Meetings

Atmospheric CO₂, climate and evolution – lessons from the past

A history of atmospheric CO₂ and its effects on plants, animals and ecosystems, Snowbird, UT, USA, December 2001

The global changes in atmospheric composition, land cover, and biogeochemistry caused by human activities during the recent past – just the 20th century – have brought about a renewed interest in the study of the processes that influence the earth system as a whole. By its nature, earth system science is not a traditional discipline in itself, but the intersection of our understanding of geological processes, atmospheric chemistry and transport, ocean science, biological processes and ecosystem function. These interactions have become increasingly evident in studies of the global carbon cycle. However, an understanding of the nature of recent perturbations to the carbon cycle and the likely implications for the future is impossible without a detailed consideration of the more distant past – feedbacks between atmospheric CO₂ concentrations, climate and the evolution of life on earth over millions of years. These questions were considered at a recent conference in Snowbird, Utah, USA. Here, some of the critical past feedbacks between atmospheric CO₂ and terrestrial ecosystems are highlighted, with an emphasis on the role of plant evolution, form and function.

‘We enter an era of CO₂ concentrations unprecedented for at least the past 1 million years’

Atmospheric CO₂ and early vascular plants

Though the data are sparse, the isotopic paleosol record indicates that atmospheric CO₂ was 15 – 20 times the preindustrial value before the Early Devonian 400 mya. Following this period from 400 to 360 mya, CO₂ concentrations appear to have dropped precipitously to values much closer to the present day (Berner, 1997). Two marked events in the fossil record are apparent during this period: the spread of rooted, vascular plants to upland areas; and, towards of the end of this period, the widespread dominance of plant forms featuring the planate, megaphyll leaves common today over microphyll or leafless plant types. These events highlight the close interaction between the effects of plant function on the atmosphere, as well as atmospheric effects on plant evolution.

CO₂ concentrations in the last 550 million years have been modeled by R. A. Berner and colleagues at Yale University (CT, USA) with the ‘GEOCARB’ model. Their simulations closely reproduce the trends in the paleosol record when the influence of plant weathering in the Devonian is represented. As vascular plants spread across the terrestrial land surface, the influence of organic acids in the rhizosphere, reduced erosion by deep rooting, and the effect of transpiration on precipitation may have caused an increase in global weathering rates which resulted in a large removal of CO₂ from the atmosphere (Berner, 1997). The parameterization of the plant-induced weathering effect is subject to a great degree of uncertainty that requires modern-day studies on the impacts of terrestrial vegetation on mineral weathering during primary succession (Moulton et al., 2000).

Atmospheric CO₂ concentrations are widely known to impact plant physiology and morphology. The consequences of declining CO₂ in the Devonian on the form of vascular plants were described by D. J. Beerling (University of Sheffield, UK). Vascular plant form was dominated by leafless or microphyll morphology 400 mya, although the existence of a small number of Early Devonian fossils with larger, planate leaves indicates that the potential for megaphylls existed at this time (Beerling et al., 2001). While planate leaves in direct sunlight may intercept up to 200% more radiation than erect, photosynthetic axes (Beerling et al., 2001), other selective pressures were clearly operating in the Early Devonian. Stomatal density has been shown to be closely and inversely correlated with CO₂ concentration in the fossil record (Chen et al., 2001) and has implications for transpirational cooling of leaves in addition to photosynthetic capacity. Calculations by Beerling et al. (2001) indicated that at the high CO₂ concentrations and low stomatal density of the Early Devonian, transpiration rates would be insufficient to prevent high temperature injury to the photosynthetic apparatus in large leaves. As CO₂ concentrations dropped and stomatal densities rose, transpiration became sufficient to support increasingly large, planate leaf structures that promoted higher productivity and a selective

The rise of C\textsubscript{4} photosynthesis
The oldest indications of C\textsubscript{4} photosynthesis in the fossil record suggest that C\textsubscript{4} plants were present at least 12–15 mya (Sage, 2001). As described by R. F. Sage from the University of Toronto (Canada), the C\textsubscript{4} photosynthetic pathway arose multiple times from at least 30 distinct evolutionary origins. C\textsubscript{4} photosynthesis is an adaptation to the high rates of photorespiration, or fixation of oxygen by Rubisco, that occur at high temperatures and relatively high ratios of atmospheric O\textsubscript{2}/CO\textsubscript{2} in C\textsubscript{3} plants. The mid-Tertiary period when C\textsubscript{4} photosynthesis presumably arose was associated with global cooling, not elevated temperatures, so that the necessary precondition for C\textsubscript{4} evolution was likely declining atmospheric CO\textsubscript{2} concentrations, which appear to have dropped below 500 ppm and a theoretical oxygenation : atmospheric CO\textsubscript{2} ratio of 220 ppm (although this decline has been recently challenged by Pagani et al., 1999). Rather, at the same time that major species extinctions and speciations occurred, such as a crash in diversity of equids in North America and the rise of boids in Africa, the prevalence of C\textsubscript{4} plants also increased dramatically in the fossil record. T. E. Cerling of the University of Utah suggested that these events were linked by the continued decline of atmospheric CO\textsubscript{2} to 180–220 ppm (although this decline has been recently challenged by Pagani et al., 1999), and the reduced availability of protein in C\textsubscript{4} leaves relative to C\textsubscript{3}. Low CO\textsubscript{2} conditions may have promoted the rapid spread of C\textsubscript{4} plants, previously a small component of global flora, and an associated expansion of grasslands into areas formerly occupied by forest. Such ecological changes would have had important implications for faunal diversity, as C\textsubscript{4} leaves require morphological and physiological adaptations if used as a major food source.

