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Initial Expansion of C_4 Vegetation in Australia During the Late Pliocene

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Key Points

- Onset of C_4 expansion during the Late Pliocene in Australia, later than other geographic regions
- Palynological analysis reveals increasingly open landscapes in the lead-up to C_4 expansion
- Northern Australian monsoon initiation linked to East Asian winter monsoon intensification is hypothesized as a driver

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Abstract

Since the late Miocene, plants using the C_4 photosynthetic pathway have increased to become major components of many tropical and subtropical ecosystems. However, the drivers for this expansion remain under debate, in part because of the varied histories of C_4 vegetation on different continents. Australia hosts the highest dominance of C_4 vegetation of all continents, but little is known about the history of C_4 vegetation there. Analysis of plant wax carbon isotopes in scientific ocean drilling sediments off north-western Australia reveal the onset of Australian C_4 expansion at ~ 3.5 Ma, later than in many other regions. Pollen analysis from the same sediments reveals increasingly open C_3-dominated biomes preceding the shift to open C_4-dominated biomes by several million years. We hypothesize that the development of a summer monsoon climate beginning in the Late Pliocene promoted a highly seasonal precipitation regime favorable to the expansion of C_4 vegetation.

Plain Language Summary

This study documents for the first time that C_4 vegetation initially expanded on the Australian continent in the Late Pliocene, several million years later than in Asia, Africa, North America and South America. The expansion of C_4 plants displaced C_3 open habitat vegetation. Understanding the timing and sequence of expansion of C_4-dominated biomes enables us to better constrain the key environmental and evolutionary factors in their development and provides a basis for future conservation of these widespread and important biomes.

1 Introduction

Vegetation utilizing the C_4 photosynthetic pathway is an important component of modern ecosystems globally, comprising ~23% of global gross primary productivity (Still et al., 2003). Biomes dominated by C_4 plants are mainly 'open' habitats, i.e. with sparse tree canopy density. Australia has the highest proportional area dominated by C_4 vegetation of all continents (Murphy & Bowman, 2007; Still et al., 2003). The majority of the continent is dominated by C_4 rather than C_3 grasses, and the relative abundance of C_4 species within grass communities is closely related to seasonal water availability (Murphy & Bowman, 2007). Survey data on modern Australian vegetation compiled in this study further support a close association between warm-season precipitation and C_4 dominance (Figure 1; Text S1.1 in the SI). Australian biomes with significant C_4 taxa include arid and tropical to sub-tropical grasslands and savannas, dominating in the north, and chenopod shrublands, dominating in the south (Hattersley, 1983; Leigh, 1994; Murphy & Bowman, 2007).

On many continents, C_4 vegetation began to proliferate by the Late Miocene, with this expansion recorded as carbon isotope shifts in plant-fixed carbon stored within a wide range of terrestrial and marine sediments and paleosols, as well as in fossil tooth enamel (Cerling et al., 1997; Strömberg, 2011; Tipple & Pagani, 2007). C_4 expansion on these continents occurred as the final stage in what has been inferred as a step-wise progression of ecosystem transformation in which C_3 forest transitioned to C_3 open landscapes, and then to C_4 open landscapes (Cerling et al., 1997; Edwards et al., 2010; Strömberg, 2011).

Despite being the most C_4 dominated continent today, little is known about the timing and pattern of C_4 expansion in Australia. Evidence exists for open habitat vegetation increasing in abundance in the Late Miocene (e.g. Locker & Martini, 1986; Macphail, 1997; Martin, 2006; Martin & McMinn, 1994; Sniderman et al., 2016). However, it is unknown whether Late Miocene Australian grasses and chenopods employed the C_3 or C_4 photosynthetic pathway. Reconstructing changes in the dominant photosynthetic pathway has been limited by the spatial and temporal discontinuity of Australian terrestrial geological records (Kershaw et al., 1994; Macphail, 1997). In this paper, we present ~10 My records of plant wax *n*-alkane carbon isotopes and pollen abundances from sediments of Ocean Drilling Program (ODP) Hole 763A (hereafter ODP 763A), off north-western Australia, to determine when, how and why C_4 vegetation expanded on the Australian continent.

