



Supporting Online Material for

The Origins of C₄ Grasslands: Integrating Evolutionary and Ecosystem Science

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Supporting Online Material

Data sources and methods for Figure 1

The simplified land cover classification for Fig. 1A was derived by grouping ISLSCP land cover categories (*S1*) as follows:

ISLSCP no.	Landcover class	Fig. 1 category
1	Broadleaf evergreen forest	Forest
2	Broadleaf deciduous forest / woodland	Forest
3	Mix of 2 and coniferous forest	Forest
4	Coniferous forest and woodland	Forest
5	High latitude, deciduous forest / woodland	Forest
6,8	Wooded C ₄ grassland	C ₄ grassland
7	C ₄ grassland	C ₄ grassland
9	Shrubs and bare ground	Bare
10	Tundra	Bare
11	Desert, bare ground	Bare
12	Cultivation	Cropland
13	Ice	Bare
14	C ₃ wooded grassland, shrublands	C ₃ grassland
15	C ₃ grassland	C ₃ grassland

Data sources and methods for Figure 2

Atmosphere, climate and fire

Paleo CO₂ estimates and errors are from Royer (*S2*) and sources therein with the addition of stomatal frequency estimates from Kürschner et al. (*S3*), B/Ca ratios of surface-dwelling foraminifera from Tripathi et al. (*S4*) and boron isotope ($\delta^{11}\text{B}$) analysis of the carbonate shells of upper-ocean planktonic foraminifera from Pearson et al. (*S5*).

Paleo relative temperature ($\delta^{18}\text{O}$ of foraminifera shells) estimates were compiled by Zachos et al. (*S6*).

Northern Hemisphere ice sheet proxies include firm evidence for terrestrial glaciation (solid color) (*S6*) and evidence for onset of conditions permitting terrestrial glaciation (dashed color) (*S7,S8*).

Charcoal abundance in marine sediments from various sources (*S9, S10*), summarized by Keeley and Rundel (*S11, S12*).

Grass fossils and molecular dates

BEP = BEP clade; PAC = PACMAD clade (C₃ or C₄); PAC? = PACMAD clade or related; BEP+ PAC = clade that includes the BEP + PACMAD clades; B= Bambusoideae; P = Pooideae; C = Chloridoideae; Pan = Panicoideae; An = Andropogoneae; Ar = Arundinoideae.

Grass fossil evidence includes phytolith assemblage data (S13) and macrofossils (S14-S19) information from USA, China, Iran, Kenya, and India.

Molecular dates for origin and diversification of C₄ grass lineages and other clades mainly from Christin et al. (S20) and Vicentini et al. (S21).

Data sources and methods for Figure 3

Vegetation structure, that is, the shift from forests or other grass-free environments to habitats with a substantial amount of grass (savanna, woodland, grassland, mosaic) is based on different sources of data for each region:

- Eastern Mediterranean (Greece-Turkey-Iran): phytolith assemblage data (S22) indicate open habitats by ~20 Ma, faunal functional morphology (mean faunal hypsodonty) support open habitats prior to 10 Ma (S23).
- China: palynological studies (S24, S25) show grass-dominated habitats in western north and interior of China.
- North America (Great Plains): phytolith assemblage data suggest a shift to open, grass-dominated habitats by the earliest Miocene (S26, S27); fossil soils support the spread of grasslands prior to the Early Miocene (S28, S29); faunal functional morphology (hypsodonty in ungulates) support grasslands by the Middle Miocene (S30-S32).
- Pakistan (Siwaliks): faunal functional morphology, toothwear data, and $\delta^{13}\text{C}$ from tooth enamel (S33-S37) all indicate that parts of the landscape were grass-dominated by 9.3 Ma.
- Kenya: faunal functional morphology, tooth wear (S38), $\delta^{13}\text{C}$ of ungulate tooth enamel (S38), plant fossils (S15), and fossil soil data (S39-S41) support the presence of habitats dominated by grass by 13.7-15 Ma, in light of revised geochronology of the key locality Fort Ternan (S42). Additional plant macrofossil and gastropod evidence from neighboring Uganda for grasslands at 17.5 Ma (S43).
- Argentina: faunal functional morphology (evolution of hypsodonty) and phytolith data suggest that the spread of open, grass-dominated habitats occurred at least by 30 Ma (S32, S44, S45).

