Climate, CO$_2$ and plant abundance

SIR — Cole and Monger[1] presented $\delta^{13}C_{PDB}$ and $\delta^{18}O_{PDB}$ records for pedogenic carbonates in palaeosols representing the past 30,000 yr BP (before present) in the northern Chihuahuan desert, New Mexico. Their $\delta^{13}C_{PDB}$ values indicated that C4 grassland dominated from 30,000 to 8,000 yr BP, but was replaced around 8,000 yr BP by a C3-dominated flora (probably desert shrubland). They proposed that this C4-to-C3 shift was caused by an increase in atmospheric CO$_2$ concentration (pCO$_2$) from 200 to 280 p.p.m.v. during the late Quaternary. They also recommended that $\delta^{13}C_{PDB}$ values of palaeosols could be used as a proxy for past pCO$_2$ changes. But the ecophysiological characteristics of C3 and C4 plants, uncertainty regarding ecosystem-level responses to pCO$_2$ increase, and $\delta^{13}C$ measurements of palaeosols in other regions, indicate that these results should be interpreted with caution.

A change in atmospheric pCO$_2$ from 200 to 280 p.p.m.v. significantly increases photosynthesis, water-use efficiency and biomass production of C3 species at the leaf and whole-plant levels[2]. However, even at the present pCO$_2$ of 350 p.p.m.v., C4 species still have quantum yields, photosynthetic rates and water-use efficiencies comparable to or greater than those of coexisting C3 plants[3,4]. Some C4 species also show enhanced carbon and water relations and increased growth with increasing pCO$_2$ (refs 3,5). In addition, net photosynthesis by C3 plants is reduced 25–40% by photorespiration under present atmospheric CO$_2$ and O$_2$ concentrations[4]; this reduction may have been greater during the late Quaternary when the CO$_2$/O$_2$ ratio was lower than at present. Thus, although carbon and water relations of C3 plants may have improved as pCO$_2$ increased from 200 to 280 p.p.m.v. during the late Quaternary, ecophysiological evidence does not suggest this increase in pCO$_2$ would have shifted competitive interactions to promote replacement of C4 grassland by C3 desert shrubland. In fact, C4 plants still comprise 50–90% of standing crop biomass in some contemporary Chihuahuan desert plant communities[6], and C4 plants continue to dominate many grasslands throughout the world characterized by high light intensity, warm temperatures and limited water availability[4].

Atmospheric pCO$_2$ is only one of many environmental factors that can influence plant communities, and direct effects of pCO$_2$ on leaf and whole-plant ecophysiology may be poor predictors of community, ecosystem or regional vegetation composition and dynamics[7]. It is possible that late Quaternary changes in pCO$_2$ enhanced carbon and water relations of C3 and/or C4 plants and played some part in the evolution and dynamics of plant communities with coexisting C3 and C4 species. However, interactions between pCO$_2$ and other environmental limitations (temperature, amount and distribution of precipitation, soil fertility, frequency and intensity of disturbance) or intrinsic biological characteristics of the plants themselves (allocation patterns, growth form, life history) could potentially reduce or negate plant responses to elevated pCO$_2$ (refs 5, 7).