2 Materials and Methods

2.1 ODP 763A Sample Preparation

Samples constitute 26 portions of foraminifera to nanno-fossil ooze or foraminifera-bearing nanno-fossil chalk (Haq et al., 1990) from ODP 763A (collected August 1988). To minimize contamination, 0.5 cm of all exposed faces of the samples was removed and all tools and equipment were thoroughly cleaned (washed with dilute Decon 90® decontaminant solution followed by three rinses of reverse osmosis water, and three rinses each of methanol, dichloromethane (DCM) and *n*-hexane). Samples were lyophilized in ashed borosilicate glass containers, prior to homogenization using a mortar and pestle. Total lipids were extracted from 9.5 to 18.9 g of each sample (mean: 13.9 g) using a Thermo Scientific™ Dionex™ ASE™ 350. Samples underwent five cycles of solvent rinse (five minute static rinse with 9:1 DCM:methanol) and purge (two minutes) at a temperature of 100°C and a pressure of ~11000 kPa. Solvents were evaporated from the total lipid extract (TLE) under N_2 on a FlexiVap™ heated evaporator. Non-polar and polar components were separated by solid phase extraction through ~0.5 g of solvent cleaned activated silica gel of 0.035 mm to 0.070 mm mesh using 4 mL of *n*-hexane and 4 mL 1:1 DCM:methanol, respectively. Elemental sulfur was removed using copper shavings activated in hydrochloric acid.

2.2 Biomarker Quantitation and Compound-Specific Carbon Isotope Analysis

n-Alkanes (C_{16} to C_{35}) were characterized and quantified on a Perkin Elmer Clarus 580 gas chromatograph-mass spectrometer (GC-MS) fitted with a PE Elite 5MS capillary column. Samples were dissolved in 100 µL *n*-hexane with 1µg mL^{-1} 1-1' binaphthyl as

internal standard. Quantitation standards were prepared by dilution of a Certified Reference Material (C7-C40 Saturated Alkanes Standard, Supelco 49452-U) with 1-1' binaphthyl as internal standard for concurrent analysis with the sample batch (See Text S1.2 in the SI for full GC-MS instrument setup specifications).

Compound-specific $\delta^{13}C$ measurements were performed for *n*-alkanes (C_{25}-C_{35}) using a Thermo Delta V isotope ratio mass spectrometer (IRMS) coupled to a Thermo Trace gas chromatograph (GC) Ultra and Isolink through a ConFlo IV interface. Samples were injected into a PTV injector with 2 mm i.d. silicosteel liner packed with glass wool. The inlet was held splitless at 60 °C during injection and then ramped ballistically to 320 °C where it was held for 1.5 minutes during the transfer phase. Compounds were separated on an HP-5MS column (30 m length, 0.25 mm i.d., 0.25 µm phase thickness) with a constant helium flow of 1.0 mL min^{-1}. The GC oven was held at 60 °C for 1.5 minutes, ramped at 15 °C min^{-1} to 150 °C and then at 4 °C min^{-1} to 320 °C and held for 10 minutes. The GC effluent was connected to a custom-made combustion reactor consisting of 1 strand each of 0.1 mm nickel, copper, and platinum wires inside a 0.5 mm i.d. fused alumina tube held at 1000 °C. Continued oxidation and complete combustion of compounds was ensured with the introduction of a trickle of 1% O_2 in helium. Water was removed from the combustion effluent with a custom-built cryotrap consisting of a 20 cm loop of 0.25 mm i.d. deactivated fused silica capillary immersed in an ethanol bath at -85 °C. The trap was periodically thawed and purged to prevent plugging from the build-up of ice. Standard mixtures of *n*-alkanes with known $\delta^{13}C$ values (Mixes B4 and A5 purchased from Arndt Schimmelmann, Indiana University) were interspersed between sample measurements to calibrate the isotopic measurements. Measurement uncertainties (standard error of the mean), including both analytical uncertainty and uncertainty in realizing the VPDB reporting scale were calculated after Polissar and D'Andrea (2014).