Relative abundance of C₄ in vegetation and diet is based on stable carbon isotope ratios of fossil soil carbonate nodules and ungulate tooth enamel, respectively. Sources for the raw $\delta^{13}\text{C}$ values are listed by region:

- Eastern Mediterranean (Greece-Turkey-Iran): fossil soil $\delta^{13}\text{C}$ data from Quade et al (S46); ungulate tooth enamel $\delta^{13}\text{C}$ only from three sites in Greece and Turkey (S46, S47).
- China: fossil soil and tooth enamel $\delta^{13}\text{C}$ values compiled from several localities in northern China (S48).
- North America (Great Plains): $\delta^{13}\text{C}$ measurements of fossil soils (S49) and ungulate tooth enamel (S50-S52) from central and southern Great Plains.
- Pakistan (Siwaliks): $\delta^{13}\text{C}$ values for fossil soils from various sources (S53-S56); ungulate tooth enamel stable carbon isotope ratios from several studies (S35, S37, S52, S57).
- Kenya: fossil soil $\delta^{13}\text{C}$ values from Kingston et al (S58) and Levin et al (S59), supported by $\delta^{13}\text{C}$ of *n*-alkanoic acids preserved in marine sediments off the east African coast (S60). Ungulate tooth $\delta^{13}\text{C}$ values from various sources (S35, S52, S61, S62).
- Argentina: fossil soil stable carbon isotope ratios are from two sites in northwestern Argentina (26-35°S) (S63); ungulate tooth enamel $\delta^{13}\text{C}$ span a wider latitudinal range (20-50°S) (S64).

For each million-year period, the maximum and minimum $\delta^{13}\text{C}$ values were taken and plotted at the midpoint of that million-year interval (e.g., at 15.5 Ma for the interval 15-16 Ma). In cases where data were only available for, for example, 15 Ma, the max and min values were plotted at 15 Ma. The raw $\delta^{13}\text{C}$ data were converted to % C₄ in vegetation/diet using age-specific calibration values established by Passey et al (S48). The maximum isotopic value for water-stressed C₃ vegetation corresponds to ~20% C₄ biomass using canonical C₃ and C₄ end-members; this cutoff value is considered the conservative estimate for the presence of C₄.

Data sources and methods for Figure 4

Phylogenetic tree reconstruction

We assembled a DNA sequence matrix for Poales (4,394 taxa) using NCBI archived data from seven commonly sequenced regions for grasses from both chloroplast (*atpB*, *matK*, *ndhF*, *rbcL*, *rpl16*, and *trnL-trnF*) and nuclear (*phyB*, ITS) genomes using the software program PHLAWD (S65) (<http://code.google.com/p/phlawd>). All sequence alignments were conducted using Muscle (vers. 3.6) (S66). The phylogeny was constructed using RAxML 7.1.0 (S67) with all genes partitioned, allowing each gene region to have independent parameter estimates for molecular rate matrices. We employed a GTRGAMMA model of nucleotide substitution, with a GTR substitution model and a Γ model of among-site rate heterogeneity. For subsequent analyses we pruned Poaceae and immediate outgroups (2,684 taxa) from the larger Poales tree. The maximum likelihood Poales phylogeny (“Poales.tre”), Poaceae phylogeny (“Poaceae.tre”) and the original DNA sequence matrix (in phylip format; “Poales.phy”) are available for download on *Science* online.

Character coding

Photosynthetic type (C₃ vs C₄) for each species was determined using previously published datasets (S68-S70).

Dominance was determined from a newly constructed database of all grass species that have been recorded as attaining high abundance in a grass community. Briefly, we surveyed all grassland and savanna species lists that have been compiled in a series of encyclopedic books (S71-S73), and recorded every grass species that was specifically listed as ‘dominant’ by the authors. We excluded grass communities that were specialized to particularly stressful edaphic factors, such as salinity and flooding, in an attempt to capture only grass species that play significant roles in the major grasslands of the world. In a few cases, actual percentage values for abundances for the grass species were provided by the authors; however, in the majority of cases, species were simply listed as “dominant.”

This newly compiled database is obviously very coarse, and is based largely upon subjective observations by many workers in grassland ecology over many years. Ideally, contributions to an improved “global grass dominants database” would adhere to a very standard and quantitative methodology of determining dominance in various communities. This current list of species is meant to be mostly illustrative, and provides a rough first attempt to explore how grassland ‘dominants’ are distributed across the grass phylogeny. The list of dominant species generated from this literature search is presented in a tab-delineated text file as Supplemental Table 1.

Character evolution analyses

Ancestral character reconstructions were performed with maximum likelihood using the computer software program LsrDISC (S74). To test whether dominant species are phylogenetically clustered, we randomized the distributions of dominance across the tree 1,000 times to generate a null expectation of occurrences. For each simulation we scored the total path length of character change across the tree (using maximum parsimony), and compared the observed path length to the distribution of path lengths generated by the simulations. The observed number of changes fell outside of the lower tail of the simulated path length distribution, meaning that the number of actual shifts in dominance was significantly smaller than expected ($p < 0.05$). All simulations and path length calculations were performed using the software program Mesquite v.2.6 (S75).

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