

Late Pliocene–Pleistocene expansion of C₄ vegetation in semiarid East Asia linked to increased burning

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ABSTRACT

Plants using the C₄ photosynthetic pathway, commonly tropical and subtropical grasses, increased in abundance in East Asia during the late Cenozoic. Determining the exact timing and likely factors leading to this major vegetation change requires region-specific studies. Here variations in pyrogenic carbon mass accumulation rate (PyC-MAR) and isotope composition ($\delta^{13}\text{C}_{\text{PyC}}$) from an ~7-m.y.-long depositional sequence from the central Loess Plateau, China, suggest increased biomass burning and an increased contribution to combusted material from C₄ taxa from 2.6 Ma. Changes in the composition of PyC after 0.6 Ma likely reflect the effects of lower temperatures, particularly during glacial periods, and changes in seasonality of precipitation. Increased PyC-MAR without concomitant changes in $\delta^{13}\text{C}_{\text{PyC}}$ at ca. 0.15 Ma appears to indicate a decoupling of feedbacks between changes in climate, fire regime, and vegetation, and may mark the onset of anthropogenic burning in the region. These new data suggest that C₄ taxa were present on the Loess Plateau from at least the late Miocene, rising to prominence at ca. 2.6 Ma following changes in climate and, critically, an increase in biomass fires.

INTRODUCTION

The expansion of plants using the C₄ photosynthetic pathway (largely subtropical and tropical grasses) over those using the C₃ pathway (trees, shrubs, and temperate-climate grasses) during and since the late Miocene, ~25 m.y. after their first evolutionary radiation (Strömberg, 2011), constitutes one of the most important ecosystem transformations of the Cenozoic (Cerling et al., 1997). However, the patterns and timing of the rise to prominence of C₄ taxa were not uniform throughout tropical and subtropical latitudes, and neither were the drivers of expansion (Edwards et al., 2010). Conditions of low CO₂ concentration (*p*CO₂), high temperature, moisture stress, and disturbances (notably fire) may have provided C₄ species with a competitive advantage over C₃ taxa (Hoetzel et al., 2013). Any one, or a combination, of these factors could have driven a rise to prominence of C₄ taxa in a particular location, and their identification is thus dependent on detailed, region-based studies (Strömberg, 2011).

Fire has a demonstrably large impact on modern ecosystems and global biogeochemical cycles. Pyrogenic carbon (PyC; also known as biochar, charcoal, black carbon, and soot; Bird and Ascough, 2012) produced

by biomass burning can be extracted from sediments using chemical oxidation (Bird and Gröcke, 1997). Sedimentary records of PyC abundance have the potential to document past fire activity over geological time scales. The stable carbon isotope composition of PyC ($\delta^{13}\text{C}_{\text{PyC}}$) is unlikely to be subject to significant alteration once buried in a sedimentary sequence (Bird and Gröcke, 1997; Liu et al., 2013). $\delta^{13}\text{C}_{\text{PyC}}$ thus records the original relative contributions from C₃ and C₄ plants to combusted biomass (Zhou et al., 2009). The quantification of both PyC and $\delta^{13}\text{C}_{\text{PyC}}$ can therefore provide important insights into the history of interactions between climate, fire, and vegetation. Here we report variations in $\delta^{13}\text{C}_{\text{PyC}}$ composition and mass accumulation rate (PyC-MAR) of biomass-burning–derived PyC from the central part of the Loess Plateau, China, since ca. 7 Ma.

MATERIALS AND METHODS

Field sampling focused on a sequence of windblown Tertiary-age Red Clay Formation overlain by Quaternary loess at Lingtai, central Loess Plateau, China (1340 m above sea level; Fig. DR1 in the GSA Data Repository¹). Magnetostratigraphy was used to establish polarity boundaries within the sequence, and interpolation and extrapolation were used to estimate ages of sediments between polarity boundaries and at the base of the sequence (Sun et al., 1998).