2.3 ODP 763A Age Model

Sample ages were calculated using linear interpolations between tie-points in an age-depth model established in Karas et al. (2011), complemented by palaeomagnetic reversal event datum tie-points established in Tang (1992) and updated to Hilgen et al. (2012).

2.4 Adjustment for Pre-Industrial Atmospheric $\delta^{13}C$, and Modelling Percent C_4

The sedimentary *n*-alkane $\delta^{13}C$ values were normalized to pre-industrial atmospheric $\delta^{13}C$, by applying the offset between $\delta^{13}C_{atm}$ for a given sample age estimated from a 3 Myr moving average benthic foraminifera record and $\delta^{13}C_{atm}$ of -6.5‰ (Tipple et al., 2010; Uno et al., 2016). Fraction of C_4 vegetation was calculated from the carbon isotopic composition of C_{31} in the sediments using a linear two end-member mixing model incorporating the mean carbon isotopic composition of C_{31} in a calibration set of modern C_3 (n=106) and C_4 (n=45) plants, also normalized to pre-industrial atmospheric $\delta^{13}C$ of -6.5‰ (Garcin et al., 2014). The C_{31} alkane was used to minimize plant wax production biases related to plant functional type (Garcin et al., 2014).

2.5 Pollen

Fossil pollen was extracted from 12 sample splits using palynological methods adapted from Moore et al. (1991). Samples were digested in cold HCl, followed by treatment with hot 10% KOH, acetolysis (a 9:1 mixture of acetic anhydride and concentrated sulfuric acid), and overnight immersion in concentrated HF, followed by heavy liquid separation using a Na-polytungstate liquid of specific gravity 2.0 (Munsterman & Kerstholt, 1996). The acid- and alkali-resistant residues were then dehydrated in ethanol and mounted on glass slides in glycerol. Pollen was counted along transects at 300x and 600x magnification on a Zeiss AxioScope A.1 with EC Plan Neofluar objectives, until at least 100 pollen grains were counted. Pollen was identified by comparison with modern reference collections and with images stored in the Australasian Pollen and Spore Atlas (APSA Members, 2007).

3 Results

3.1 Plant Wax *n*-Alkane Distributions and Carbon Isotope Ratios

Sedimentary *n*-alkanes in samples from 8.8-1.0 Ma display unimodal homolog distributions, peaking at C_{29}, C_{31} or C_{33}, with a strong odd-over-even predominance (carbon preference index, CPI >2) (Dataset S1 in the SI) that is indicative of a higher plant origin (Bush & McInerney, 2013). The oldest sample, at 9.5 Ma, has a bimodal distribution with peaks at C_{26} and C_{29} and a weak odd-over-even predominance (CPI<2) (Dataset S1 in the SI), suggestive of petrogenic hydrocarbons from unknown sources that obscure plant-derived $\delta^{13}C$ and chain-length distributions. Thus, we disregard the oldest sample as it is likely not of terrestrial plant origin. The proportional abundance of C_{33} compared to C_{29} *n*-alkanes increases significantly throughout the record (Figure 2; Dataset S1 in the SI).