Therefore, the conversion of forested areas to open grassland and the spread of plants utilizing Kranz anatomy may have strongly influenced faunal evolution (Cerling et al., 1998). Indeed, these global changes in atmospheric and floral composition may have been associated with the evolutionary path of our own early hominin ancestors (Avery, 1995).

Atmospheric CO\textsubscript{2}-induced changes in C\textsubscript{3}–C\textsubscript{4} composition were likely to have continued into the Quaternary. Compound-specific, carbon isotope analyses of African tropical lake sediments show large changes in floral composition during the last glacial maximum in the Holocene (F. A. Street-Perrott, University of Wales, UK). These results indicate that the glacial-interglacial cycles in CO\textsubscript{2} concentration from c. 190–280 ppm caused retreats and advances in tropical forests, with major shifts in tree species composition as shifts in treeline due to large changes in global temperature (Street-Perrott et al., 1997). Street-Perrott reported that additional lake sediment data from the Americas revealed strong influences of local precipitation on floral shifts as well as low CO\textsubscript{2}. These results have important implications for future changes in terrestrial ecosystem composition as a consequence of human-induced changes in atmospheric CO\textsubscript{2} and climate.

The future of atmospheric CO\textsubscript{2}
Atmospheric CO\textsubscript{2} and human society have always been closely linked. Glacial and interglacial cycles associated with oscillating atmospheric CO\textsubscript{2} concentrations played a role in human genetic and cultural evolution (Hewitt, 2000), as did the domestication of C\textsubscript{4} plants such as millet, maize and sugar cane, which influenced the development of cultures around the world and continues to affect modern society (N. J. van der Merwe, University of Cape Town, South Africa; van der Merwe & Tischner, 1999). Today, as we enter an era of CO\textsubscript{2} concentrations unprecedented for at least the past million years, never have the associations between human activity and the atmospheric pool of carbon been as evident. Human consumption of fossil fuel has already increased atmospheric CO\textsubscript{2} by 30% since the dawn of the industrial revolution – this effect is likely to rise to double the preindustrial value or more by the close of the 21st century (Prentice et al., 2001). Impacts of these changes on terrestrial vegetation and the role of biota in buffering increases in atmospheric CO\textsubscript{2} have been the subject of intense study, as discussed by R. J. Norby (Oak Ridge National Laboratory, TN, USA) for forest ecosystems and R. Shaw (Carnegie Institution of Washington, DC, USA) for arid and semiarid systems. Although much progress has been made in understanding the physiological effects of elevated CO\textsubscript{2} on plants, important questions remain for the future of terrestrial ecosystems, particularly in scaling the results of relatively small-scale and short-term experiments to larger spatial scales and longer time periods.
and in studying the effects of multiple global drivers on whole ecosystem processes.

In order to gain our best understanding of the likelihood of atmospheric and climatic changes in the next century and beyond, the linkages between plants, animals, humans and the atmosphere that have proved so crucial to understanding the past must be extended to projections of the future. Some of the keys to unlocking the uncertainties of future changes lie in the past, such as the role of adaptations to past environments in influencing future plant responses (J. K. Ward, University of Utah; Ward et al., 2000) and the coevolution of plants and herbivores that may be altered by future CO2 regimes (R. L. Lindroth, University of Wisconsin, WI, USA; M. D. Dearing, University of Utah). Process-based models and atmospheric inversions of past atmospheric CO2 data may provide important information about the present carbon cycle (J. O. Kaplan, MPI-Biogeochemistry, Jena, Germany; C. Trudinger, CSIRO, Canberra, Australia), which continues to be a critical topic of research at ecosystem, regional and global scales due to uncertainties in the distribution and mechanisms of the terrestrial carbon sink (Schimel et al., 2001). In the future, human activities will likely dominate the trajectory of atmospheric CO2, presenting new challenges in linking the drivers of human consumption of fossil fuels with ecosystem function and atmospheric change. The research presented at Snowbird illustrated that linkages between ecology, evolution and geoscience continue to advance our understanding of earth system science, and are a model for the interdisciplinary collaborations required for future research.

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