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Some ecological implications of palaeoatmospheric variations

P. D. MOORE

Division of Biosphere Sciences, King's College London, Campden Hill Road, London W8 7AH, UK

Abstract: The past composition of the atmosphere is gradually being elucidated with increasing precision. But advances in the understanding of the ecological and evolutionary implications of atmospheric changes are not keeping pace. A graphic model is presented here to indicate the complexity of interacting forces resulting from a change in atmospheric carbon dioxide level, and it can be seen that any resultant ecological outcome will be influenced by a series of (sometimes opposing) factors. This is particularly true of the hydrological consequences of atmospheric change and hydrology will undoubtedly prove a major influence on vegetation.

Changes in the levels of both atmospheric carbon dioxide and oxygen have had profound effects on the evolution of plant life by modifying the selective pressures favouring alternative systems of carbon assimilation. These photosynthetic strategies are also closely related to local hydrology. More ecological and physiological information is clearly needed before the biological consequences of variations in the atmosphere of the past can be appreciated.

There have been numerous attempts in recent years to elucidate in a quantitative fashion the changes that have occurred in the atmosphere during the course of the Earth's history. Many of the techniques employed and conclusions reached are described in this thematic set. As yet many of these results are of a preliminary nature; techniques need refining and analyses need to be extensively duplicated before precise conclusions can be obtained regarding the extent and timing of past atmospheric changes. However, it now seems well established that significant atmospheric changes that may well have had important ecological and evolutionary repercussions have taken place and continue to do so. It is the aim of this contribution to examine some of these influences and to consider their interactions.

Palaeoatmospheric studies of the Phanerozoic have largely concentrated upon two of the component gases, oxygen and carbon dioxide. Other components, such as the noble gases (Turner this issue), have not been regarded as biologically influential, or, like nitrogen (Raven & Sprent this issue), have not been regarded as limiting to evolutionary processes, though the development of microbial fixation mechanisms must be regarded as a most important step in the establishment of nutrient cycles in primitive ecosystems (Raven & Sprent this issue). Attention here will concentrate on the ecological implications of variations in carbon dioxide and oxygen levels in the atmosphere.

Carbon dioxide and ecology

Past and present variations in the carbon dioxide levels of the atmosphere have been outlined and discussed by Hall (this issue). They have made it clear that considerable variations have taken place in the past and further changes can confidently be predicted for the future. The rates of change and the quantitative levels of change are still not entirely clear. The analysis of foraminiferal carbon suggests that the atmosphere of the last interglacial (stage 5e) may have contained as much as 350 ppm CO_2, falling to about 200–225 ppm during the last glacial and perhaps rising to 280 ppm before the effects of the industrial revolution (Shackleton *et al.* 1983). On the basis of ice core bubbles, Delmas *et al.* (1980) placed the cold-stage carbon dioxide level as low as 160 ppm, just half of the present value. The most recently published data from the Byrd station in West Antarctica (Neftel *et al.* 1988) suggest levels of between 180 and 200 ppm during the last glacial. Raynaud & Barnola (1985) suggest a pre-industrial carbon dioxide level of 260 ppm. Estimates of carbon dioxide partial pressures in earlier times are far less precise, but much higher values are proposed for the Cretaceous.

Given that carbon dioxide has varied in the past, the question remains concerning the ecological effects of such variations. Figure 1 provides an indication of the complexity of interactions arising from a putative increase in carbon dioxide. In this diagram, an arrow represents an influence of one effect upon another.

Groves *et al.* (1978) proposed that an increase in atmospheric carbon dioxide would lead to cooling of the upper stratosphere. When carbon dioxide diffuses into the upper stratosphere it emits more infrared radiation to space than it absorbs, thus reducing the stratospheric temperature. This is turn favours ozone production. Work by Bischof *et al.* (1985) has demonstrated that the necessary upward diffusion of CO_2 does take place, so one consequence of raised atmospheric CO_2 could be an increase in stratospheric ozone. The reduced ultra-violet radiation penetration resulting from higher ozone levels would permit the maintenance of high phytoplankton population densities in the surface layers of the ocean, thus increasing planktonic productivity and ultimately the carbon sink in the oceans, not only through the well-known planktonic food-chains, but also through the decomposer route provided by bacterioplankton (Ducklow *et al.* 1986). The latter could account for some of the lost carbon in recent budget estimates (Hall this issue), as could the unexpectedly high flux of pteropod shells from surface to deep ocean waters, commented on by Whitfield (1984).

Increased atmospheric carbon dioxide could also result in an increase in the primary productivity of land plants. Plants using a C_3 (Calvin cycle) system of photosynthesis are generally limited by the level of ambient carbon dioxide.

