

Bax/Bak action in mitochondria. These agents release  $\text{Ca}^{2+}$  themselves and kill more efficiently when  $\text{Ca}^{2+}$  is further increased by physiological or pathological stimuli, accounting for the “ $\text{Ca}^{2+}$ -preconditioning” observed in previous studies (5). Killing absolutely requires an increase in mitochondrial  $\text{Ca}^{2+}$ , and thus strictly depends on ER  $\text{Ca}^{2+}$  levels. In the second category are agents, such as tBid, that require the presence of Bax or Bak in the mitochondria but do not engage the ER  $\text{Ca}^{2+}$  gateway. These agents do not require mitochondrial  $\text{Ca}^{2+}$  and kill efficiently at all ER  $\text{Ca}^{2+}$  loads. The third category is constituted of agents—such as etoposide, staurosporine, brefeldin A, and T cell receptor activation—that engage both pathways. These agents require both  $\text{Ca}^{2+}$  and the presence of Bax or Bak in mitochondria, and both ER  $\text{Ca}^{2+}$  and Bax/Bak levels modulate their killing potency.

The Bax/Bak-deficient mouse cells of Scorrano *et al.* are the first loss-of-function model in which an alteration in  $\text{Ca}^{2+}$  handling is causally linked to cell killing, but the mechanism leading to decreased ER  $\text{Ca}^{2+}$  is not established. The presence of normal amounts of  $\text{Ca}^{2+}$  signaling proteins in Bax/Bak-deficient cells suggests that the defect is either directly caused by the Bax/Bak proteins themselves or is mediated

by a change in activity, rather than content, of a  $\text{Ca}^{2+}$  handling protein. A possible candidate for such modulation is the  $\text{IP}_3$  receptor, the principal  $\text{Ca}^{2+}$ -release channel of the ER, whose activity undergoes complex regulation by  $\text{Ca}^{2+}$ , ATP, and phosphorylation. SERCA proteins are also subject to modulation, and it will be interesting to see whether Bax/Bak inactivation is associated with changes in activity of the  $\text{IP}_3$  channel or of SERCA. Another likely partner is the antiapoptotic protein Bcl-2. The effects of Bak/Bax inactivation mimic those of Bcl-2 overexpression, suggesting that the balance between Bax/Bak and Bcl-2, rather than the amounts of the individual proteins, determines ER  $\text{Ca}^{2+}$  load. Manipulation of Bcl-2 expression in Bax/Bak-ablated cells will allow researchers to test directly this “rheostat” model, and to confirm whether Bcl-2 and Bax/Bak indeed coregulate ER  $\text{Ca}^{2+}$ .

The Scorrano *et al.* study defines a new role for the ER-mitochondria  $\text{Ca}^{2+}$  connection. The ER is now envisioned as a gun pointed at the mitochondria, which can be loaded and unloaded with  $\text{Ca}^{2+}$  by Bax and Bcl-2 proteins. Some, but not all, apoptotic signals are able to pull the ER  $\text{Ca}^{2+}$  trigger, and hence to kill cells in a strictly  $\text{Ca}^{2+}$ -dependent manner. Future studies will determine whether this mechanism al-

so occurs when Bcl-2 family members are expressed at physiological levels in vivo, and whether physiological death signals are able to pull the  $\text{Ca}^{2+}$  trigger.

## References

1. D. R. Green, J. C. Reed, *Science* **281**, 1309 (1998).
2. J. C. Martinou, D. R. Green, *Nature Rev. Mol. Cell. Biol.* **2**, 63 (2001).
3. M. J. Berridge, P. Lipp, M. D. Bootman, *Nature Rev. Mol. Cell. Biol.* **1**, 11 (2000).
4. G. Hajnoczky, G. Csordas, M. Madesh, P. Pacher, *Cell Calcium* **28**, 349 (2000).
5. G. Szalai, R. Krishnamurthy, G. Hajnoczky, *EMBO J.* **18**, 6349 (1999).
6. L. Scorrano *et al.*, *Science* **300**, 135 (2003); published online 6 March 2003 (10.1126/science.1081208).
7. R. Rizzuto, M. Brini, M. Murgia, T. Pozzan, *Science* **262**, 744 (1993).
8. L. S. Jouaville, F. Ichas, E. L. Holmuhamedov, P. Camacho, J. D. Lechleiter, *Nature* **377**, 438 (1995).
9. S. Arnaudeau, W. L. Kelley, J. V. Walsh Jr., N. Demareux, *J. Biol. Chem.* **276**, 29430 (2001).
10. G. Hajnoczky, L. D. Robb-Gaspers, M. B. Seitz, A. P. Thomas, *Cell* **82**, 415 (1995).
11. P. Pacher, G. Hajnoczky, *EMBO J.* **20**, 4107 (2001).
12. G. Hajnoczky, G. Csordas, M. Yi, *Cell Calcium* **32**, 363 (2002).
13. K. Nakamura *et al.*, *J. Cell Biol.* **150**, 731 (2000).
14. P. Pinton *et al.*, *EMBO J.* **20**, 2690 (2001).
15. S. Arnaudeau *et al.*, *J. Biol. Chem.* **277**, 46696 (2002).
16. E. Rappaport *et al.*, *J. Cell Biol.* **159**, 613 (2002).
17. R. Foyouzi-Youssefi *et al.*, *Proc. Natl. Acad. Sci. U.S.A.* **97**, 5723 (2000).
18. P. Pinton *et al.*, *J. Cell Biol.* **148**, 857 (2000).
19. L. K. Nutt *et al.*, *J. Biol. Chem.* **277**, 20301 (2002).
20. L. K. Nutt *et al.*, *J. Biol. Chem.* **277**, 9219 (2002).
21. N. S. Wang *et al.*, *J. Biol. Chem.* **276**, 44117 (2001).
22. M. J. Thomenius *et al.*, *J. Biol. Chem.* **278**, 6243 (2003).
23. M. C. Wei *et al.*, *Science* **292**, 727 (2001).