If the C4-to-C3 shift in the Chihuahuan desert was driven by rising pCO$_2$, then similar shifts should be evident elsewhere at 7,000 to 9,000 yr BP. The $\delta^{13}C_{PDB}$ of organic carbon in palaeosols in the southern Great Plains[8] (a in the figure) contradict this prediction, and indicate that the relative importance of C4 grass production increased from 9,000 to 5,000 yr BP. Estimates of C4-derived carbon at this site correlate with both mean global temperature variations (b in the figure) and regional climate reconstructions[8] over the past 9,000 yr BP, consistent with previous research demonstrating that C4 distribution and performance are correlated strongly with temperature[4]. Other $\delta^{13}C_{PDB}$ records from palaeosols throughout the Great Plains[9-11] also document significant increases in C4-derived carbon that correlate with climate, but not the pCO$_2$ record, during the early and middle Holocene. These
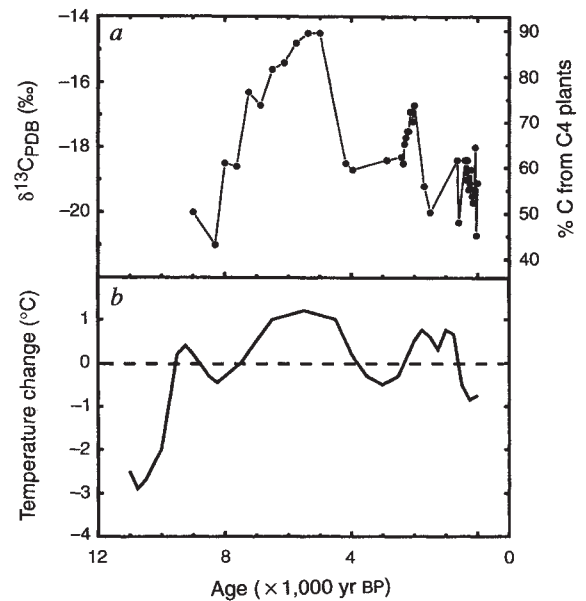
a, $\delta^{13}C_{PDB}$ of organic matter in palaeosols and sediments from Fort Hood Military Reservation in the southern Great Plains of central Texas. b, Global mean temperature variations during the Holocene. Stratigraphy, geomorphology, chronology and isotope methodology associated with the palaeosols have been described in detail elsewhere[8]. Precision (± 1 s.d.) of $\delta^{13}C_{PDB}$ values was ≤0.2 ‰. The proportion of carbon derived from C4 plants was estimated by mass balance using -13 ‰ and -27 ‰ as mean $\delta^{13}C_{PDB}$ values for C4 and C3 plants, respectively. Holocene global temperature variations (b) are adapted from ref. 13 and expressed relative to mean global temperature near the beginning of the twentieth century (~15°C).

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results[8-11] indicate that $\delta^{18}C_{PDB}$ of soil carbon is not always a reliable proxy for pCO$_2$.

Cole and Monger[1] report that their C4-to-C3 vegetation change at 8,000 yr BP was coincident with increased aridity in the southwestern United States, as indicated by climate modelling, palaeovegetation and geomorphic reconstructions, and packrat middens. This shift from C4-to-C3 might, therefore, reflect the replacement of C4 mesophytic grasses by C3 xeromorphic woody growth forms better adapted to warmer, drier conditions despite having the C3 pathway. However, because $\delta^{18}O_{PDB}$ in their pedogenic carbonates varied little at the time of the C4-to-C3 transition, Cole and Monger argued that climate was not responsible for the vegetation change. Considering the uncertainties associated with the climatic significance of $\delta^{18}O_{PDB}$ in continental carbonates[12], this result may not constitute unequivocal evidence for constant climate. The area studied in ref. 1 lies near the ecotone between the grassland and desert biomes of North America, where desert scrub and grassland communities intergrade over broad areas. As a result, small changes in temperature and distribution and amount of precipitation that might be undetectable in the $\delta^{18}O$ record, and/or changes in disturbance regime, could produce relatively large changes in

vegetation composition. Although the precise mechanism responsible for the vegetation change documented by Cole and Monger remains unknown, it seems unlikely that increased pCO_2 was the only driving force.

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MONGER AND COLE REPLY — The purpose of our paper[1] was to show the correlation between a decline of C4 grasses recorded by soil $\delta^{13}C$ values and increased pCO_2 recorded by ice cores[2-5]. We think this correlation is important in the light of recent experimental results showing that increased pCO_2 may give C3 plants a competitive advantage[6], and that the expansion of Miocene C4 biomass was potentially related to lower pCO_2 levels[7].

