. 1a,b). The total C_4 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 C_4 species abundance is strongly and positively related with mean annual temperature (T_m) ($R^2 = 0.56$, $P < 0.0001$) and mean annual precipitation (P_m) ($R^2 = 0.47$, $P < 0.0001$; Fig. 2a–c). Multiple regression of the total C_4 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_I) as model:

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

This indicates that these climate factors affect the distribution of total C_4 species abundance in China. Stepwise multiple regression analysis exhibits that T_m has highest contributions (61.5%) to total C_4 species distribution, while the impacts of P_m (2.0%) and A_I (2.6%) are relative less (Table 2).

C_4/C_3 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 C_4/C_3, even though the occurrence of C_4 species is high in these regions. There are no significant relations between C_4/C_3 proportions and climate variables in present-day vegetation in China ($P > 0.05$; Fig. 2d–f), indicating that C_4/C_3 proportion dose not exhibit certain ecological pattern, even the C_4 occurrence dose significantly related with plant abundance at large-scale region.

C_4 distribution patterns predicted by total C_4 species abundance appear to be insensitive to climate factors known to influence C_4 occurrence and expansion because of the different adaptive strategies for C_4 taxa to climate variables. Both grass and sedge C_4 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 ($R^2 = 0.23$, $P < 0.01$; $R^2 = 0.55$, $P < 0.001$) (Fig. 4a–c). Multiple regressions of grass C_4 species abundance ($Y_{grassC4}$) and sedge C_4 species abundance ($Y_{sedgeC4}$) against climate variables manifest that $Y_{grassC4}$ and $Y_{sedgeC4}$ are strong correlated with T_m, P_m and A_I as models:

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

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

But stepwise multiple regression analysis demonstrates that grass C_4 plant distribution is largely restricted to P_m (50.6%), and T_m and A_I functions are not significant ($P > 0.05$). Sedge C_4 species is mainly limited to T_m (64.7%) and the impacts of P_m (0.2%) and A_I (2.3%) are very less and no significant ($P > 0.05$; Table 2).

On the contrary, Chenopod C_4 plant abundance is strongly and positively related with A_I ($R^2 = 0.88$, $P < 0.001$), 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 C_4 plant abundance against climate variables shows that there is a strong correlation between $Y_{Chenopod\ C4}$ and T_m, P_m and A_I as model:

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

Stepwise multiple regression analysis exhibits that Chenopod C_4 plants is confined to arid index (88.2%) in present-day vegetation at whole China. These suggest the distributions of C_4 taxa are restricted to different climate factors at present-day vegetation in China.