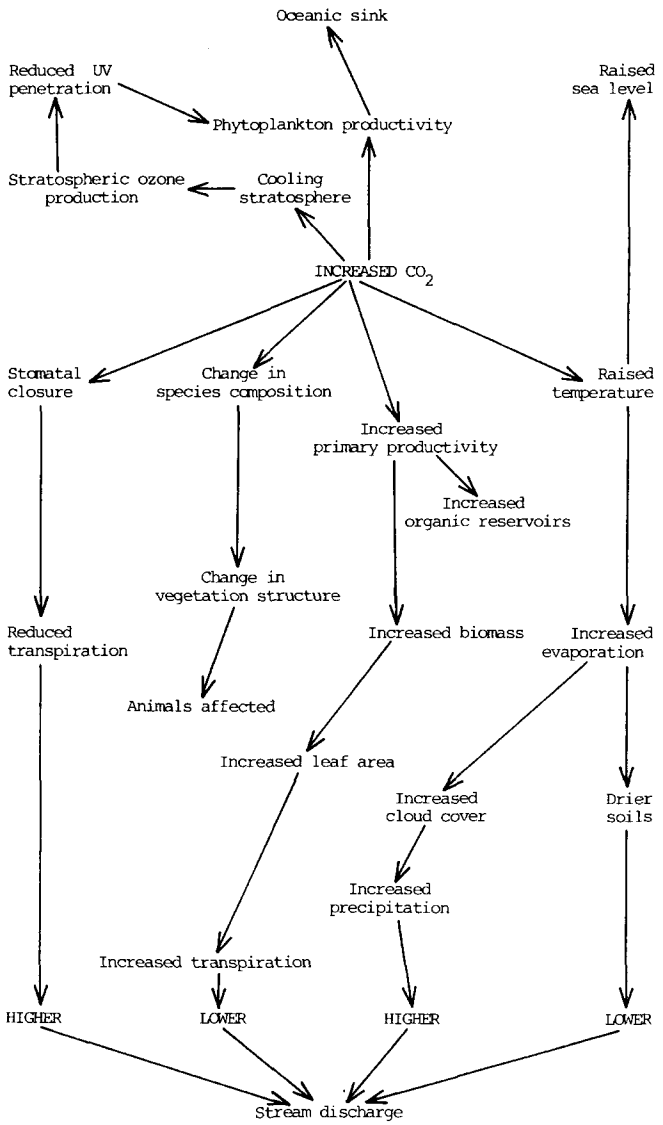

Fig. 1. Graphic model of some possible consequences of raised atmospheric carbon dioxide levels, together with their ecological repercussions.

The current increase in atmospheric CO_2 may already be influencing global primary productivity, and this may be detected by observing changes in the amplitude of seasonal variations in atmospheric carbon dioxide. Hall *et al.* (1975) pioneered this approach and examined 'hemispheric metabolism' from data on atmospheric CO_2 variation at the Mauna Loa monitoring station in Hawaii. By subtracting the trough in CO_2 levels for each summer from that for the preceding winter, they determined the net seasonal uptake of CO_2 by photosynthesis, and using the difference between each trough and the following crest, they estimated net hemispheric respiration. Between 1959 and 1972, however, they could detect no change in seasonal amplitude of atmospheric CO_2 variation. D'Arrigo *et al.* (1987) have presented data suggesting that global biomass changes are now detectable and that up to 50% of the seasonal variation in CO_2 in Alaska and 30% in Hawaii is due to the growth of the boreal forests in the northern hemisphere.

An alternative approach to the study of plant growth response to an increase atmospheric carbon dioxide is the analysis of growth rings in trees. D'Arrigo *et al.* (1987) have used this method in the boreal forests using white spruce (*Picea glauca*) and LaMarche *et al.* (1984) have conducted similar studies on bristlecone pine (*Pine aristata*) in the White Mountains of California. They show an increase in pine growth rates during the last two centuries and especially in the last 20 years. More extensive studies are needed to corroborate these indications, but an increase in global phytomass is precisely what might be expected of raised atmospheric CO_2 levels.

