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Relationship between climatic conditions and the relative abundance of modern C_3 and C_4 plants in three regions around the North Pacific

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Using −24‰ and −14‰ as the endpoints of stable carbon isotopic composition of total organic carbon ($\delta^{13}C_{TOC}$) of surface soil under pure C_3 and C_4 vegetation, and surface soil $\delta^{13}C_{TOC}$ data from eastern China, Australia and the Great Plains of North America, we estimate the relative abundance of C_3/C_4 plants (i.e., the ratio of C_3 or C_4 biomass to local primary production) in modern vegetation for each region. The relative abundance of modern C_3/C_4 vegetation from each region is compared to the corresponding climatic parameters (mean annual temperature and precipitation) to explore the relationship between relative C_4 abundance and climate. The results indicate that temperature controls the growth of C_4 plants. However, even where temperature is high enough for the growth of C_4 plants, they will only dominate the landscape when precipitation declines as temperatures increase. Our results are consistent with those of other investigations of the geographic distribution of modern C_4 plant species. Therefore, our results provide an important reference for interpretation of past C_3/C_4 relative abundance records in these three regions.

organic carbon isotopes, modern C_3/C_4 relative abundance, climatic factors, temperature, precipitation

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Terrestrial higher plants assimilate atmospheric carbon dioxide into organic matter mainly by one of two photosynthetic pathways, commonly called C_3 or C_4 pathways. All trees, most shrubs and most grasses are C_3 plants, while C_4 plants are sedges, grasses and shrubs [1–4]. Due to their different physiological processes, C_3 and C_4 plants have different growth advantages in different entironments and their carbon isotopic composition is significantly different. Therefore, theoretically speaking, the relative abundance of C_3/C_4 plants in local terrestrial ecosystems during historical and geological periods can be used to reconstruct paleoenvironmental change. Until now, such paleoenvironmental reconstruction has been widely conducted in lacustrine sediments [5–7], loess/paleosol sequences [8–11], marine sediments [12,13] and other geological archives around the world.

Nowadays, the available knowledge about the relationship between the growth of C_4 plants and climatic conditions comes mainly from the investigation of the geographic distribution of modern C_4 species. For example, the relationship between climate conditions and the geographic distribution of modern C_4 species in mainland China has been systematically investigated by Yin and Li [14]. Similarly, Sage et al. [15] summarized the global geographic distribution of modern C_4 plants. These efforts contributed significantly to our understanding of the relationship between the growth of C_4 plants and climate. However, C_3/C_4 relative abundance, defined as the ratio of C_3 or C_4 biomass to local primary production, is different from the geographic

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*Corresponding author (email: raozhg@lzu.edu.cn) distribution of C_4 species, and also different from the ratio of C_4 species to all plant species in a specific ecosystem. In regions with few C_4 species, such as the region over 60°N where only 3 to 5 C_4 species have been found [15], both the ratio of C_4 species to all plants species (i.e., the C_4 species abundance) and the relative abundance of C_4 biomass in the local ecosystem is close to zero. Similarly, in regions with abundant C_4 plants, such as a savanna ecosystem where the ratio of C_4 species to all plant species is normally higher than 90%, the relative abundance of C_4 biomass may also be very high [15]. In other regions, however, the C_4 species abundance and the relative abundance of C_4 biomass may differ significantly. Sedimentary organic carbon isotopic analyses may provide information about past C_3/C_4 relative abundance, but says nothing about the species abundance of C_4 plants.

Organic carbon isotopic compositions ($\delta^{13}C_{TOC}$) of surace soil in different regions have been evaluated for their relationship to climate. Modern $\delta^{13}C_{TOC}$ data of 18 surface soil samples from the central Chinese Loess Plateau (34°N to 38°N) range from –21.4‰ to –24.8‰, with an average value of –23.3‰, indicating the region is dominated by C_3 plants [16]. Many $\delta^{13}C_{TOC}$ data of surface soil samples in central-east Asia (from 34°N to 52°N) from the northern slope of the Qinling Mountains near Baoji (China) to Hanhayn Huryee near the Mongolia-Russian border, reported by Feng et al. [17], are also very negative, indicating that C_3 plants dominate this region as well. However, between 42°N and 46°N in the same region, the $\delta^{13}C_{TOC}$ values are relatively higher, which may suggest that carbon isotopic values of C_3 plants are greater under drier conditions [18]. This is further bolstered by the fact that the sampling area is desert or desert steppe [17]. Surface soil $\delta^{13}C_{TOC}$ data from these two regions have been used to analyze their relationship with environmental conditions [16,17,19], however, C_3/C_4 relative abundance of modern vegetation and its relationship with climatic condition could not be well established for these two regions, primarily because the two regions are dominated by C_3 plants.

