degree of freedom. This gives a probability of only 0.02, so even though the sample size is small, it is unlikely that we would obtain the present observations under hypothesis Exciting. A similar conclusion is reached if we use the MVL database of Valet *et al.*[5].

Recent volcanic data and analyses[11,12], although apparently supportive of hypothesis Exciting, are as yet not compelling. This is because the database suffers from problems similar to the sedimentary database, so careful analysis is required to exclude causes such as the correlations now apparent in the sedimentary database.

The most important issue to resolve at this stage is the cause of the apparent ±90° preferential grouping for (EC-site). Two points should be noted. First, because the preferred-EC bands are 60° wide, only a small bias away from uniform randomness towards ±90° in (EC-site) is needed. For example, one can construct systematic rock magnetic effects such as increased inclination errors in sediments at low field intensity[13] that would contribute to such a bias. Furthermore, Egbert[10] has shown that, under a wide range of circumstances, one could expect VGP longitude distributions to peak ±90° in longitude away from the observation site. Such possibilities must be seriously considered. Second, until there are sufficient data to perform testing for each reversal independently, and then test composite results from the different reversals, any conclusion must be considered tentative. Notwithstanding this second point, it seems premature to embrace hypothesis Exciting when the very data on which this hypothesis is based do not support it. More data are certainly required. Further data that fall into group (1*a*) are almost counterproductive, however, and it is crucial that further data be obtained from sites that fall well outside the present preferred-site bands. ☐

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Expansion of C4 ecosystems as an indicator of global ecological change in the late Miocene

Thure E. Cerling*, Yang Wang* & Jay Quade†

* Department of Geology and Geophysics, University of Utah,
Salt Lake City, Utah 84112, USA
† Department of Geosciences, University of Arizona, Tucson,
Arizona 85705, USA

THE most common and the most primitive pathway of the three different photosynthetic pathways used by plants is the C3 pathway, or Calvin cycle, which is characterized by an initial CO_2 carboxylation to form phosphoglyceric acid, a 3-carbon acid. The carbon isotope composition (δ^{13}C) of C3 plants varies from about −23 to −35‰[1-3] and averages about −26‰. Virtually all trees, most shrubs, herbs and forbs, and cool-season grasses and sedges use the C3 pathway. In the C4 pathway (Hatch–Slack cycle), CO_2 initially combines with phosphoenol pyruvate to form the 4-carbon acids malate or aspartic acid, which are translocated to bundle sheath cells where CO_2 is released and used in Calvin cycle reactions[1-4]. The carbon isotope composition of C4 plants ranges from about −10 to −14‰, averaging about −13‰ for modern plants[1-3]. Warm-season grasses and sedges are the most abundant C4 plants, although C4 photosynthesis is found in about twenty families[5]. The third photosynthetic pathway, CAM, combines features of both C3 and C4 pathways. CAM plants, which include many succulents, have intermediate carbon isotope compositions and are also adapted to conditions of water and CO_2 stress. The modern global ecosystem has a significant component of C4 plants, primarily in tropical savannas, temperate grasslands and semi-desert scrublands. Studies of palaeovegetation from palaeosols and palaeodiet from fossil tooth enamel indicate a rapid expansion of C4 biomass in both the Old World and the New World starting 7 to 5 million years ago. We propose that the global expansion of C4 biomass may be related to lower atmospheric carbon dioxide levels because C4 photosynthesis is favoured over C3 photosynthesis when there are low concentrations of carbon dioxide in the atmosphere.

Fossil soils and fossil tooth enamel are important indicators of the presence of C4 biomass in local ecosystems. The carbon isotope composition of soil carbonate is related to the isotope composition of the local biomass, being enriched in ^{13}C by about 14 to 17‰ compared to the local biomass[6,7]; the carbon isotope composition of tooth enamel is enriched in ^{13}C by about 12‰ compared to the diet[8,9]. Palaeosol (fossil soil) carbonate and fossil tooth enamel are robust indicators of palaeoenvironment[10-13] and palaeodiet[14-16], respectively, and have been shown to retain their isotope composition through diagenesis[17,18]. The large range in the δ^{13}C values for C3 plants (where $\delta^{13}\mathrm{C} = [(^{13}\mathrm{C}/^{12}\mathrm{C})\ \mathrm{sample}/(^{13}\mathrm{C}/^{12}\mathrm{C})_{\mathrm{PDB}} - 1] \times 1{,}000$ and PDB is the stable isotope reference standard) results in some ambiguity in interpretation of the δ^{13}C values for pedogenic carbonate and tooth enamel. Under conditions of moisture stress, the isotope composition of C3 plants can be several ‰ enriched in ^{13}C (refs 3, 19, 20), so that ecosystems with δ^{13}C values as high as −23‰ could be essentially pure C3 ecosystems, with resultant δ^{13}C of soil carbonate of −8‰ and tooth enamel of −10‰. As many animals are highly selective in their dietary intake, δ^{13}C values as high as −8 or −9‰ could result from a diet of C3 plants in semi-arid regions that are isotopically enriched in ^{13}C compared to more mesic ecosystems. δ^{13}C values of −20‰ have been reported for C3 plants growing in arid environments where stomatal conductance is limited[21].

Palaeosols from Pakistan show a very well defined change in the isotope composition of palaeosol carbonate from about −9 to −12‰ beginning at about 7.4 Myr, to −2 to +2‰ by about 5 Myr[12]. (Figure 1 shows data from ref. 12 as a five-point running average, with a sampling density of about 1 palaeosol per 130,000 years over 17 Myr.) The palaeosol data from Pakistan indicate a virtually pure C3 ecosystem before 7 Myr, which was replaced by an ecosystem dominated by C4 biomass by 5 Myr. It is unlikely that more than a small fraction of the biomass could have been using the C4 or CAM photosynthetic pathways before 7 Myr. Because of the possibility of C3 plants being isotopically enriched in semi-arid environments, which are those in which pedogenic carbonate formation is favoured[22,23], even the most positive δ^{13}C values for Pakistan palaeosols before 7.5 Myr ago represent essentially pure C3 ecosystems.