From 8.8–3.6 Ma, carbon isotope ratios of C_{29}, C_{31} and C_{33} are stable with values indicative of predominantly C_3 vegetation. Beginning at 3.5 Ma, $\delta^{13}C$ values progressively increase, becoming more enriched in ^{13}C (Figure 2; Dataset S1 in the SI). In addition, at 3.5 Ma, the $\delta^{13}C$ values of C_{29}, C_{31} and C_{33} *n*-alkanes begin to diverge, causing an increasingly greater difference between $\delta^{13}C$ values of C_{33} and C_{29} after that time (Figure 2; Dataset S1 in the SI). The fraction of the source vegetation that is C_4 plants is estimated from the carbon isotopic composition of the sedimentary C_{31} *n*-alkane (Figure 2, 3). Estimated C_4 fraction from 8.8–3.6 Ma is low, ranging from 9.2 $^{+27.5}_{-9.2}$ % to 19.2 $^{+26.5}_{-19.2}$ % (modern plant end-member 1-sigma calculation uncertainty). At ~3.5 Ma, the estimated C_4 fraction begins progressively increasing, save for one sample at 2.8 Ma. Percent C_4 reaches a maximum of 59.2 ± 22.4 % at 1.0 Ma (Figure 2, 3; Dataset S1 in the SI). It must be noted that the uncertainties in calculations of fraction C_4 vegetation are likely overestimated, due to the geographically and climatically broad modern plant calibration set used (Garcin et al., 2014). Variability in the isotopic composition of the C_{31} *n*-alkane in modern C_3 and C_4 plant endmembers from any one region is likely to be less than the calibration set.

3.2 Palynological Results

Pollen analysis was undertaken on samples ranging in age from 6.8-1.0 Ma and results are presented as a summary pollen percentage diagram (Figure 2). During the latest

Miocene, Gyrostemonaceae, Casuarinaceae, *Acacia* and *Dodonaea* are important components of the pollen sum. Poaceae, Asteraceae and *Eucalyptus* pollen are also present in substantial proportions during the latest Miocene. Across the Miocene-Pliocene boundary, values of Gyrostemonaceae, Casuarinaceae, *Acacia* and *Dodonaea* decline, while those for Restionaceae, indeterminate Myrtaceae pollen, Cyperaceae, and ferns (Polypodiaceae and *Cyathea*) increase steadily until collapsing at ca. 4.9 Ma. Poaceae, Asteraceae and chenopod maintain steady or increasing values through the Early Pliocene. Around the Early-Late Pliocene boundary (3.5-3.6 Ma), the vegetation becomes strongly dominated by Poaceae and Asteraceae, with varying contributions from *Eucalyptus*, Myrtaceae and chenopods, which persists with little subsequent change for the remainder of the record (note, all pollen taxa presented in Figure S3 and Dataset S2 in the SI).

4 Discussion and Conclusions

4.1 Pliocene Expansion of C_4 Vegetation

The carbon isotope ratios of leaf wax *n*-alkanes begin to become enriched in ^{13}C at ~3.5 Ma (Figure 2) implying an expansion of C_4 vegetation in north-western Australia. In addition, beginning at ~3.5 Ma, the $\delta^{13}C$ of the C_{33} *n*-alkane becomes increasingly enriched in ^{13}C compared to the other shorter chain-lengths (Figure 2). Modern Australian grasses produce a higher proportion of C_{33} than trees or shrubs (Figure S2, Table S1, Text S1.3 and Dataset S3 in the SI). This pattern is mirrored in North America and Africa, where grasses have higher abundances of longer chain *n*-alkanes (C_{33} and C_{35}) than trees that instead show higher abundances of shorter chain *n*-alkanes (C_{27} and C_{29}) (Bush & McInerney, 2013; Garcin et al., 2014; Rommerskirchen et al., 2006; Vogts et al., 2009). C_{33} is therefore proposed to be more sensitive to the presence of C_4 grasses on the landscape (Uno et al., 2016), while C_{29} is less influenced by grasses. Carbon-13 enrichment and the beginning of isotopic divergence between C_{29} and C_{33} in our sedimentary record at ~ 3.5 Ma marks the onset of the expansion of C_4 vegetation. Phylogenetic evidence suggests that the moderately diverse C_4 grass tribe Triodiinae, characteristic of central Australian arid vegetation today, radiated in the Australian interior during the late Miocene (Toon et al., 2015). Nonetheless, any Late Miocene C_4 vegetation must have been sparse, as it is not detectable in our C_{29}-C_{33} *n*-alkane record. However, ^{13}C-enrichment of the C_{35} *n*-alkanes relative to C_{29}-C_{33} (Figure S1 in the SI) could be an indication of trace amounts of C_4 vegetation on the landscape prior to 3.5 Ma. The significant expansion in C_4 vegetation beginning at 3.5 Ma indicated by the inflection in our carbon isotope record reflects widespread biologically-productive C_4 vegetation like that supported in the Australian monsoon tropics today (Williams et al., 2017). This timing postdates the onset of most C_4 expansions in Asia, Africa, North America and South America, which occurred across the middle to Late Miocene (Cerling et al., 1997; Dupont et al., 2013; Feakins et al., 2013; Fox et al., 2012; Fox & Koch, 2004; Ghosh et al., 2017; Hoetzel et al., 2013; MacFadden et al., 1996; Passey et al., 2009; Passey et al., 2002; Quade & Cerling, 1995; Uno et al., 2016).

