

rad1 and *rad10* mutants do not show defects in other pathways of mitotic recombination, or meiotic recombination, which would be characteristic of a loss of Holliday junction resolvase activity. The role of Rad1 and Rad10 in recombination is more probably related to their function in the processing of double-strand breaks by the removal of unpaired 3' ends⁹.

Stephen C. West

Imperial Cancer Research Fund,
Clare Hall Laboratories,
South Mimms EN6 3LD, UK

Impact modellers not surprised

SIR — Weissman¹ and Chapman² in their News and Views articles made it clear that many astronomers were not expecting to observe effects of the impact of comet Shoemaker–Levy 9 on Jupiter, let alone luminous fireballs and light-scattering plumes rising over the limb. But modellers had predicted that hot debris clouds would rise over Jupiter's limb for sufficiently large impacts^{3–6}.

Chapman² pointed out that there is some variation between the models, and suggested that numerical modellers return to the drawing board because of an apparent lack of evidence from preliminary data from Galileo's photopolarimeter–radiometer for the fireballs that had been predicted. But the half-minute-long light pulses initially interpreted by Chapman as meteor flashes are fully consistent with bolide entry immediately followed by fireball expansion. The channel of hot gas left by the entry radiated the light that Galileo observed, and it is this material in the entry channel that becomes the ballistic fireball. Newer Galileo data and further analysis have now provided strong evidence for this suggestion⁷. We think that Chapman's rejection of the models was premature. Certainly, the next step is to analyse the Shoemaker–Levy 9 impact data and to interpret the results in terms of the computational models. Although the models might need some fine-tuning, they are all in reasonable agreement with many of the observed phenomena.

Mark B. Boslough

David A. Crawford

Experimental Impact Physics Department,
Sandia National Laboratories, Albuquerque,
New Mexico 87185-0821, USA

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Growth limits on phytoplankton

SIR — Morel *et al.*¹ have demonstrated that growth of the planktonic diatom *Thalassiosira weissflogii* decreased in response to zinc limitation. The fact that most of the cellular Zn was found to be associated with carbonic anhydrase, an enzyme central to carbon metabolism, gave rise to the concept of Zn and carbon co-limitation. This, indeed, was supported by the observation that the growth-reducing effect of Zn limitation was partly compensated by increasing CO₂ availability.

Based on these results, Morel *et al.* hypothesized that diminished growth rates under low Zn concentrations reflected a decrease in HCO₃⁻ uptake due to reduced carbonic anhydrase activity. To test this hypothesis the authors made use of the equilibrium fractionation of ¹³C between HCO₃⁻ and CO₂. Because CO₂ dissolved in water is significantly depleted in ¹³C relative to HCO₃⁻ (10.7‰ more negative at T = 10 °C; ref. 2), a decrease in HCO₃⁻ uptake relative to CO₂ uptake should result in a more negative organic matter δ¹³C. A lower δ¹³C value in response to Zn limitation was, in fact, observed when Zn-limited cells of *T. weissflogii* were compared with iron-limited cells kept under similarly reduced growth rates. Based on this finding, Morel *et al.* concluded that HCO₃⁻ uptake did occur in *T. weissflogii* and was reduced under low Zn concentrations.

Central to the authors' reasoning is the assumption that HCO₃⁻ uptake involves carbonic anhydrase (for which, in fact, there is no conclusive evidence). If this assumption were true, however, isotope fractionation by carbonic anhydrase, which for the catalysed conversion of HCO₃⁻ to CO₂ is 10.1‰ (ref. 3), would largely cancel the initial difference in δ¹³C of 10.7‰ between HCO₃⁻ and CO₂. The δ¹³C signal resulting from carbonic anhydrase-mediated HCO₃⁻ uptake and CO₂ uptake would essentially be indistinguishable. Thus, a change in the contribution of carbonic anhydrase-mediated HCO₃⁻ uptake in overall carbon acquisition remains undetectable by δ¹³C measurements. (The observed difference in δ¹³C between Zn- and Fe-limited *T. weissflogii* may simply reflect the different metabolic functions of Zn and Fe — Zn in carbon metabolism and Fe in nitrogen metabolism.) In consequence, the results of Morel *et al.* do not permit any conclusion about the source of inorganic carbon acquired by the cell.

Because carbonic anhydrase in *T. weissflogii* is located both extra- and intracellularly, Zn limitation is bound to affect carbonic anhydrase-mediated carbon

uptake as well as assimilation. Variables reflecting the physiological condition of whole cells, such as cell growth, however, do not allow a distinction between intra- and extracellular carbonic anhydrase responses to Zn limitation. The results of Morel *et al.* therefore do not provide conclusive evidence regarding the specific processes influenced by Zn limitation. Although the authors have demonstrated an effect of low Zn availability on carbon metabolism, the origin of this effect remains an open question.

Ulf Riebesell

Dieter Wolf-Gladrow

Alfred Wegener Institute for Polar and
Marine Research,

MOREL AND REINFELDER REPLY — In line with their earlier article⁴ (which showed low growth rates in high pH cultures), Riebesell and Wolf-Gladrow appear to believe that only CO₂ is taken up by marine phytoplankton. As already pointed out by Turpin⁵, however, the uptake of HCO₃⁻ by microalgae is not in doubt, and neither is the involvement of carbonic anhydrase in inorganic carbon accumulation (possibly through a simple extracellular catalysis of HCO₃⁻/CO₂ conversion). It would be most surprising if the ability to take up HCO₃⁻ were not shared by most oceanic phytoplankton growing at low CO₂.

Nonetheless, Riebesell and Wolf-Gladrow are right to say that high δ¹³C values in phytoplankton organic matter cannot in themselves prove HCO₃⁻ uptake, even if many authors have made this inference. Not knowing the exact steps involved in inorganic carbon uptake in marine phytoplankton, we are free to imagine many possible ways other than HCO₃⁻ uptake, by which high δ¹³C values can be achieved. Short-term kinetic studies of carbon uptake and characterization and localization of the proteins involved are needed to solve this important problem.

For now, we note that the enhancement of growth rate by Zn in our CO₂-limited cultures implies enhancement of either CO₂ or HCO₃⁻ uptake. Based on the literature and our ¹³C and carbonic anhydrase data, we believe the latter to be more likely, but either mechanism would be consistent with our claim that low Zn concentrations may effect CO₂ limitation of phytoplankton in the oceans.

François M. M. Morel

John R. Reinfelder

Department of Geological and
Geophysical Sciences,
Guyot Hall, Princeton University,
Princeton, New Jersey 08544, USA

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