PyC was extracted from a total of 1142 samples using the method of Bird and Gröcke (1997). PyC abundances were determined by combustion and cryogenic purification of CO₂, followed by $\delta^{13}\text{C}_{\text{PyC}}$ determination of the gas using a Finnigan MAT 251 mass spectrometer. Isotopic compositions are expressed as deviations relative to the Vienna Peedee belemnite standard with a precision of $\pm 0.2\text{‰}$ or better. PyC-MAR and the relative contribution to combusted biomass from C₃ and C₄ taxa can be determined from the PyC abundance, sedimentation rate, and $\delta^{13}\text{C}_{\text{PyC}}$ data (see the Data Repository and Table DR1 therein).

Wavelet transform and a multitaper method (Thomson, 1982) were implemented on the PyC-MAR and combusted C₄ contribution (derived from $\delta^{13}\text{C}_{\text{PyC}}$) data for the period since 3 Ma, using the MATLAB program (see Grinsted et al., 2004), to resolve possible relationships between climate, fire, and C₄ biomass.

¹GSA Data Repository item 2014367, supplemental information on sampling site and settings, result calculations, and comparison between $\delta^{13}\text{C}_{\text{PyC}}$ in Lingtai and $\delta^{13}\text{C}_{\text{TOC}}$ in other sections, is available online at www.geosociety.org/pubs/ft2014.htm, or on request from editing@geosociety.org or Documents Secretary, GSA, P.O. Box 9140, Boulder, CO 80301, USA.

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RESULTS AND DISCUSSION

The sequence of samples analyzed accumulated over the past ~7 m.y.; the Red Clay Formation-loess boundary is dated at ca. 2.6 Ma (Fig. 1). Four distinct periods can be distinguished in the PyC-MAR data: ca. 7.0 Ma to ca. 2.6 Ma; ca. 2.6 Ma to ca. 0.6 Ma; ca. 0.6 Ma to ca. 0.15 Ma; and after ca. 0.15 Ma (Fig. 1; Table DR1). PyC-MAR fluctuated but was generally low in the early part of the record (an average of 0.52 mg cm⁻² k.y.⁻¹, n = 294), showing a sustained increase from ca. 2.6 Ma, with a more rapid increase during the past ~0.15 m.y. (average of 8.53 mg cm⁻² k.y.⁻¹, n = 71) (Fig. 1E). δ¹³C_{PyC} averaged -22.7‰ prior to ca. 2.6 Ma (with a marked oscillation at ca. 3.3 Ma), and increased to -16.9‰ by 0.6 Ma, before declining abruptly to ~-24.4‰, after which point values remained generally low (Figs. 2D and 2F).

Prior to 2.6 Ma, the results suggest low levels of biomass burning, with C₃ plants making the predominant contribution to combusted material. On average, ~20% of the total PyC was derived from C₄ biomass, although the C₄ contribution to combusted biomass temporarily increased at ca. 6.8, 5.2, and 3.3 Ma. An increased C₄ contribution to combusted biomass likely reflects a greater prominence in source vegetation, presumably as a result of the conferring on C₄ taxa of a competitive advantage during brief episodes of increased aridity, as inferred from records of dust flux (Fig. 2H). The increase in C₄ contribution to combusted biomass to ~38% at ca. 6.8 Ma is consistent with previous estimates for the proportional presence of C₄ in vegetation at this time, based on the isotopic com-

position of pedogenic carbonate (Ding and Yang, 2000; An et al., 2005), and supports previous suggestions that C₄ plants were established on the Asian continent by ca. 8 Ma (Cerling et al., 1997) or even earlier (Jia et al., 2003). Nevertheless, pollen data suggest that trees and shrubs (mostly C₃ plants) were dominant during the Miocene and the Pliocene (Ma et al., 2005), creating suboptimal canopy and microclimatic conditions for C₄ taxa (Ehleringer et al., 1997).