4.2 Late Miocene/Early Pliocene Opening of the Landscape

Substantial Poaceae, Asteraceae, and *Eucalyptus* pollen suggest that north-west Australia was dominated by very open woodland and/or shrubland in the latest Miocene. The prominence of Gyrostemonaceae and Casuarinaceae suggests this vegetation may have had similarities to contemporaneous Late Miocene open shrubland recorded on the Nullarbor Plain in the south of the continent, which was dominated palynologically by these two families (Sniderman et al., 2016). Increases in Restionaceae pollen percentages across the Late Miocene/Early Pliocene transition suggests an increase in effective precipitation, based on the preference of Restionaceae for seasonally moist wetland habitats (Briggs, 2001). Peaks in representation of Myrtaceae, Cyperaceae and ferns are consistent with a peak in moisture at ca. 4.9 Ma, just before these taxa decline abruptly. Rising values of Poaceae, Asteraceae and chenopod pollen during the Early Pliocene imply the increasing dominance of very open vegetation, in which grass and chenopods were more important than previously. Increasing relative abundance of the C_{33} compared to C_{29} *n*-alkane homolog beginning between 7 and 6 Ma also suggests increasing contributions from grasses (Figure 2). Our carbon isotope record indicates that C_4 vegetation did not begin to compose a significant fraction of the increasingly open landscape until ~3.5 Ma. From these data, we interpret an initial Late Miocene expansion of C_3 grasses and/or chenopods, followed by a shift to C_4 grasses and/or chenopods near the Early/Late Pliocene boundary. Fossil fauna tooth enamel isotope data showing mixed C_3 and C_4 diets from the bio-stratigraphically dated Late Pliocene Chinchilla Sands of south-eastern Queensland are consistent with this timing (Montanari et al., 2013). We infer from our record a pattern of ecosystem changes on the Australian continent not dissimilar to other geographic regions (Edwards et al., 2010; Strömberg, 2011), though delayed by several million years.

4.3 Drivers of Late C_4 Expansion on the Australian Continent

Environmental conditions that tend to promote C_4 over C_3 photosynthesis are low atmospheric pCO_2, high temperature, aridity, warm-season precipitation, high irradiance, and fire (Ehleringer, 2005; Keeley & Bond, 2001; Knapp & Medina, 1999; Long, 1999). Decreased pCO_2 has been postulated as a major control on the onset of C_4 expansion globally (Cerling et al., 1997; Cerling et al., 1993; Ehleringer et al., 1991), with new developments in atmospheric pCO_2 reconstruction suggesting a significant decrease through the Late Miocene (Bolton et al., 2016; Mejía et al., 2017). However, heterogeneous timing of C_4 expansion across the globe (Figure S4 in the SI) indicates that decreased pCO_2 cannot be the only driving factor. This assertion is supported by models showing that while changes in pCO_2 have the potential to transform global vegetation states, the timing of transformation will vary due to regional differences in the timing and rates of change of temperature, rainfall amount and seasonality, and fire severity (Higgins & Scheiter, 2012). We argue the relative importance of pCO_2 and environmental factors will likely vary by region.