Until now, a systematic summary of the results of the studies on the relationship between modern C_3/C_4 relative abundance and climate across large areas, has not been available. Yet it is widely recognized that such summaries are critical to plaeoenvironmental reconstructions that evaluate change in C_3/C_4 relative abundance over time. In this paper, we estimate modern C_3/C_4 relative abundance in eastern China, Australia and the Great Plains of North America using a unique method to examine previously reported surface soil $\delta^{13}C_{TOC}$ data from each region [20–23]. The estimated modern C_3/C_4 relative abundance for each region is then compared to corresponding data for mean annual temperature (MAT) and precipitation (MAP) to explore the relationship between modern C_3/C_4 relative abundance and climatic condition in an extremely wide region with variable climatic and vegetational types.

1 Materials and methods

Worldwide investigations demonstrate that the carbon isotopic composition of C_3 plants ranges from –20‰ to –34‰, with a mean around –27‰, while the carbon isotopic composition of C_4 plants ranges from –9‰ to –19‰, with a mean value of –13‰ [1–4]. From this two important points emerge: first, the carbon isotopic composition of modern plants is variable under different environments [18,24]; and second, the carbon isotopic composition of plant remains may change during the burial and decomposition process, and this change is variable [16,25]. Because of this, using the mean carbon isotopic composition of modern plants (–27‰ and –13‰) as the endpoints to estimate C_3/C_4 relative abundance may result in significant errors. Referring to the study of surface soil $\delta^{13}C_{TOC}$ data from the Great Plains of North America [22] and Australia [23], Gu et al. [8] chose –24‰ and –14‰ as the endpoints of $\delta^{13}C_{TOC}$ data of soil under pure C_3 and C_4 vegetation to establish a history of change in C_3/C_4 relative abundance from the last glacial to the Holocene in several loess/paleosol sequences from the Chinese Loess Plateau. A comparison of different estimation methods demonstrates that the method of Gu et al. [8] is relatively suitable for the estimation of C_3/C_4 relative abundance with $\delta^{13}C_{TOC}$ data [26]. In this study, we follow Gu et al. in using –19‰ as the threshold between C_3 and C_4 dominance. Specifically, surface soil $\delta^{13}C_{TOC}$ values greater than –14‰ indicate pure C_4 vegetation (the relative abundance of C_4 plants is 100%); surface soil $\delta^{13}C_{TOC}$ values between –19‰ and –14‰ represent vegetation dominated by C_4 plants (the relative abundance of C_4 plants is between 50% to 100%); surface soil $\delta^{13}C_{TOC}$ values between –19‰ and –24‰ reflect C_3/C_4 mixed vegetation dominated by C_3 plants (the relative abundance of C_4 plants is between 0% to 50%); and surface soil $\delta^{13}C_{TOC}$ values less than –24‰ indicate pure C_3 vegetation (the relative abundance of C_4 plants is 0%).

The surface soil $\delta^{13}C_{TOC}$ data used in this paper come from eastern China [21], the Great Plains in North America [22] and Australia [23], and the approximate distribution of these three regions is shown in Figure 1. Our previous study results demonstrate that the spatial distribution of surface soil $\delta^{13}C_{TOC}$ values (Figure 2(a)) is similar to the spatial distribution of carbon isotopic compositions for long-chain *n*-alkanes (n-C_{27}, n-C_{29} and n-C_{31}) with significant odd-to-even carbon preference derived from terrestrial higher plants in eastern China. Both of these carbon isotopic data sets are more positive in the area between 31°N and 40°N, and very negative in the area that above 40°N (for $\delta^{13}C_{TOC}$ data, most of them are less than –24‰). In the area below 31°N, both sets of carbon isotopic data are dispersed and more negative than in the mid-latitude area as a whole (for $\delta^{13}C_{TOC}$ data, most of them are less than –19‰) [21]. Such a spatial change trend is consistent with carbon isotopic data