Seasonality and aridity increased in East Asia after ca. 3.6 Ma, driven by uplift of the Tibetan Plateau and ongoing global cooling (An et al., 2001; Guo et al., 2002). The increase in warm-season rainfall likely favored an expansion of C₄ grasses, with their higher water-use efficiency relative to C₃ taxa (Osborne and Sack, 2012), in semiarid steppe grassland. In addition, greater seasonality of rainfall is likely to have provided conditions conducive to intense biomass fires (Keeley and Rundel, 2005), with increased fire activity leading to more open-canopied forms of vegetation predisposed to burning. The relative abundance of C₄ taxa may be boosted by burning (Beerling and Osborne, 2006), owing to traits in keeping with both the promotion of, and rapid recovery following, fire (Keeley and Rundel, 2005; Bond, 2008). This coupling appears evident from ca. 2.6 Ma, when burning and the relative contribution of C₄ to combusted biomass both increased, and implies that increased seasonality, superimposed upon a long-term trend to greater aridity, may have led to the progressive establishment of conditions conducive to coexpansion of C₄ biomass and fire.

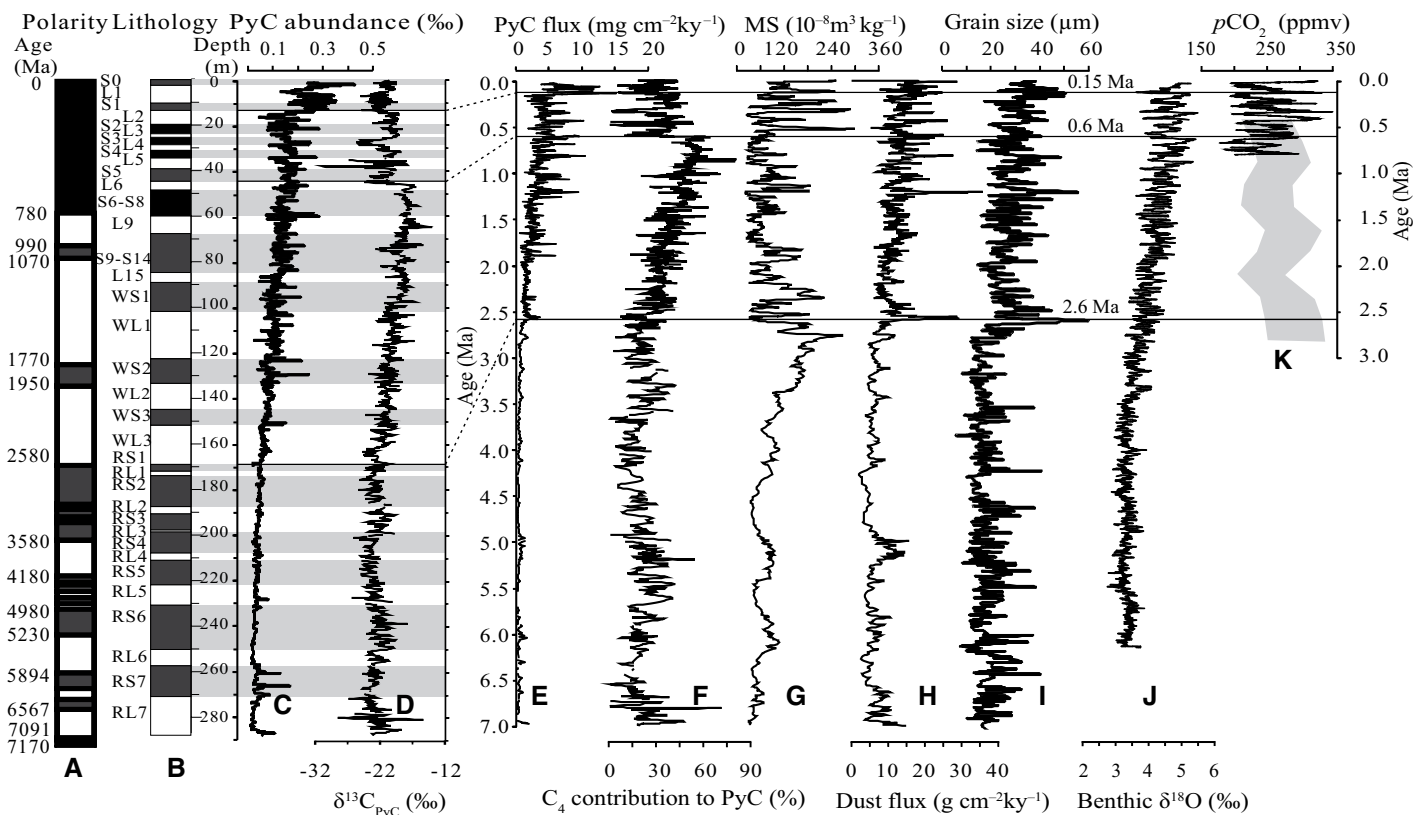


