

vegetation composition. Although the precise mechanism responsible for the vegetation change documented by Cole and Monger remains unknown, it seems unlikely that increased pCO₂ was the only driving force.

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MONGER AND COLE REPLY — The purpose of our paper¹ was to show the correlation between a decline of C4 grasses recorded by soil δ¹³C values and increased pCO₂ recorded by ice cores²⁻⁵. We think this correlation is important in the light of recent experimental results showing that increased pCO₂ may give C3 plants a competitive advantage⁶, and that the expansion of Miocene C4 biomass was potentially related to lower pCO₂ levels⁷.

We agree with Boutton *et al.* that a pCO₂-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 system¹. Such alluvial fan systems located in desert scrub/grassland ecotones may offer the best place to 'prospect' for floral responses to changing pCO₂ 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 runoff and have high water-holding capacities exhibit only moderate isotope shifts at 7,000–9,000 years BP⁸.

Therefore, considering the magnitude of pCO₂ change during the last deglaciation, we would not expect to see a floral shift driven by increasing pCO₂ 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 Texas⁹, whereas a decline in C4 grasses occurred at the same time on alluvial fans in southern New Mexico¹. Both areas experienced aridity and increased pCO₂. In southern New Mexico increased pCO₂, which potentially gives C3 desert scrub a competitive advantage⁶, 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 pCO₂ in central Texas were probably offset by aridity, which promoted C4 prairie expansion.

Important clues about the relative roles of pCO₂ and climate on vegetation shifts can be provided by δ¹⁸O 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 δ¹⁸O and δ¹³C, purportedly due to climatically driven vegetation changes, our results show profound ¹³C/¹⁸O discordance. Because δ¹⁸O values remained relatively constant (±1‰) whereas δ¹³C values changed approximately 6–8‰, we regard the discordant trajectories as an indication that another variable, pCO₂, 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 pCO₂ 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 δ¹³C values in palaeosol carbonate may be an important indicator of past CO₂ changes.

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CO₂ effects at high temperature

SIR — Oechel *et al.*¹ report that initial increases in carbon fixation by an Arctic tundra ecosystem exposed to elevated CO₂ concentrations (680 p.p.m.) were not detectable after 3 years at ambient temperatures; in contrast, experimental areas exposed to elevated CO₂ and temperature (+4 °C) continued as net sinks for CO₂ 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 CO₂ at ambient temperatures and enhanced CO₂ 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 CO₂. Simply, enhanced CO₂ uptake in year three may have been a temperature effect.

We are now exploring in the Ecotron^{2,3} ecosystem-level impacts of enhanced CO₂, 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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