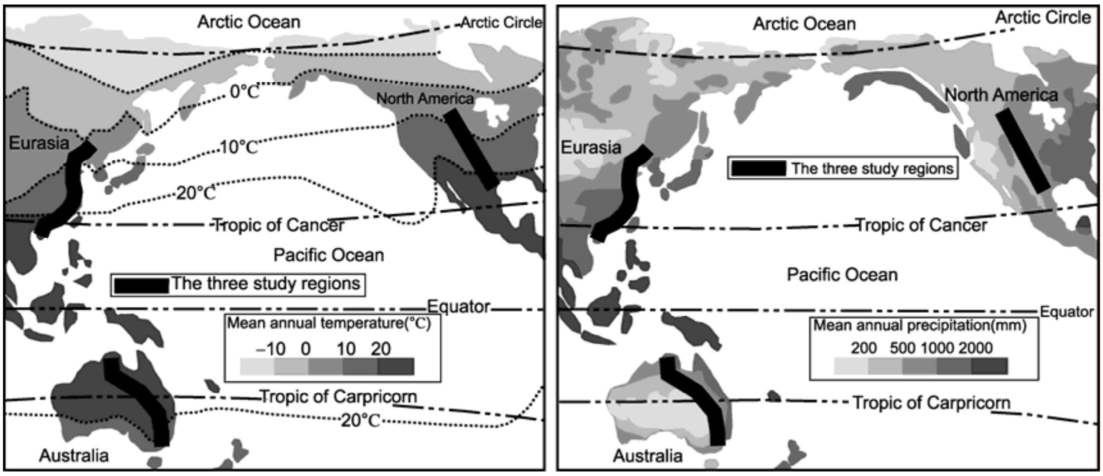

Figure 1 The regions where surface soil $\delta^{13}C_{TOC}$ data come from and the distribution of the mean annual temperature and precipitation around the North Pacific.