Strain (1987) is conducting experiments into the effects of raised atmospheric CO_2 and higher temperature on whole ecosystems in the Alaskan tundra. He has conducted a three year experiment with treatments involving enriched CO_2 and raised temperature (+4 °C), and has discovered that narrow-leaved monocots, such as *Eriophorum* and *Carex* responded more strongly to both factors than such dwarf shrubs as *Vaccinium, Ledum* and *Betula nana.* These results imply that important changes in the competitive ability of plants will occur in response to raised CO_2 and temperature, which may lead to changes in the composition of plant communities. Such changes in the species composition of communities could have considerable impact on animal populations, not only because of the reduction of certain potential food plants and the increase of others, but also because of the changes in ecosystem structure (that is, the architecture of the plant canopy) which could result when particular life-forms of plants are affected, as in the tundra studies. In general, the diversity of animals, especially invertebrates, is more closely related to ecosystem structure than to plant diversity.

It is possible that some of the increased terrestrial primary production would pass not into grazing or decomposer food chains, but into the accumulation of organic reserves in the form of peats. Peat-forming processes, however, are generally regulated by decomposition rather than production rates (Moore 1987), and these in turn depend upon waterlogging, so hydrological changes are more likely to be of importance in determing this alteration in energy pathways than is primary productivity. Even if conditions favoured the accumulation of such reserves, as in Carboniferous times, it is unlikely that the rate of accretion of fossil carbon would have had a significant effect on contemporaneous atmospheric carbon dioxide levels (Moore 1983).

One effect of higher concentrations of carbon dioxide in the atmosphere which is generally agreed upon is the overall raising of the temperature of the troposphere and the Earth's surface. Many models have been constructed to provide a basis for estimating the effects of a doubling of CO_2 levels. These are reviewed and discussed by Kerr (1986). Estimates mainly fall between 2° and 4 °C rise in global temperature and such a temperature rise would also contribute to increased primary productivity, but geographical factors would have to be taken into consideration, particularly as they affect water availability.

It is when we consider hydrology that the effects of changing carbon dioxide are most difficult to envisage. For most plants, a rise in ambient CO_2 leads to stomatal closure, so one might expect lower global transpiration rates to ensue. Idso & Brazel (1984) have estimated that streamflow in the western United States could increase by 40–60% as a consequence of a doubling of atmospheric CO_2 levels and its

consequent effect on transpiration. Their model is complex, however, for increased temperature, as well as increased carbon dioxide, will stimulate photosynthetic production and thus possibly increase plant biomass over the land surface of the earth. This will generate a corresponding increase in leaf area and hence transpiration. A high global leaf area, in turn, will tend to decrease run-off and stream discharge.

It could be argued, on the other hand, that any increase in productivity on the part of the vegetation would be matched by an increase in respiration. A rise in overall metabolism would thus not necessarily result in a plant biomass increase.

There are many other variables to consider. The direct effect of carbon dioxide on atmospheric circulation patterns and precipitation is one of these. Manabe & Wetherald (1987) have provided a detailed model to account for geographical variations in soil moisture as an outcome of a global temperature rise. They show that a considerable reduction is expected over continental North America, western Europe and northern Canada, perhaps of the order of 10%. As Mitchell & Warrilow (1987) have pointed out, however, much depends on the physical attributes of the soils within these regions. For example, a light sandy soil in a prairie region will respond in a different manner from a peaty substrate under the influence of permafrost in the Canadian tundra.

Clearly, any modelling of the ecological impact of carbon dioxide levels on stream discharge and erosion needs to take many factors into consideration.

Carbon dioxide, oxygen and photosynthetic strategies

One of the major distinctions between the C_3, C_4 and CAM photosynthetic systems is the sensitivity of the former to ambient carbon dioxide levels. The enzyme responsible for initial carbon assimilation in a C_3 plant (ribulose 1–5 bisphosphate carboxylase—RuBisCo), has a lower affinity for CO_2 than does its equivalent in C_4 and CAM plants (phospho-enol pyruvate carboxylase). Thus any reduction in CO_2 will put C_4 and CAM plants at a physiological advantage, whereas raised CO_2 levels will favour C_3 plants (Moore 1983).

Another characteristic of the C_3 system is its sensitivity to oxygen levels. Oxygen competes with carbon dioxide for active sites on the RuBisCo enzyme, so that carbon fixation in an atmosphere containing oxygen is less efficient than one which is oxygen free. This inefficient use of available carbon is termed photorespiration (Rao & Hall 1982). Any reduction in atmospheric oxygen will therefore provide advantages to C_3 plants, whereas increases in oxygen will favour CAM and C_4 species. Both the evolution of photosynthetic pathways in the past and the selection for particular species in given habitats must have been influenced by the varying proportions of oxygen and carbon dioxide (Fig. 2).

The influence of CO_2 on global temperature must also be taken into consideration. Raised temperatures generally place C_4 species at an advantage, hence their current preponderance in low latitudes.