Figure 1. Time series of calculated pyrogenic carbon mass accumulation rate (PyC-MAR) and C₄ contribution to combusted biomass for sequence of samples from Lingtai, China, and comparison with other proxies (see text). **A:** Magnetic polarity column (from Sun et al., 1998). Black bars represent normal polarity, white bars represent reversed polarity. **B:** Stratigraphy of the sequence characterized by alternating lighter loess and/or silty loess and darker paleosol layers. Black bars represent paleosols (prefix S) and white loess (L). W—early Pleistocene loess-paleosol; R—late Miocene-Pliocene Red Clay Formation paleosol deposits. **C, D:** Variations in PyC abundance and PyC isotopic composition with depth. **E, F:** Variations in PyC-MAR and percentage contribution of C₄ plants to combusted biomass over the past 7 m.y. **G–I:** Magnetic susceptibility (MS), dust flux, and grain size curves from Sun et al. (2006); high values indicate strong summer monsoon, winter monsoon, and aridity, respectively. **J:** The LR04 benthic oxygen isotope stack (5.3 m.y. stack of benthic δ¹⁸O records from 57 sites; Liesiecki and Raymo, 2005), reflecting changes in global ice volume. **K:** Ice core record of atmospheric pCO₂ in the past 800 k.y. (solid gray line) (Siegenthaler et al., 2005), and alkenone-based atmospheric CO₂ concentration since ca. 3 Ma (broad shaded curve) (Pagani et al., 2009). Tie lines through C to I mark ca. 2.6, ca. 0.60, and ca. 0.15 Ma; divisions are based on marked changes in δ¹³C_{PyC} and/or PyC-MAR.

