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Invited review

Relationship between the stable carbon isotopic composition of modern plants and surface soils and climate: A global review

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ABSTRACT

Analysis of the stable carbon isotopes ($\delta^{13}C$) in organic material in various geological archives has been widely used for paleoclimatic reconstruction. Consequently, it is important to characterize the $\delta^{13}C$ values of modern plants and surface soils to provide analogues for strengthening paleoclimatic reconstructions. In this paper, > 10.000 previously reported $\delta^{13}C$ values from modern plants and surface soils at globally distributed sites, together with newly obtained surface soil $\delta^{13}C$ data from 107 sites in inland China, are used to establish relationships with corresponding mean annual temperature (MAT) and precipitation amount (MAP). Using a $\delta^{13}C$ value of −24‰ of surface soil as the discriminator between pure C_3 vegetation and C_3/C_4 mixed vegetation, our results demonstrate a close relationship between MAT and C_4 relative abundance, implying that temperature is the primary climatic factor determining the C_3/C_4 relative abundance. Both the $\delta^{13}C$ values of modern C_3 plants and surface soils under pure C_3 vegetation are significantly negatively correlated with MAP, confirming that the $\delta^{13}C$ of material sourced from pure C_3 vegetation can be used for paleoprecipitation reconstruction. However, unlike C_3 plants, the $\delta^{13}C$ values of modern C_4 plants are significantly positively correlated with MAP. Thus our results can serve as a reference for the paleoclimatic interpretation of sedimentary $\delta^{13}C$ data.

Contents

1. Introduction

Terrestrial higher plants are commonly designated as C_3, C_4 and CAM (crassulacean acid metabolism; Osmond, 1978), according to their photosynthetic pathways. CAM plants will not be considered in this paper, because they are only present in highly specialized ecosystems (such

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as deserts). The carbon isotopic composition ($\delta^{13}C$) of modern C_3 plants (normally refers to the value of bulk leaf tissue, and is expressed as plant $\delta^{13}C$ in this paper) ranges mainly from −20‰ to −34‰, with the most frequent values around −27‰, under modern atmospheric CO_2 conditions (1980s: atmospheric pCO_2 ca. 340 ppm; $\delta^{13}C$ of ca. −7.6‰). The $\delta^{13}C$ values of modern C_4 plants range principally from −9‰ to −19‰, with the most frequent values around −13‰ (Deines, 1980; O'Leary, 1981, 1988; Farquhar et al., 1989; Sage et al., 1999).

Different environmental factors can affect the carbon isotopic fractionation during the photosynthetic processes of both C_3 and C_4 plants. Among them, precipitation amount and temperature are the most important climatic factors. The more negative $\delta^{13}C$ values of C_3 plants normally occur under relatively humid conditions, due to the relatively high stomatal conductance of C_3 plants and therefore increased intercellular partial pressures of CO_2 under such conditions (e.g. Farquhar et al., 1989). The relationship between temperature and $\delta^{13}C$ values of C_3 and C_4 plants is more complex (e.g. Wang et al., 2013; Jia et al., 2016), because both the activity of photosynthetic enzymes and the stomatal conductance of plants can be affected by temperature. Generally, with temperature increase from very low values, the enhanced activity of photosynthetic enzymes and enlarged stomatal conductance will result in more negative $\delta^{13}C$ values of plants. Then, with a further increase in temperature, in order to maintain their water supply, plants will close some stomas and therefore the stomatal conductance of plants will be decreased. Meanwhile, the activity of photosynthetic enzymes will be limited under very high temperature. Both the decreased stomatal conductance and limited activity of photosynthetic enzymes will finally result in more positive $\delta^{13}C$ values of plants. That is why the relationships between temperature and $\delta^{13}C$ data of plants present a complex picture. Furthermore, C_3 plants have competitive growth advantages under environmental conditions of low temperature, high humidity and high atmospheric CO_2 concentration; C_4 plants have a relative growth advantage under environmental conditions of high temperature, aridity and low atmospheric CO_2 concentration (e.g. Deines, 1980; O'Leary, 1981, 1988; Farquhar et al., 1989; Sage et al., 1999).

These observations provide the theoretical basis for the interpretation of $\delta^{13}C$ values measured in geological archives containing the remains of terrestrial higher plants, the $\delta^{13}C$ values of which are normally used as an indicator of past variations in C_3/C_4 relative abundance and thus for paleoclimatic reconstruction. $\delta^{13}C$ data (not only limited to bulk organic $\delta^{13}C$ data) have been obtained from sedimentary archives, such as loess deposits (e.g. Lin et al., 1991, 1992; Zhang et al., 2003; Rao et al., 2006, 2013a, 2015), lake sediments (e.g. Street-Perrott et al., 1997; Huang et al., 2001) and marine sediments (e.g. Ratnayake et al., 2006; Galy et al., 2008). These sites are globally distributed, and the results have been used to reconstruct paleovegetation and paleoclimate on various timescales (Rao et al., 2012). However, several fundamental issues remain unclear regarding the interpretation of the data and therefore require further study. These issues are summarized below.

