

LETTER TO THE EDITOR

Do Low CO₂ Concentrations Affect Pollen-Based Reconstructions of LGM Climates? A Response to “Physiological Significance of Low Atmospheric CO₂ for Plant–Climate Interactions” by Cowling and Sykes

We applaud the recent review, by Cowling and Sykes (1999), of the experimental evidence for interactions among CO₂, climate, and plant physiology, and the implications for pollen-based paleoclimatic reconstructions. Atmospheric concentrations of CO₂, a basic nutrient for plants, have a long history of variation (Berner, 1997). Ice core records from the last 420,000 years show glacial concentrations as low as 200 ppm and interglacial levels up to 280 ppm (Petit *et al.*, 1999). The physiological responses of plants to different concentrations of atmospheric CO₂ may in turn affect their climatic optima, by altering such properties as their water use efficiency and thermal optima for maximal growth (Polley *et al.*, 1993, 1995).

If full glacial CO₂ concentrations of 200 ppm in fact affected plant–climate interactions, then, as Cowling and Sykes (1999) rightly point out, this effect would weaken a key assumption underlying pollen-based paleoclimatic reconstructions: that the observed relationship between modern pollen abundances and climate can be transferred to fossil pollen abundances (Bartlein *et al.*, 1986; Prentice *et al.*, 1991; Webb *et al.*, 1993). The type of photosynthetic pathway (C₃ or C₄) available to a plant largely determines its response to changes in atmospheric CO₂ concentrations, so that the greatest effects of CO₂ upon community composition should occur in mixed communities or at ecotones between C₃- and C₄-dominated communities. Because accurate estimates of past climates are important, so is the rapidly improving knowledge of plant–CO₂ interactions coming forward from physiological studies.

From their review of the physiological evidence, Cowling and Sykes (1999) draw two main conclusions: (1) the pollen-based reconstructions of climate during the last glacial maximum (LGM) may be overestimating its dryness, and (2) LGM climates may have been cooler than inferred from the fossil pollen. We concur with their point about dryness but doubt their case for a warm bias in the pollen-based temperature reconstructions.

CO₂, PLANTS, AND MOISTURE RECONSTRUCTIONS

The evidence is compelling that low CO₂ concentrations during the LGM may cause pollen-based reconstructions to overestimate LGM aridity. If atmospheric CO₂ concentrations are low, C₃ plants respond by increasing stomatal conductance to maintain a

sufficient intake of CO₂, and thus incur a cost of increased water loss (Farquhar and Sharkey, 1982; Field *et al.*, 1995). Growth chamber studies have shown that the stomatal conductance of C₃ plants increases linearly and water use efficiency decreases linearly with decreasing concentrations of ambient CO₂ (Cowling and Sage, 1998; Polley *et al.*, 1993, 1995). The water use efficiency of C₄ plants is expected to be less affected by changes in CO₂ because C₄ plants are able to efficiently pump CO₂ from the mesophyll cells, the primary location for leaf–atmosphere gas exchange, to their bundle sheath cells, where carbon fixation takes place (Ehleringer *et al.*, 1991; Larcher, 1995). A decline in CO₂ concentrations therefore may be qualitatively identical to decreasing moisture availability, thereby increasing the competitive success of C₄ plants and drought-tolerant C₃ taxa. This effect may have been strong enough to influence the taxonomic composition of plant communities (Idso, 1989), and may in part explain why the LGM forests of eastern North America were more open than at present (Cowling, 1999; Davis, 1989). In tropical Africa, low CO₂ concentrations may explain the observed lowering of montane vegetation zones during the LGM (Jolly and Haxeltine, 1997; Street-Perrott *et al.*, 1997).

Nevertheless, the signal of dryer-than-present conditions at the LGM obtained from fossil pollen records is not wholly an artifact of a low CO₂, because other paleoclimatic proxies support the palynological reconstructions. Dust records from marine and ice cores also indicate an increased eolian flux during the LGM, which has been hypothesized to have resulted from a combination of increased wind velocities, glacial sources, and drier conditions (Mahowald *et al.*, 1999). Lake-level records, which are regionally lower in several areas, including eastern North America, seem to provide support for palynological paleoclimatic reconstructions, but lake levels may also be influenced indirectly by atmospheric CO₂ through its control on plant transpiration. Partitioning the effect of CO₂ and low precipitation upon LGM community composition and pollen-based reconstructions requires modeling studies such as those performed by Cowling (1999) and Jolly and Haxeltine (1997). Pollen-based studies remain useful for showing past vegetation distributions (Jackson *et al.*, 2000), and pollen-derived climate estimates set a lower bound for the aridity of the LGM.

CO₂, PLANTS, AND TEMPERATURE RECONSTRUCTIONS

We disagree with the assertion that “if growth optima were in fact significantly lower in glacial plants relative to today, then pollen-reconstructed temperature decreases for the LGM may be currently underestimated” (Cowling and Sykes, 1999, p. 239). For pollen-derived temperature estimates to be affected by plant–CO₂ interactions, it must be shown that changes in the physiology of individual plants produced ecosystem-scale shifts in the composition and structure of past plant communities, and that such shifts were likely to have altered the composition of the pollen rain collected in quiet-water sediments.