The timing of the expansion of C_4 vegetation documented here coincides closely with evidence for cooling and aridification in north-west Australia. Sea surface temperatures cool significantly in the region at 3.44 Ma (Karas et al., 2011; Sniderman et al., 2016) (Figure 3), while at 3.3 Ma, there is evidence for the beginning of a transition from a humid to a more arid and/or more seasonal climate (Christensen et al., 2017) (Figure 3). On the Nullarbor

Plain, Sniderman et al. (2016) found no pollen in Pliocene speleothems younger than 3.4 Ma, suggesting that increasing aridity slowed speleothem growth after this time. The drivers of Australian aridification are debated; restriction of the Indonesian Throughflow (ITF) has been hypothesized as the driver of changes in precipitation in north-western Australia during the Pliocene (Christensen et al., 2017; Krebs et al., 2011). Krebs et al. (2011) simulated a constricted ITF based on Pliocene ocean bathymetry, finding that this could have caused a precipitation decrease of up to 30% over the eastern Indian Ocean. Conversely, other modelling experiments have indicated that ITF restriction was not associated with a decrease in precipitation over the eastern Indian Ocean, nor was it associated with significant globally pervasive impact on climate (Brierley & Fedorov, 2016; Jochum et al., 2009). Regardless of the driver of Late Pliocene aridification, there is also evidence for aridity in north-western Australia during the Late Miocene, from ~16-6 Ma (Groeneveld et al., 2017), that did not lead to an expansion of C_4 vegetation (Figure 3). This suggests that aridity by itself was not the primary driver of Late Pliocene C_4 expansion, an inference that is substantiated by globally inconsistent relationships between C_4 plant distributions and modern climate (Sage et al., 1999).

Opening of the landscape, increased seasonality of precipitation, as well as increased incidence of fire are suggested to have played significant roles in promoting the expansion of C_4 vegetation on other continents (Beerling & Osborne, 2006; Edwards et al., 2010; Osborne, 2008; Scheiter et al., 2012; Zhou et al., 2017). Our pollen record suggests that Australian vegetation structure was already open by the Late Miocene/Early Pliocene (Long, 1999). Our record of C_4 expansion also coincides very closely with evidence of increased east Asian dust flux into marine sediments, at ~ 3.5 Ma (Figure 3) (Rea et al., 1998; Snoeckx et al., 1995), widely interpreted as marking the initial intensification of the East Asian winter monsoon (EAWM) or Siberian High (An et al., 2001; Guo et al., 2004; Rea et al., 1998; Sun et al., 1998; Zheng et al., 2004). Controls governing the Australian monsoon over late Neogene to Quaternary timescales are complex (Z. Liu et al., 2003; Wyrwoll & Valdes, 2003), but are dominated by two opposed influences: within-hemisphere insolation forcing (Wyrwoll et al., 2007; Wyrwoll & Valdes, 2003), that is comparatively weak because of the relatively small, low relief land surface of northern Australia; and remote forcing driven by cross-equatorial thermal and pressure gradients between Australia and East Asia (An, 2000). The persistence of an East Asian-Australian precipitation teleconnection, in which Northern cooling leads to southward migration of the Inter Tropical Convergence Zone (ITCZ), has been indicated at a range of Quaternary timescales from centennial-millennial (Denniston et al., 2013; Eroglu et al., 2016) to orbital (Y. Liu et al., 2015), and has been observed in sedimentary records from the Holocene (Eroglu et al., 2016), the last deglaciation (Yancheva et al., 2007), and as far back as the mid-Pleistocene (Y. Liu et al., 2015). The sensitivity of the cross-equatorial meridional circulation linking the EAWM and the Australian monsoon to orbital obliquity has been explored using climate model simulations (Shi et al., 2011).