It is difficult to discriminate the primary climatic factor that drives the variation in C_3/C_4 relative abundance on geological time scales, due to the co-variation of temperature and precipitation. For example, in the central and eastern Chinese Loess Plateau, results from several profiles with more positive $\delta^{13}C$ values in Holocene paleosol layers than that in last glacial loess layers have been considered to reflect increased C_4 relative abundance from the last glacial to the Holocene (e.g. Lin et al., 1991, 1992; Rao et al., 2006, 2013b; Yang et al., 2015). However, there are two opposing viewpoints regarding the major factor responsible for the increased C_4 relative abundance in the region. One viewpoint emphasizes the effect of the East Asian summer monsoon (related to precipitation amount; Lin et al., 1992; Lin and Liu, 1992; He et al., 2002; Liu et al., 2005a); and the other highlights the influence of temperature (e.g. Gu et al., 2003; Zhang et al., 2003; Vidic and Montañez, 2004). Investigation of the modern relationship between C_3/C_4 relative abundance and climate on a large spatial scale can potentially contribute to determining the primary climatic factor influencing C_4 relative abundance in the geological past.

It has been widely noted that the $\delta^{13}C$ values of C_3 plants mainly respond to precipitation amount, from climatic perspective mentioned above, with more negative $\delta^{13}C$ values occurring with increasing precipitation amount (e.g. Stewart et al., 1995; Wang et al., 2003; Zheng and Shangguan, 2007; Diefendorf et al., 2010; Kohn, 2010). Thus the $\delta^{13}C$ values of organic material in sedimentary archives derived from pure C_3 vegetation, especially those from aeolian sediments, potentially reflect paleoprecipitation. Quantitative paleoprecipitation reconstruction based on $\delta^{13}C$ data has been applied to studies of both European loess (Hatté et al., 2001) and the loess of the western Chinese Loess Plateau (Rao et al., 2013b). However, it is noteworthy that the response of $\delta^{13}C$ values to precipitation amount varies among different C_3 species. This has been demonstrated by the correlations between precipitation amount and the $\delta^{13}C$ values of three C_3 species studied by Liu et al. (2005b) and of four C_3 species studied by Wang and Han (2001) (Fig. 1; see the Supplementary Information of Rao et al., 2013b for more information). Given that sedimentary $\delta^{13}C$ data consist of a mixture of isotopic signals from many plant species, and that modern plant $\delta^{13}C$ studies have only been conducted on a limited proportion of C_3 species, the observed statistical relationship between the $\delta^{13}C$ values of modern C_3 species and precipitation should not be used directly for paleoprecipitation reconstruction. Clearly, a greater number of studies of the modern relationship between the $\delta^{13}C$ values of surface soils under pure C_3 vegetation (as an integrator of ecosystem diversity) and the corresponding precipitation amount are required for reliable paleoprecipitation reconstruction. In the case of quantitative paleoprecipitation reconstruction based on high-resolution loess $\delta^{13}C$ data from the western Chinese Loess Plateau, the results of a study of surface soil $\delta^{13}C$ values in arid central Asia (Lee et al., 2005; Feng et al., 2008) have been adopted as the modern reference and therefore more reliable paleoprecipitation reconstruction results have been obtained (Rao et al., 2013b). Although the results of $\delta^{13}C$ analyses of modern C_3 plants have been well summarized (e.g. Diefendorf et al., 2010; Kohn, 2010), a corresponding summary of the results of $\delta^{13}C$ analyses of surface soils is still needed.

Unlike C_3 plants, the relationship between the $\delta^{13}C$ values of C_4 species and precipitation is not well constrained. For example, the results from 19 sites in North China demonstrated that the $\delta^{13}C$ values ($n = 89$) of C_4 species became more positive with increasing precipitation amount, and that the $\delta^{13}C$ values of five C_4 species from a specific location were all more positive in the wet season than in the dry season (Wang et al., 2006), in contradistinction to the results for modern C_3 plants (e.g. Stewart et al., 1995; Wang et al., 2003; Zheng and Shangguan, 2007; Diefendorf et al., 2010; Kohn, 2010). However, the $\delta^{13}C$ values ($n = 28$) of *Bothriochloa ischaemum* (C_4) were negatively correlated with precipitation amount (−0.61%/100 mm; Liu et al., 2005b) along a mean annual precipitation (MAP) gradient from 350 to 700 mm in North China, which is the opposite to the findings of Wang et al. (2006). Apparently, study of a much larger number of C_4 species is needed, considering that different responses of $\delta^{13}C$ values to precipitation among different C_4 species (as is the case for C_3 species) are highly possible.

In the present study, we compiled $\delta^{13}C$ data from surface soils ($n = 5655$; Supplementary Table S1, including newly obtained surface soil $\delta^{13}C$ data from 107 sites in inland China) and of modern plants ($n = 4908$; Supplementary Table S2), from globally distributed sites and previously reported in the literature. We used the data to statistically examine the relationship between plant and soil $\delta^{13}C$ and mean annual temperature (MAT) and precipitation amount (MAP).

2. Methods

The spatial distribution of the $\delta^{13}C$ study sites for surface soils and modern plants cited in this paper is shown in Fig. 2 (Supplementary