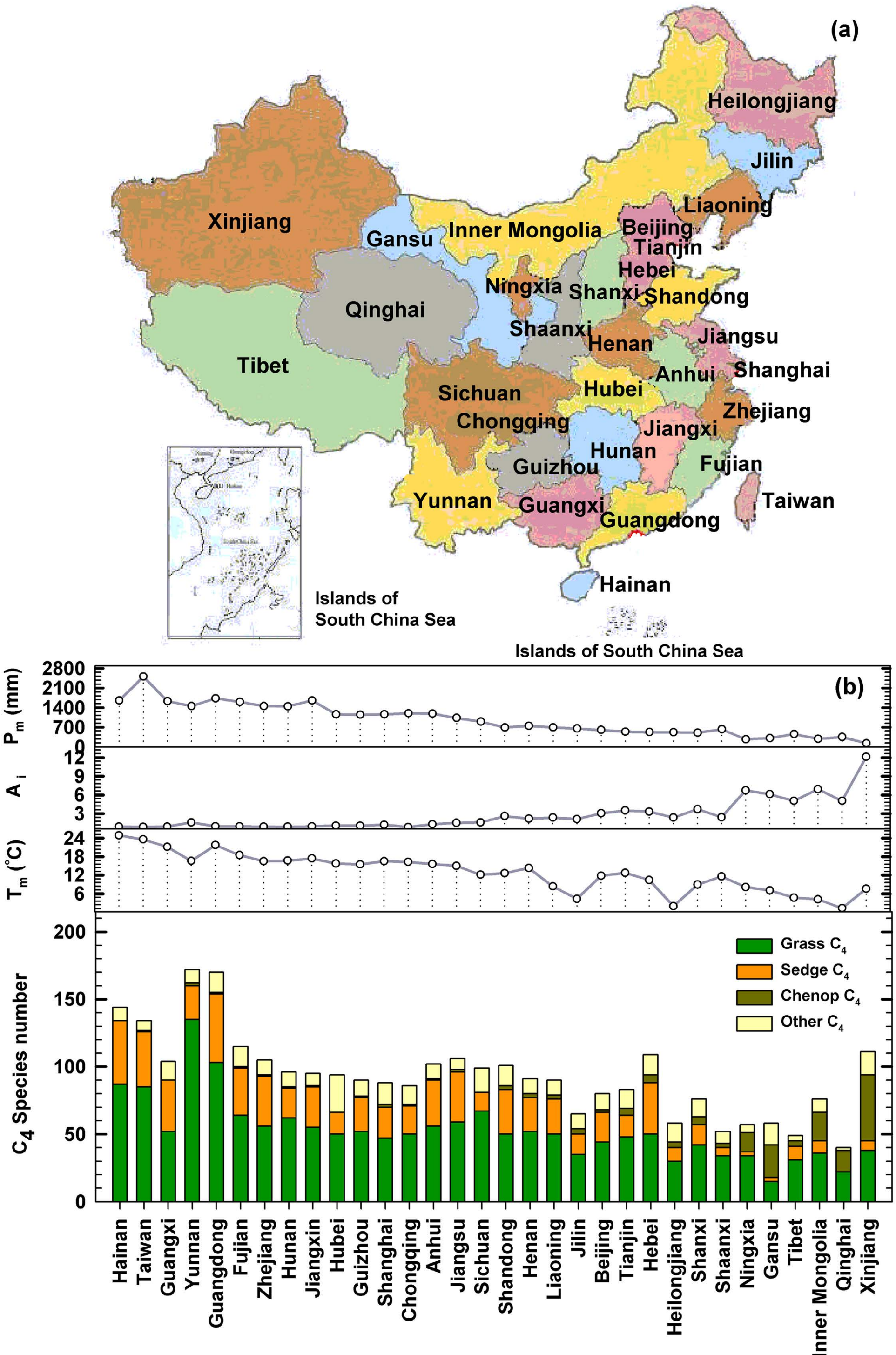

Figure 1. Geographical distribution (**a**), climate variables and numbers of C_4 species occurrence in 32 provinces and municipalities of China (**b**). The map was generated by *ArcGIS 93 SLX* (http://www.esri.com/software/arcgis/). *Abbreviations* – P_m, mean annual precipitation; Ai, arid index; T_m, mean annual temperature; Chenop C_4, C_4 species in *Chenopodiaceae*. *Scientific Reports* remains neutral with regard to contested jurisdictional claims in published maps.

Discussion

There were many studies on the C_4 plant expansion and distribution in relation to climate over the past couple of decades[1,16–19], but only few manifested the detail floristic data of C_4 occurrence in large regional scale (*e.g.*