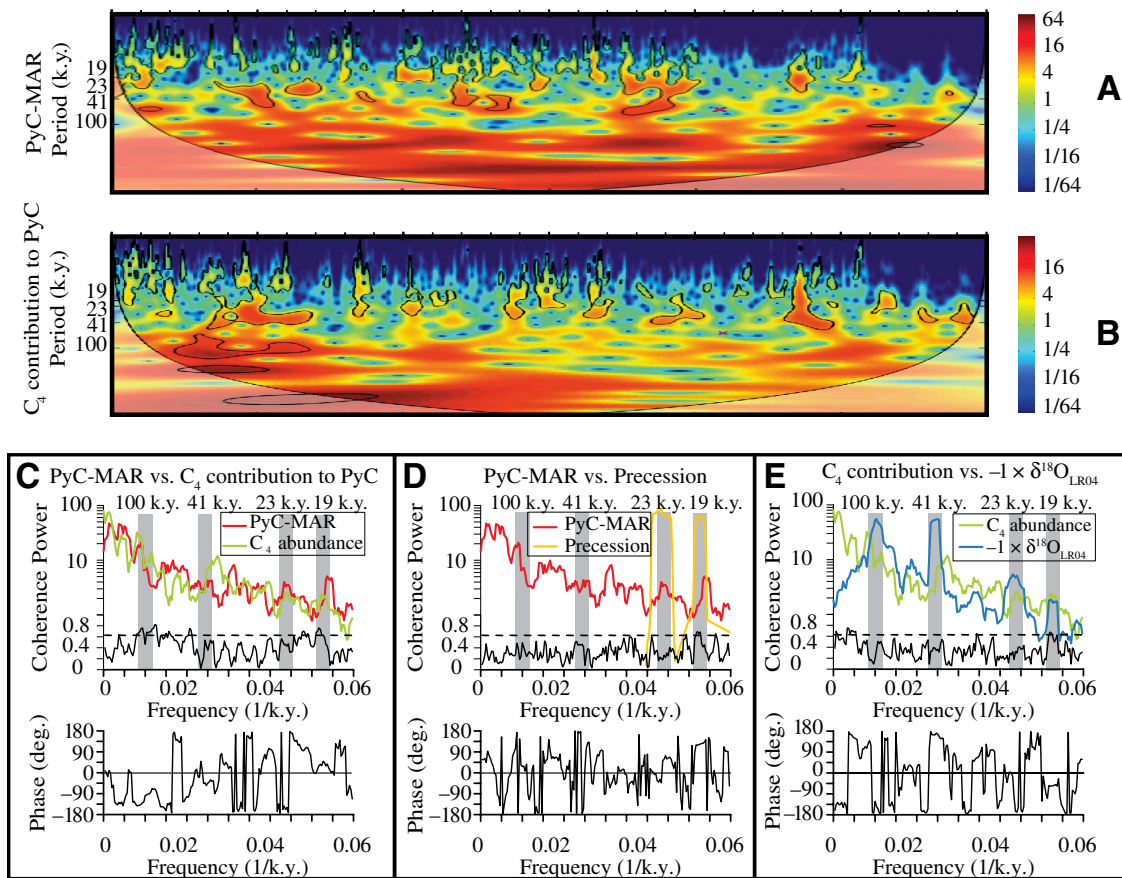


Figure 2. Wavelet spectra of pyrogenic carbon mass accumulation rate (PyC-MAR) and percent of C_4 biomass contributing to PyC for the past 3 m.y. and cross-spectral results of PyC-MAR, C_4 abundance, and other climatic factors. **A:** Wavelet spectra of PyC-MAR abundance. **B:** Wavelet spectra of C_4 abundance. **C:** Cross-spectral results of PyC-MAR (red) versus C_4 contribution (green). **D:** Cross-spectral results of PyC-MAR (red) versus precession (yellow). **E:** Cross-spectral results of C_4 contribution (green) versus $-1 \times \delta^{18}O_{LR04}$ (LR04 stack of Liesiecki and Raymo, 2005) (blue). Axis markers in **A** and **B** denote the frequencies of 19, 23, 41, and 100 k.y., and black contours show the 95% confidence level. Shaded bars in the upper panels of **C–E** denote the frequencies of 19, 23, 41, and 100 k.y. Horizontal dashed lines indicate 95% confidence level. Log transformation was implemented on PyC-MAR to make the variance stationary.

PyC-MAR systematically increased with $\delta^{13}C_{PyC}$ between 2.6 and 0.6 Ma (Figs. 2A and 2C), suggesting that a positive feedback between fire and C_4 abundance was maintained (Edwards and Smith, 2010; Scheiter et al., 2012). Increased C_4 abundance and PyC-MAR coincide with decreasing magnetic susceptibility and increasing benthic $\delta^{18}O$ on a tectonic time scale. Northern Hemisphere glaciation was initiated at ca. 2.6 Ma, strongly influencing monsoonal activity and drying in East Asia (An et al., 2001; Lu et al., 2010). As the summer monsoon is the main determinant of rainfall in the region, a weakening of the East Asian summer monsoon would have further intensified and prolonged aridity. Increased aridity and/or seasonality can promote both C_4 expansion and fire. Over glacial-interglacial cycles, high PyC-MAR values in paleosol layers indicate enhanced fire activity as a result of the availability of high levels of combustible biomass during interglacials (Zhou et al., 2009). Variations in the relative contributions of C_4 and C_3 plants to combusted biomass thus appear in step with glacial-interglacial cycles, with relatively higher average proportions of C_4 -derived carbon contributing to total PyC during the formation of paleosol layers 2.6–1.2 Ma. After 1.2 Ma, increased representation of C_3 in combusted biomass during interglacial periods could reflect the effects of monsoon variability superimposed upon those of long-term increases in aridity and fire activity (Fig. 1F), while pCO_2 remained relatively stable (Siegenthaler et al., 2005; Pagani et al., 2009) (Fig. 1K).

