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Invited lecture: Atmospheric CO_2, terrestrial ecology, and mammalian evolution

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ABSTRACT: The distribution of C_3 versus C_4 plants in the modern world is related to temperature. However, because of the sensitivity of C_3 to the CO_2/O_2 ratio of the atmosphere it is expected that global changes in the distribution of C_3 versus C_4 plants should accompany atmospheric CO_2 changes in geological time. The period from 6 to 8 million years ago was a time of C_4 expansion in many parts of the globe.

1 INTRODUCTION

There is strong ecological, geographical, and palaeoecological evidence that abundance and distribution of plants using C_4 photosynthesis are related to climate, specifically to atmospheric carbon dioxide concentration and temperature. C_4 plants are mainly grasses, especially the tropical and subtropical grasses (Sage et al. 1999).

2 RESULTS AND DISCUSSION

The C_3 photosynthetic pathway evolved under very high atmospheric CO_2 concentrations whereas the C_4 photosynthetic pathway is a much more recent development, representing adaptation to relatively low atmospheric CO_2 concentrations. A model of quantum yield of plants using the C_3 versus C_4 photosynthetic pathways shows that the crossover temperatures for C_3 plants compared to C_4 monocots is about 22°C for the modern condition (Cerling et al. 1997). This results from photorespiration in C_3 plants at low CO_2/O_2 ratios. The model further shows that the crossover is strongly dependent on both temperature and atmospheric CO_2 (Figure 1). C_4 dicots are more rare than C_4 monocots and have significantly lower crossover temperatures; they are favored only showing the crossoverunder extremely low CO_2 conditions, such as are found under full Glacial conditions (Ehleringer et al. 1997). The "C_4-world", where C_4 plants make up a significant fraction of tropical to temperate ecosystems, began at the end of the Miocene due to low atmospheric CO_2 concentrations; since then C_3 plants have been starved for CO_2. C_4 grasses are the dominant grass from 0 to 45 degrees latitude, and thus modern savannas are important ecosystems that characterize the "C_4-world" of the Plio-Pleistocene. Mammalian evolution during the Plio-Pleistocene was directly related to the low CO_2 concentrations of the atmosphere, because competition between C_4 and C_3 plants (and even between different C_3 plants) resulted from CO_2 starvation of C_3 plants due to photorespiration. Some mammals, such as equids, were already grazing on C_3 grasses and immediately used this new resource when it became more readily available at the end of the Miocene. Figure 2 shows that equids had already apparently adapted to a grazing diet in North America by about 15 million years ago as indicated by their development of hypsodont (high crowned) teeth, but changed to a C_4 diet abruptly between 6 and 7 million years ago. The change to high crowned teeth in equids was during a period of diversification within the equids,

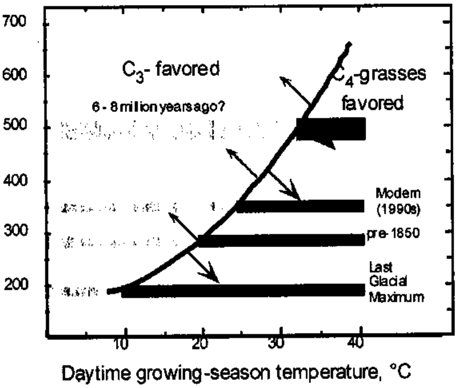

Figure 1. Model of C_3 versus C_4 photosynthesis based on relative quantum yields.