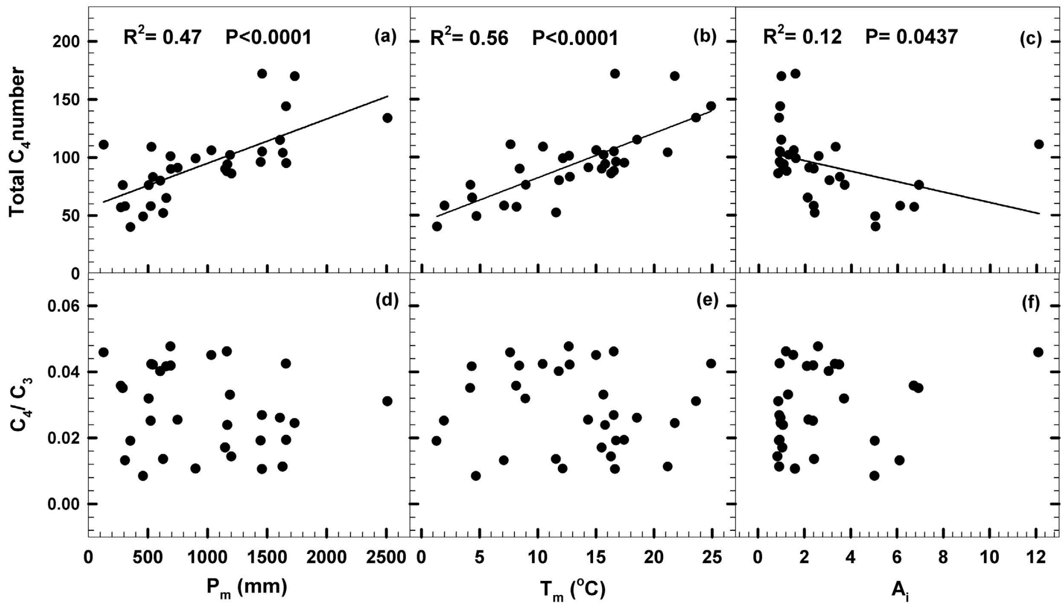

Figure 2. Regression of the total C_4 species numbers and C_4/C_3 versus mean annual precipitation (P_m), mean annual temperature (T_m) and arid index (Ai) in China.

	P_m		T_m		A_i	
	Partial R^2	Probability	Partial R^2	Probability	Partial R^2	Probability
Total C_4	0.020	0.243	0.615	0.000	0.026	0.180
Grass C_4	0.506	0.000	0.031	0.176	0.002	0.710
Sedge C_4	0.002	0.703	0.647	0.000	0.023	0.170
Chenop C_4	0.027	0.006	0.000	0.945	0.882	0.000

Table 2. Results of stepwise multiple regression analyses. Dependent variables: total C_4, grass C_4, sedge C_4 and Chenop C_4; Independent variables: mean annual precipitation (P_m), mean annual temperature (T_m) and arid index (A_i). The values of parameter estimate refer positive/ negative relationships between the examined dependent variable and the independent variables.

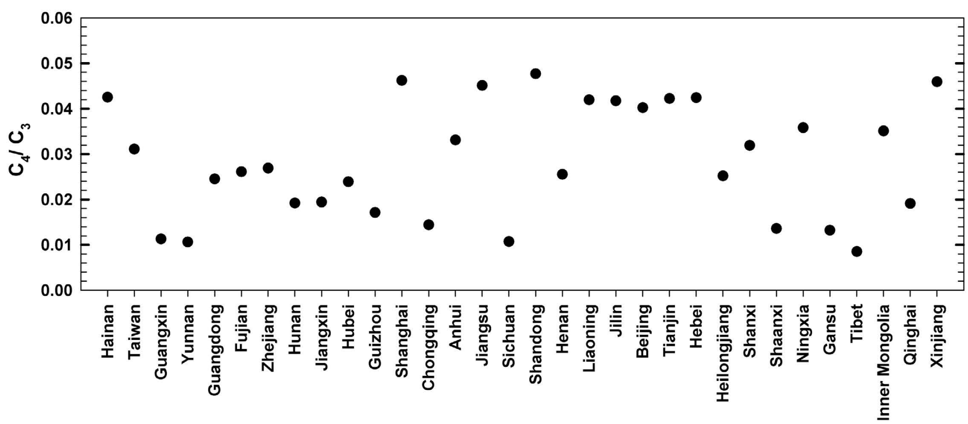

Figure 3. The C_4/C_3 fractions in 32 provinces and municipalities of China.

Europe[9,10], Middle East[13], Central Asia[14]). 371 identified C_4 species within China account for roughly 20% of known C_4 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 C_4 photosynthesis (Fig. 1; Supplementary Table S1). The total number of C_4 species in China (Table 1), mainly grasses (53.64%), sedges (19.67%) and Chenopods (17.52%), is much greater than that in Europe[9] and Middle East[13]. However, the number

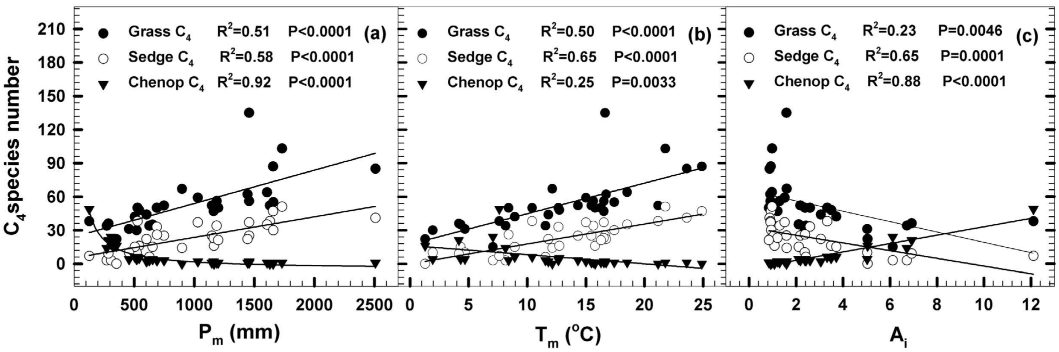

Figure 4. Relations of grass, sedge and Chenop C_4 plant abundances with mean annual precipitation (P_m), mean annual temperature (T_m) and arid index (Ai) in China.

