PERSPECTIVES

CLIMATE CHANGE

Carbon Dioxide and Vegetation

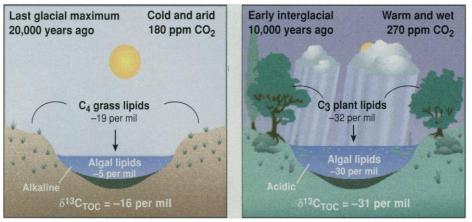
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What happens to vegetation when greenhouse gases (mainly carbon dioxide) increase in concentration and the temperature goes up? The Framework Convention on Climate Change commits the signatories to avoiding dangerous interference with the climate system, interference that might harm the world's agriculture and natural ecosystems. But just what are the likely responses of vegetation? Much attention is paid to the effects of temperature and other climatic changes. As Street-Perrott et al. report on page 1422 of this issue, there is now evidence that, at an ecosystem level, the direct effects of an increase in carbon dioxide are themselves important (1).

Street-Perrott and her colleagues have studied the paleoenvironmental history of high-altitude lakes and the surrounding vegetation in East Africa. They examined the lake sediments, the pollen and leaf waxes in them, and the carbon isotope composition of bulk organic matter and of specific biomarkers. They conclude that the increasing concentration of carbon dioxide in the atmosphere since the last glacial period has allowed trees to grow where the vegetation was (before 13,000 years ago) restricted to an almost treeless, grassy heathland.

Street-Perrott et al. found that the increase in CO₂ concentration was correlated with a decrease in the amount, measured as δ^{13} C, of the heavier stable isotope. This result is consistent with a shift from the photosynthetic pathway common in tropical grasses (denoted C_4) to the pathway found in trees (denoted C_3). However, a number of factors can influence the composition of sediments, and hence, the importance of the authors' careful work in measuring composition of particular biomarkers to separate terrestrial, aquatic, and bacterial sources. C4 plants utilize a CO₂-concentrating mechanism that is advantageous at low concentrations but is more "costly" to the plant than C₃ metabolism as CO_2 levels increase. The very evolution of C₄ was probably in response to low CO₂ concentrations, with rapid expansion about 7 million years ago (2).

The findings offer an explanation for a paleoecological puzzle. Previous estimates of the cooling of tropical land areas at the last glacial maximum (LGM) (about 20,000 years ago) were large, so large as to be incompatible with the decrease in sea-surface temperatures (<2°C) deduced from deep-sea cores. The terrestrial estimates had been made by examining changes in the elevation of tree lines and ascribing those changes to temperature alone. Acknowledging that



The increase of CO₂ concentration and temperature from the LGM to the early interglacial led to an increase in the hydrological cycle, the greater growth of trees, which use the C₃ pathway of photosynthesis, less reliance on CO₂-concentrating mechanisms on land and in the water, and the consequent depletion of ¹³C (more negative δ^{13} C) in the total organic matter (TOC, total organic carbon) found in the lake sediments (1).

 CO_2 concentration itself affects the growth of trees enables us to see that the cooling of tropical land was not so great. During the glacial times, the trees were being starved of the substrate for photosynthesis. Along these same lines, Sage has argued (3) that agriculture became viable at several places around the world between 11,000 and 6000 years ago, only when the CO₂ concentration became sufficiently large to sustain decent yields for our first farmers.

For the individual plant, water-use efficiency is almost directly proportional to the level of CO_2 for a given regime of temperature and humidity (4). So concentrations of 180 parts per million (ppm) (such as occurred during the LGM), being half the current levels, would mean that plants had to transpire twice as much water then as now to achieve the same level of photosynthesis (see figure). Put another way, doubling the CO₂ concentration is almost like doubling the rainfall as far as plant water availability is concerned. Further, increased greenhouse forcing also speeds up the global hydrological cycle, and so, on avercrease from the LGM to the present 360 ppm should be much greater than the effects of going from 360 to 540 ppm, the latter being twice the preindustrial level (about 270 ppm). The plants of today are much less water- and CO₂-limited than they were at the LGM. Nevertheless, one suspects that the direction of change in the near future will be the same as that following the LGM, one of increased "effective rainfall," with the agricultural and ecological consequences that follow. Given that the availability of water for agriculture is already becoming such a problem, this aspect, at least, of atmospheric change is a welcome one.

age, the actual rainfall increases with increas-

ing CO_2 concentration. Many of the paleorecords indicate arid conditions during the

LGM. Much of this was probably caused by drier conditions, whereas some records that rely on the amounts of pollen, for example,

could rather be reflecting the physiological aridity caused by low atmospheric CO_2 levels. The results help explain the findings (5) that the terrestrial biosphere in the preindustrial

era (about 270 ppm) stored about 30% more

greenhouse effect are more sensitive to CO₂

levels when the concentrations are low. The

translation of increased photosynthesis to

increased growth rate is not straightfor-

ward, depending on developmental pro-

cesses (6). The effects of the 180-ppm in-

Both photosynthesis and the enhanced

carbon than it did at the LGM.

References

- 1. F. A. Street-Perrott et al., Science 278, 1422
 - 2.
- F. A. Outer.
 (1997).
 T. E. Cerling *et al.*, *Nature* **389**, 153 (1997).
 R. F. Sage, *Global Change Biol.* **1**, 93 (1995).
 C. Wong, I. R. Cowan, G. D. Farquhar, *Na* S. C. Wong, I. R. Cowan, G. D. Farquhar, Nature 4. 282, 424 (1979).
- 5. M. J. Bird, J. J. Lloyd, G. D. Farquhar, ibid. 371,
- 566 (1994). J. Masle, G. S. Hudson, M. R. Badger, *Plant Physiol.* **103**, 1075 (1993). 6.

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