There is one further complication when considering influences on the balance of photosynthetic strategies, namely the water balance of the environment. One ecological

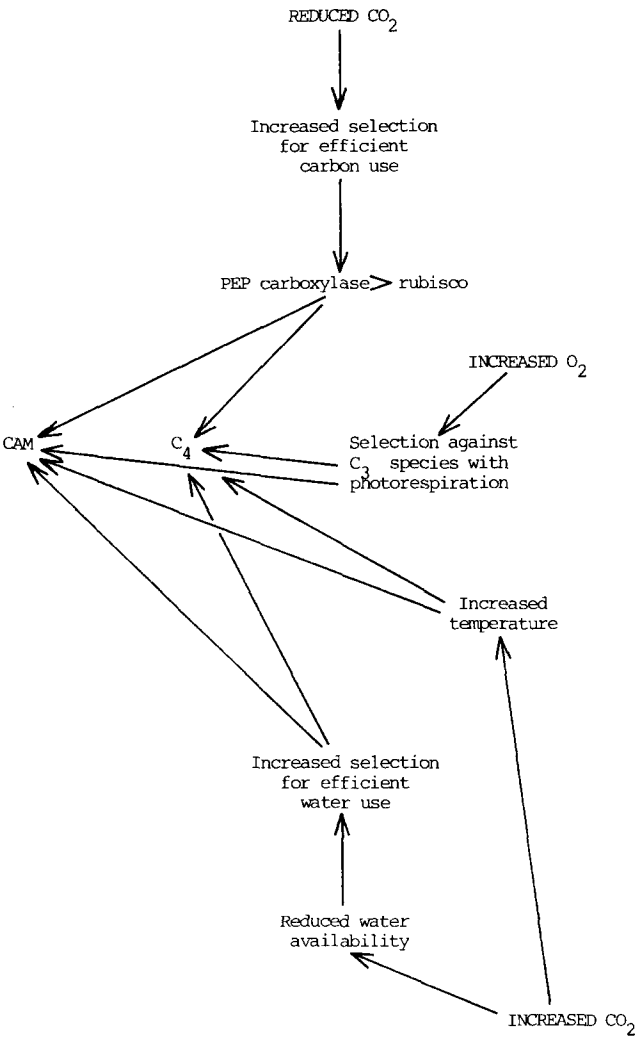

Fig. 2. A model illustrating the possible effects of carbon dioxide and oxygen variations upon photosynthetic strategies in plants. CAM, Crassulacean Acid Metabolism.

advantage of C_4 and CAM photosynthesis is their enhanced water-use efficiency. In present-day biogeography this means that these strategies are more prevalent in dry habitats (Teeri & Stowe 1976). As has been discussed, a raised carbon dioxide level could affect water budgets in a number of ways and the precise outcome in any location would be influenced by local geographic, topographic and edaphic factors.

Conclusions

Considerable advances have recently been made in the reconstruction of past atmospheric compositions, many of which are reported in the series of papers gathered here. There has not, however, been an equivalent advance in the understanding of the ecological consequences of a changed atmosphere. From the arguments presented in this paper, it can be seen that this area of modelling is complex and factors cannot be taken in isolation from one another. More experiments, similar to those of Strain (1987) using multiple variables, are needed in modern natural and man-made systems if these interactions are to be better understood and quantified. In addition, the current rise in atmospheric

carbon dioxide could provide a valuable opportunity to document the ecological and biogeographic consequences of this inadvertent global experiment. The changes that might be expected to ensue, such as modifications to the Earth's total biomass, will be difficult to detect, but they may provide students of the palaeoatmosphere with some assistance in the reconstruction of the past. The value of such information, however, is limited by the lack of precise modern analogues for past conditions.

The present can never be a complete key to the past in matters as complex as the investigation of palaeoatmospheres and their biological repercussions. The responses of plants now extinct to atmospheric variations of the type considered here can never be fully known. Also, as pointed out by Rea *et al.* (1985), it is not only the chemical composition of the atmosphere which must be examined, but also the history and past strength of atmospheric circulation patterns. These workers have studied aeolian particle deposition in deep-sea sediments and have used this as a means of tracing the strength of air-mass movements. The climate experienced in a given part of the globe will clearly be influenced by the direction and strength of such atmospheric movements.

In addition, there is the problem of past supercontinents and their impact on climatic patterns. A land mass the size of Gondwanaland, for example, may have exerted a greater influence on climate patterns, especially their seasonal variation, than that of carbon dioxide levels (Crowley *et al.* 1987). The continentality of the interior of such a land mass would contrast strongly with the oceanicity of its coasts.

Clearly, a knowledge of palaeoatmospheric chemistry represents only one component in the understanding of global palaeoecology.

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