of Chenopod C_4 species is only 1/3 of that in Middle East and 1.5 times of that in Mongolia[14], probably because China arid regions is smaller than Middle East, but larger than Mongolia. This knowledge is essential for building global C_4 plant database and formulating generalization regarding their relation to global climate.

What is the driving factor for C_4 plant expansion and distribution remains controversial. The evidences of palaeovegetation and fossil tooth enamel indicated the global expansion of C_4 plants may be related to lower PCO_2 in the Miocene[1,16,17], but some evidences suggested that C_4 plant expansion was likely driven by climate variables and fire in both old world and present-day vegetation[19,20]. Our data clearly demonstrate that C_4 plant distributions are restricted to mean annual climate variables (*e.g.* T_m, P_m and A_I) in the present-day vegetation in China (Fig. 2). From the south to the north, T_m governs the vegetation changes, while from the east to the west moisture gradient (P_m) drives plant distributions[23,24]. Within China, the total C_4 species abundance is strongly and positively related with T_m and P_m, this suggests that there is remarkably strong tendency for C_4 species to grow in hot and wet conditions, even though the stepwise multiple regression analysis exhibits that the impact of P_m is relative less (Table 2). This is much different with previous observations[6,11,25], their evidences manifest that July average daily temperature is a critical factor for C_4 distribution and the precipitation gradients seem to have much less impacts. Such significant difference is probably because almost 2/3 identified C_4 species are perennial grasses, sedges and some Polygonaceae species, relative higher P_m and T_m are not only favor for their growth in growing seasons, but also for their survival in winters[15,23,24]. This is also partly supported by the observation of soil organic carbon and present vegetation which indicates that C_4 fraction of Inner Mongolia grassland has increased by approximately 10% in the past decades because of increasing of temperature[26].

The C_4/C_3 proportion in China flora is about 1.2% and much lower than 3% estimated at global scale[4,18]. This is mainly due to complex relief in China, 2/3 of the total area is mountains and plateaus[23]. 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 C_3 and C_4 plants are much high in the southern regions. In addition, lower C_4 plant occurrence in China is for the absence of tropical savannas, which is estimated with more C_4 grasses[1], but large area of temperate grasslands and deserts (40% of China land) devotes considerable C_4 plant resources[5,15]. There are no significant relations ($P > 0.05$) between C_4/C_3 proportions and climate variables in present-day vegetation in China (Fig. 2d–f), indicating that C_4/C_3 proportions do not show certain ecological pattern (Fig. 3), even though C_4 occurrence dose significantly related with plant abundance at large-scale region.

Separate analysis for different C_4 taxa succeed in detecting C_4 distribution patterns accurately at continental scale, for the separate analysis can eliminate the noise signal from the C_4 taxon with different responses to climate variables and adaptive strategies. Previous studies had found that grass and sedge C_4 plants were largely restricted to July average daily temperature[6,11,18,25]. However, it is different in China, separate multiple regression analyses display that the grass and sedge C_4 plant abundances are mainly restricted to P_m and T_m respectively (Table 2). Most grass C_4 species are terrarium plants and their distributions are mainly restricted to P_m, while almost all sedge C_4 species are aquatic plants and the distributions of sedge C_4 taxon is governed by T_m in China. This explanation is also supported by the relative higher proportions of perennial C_4 grasses and sedges in the floristic data (Supplementary Table S1). Unlike the grass and sedge C_4 plants, the distribution of Chenopod C_4 taxon is drove by aridity (Table 2; Fig. 4). Chenopod C_4 plants are favored arid regions with hot summer and sufficient summer precipitation, because most of Chenopod C_4 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[15]. Even though there are a few studies on the occurrence of C_4 Chenopods in particular regions[13,14], but C_4 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[15]. In the dry west China (*e.g.* Xinjiang, Qinghai and Inner Mongolia), 30–45% of the total C_4 species is Chenopod plants, while that in the east and south China is less than 1%. Predominant C_4 Chenopods in hot and arid ecosystems, as well as strong relations with aridity (Fig. 4), imply that the expansion of C_4 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 C_4 plants in water-limited deserts are not considered critical for establishing C_4 grass distribution pattern, and are commonly invoked to explain the dominance of C_4 dicots[21,27], even though they did not separate Chenopod C_4 species from dicots.