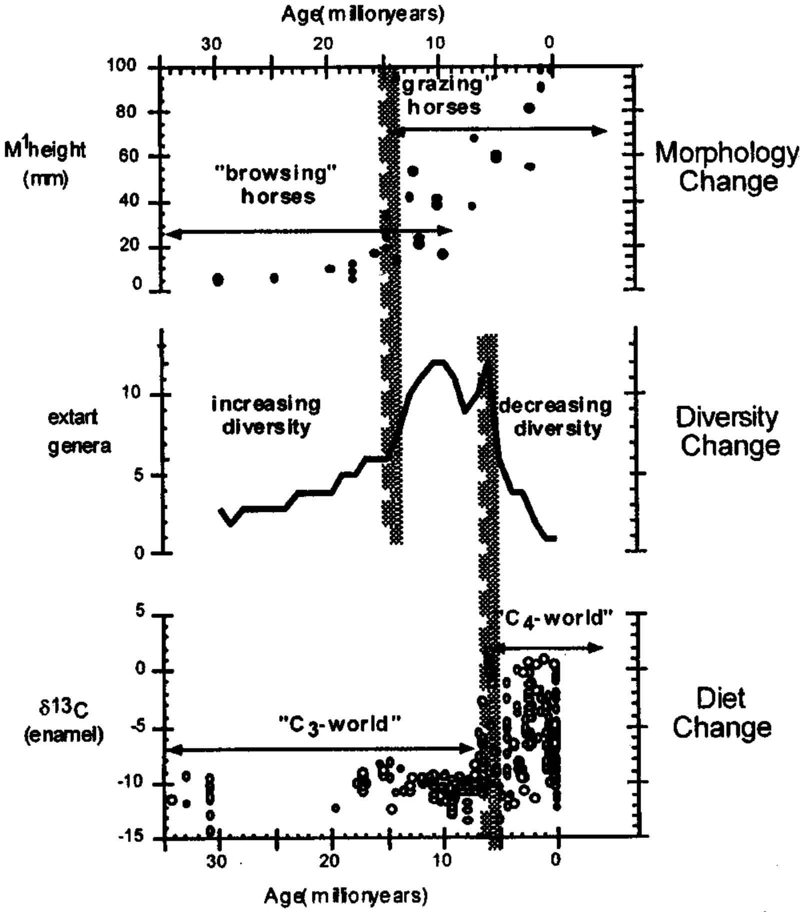

Figure 2. Index of hypsodonty for North American equids, the number of extant genera, and $\delta^{13}C$ of equid tooth enamel from North America in the Neogene.

whereas the time of C_4 expansion was accompanied by a rapid decline in equid diversity (Figure 2).

The change to a C_4 diets in mammals was abrupt: Figure 3 shows that 10 million years ago Asian, African, and the North American equids had a C_3 diet, but changed to a C_4 diet between 6 and 8 million years ago. Entire mammalian communities on all continents (except Antarctica) underwent a great change from the "C_3-world" at the end of the Miocene to the Plio-Pleistocene "C_4-world", even in regions where C_4 plants have never been abundant (e.g., Europe).

Many vegetation changes in the Pliocene and Pleistocene have been explained as being the result of changes in seasonality or changes in aridity (e.g., Janis 1993). However, water loss from plants occurs through the stomata which is where CO_2 is taken up by plants through diffusion. Thus, reduction in photosynthesis and ultimately growth rate, could be due to lower atmospheric CO_2 concentrations instead of aridity. For this reason, changes in CO_2 concentration also should be considered in climate reconstruction because the direct impact of CO_2 on plant productivity is independent of water and temperature constraints.

3 CONCLUSIONS

Global changes in terrestrial ecology are expected to result from changes in the CO_2/O_2 ratio. At CO_2 concentrations less than about 500 ppmV C_3 plants increasingly become less efficient due to photorespiration. Therefore changes in the fraction of C_3 versus C_4 plants may be related to changes in the atmospheric CO_2 concentration. The late Miocene to early Pliocene was a period of global vegetation change as well as a period of faunal

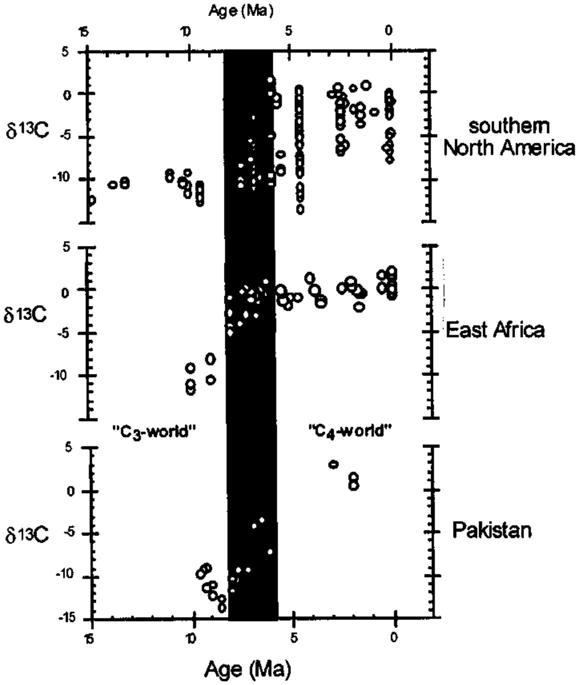

Figure 3. Global diet change in equids shown for North America, Africa, and Asia based on the $\delta^{13}C$ values of equid tooth enamel

turnover in the mammals. The last 6 to 8 million years can be characterized as a "C_4-world" which differed greatly in terrestrial ecology than the previous "C_3-world".

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