Spectral analysis provides further evidence for the influence of monsoon variability on vegetation type and an apparent coupling between fire activity and proportional contribution of C_4 to combusted biomass. During the period ca. 2.6–0.6 Ma, 41 k.y. and 19 k.y. periodicities (the two main orbital cycles associated with winter and summer monsoons) are evident in both the PyC-MAR and $\delta^{13}C_{PyC}$ data (Figs. 2A and 2B). The PyC-MAR and estimated proportional contribution of C_4 are in phase at

a periodicity of 19 k.y. (Fig. 2C), indicating greater C_4 biomass at times of increased fires.

After ca. 0.6 Ma, $\delta^{13}C_{PyC}$ values decreased abruptly, indicating a decreased contribution from C_4 biomass. Similar pCO_2 levels through this period (Fig. 1K) indicate the absence of a direct link between CO_2 and C_4 abundance. Instead, increased competitive advantage of C_3 vegetation, also evident from the available pollen record (Wu et al., 2007), may have been triggered by a fall in growing season temperature below the threshold favoring C_4 taxa (Huang et al., 2001). The dominance of 100 k.y. and 41 k.y. periodicities in C_4 abundance from ca. 0.6 Ma to ca. 0.2 Ma (Fig. 2B) further indicates that temperature and aridity are the main drivers of a C_4 contribution. Evidence from Lingtai for a decline in C_4 abundance from ca. 0.6 Ma thus contradicts $\delta^{13}C$ data from pedogenic organic matter from Lantian (769 m above mean sea level; An et al., 2005) and from Yanyu (620 m above mean sea level; Sun et al., 2012), close to the southern edge of the Loess Plateau, both of which suggest substantial overall increases in abundance of C_4 biomass in the past 0.6 m.y. (Fig. DR2). These apparently contradictory records may reflect an altitudinal effect, as temperatures at the higher altitude site of Lingtai may have become too cold to support C_4 taxa from ca. 0.6 Ma, and/or reflect differences in provenance, with PyC data representing region-wide changes as opposed to the very local variability likely to be recorded by pedogenic organics.

Increased abundance in PyC-MAR without any systematic change in $\delta^{13}C_{PyC}$ at ca. 0.15 Ma (Figs. 1E and 1F) indicates a decoupling of the two proxies. Abundant PyC at this time may have been the result of increased fire activity associated with the activities of hominins (Roland, 2000). The proportion of C_4 -derived PyC in the Holocene part of the sequence (~31%) is consistent with modern observations of vegetation and measurements of the isotope composition of pedogenic and organic carbon (An et al., 2005; Liu et al., 2013).

CONCLUSION

Results presented here highlight the important role played by fire in a rise to prominence of C_4 taxa in semiarid grasslands on the central Loess Plateau from ca. 2.6 Ma, along with increasing aridity and seasonality. This rise occurred significantly later than in other subtropical and tropical regions. Since ca. 2.6 Ma, the effects of burning, superimposed on the impacts of the initiation and evolution of Northern Hemisphere glaciation and tectonic uplift, have contributed to a history of vegetation in which C_4 grasses are prominent components. More recently, long-term coupling between fire frequency, vegetation, and climate appears to have been disrupted, possibly by anthropogenic burning. A combination of temperature, rainfall, and fire thus appears to have been much more influential than variations in atmospheric pCO_2 in determining the relative contributions of C_3 and C_4 plants to biomass in East Asia.

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