The isotope composition of fossil tooth enamel from mammals from the Siwaliks in Pakistan and from horses in western North America indicate that C4 plants were an important part of the diet starting between 7 and 6 Myr ago (Fig. 1), which is the same time that C4 biomass became important in Pakistan. Major faunal turnover, including the local extinction of hominoids, occurred in the Siwaliks between 7 and 5 Myr ago[24-27]. The shift in the δ^{13}C of enamel from North American horse teeth does not correspond to the noted change in hypsodonty that occurred in the early to middle Miocene[28]. This observation will require a revision in the interpretation of mammalian dentition and its relationship to the spread of savanna ecosystems in the Miocene. Preliminary studies of palaeosol carbonate from East Africa suggest that C4 biomass was of minor importance in the Miocene, but expanded significantly in the Pliocene and Pleistocene[13].

The palaeosol carbonate and fossil tooth enamel data suggest that the expansion of C4 ecosystems took place rapidly between 7 and 5 Myr ago in both the New World and the Old World. Synchronous expansion of C4 ecosystems in both the New World and the Old World suggests a change in global conditions, rather than local development and gradual expansion around the world. We suggest that the change may have been due to a decrease in atmospheric CO_2 levels. The C4 pathway is an adaptation to reduce photorespiration that occurs in C3 plants. Under conditions of increased CO_2, C3 photosynthesis is more efficient than C4 or CAM photosynthesis[4]. But when the CO_2 concentration in intercellular gases in C3 plants falls below about 400 p.p.m.v., the CO_2/O_2 ratio decreases sufficiently to increase photorespiration rates, reducing the inherent advantage of C3 plants over C4 plants in carbon fixation[4]. At sufficiently low concentrations of atmospheric CO_2, combined with high temperatures and/or moisture stress, C4 plants are more efficient than C3 plants[4]. Therefore a rapid global expansion of C4 ecosystems may have been a result of atmospheric CO_2 falling below a critical threshold for efficient C3 photosynthesis, probably around 400 to 500 p.p.m.v. Previous studies on the palaeosols indicates that the atmospheric CO_2 during the Miocene and Pliocene was less than 800 p.p.m.v. (ref. 29). The midpoint of this rapid change in global terrestrial ecosystems, about 6.3 Myr, is also a period when the carbon isotope composition of the oceans changed significantly[30-32]. An increase the proportion of C4 biomass or a decrease in the total terrestrial biomass would result in an isotope shift in the direction observed in the oceans. The near-temporal coincidence in the changes in the isotope composition of the terrestrial and marine carbon pools may be further evidence that a critical threshold was passed that affected the carbon budget of the biosphere.

Previously we attributed the dramatic shift in δ^{13}C of palaeosol carbonate to an intensification of the Asian monsoon[12], based in part on the less dramatic δ^{18}O shift in the isotope composition of palaeosol carbonate that slightly preceeded the δ^{13}C shift. It now appears that the changes observed in the sediments of the Siwaliks are related to global changes in both the carbon budget and the meteoric water cycle, which do not preclude a link to the Asian monsoon system.

The modern global ecosystem includes tropical savannas, temperate grasslands, and semi-desert shrublands that have abundant C4 biomass. Our results indicate that C4 plants underwent significant expansion starting about 7 Myr ago in both the Old World and the New world. Although our results do not preclude C3 grasslands before 7 Myr ago, modern C3 grasslands are restricted to regions with cool growing seasons, such as montane or boreal conditions, or when the growing season is in the spring or winter (as in the Mediterranean climate). It is possible that C3 temperate and tropical grasslands could have existed under CO_2 conditions significantly higher than modern values. However, modern ecosystems with significant C4 biomass seem to be a feature of the late Neogene to present. ☐

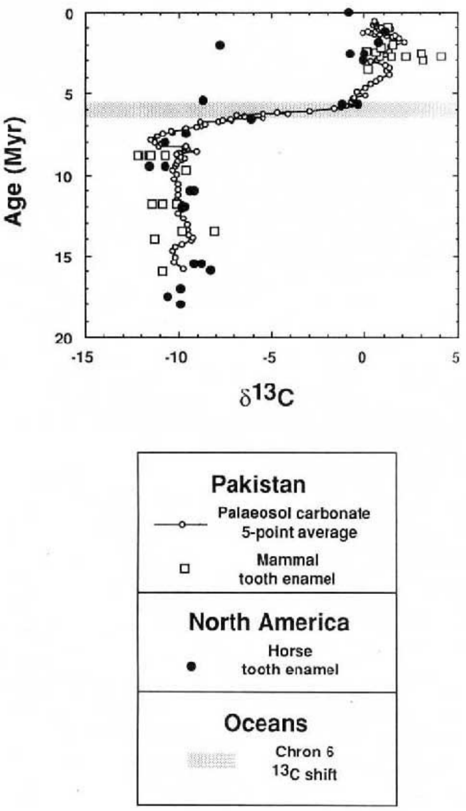

FIG. 1 Isotope transitions in North America and in Pakistan and the late Miocene carbon isotope shift in the oceans. Palaeosols from Pakistan (5-point running average shown as connected circles)[12], tooth enamel from Pakistan (squares; ref. 16, and our unpublished results) and North America (filled circles). Each shows a 10–12‰ shift between 7 and 5 Myr. The age of the marine carbon shift[30-32] is shown as a dotted area.

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