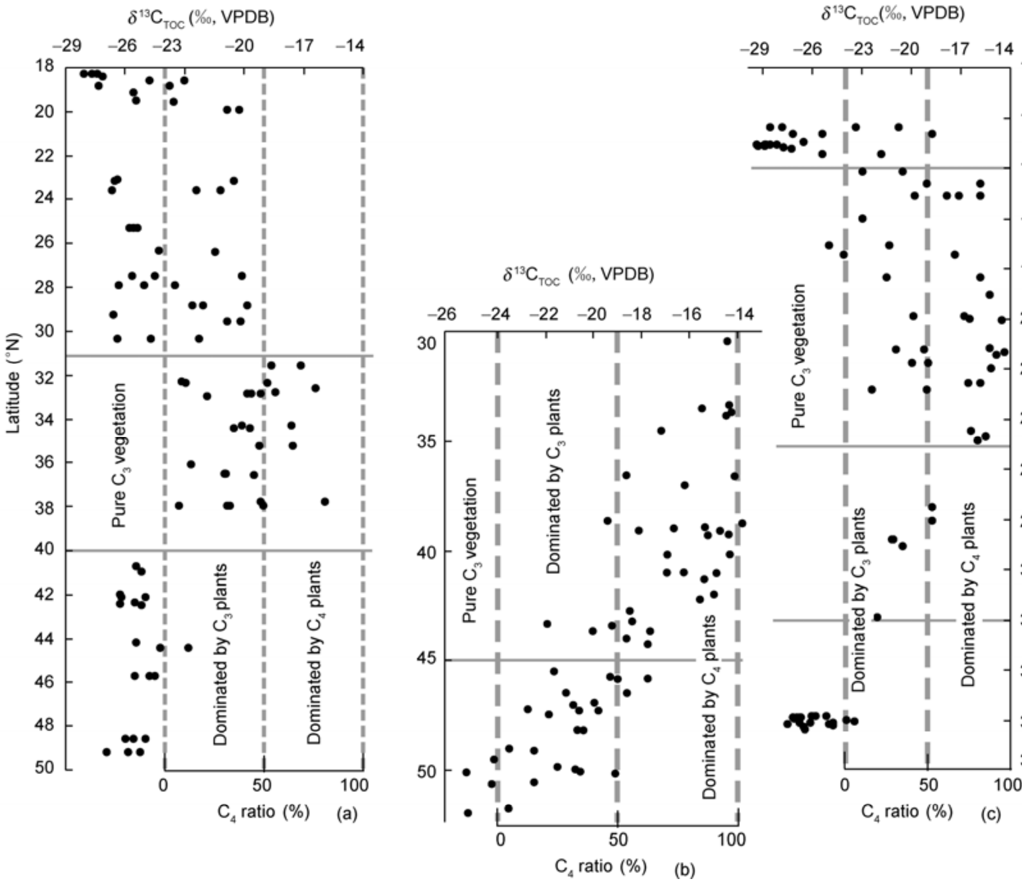

Figure 2 The pattern of spatial change in surface soil $\delta^{13}C_{TOC}$ data and corresponding estimated C_3/C_4 relative abundance in eastern China (a), the Great Plains in North America (b) and Australia (c).

of phytoliths in surface soil samples gathered in eastern China [27]. Surface soil $\delta^{13}C_{TOC}$ data from the Great Plains in North America [22] range from 30°N to 52°N, and decrease with increasing latitude (Figure 2(b)). Surface soil $\delta^{13}C_{TOC}$ data from Australia [23] are more positive between 14°S and 25°S, but increasingly negative further north and south of this area. As a whole, surface soil $\delta^{13}C_{TOC}$ values are less than –24‰ both above 14°S and below 32°S (Figure 2(c)).

2 Results and discussion

Using the above-mentioned method and surface soil $\delta^{13}C_{TOC}$ data, spatial differences in modern C_3/C_4 relative abundance for three different regions has been estimated and shown in Figure 2. Pure C_3 vegetation or C_3/C_4 mixed vegetation dominated by C_3 plants exists in the area of 18°N to 31°N in eastern China. The area of 31°N to 40°N in eastern China is occupied by C_3/C_4 mixed vegetation dominated by C_3 or C_4 plants; pure C_3 vegetation does not exist in this area. However, the area above 40°N in eastern China is dominated by pure C_3 vegetation (Figure 2(a)). In the Great Plains of North America, pure C_4 vegetation or C_3/C_4 mixed vegetation dominated by C_4 plants occupy the area of 30°N to 45°N, while the area between 45°N and 50°N is occupied by C_3/C_4 mixed vegetation dominated by C_3 plants; and pure C_3 vegetation dominates the area above 50°N (Figure 2(b)). In Australia, it is pure C_3 or C_3-dominant vegetation in the area of 10°S to 14°S. In the area of 14°S to 25°S, mostly, the vegetation is mixed C_3/C_4 but dominated by C_3 or C_4 plants, while pure C_4 vegetation still dominates several sampling sites in this area. C_3/C_4 mixed vegetation dominated by C_3 plants occupy the area of 25°S to 32°S, and pure C_3 vegetation exists in the area below 32°S (Figure 2(c)).

Climatic parameters, including MAT and MAP, have been gathered from meteorological stations nearest each surface soil sampling site in eastern China [20]. Similarly, Bird and Pousai [23] provided MAT and MAP data of each surface soil sampling site in Australia. Therefore, it is possible for us to further analyze the relationship between modern C_3/C_4 relative abundance and MAT and MAP in these two regions. This analysis may be affected by several factors related to the seasonality of plant growth: (1) because the study region has large latitudinal span, the growing season of plant varies with location, making it difficult to identify a growth season suitable to the entire study region; (2) spatial trends in mean temperature and precipitation of the growing season should be consistent with MAT and MAP in the whole study region; and (3) only MAT and MAP data were available in Australia [23]. Therefore we only analyze the relationship between modern C_3/C_4 relative abundance and MAT and MAP in eastern China and Australia (Figure 3). In eastern China, pure C_3 vegetation dominates the area where MAP is more than 1800 mm or less than 500 mm. While C_4 plants can grow when MAP is between 500 mm and 1800 mm, C_4 plants only dominate the vegetation where MAP is between 500 mm and 1200 mm (Figure 3(a)). Correspondingly, pure C_3 vegetation dominates areas with MAT lower than 12°C. While C_4 plants can grow when MAT is between 12°C and 26°C, only those places with MAT between 12°C and 16°C have vegetation dominated by C_4 plants (Figure 3(b)). In Australia, pure C_3 vegetation dominates the area with MAP less than 200 mm, C_4 plants can grow when MAP is between 200 mm and 800 mm, and only those areas with MAP between 200 mm and 500 mm have vegetation dominated by C_4 plants (Figure 3(c)). Correspondingly, pure C_3 vegetation dominates the area with MAT lower than 16°C, while C_4 plants can grow when MAT is between 16°C and 28°C. Only those areas with MAT between 21°C and 28°C have vegetation dominated by C_4 plants (Figure 3(d)). It seems the relationship between modern C_3/C_4 relative abundance and single climatic parameter is significantly different in these two regions, especially, the climatic conditions of the areas dominated by C_4 plants in these two regions. Therefore, we further compare modern C_3/C_4 relative abundance of these two regions for the same values of MAT and MAP, as shown by Figure 4. Considering the temperature of the area dominated by C_4 plants in the Great Plains of North America is higher than the corresponding area in eastern China (Figure 1), and the precipitation is more than that of the corresponding area