The abrupt increase in the abundance of C_4 plants at ~3.5 Ma is most easily explained as a vegetation response to the onset of the Australian monsoon regime. In this interpretation, the intensification of the EAWM (Figure S4 in the SI), itself thought to be related to ongoing late

Cenozoic global cooling (Ge et al., 2013; Lu et al., 2010), for the first time pushed the ITCZ far enough southward to develop a substantial summer monsoon in northern Australia, characterized by a strong seasonal precipitation contrast and potentially greater incidence of fire. The relatively late appearance of a distinctly monsoonal moisture regime in northern Australia may help to explain the Plio-Pleistocene evolution of animal clades confined to the Australian monsoon tropics today that are nested within lineages more typical of inland, arid Australia (Laver et al., 2017; Nielsen et al., 2016). The establishment of this new climatic regime would have provided the ecological opportunities necessary for the expansion of C_4 vegetation in Australia beginning at ~3.5 Ma. This supports the hypothesis that the heterogeneous rise of C_4 ecosystems globally reflects variations in the environmental factors providing competitive advantages to C_4 vegetation.

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Figure 1.
Study site in the context of modern Australian C_4 vegetation and climate. (a) Location of ODP 763A, with mapped Summer Rainfall Index (SRI) and surveyed percent C_4 plant cover (see Text S1.1 in the SI for details). SRI calculated as the proportion of summer rainfall (December, January, February) out of summed summer (December, January, February) and winter (June, July, August) rainfall (Australian Government Bureau of Meteorology, 2016). Arrows indicate modern dust transport pathways (Hesse & McTainsh, 2003). (b) The probability that C_4 vegetation is present for a given range of SRI based on survey data.

Figure 2.
Organic geochemical and palynological data derived from sediments of ODP 763A. (a) Compound specific carbon isotope ratios of *n*-alkane homologs; C_{29} (blue), C_{31} (yellow) and C_{33} (pink), with percent C_4 based on the C_{31} homolog. Error bars represent plus and minus one standard error of the mean. (b) The difference between the carbon isotope ratio of C_{33} and that of C_{29}. (c) Grouped pollen percentages indicating relative proportions of herbaceous, woody and other taxa. (d) The proportional concentration of C_{33} relative to C_{29}+C_{33}.

Figure 3.
Australian record of C_4 expansion in the context of contemporaneous climate records and interpretations. (a) Percent C_4 reconstructed from the carbon isotope ratio of the C_{31} *n*-alkane homolog, with modern plant end-member 1-sigma calculation uncertainty shown as dashed black lines. (b) Mg/Ca sea surface temperature reconstruction from ODP 763A (black line is a 15-point simple moving average, calculated using the 'TTR' package (Ulrich, 2018) in R (R Core Team, 2016). Data from Karas et al. (2011). (c) Mass accumulation rates from ODP Sites 885/886 in the central North Pacific ocean (Rea et al., 1998; Snoeckx et al., 1995), interpreted as increasing aeolian flux into sediments resulting from intensification of the East Asian winter monsoon (Dataset S5 in the SI, see Text S1.4 in the SI for methods used to calculate MAR and to update timescale). (d) Arid (tan) and humid (blue) intervals interpreted from potassium abundance in wireline logs from IODP U1463 and U1464 off north-west Australia (Christensen et al., 2017; Groeneveld et al., 2017). Dashed lines on all panels indicate approximate alignment between a SST change point at 3.44 Ma (Sniderman et al., 2016), the increase observed in percent C_4 at ~3.5 Ma, and increased aeolian dust flux into the central North Pacific ocean.