Driving factor for C_4 plant expansion at spatial and temporal large-scale is controversial. The palaeosol carbonate and fossil tooth enamel data implicated that the C_4 plant expansion may have been due to decreasing of PCO_2 in late Miocene[1], but other evidences suggested that the development of low-latitude season aridity and changes in growing conditions led to the expansion of C_4 plants at ~7 Ma[19]. These different explanations are mainly due to the lack of direct evidences and extensive data analysis. Our mass flora data analysis partly supports Pagain's perspective[19], but their evidences also can not explain the divergence distribution pattern of different C_4 taxa. The divergence in C_4 climate pattern implicates these C_4 taxa may be with different area of origins, evolutionary histories[2,21], expansion mechanism and adaptive strategies, because the Chenopod C_4 taxon has a diametrically opposed distribution pattern with grass and sedge C_4 taxa (Fig. 4). In the previous studies[6,18,25], it had been found that grass and sedge C_4 plants are governed by July average daily temperature, but the distribution of grass, sedge and Chenopod C_4 species in China are largely restricted to P_m, T_m and A_I respectively, for the mean annual climate variables (especially P_m and T_m) can accurately describe the climate restrictions of plant distributions in China[23,24]. Edwards and Still also proved that the restriction of C_4 grasses to warmer areas was due largely to their evolutionary history[2].

Comparing with most previous researches[1,16–19] this work provides detail floristic data of C_4 occurrence in large regional scale based on China flora sources, which is essential for building worldwide C_4 plant database, and also contributes direct evidence formulating generalization regarding the driving factors of C_4 plant expansion. We suggest that the restriction of C_4 distributions at continental scale is due to largely the annual climate variables (*e.g.* P_m, T_m and A_I) in present-day ecosystems in China. Different C_4 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 histories[2,21]. Our findings suggest that the expansion of C_4 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 C_4 species may decrease in the future. This may have huge impacts on vegetation dynamics and primary plant production for the C_4 plants accounts for roughly 1/4 of global terrestrial primary production[2,3].

Methods

China topography and climate. China, occupied a large area, about 9.6 million km^2 (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 plateaus[23]. 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 150–400 mm in the western deserts and semi-deserts to 500–800 mm in the central region and vast flat plains, and 800–1000 mm in the eastern and coastal areas. The main nature vegetation types include tropical rain forest, wet land, grassland, desert and tundra[23].

Obtaining C_4 taxon data and analysis. Local C_4 taxon data of 32 provinces and municipalities (Fig. 1a) were collected from the C_4 plant database of Plant Adaptation Strategy and Mechanism Group, Institute of Botany, CAS, Reipublicae Popularis Sinicae[23], Catalogue of Life China and local flora sources[28–60]. Long-term (1950–2010) climate data were provided by the National Meteorological Information Center of China Meteorological Administration. C_4/C_3 proportion refers to the ratio of C_4 species number to C_3 species number in local flora. Regressions of C_4 taxon (*e.g.* total C_4 species abundance, grass and sedge C_4 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 C_4 taxa accurately at global scale. Stepwise multiple regression analyses between C_4 taxon and climatic variables were used to quantify the critical restriction of C_4 taxon. All statistical analyses were performed using SPSS 17.0 (SPSS for Windows, Chicago, IL, USA).

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Acknowledgements

This research was funded by grants from National Scientific Foundation of China (31070228, 31170304). We are grateful for the free climate data provided by National Meteorological Information Center of China Meteorological Administration and Worldclim-Global Climate Data (http: //www. worldclim.org/).

Author Contributions

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.

Additional Information

Supplementary information accompanies this paper at http://www.nature.com/srep

Competing financial interests: The authors declare no competing financial interests.

How to cite this article: Wang, R. and Ma, L. Climate-driven C_4 plant distributions in China: divergence in C_4 taxa. *Sci. Rep.* **6**, 27977; doi: 10.1038/srep27977 (2016).