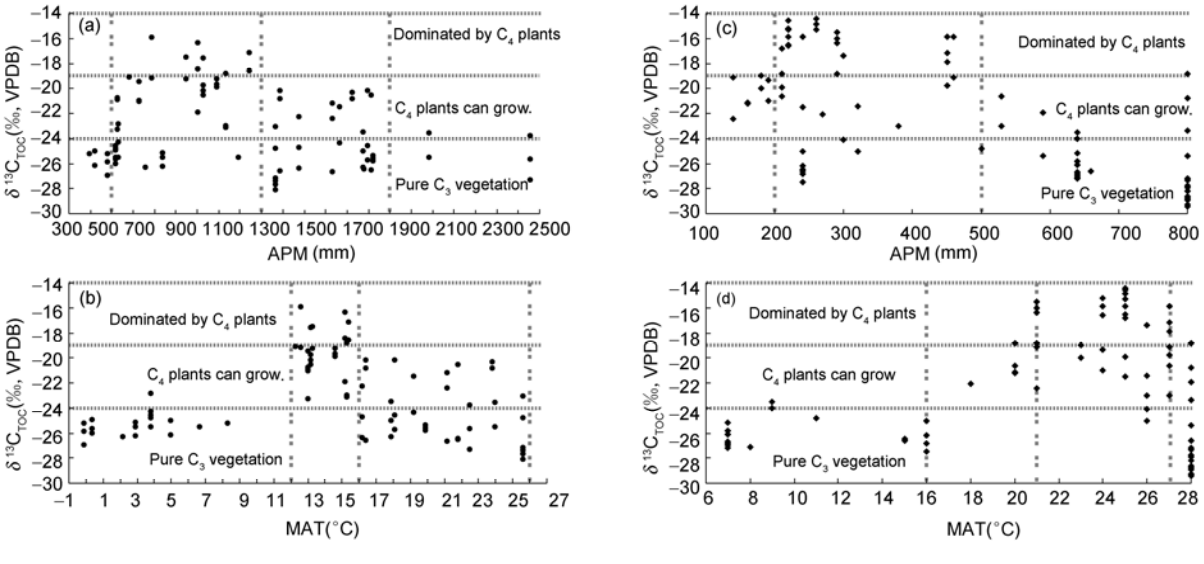

Figure 3 (a) The relationship between C_4 relative abundance and MAP in eastern China; (b) the relationship between C_4 relative abundance and MAT in eastern China; (c) the relationship between C_4 relative abundance and MAP in Australia; (d) the relationship between C_4 relative abundance and MAT in Australia.