Changes in CO₂ and temperature affect the growth optima and photosynthetic efficiency of plants via their control of plant photorespiration. During photorespiration, the Rubisco enzyme, a primary catalyst for the fixation of CO₂ during photosynthesis (Larcher, 1995), instead reacts with an O₂ molecule, thereby decreasing photosynthetic efficiency. In C₃ plants, photorespiration rates increase in response to rises in temperature and in the relative intracellular pressures of CO₂ and O₂ (Brooks and Farquhar, 1985). C₄ plants, on the other hand, pay an initial cost in photosynthetic efficiency for maintaining a carbon pumping mechanism, but are relatively insensitive to changes in temperature and CO₂ (Ehleringer *et al.*, 1991). The “crossover curve” of combinations of temperatures and CO₂ at which the C₃ pathway becomes less efficient than the C₄ pathway can be estimated, and has produced accurate predictions of the modern distribution of C₃ and C₄ grasslands (Collatz *et al.*, 1998). Differences in the photosynthetic efficiency of C₃ and C₄ plants, however, will affect community composition only if efficient light utilization provides a strong competitive advantage. Relative photosynthetic efficiency is likely to be an important factor within grassland ecosystems, where C₃ and C₄ plants have similar life forms, but not within forested or semiforested ecosystems. In these ecosystems, woody C₃ plants can prevail irrespective of photosynthetic efficiency simply by shading out the C₄ graminoids (Collatz *et al.*, 1998).

Even within grassland ecosystems, the relative importance of the late Pleistocene rises in CO₂ and temperature may have varied by latitude. In tropical regions, where temperature shifts were on the order of a few degrees Celsius (Jolly *et al.*, 1998), the rise in CO₂ from 200 ppm at the LGM to 280 ppm prior to the Industrial Revolution may have had a large impact upon grassland communities. In tropical Africa, carbon isotope records indicate that C₄ grasslands have declined in extent since the LGM (Ehleringer *et al.*, 1997), consistent with the rise in CO₂. In northern midlatitudes, however, the large temperature changes experienced in regions near the Pleistocene ice sheets may have had a greater impact upon grassland ecosystems than did the late Pleistocene rise in CO₂. This hypothesis would explain why carbon isotope and phytolith records from the Great Plains indicate that mixed C₃/C₄ ecosystems during the late Pleistocene were replaced by C₄ grasslands in the Holocene (Fredlund and Tieszen, 1997; Holli-

day, 1995; Muhs *et al.*, 1999), a shift counter to that expected from the CO₂ history. In any case, the pollen record is largely insensitive to shifts in frequency among C₃ and C₄ graminoids, because Poaceae pollen is generally not identifiable below the familial level. Therefore, much of the competitive dynamics between C₃ and C₄ grasses will not greatly affect the composition of fossil pollen records, nor should it affect the climate reconstructions based upon fossil pollen data.

The main way that changes in CO₂ could lead to biases in the pollen-based reconstructions of LGM temperatures is through its effect on leaf conductance and plant water use efficiency. Declines in the latter could lead to vegetational change in regions where moisture is a key limiting factor. In some parts of the world, such shifts could be misinterpreted to reflect changes in temperature. Using a process-based vegetation model, Jolly and Haxeltine (1997) showed that the effects of CO₂ could explain much of the observed lowering of African treelines at the LGM. However, they noted that if CO₂ is a factor in controlling the position of African treelines at the LGM, then pollen-based estimates of temperature decreases at the LGM would be overestimated—a bias opposite in direction to that asserted by Cowling and Sykes (1999).

In many regions, the LGM pollen samples remain dominated by pollen from C₃ plants; the inference of colder-than-present temperatures at the LGM from these samples is perhaps less likely to be confounded by low CO₂ concentrations. In eastern North America, for example, the estimates of lower-than-present temperatures at the LGM are driven by high pollen abundances of boreal conifers (spruce, fir, northern pine) in areas where temperate deciduous trees and southern pine dominate today (Prentice *et al.*, 1991; Webb *et al.*, 1993, 1998). The possibility that low CO₂ concentrations favored evergreen conifers at the expense of deciduous trees at the LGM cannot be ruled out, but currently the evidence from experimental studies suggests that differences in responses to CO₂ among C₃ species are much smaller than differences between C₃ and C₄ species (Bazzaz, 1990; Ehleringer *et al.*, 1997). Therefore, a more likely inference at this time is that the changes observed in eastern North American pollen records mainly reflect past changes in temperature.

The bottom line is not whether fossil pollen data should be used to infer past climates, but rather how to interpret such reconstructions. If Cowling and Sykes (1999) are correct, then the pollen-based paleoclimatic estimates should be reinterpreted as placing constraints on the state of LGM climates. For times when CO₂ concentrations were low, the pollen-based estimates set a lower boundary for past levels of precipitation and moisture, and, at worst, an upper bound for temperature. As such, the pollen data will remain a useful tool for evaluating climate simulations of the LGM. If, as we believe, only the moisture estimates are consistently biased in a known direction, then the temperature estimates should still be considered accurate, although with perhaps an asymmetric uncertainty toward lower values. In either case, the attributes of the fossil pollen data—the large number of samples in time and space, their good temporal control, and their amenability to multivar-

iate statistical techniques—mean that fossil pollen records will remain an invaluable resource for paleoclimatic reconstructions in the Quaternary. Linking the pollen data with CO₂ estimates and mechanistic vegetation models should help in producing the best possible estimates for past climates.

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