We agree with Boutton *et al.* that a pCO_2-driven shift did not happen in all C4 ecosystems worldwide approximately 7,000–9,000 years BP. We did not state that the C4-to-C3 isotope signal would be universal, but pointed out that the signal we observed was associated with an arid alluvial fan system[1]. Such alluvial fan systems located in desert scrub/grassland ecotones may offer the best place to 'prospect' for floral responses to changing pCO_2 for two reasons. First, well-preserved palaeosols necessary for the isotope record are common. Second, these areas are ecologically fragile because their soils often have low water-holding capacities, making them susceptible to environmental stresses. In contrast, intermontane basin soils adjacent to our study area that receive runon and have high water-holding capacities exhibit only moderate isotope shifts at 7,000–9,000 years BP[8].

Therefore, considering the magnitude of pCO_2 change during the last deglaciation, we would not expect to see a floral shift driven by increasing pCO_2 within prairies of central Texas or elsewhere. Using the example of Boutton *et al.*, an

increase in C4 grasses occurred from 9,000 to 5,000 years BP in central Texas[9], whereas a decline in C4 grasses occurred at the same time on alluvial fans in southern New Mexico[1]. Both areas experienced aridity and increased pCO_2. In southern New Mexico increased pCO_2, which potentially gives C3 desert scrub a competitive advantage[6], would have intensified the effects of aridity to promote a loss of C4 grasses. In contrast, the benefits to C3 trees and C3 grasses from increased pCO_2 in central Texas were probably offset by aridity, which promoted C4 prairie expansion.

Important clues about the relative roles of pCO_2 and climate on vegetation shifts can be provided by $\delta^{18}O$ values. We acknowledge the uncertainties associated with using these values in pedogenic carbonate as climatic indicators. But unlike previous studies[10,11] showing parallel shifts in $\delta^{18}O$ and $\delta^{13}C$, purportedly due to climatically driven vegetation changes, our results show profound $^{13}C/^{18}O$ discordance. Because $\delta^{18}O$ values remained relatively constant ($\pm 1\%o$) whereas $\delta^{13}C$ values changed approximately 6–8%o, we regard the discordant trajectories as an indication that another variable, pCO_2, had an important influence on the vegetation change.

There is no question that a number of variables cause C4–C3 vegetation shifts. We did not claim that pCO_2 was the only driving force. However, where fragile arid and semiarid environments are well-preserved in the geological record, and other variables such as climate change are understood, we believe $\delta^{13}C$ values in palaeosol carbonate may be an important indicator of past CO_2 changes.

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CO$_2$ effects at high temperature

SIR — Oechel *et al.*[1] report that initial increases in carbon fixation by an Arctic tundra ecosystem exposed to elevated CO_2 concentrations (680 p.p.m.) were not detectable after 3 years at ambient temperatures; in contrast, experimental areas exposed to elevated CO_2 and temperature (+4 °C) continued as net sinks for CO_2 3 years after the experiment began, albeit at a slightly lower level than in year one. Unfortunately, Oechel *et al.* do not report results for enhanced temperatures only. The data refer to control and enhanced CO_2 at ambient temperatures and enhanced CO_2 at enhanced temperatures. Responses to enhanced temperatures alone are not reported, although the methods suggest that the measurements may have been done. On the data provided it is therefore impossible to distinguish an ecosystem-level response to enhanced temperatures alone, from the effects of enhanced temperatures in combination with enhanced CO_2. Simply, enhanced CO_2 uptake in year three may have been a temperature effect.

We are now exploring in the Ecotron[2,3] ecosystem-level impacts of enhanced CO_2, enhanced temperature, and their combination in a fully factorial design, across several plant generations, allowing us to test Oechel *et al.*'s important conclusions.

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Replication step

SIR — In your article "Guesswork and randomness" (*Nature* **372**, 30; 1994), you state in regard to Spiegelman's molecular evolution experiments on Qβ that "selection for the replicase giving the most rapid replication of the whole virus eventually yielded a dramatically shorter enzyme". This is not so. The experiment, which involved serial replication of Qβ RNA by purified Qβ replicase *in vitro*, yielded a greatly shortened (biologically inactive) RNA, in which sequences required for recognition by the replicase were conserved but most coding sequences were eliminated. The selective advantage of this RNA *in vitro* was that it was replicated faster than full-length wild-type Qβ RNA. No "shorter enzyme" resulted or was involved in this experiment.

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