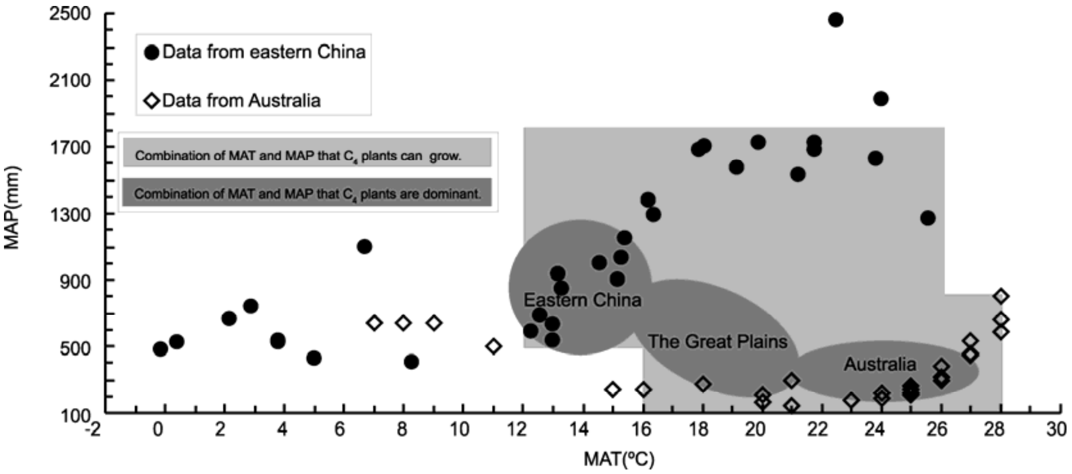

Figure 4 The change of the modern C_4 relative abundance in different combination of MAT and MAP in eastern China, the Great Plains of North America and Australia. Distribution of evidence from North America is approximate.

in Australia (Figure 1), the approximate range of MAT and MAP of the area dominated by C_4 plants in the Great Plains of North America is also plotted on Figure 4. We then see that when MAT is lower than 12°C, the vegetation can be regarded as pure C_3 vegetation no matter the change in precipitation. C_4 plants can grow in a wide range of MAP when MAT is higher than 12°C. However, with further increasing MAT, C_4 plants can keep their predominance when the MAP is decreasing.

A summary of the geographic distribution of modern C_4 plants around the world by Sage et al. [15] shows that only 3 to 5 modern C_4 species exist in the region above 60°N, and modern C_4 species are few in the region below 45°S. Carbon isotopic composition of 158 modern plant species gathered in the Qinghai-Tibet Plateau (27°42′–40°57′N, 88°93′–103°24′E and 2210–5050 m) analyzed by Wang et al. [28] demonstrate that only 8 are C_4 plant species. Based on the analyses of carbon isotopes of leaves of more that 300 modern plant species gathered along an altitudinal gradient, Li et al. [29] find only 52 C_4 plant species among more than 3500 plants species in the plateau area of Qinghai Province. A common feature of those high latitude and high altitude regions is low temperature. This is consistent with our analyses of the relationship between modern C_3/C_4 relative abundance and climatic condition. Surface soil $\delta^{13}C_{TOC}$ data from 34°N to 40°N in the central Chinese Loess Plateau [16,19] and central East Asia [17] are more negative than the corresponding data from the same latitudinal band in eastern China. This suggests that these two regions are dominated by C_3 plants and that the C_4 relative abundance in these two regions is lower than in the same latitudinal band in eastern China. This may result from the lower temperatures of these two regions relative to the same latitudinal band in eastern China (Figure 1), and may reflect the influence of temperature on the growth of C_4 plants. At the same time, these two regions are drier than the same latitudinal band in eastern China, which may suggest that below a temperature threshold, a dry environment does not promote the growth of C_4 plants. Although many rain forests or seasonal rain forests occupy low-latitude regions with high temperature and precipitation, typical C_4 vegetation-that is, savanna vegetation-normally occupies low latitudes marked by high temperature and high relative aridity. This is consistent with our understanding that so long as temperature is high enough for the growth of C_4 plants, they will predominate the landscape as temperatures increase and precipitation decreases.

3 Conclusions

The relative contribution of modern C_4 plants to local primary production in eastern China, the Great Plains in North America and Australia can be estimated using a unique method and surface soil $\delta^{13}C_{TOC}$ data from each region. The estimated modern C_4 relative abundance is semi-quantitative, and is compared across uniform values of mean annual temperature and precipitation to explore the relationship between modern C_4 relative abundance and climatic condition. Our results suggest that no matter the variation in precipitation, C_4 plants are extremely seldom when the temperature is too low such as at high altitudes and high latitudes. When temperature is high enough, C_4 plants can grow under a wide range of precipitation, however, C_4 plants can only dominate the vegetation under a limited range of precipitation. More importantly, with an increase in temperature, C_4 plants will only remain dominant where precipitation declines. Paleoenvironmental reconstructions based on sedimentary archives of change in C_3/C_4 relative abundance in the past, will benefit form these results.

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