## CLIMATE CHANGE

# Will Ocean Fertilization Work?

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Iron fertilization of the ocean—a potential strategy to remove  $\text{CO}_2$  from the atmosphere—has generated much debate among ocean and climate scientists (1–4). It is viewed as particularly attractive by geoengineers because the addition of relatively small amounts of iron to certain ocean regions may lead to a large increase in carbon sequestration at a relatively low financial cost.

To assess whether iron fertilization has potential as an effective sequestration strategy, we need to measure the ratio of iron added ( $\text{Fe}_{\text{add}}$ ) to the amount of carbon sequestered ( $\text{C}_{\text{seq}}$ ) (in the form of sinking particulate organic carbon, POC) to the deep ocean in field studies. We must then apply appropriate scaling factors to deter-

mine whether globally significant quantities of  $\text{CO}_2$  can be removed from the atmosphere to the deep ocean in this way.

The Southern Ocean (see the figure) is the most important region for possible climate regulation by iron fertilization. In this high-nitrate low-chlorophyll (HNLC) region, large quantities of surface macronutrients return to the deep ocean via the flow of intermediate and deep waters. According to the “iron hypothesis” (5), adding iron to these nutrient-rich surface waters will increase phytoplankton biomass, resulting in increased uptake of  $\text{CO}_2$  by the phytoplankton living in the surface ocean.

In the Southern Ocean, there have been three open-ocean iron-enrichment experiments: SOIREE (Southern Ocean Iron Enrichment Experiment) (6), EisenEx-1 [Eisen(=Iron) Experiment] (7), and SOFeX (Southern Ocean Iron Experiment) (8). All three produced notable increases in biomass and associated decreases in dissolved inorganic carbon and macronutrients. However, evidence of sinking particles car-



**Exploring the Southern Ocean.** The research and supply vessel *Aurora Australis* heads into an iceber field off Antarctica.

rying POC to the deep ocean was limited.

SOIREE (a 13-day experiment) and EisenEx-1 (21 days) showed no difference between particle fluxes in the fertilized and nonfertilized waters (7, 9–10). During SOFeX (28 days), we observed in the fer-

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tilized waters a measurable increase in POC flux in response to iron (11). Natural blooms at this site in the Southern Ocean have a lifetime on the order of 20 to 30 days (12), but we did not observe the termination of the SOFeX bloom, as evidenced by continued high biomass and high photosynthetic efficiency (8).

These experiments allow an initial assessment of the two key scaling factors—the export efficiency and the size of ocean area affected—both of which are needed to determine whether iron fertilization can be an effective mitigation strategy.

To estimate export efficiency, geoengineering proposals to fertilize the ocean use laboratory-based Fe:C ratios required for algal growth [Fe:C molar ratios of  $2 \times 10^{-6}$  to  $7 \times 10^{-6}$  (13)] to scale up predictions of the impact of relatively small iron additions on downward POC flux. Such upscaling is the source of claims of a low financial cost for this mitigation strategy relative to other proposed means of carbon sequestration [\$1 to \$2 per metric ton of carbon sequestered (14)].

During SOFeX 1.3 tons of elemental iron were added to the ocean, resulting in a POC flux at 100 m of 2100 tons (11). This is equivalent to a molar  $\text{Fe}_{\text{add}}:\text{C}_{\text{seq}}$  ratio of only  $1.3 \times 10^{-4}$ —two orders of magnitude higher than uptake ratios used in ocean models and geoengineering plans. It is perhaps not surprising that the  $\text{Fe}_{\text{add}}:\text{C}_{\text{seq}}$  ratio will necessarily be higher than that seen in lab cultures because not all of the added iron is bioavailable and some is lost by physical scavenging. Moreover, the fraction of planktonic carbon exiting surface waters on sinking particles is naturally low

(typically <5 to 25% of total carbon uptake rates) owing to efficient recycling of essential macronutrients and carbon by heterotrophs and microbes.

By the end of the observations, the small (200 to 250 km<sup>2</sup>) experimental patches in SOIREE and SOFeX had spread naturally to cover an area of the ocean roughly 1000 km<sup>2</sup>. If commercial iron fertilization has the same impact on export efficiency and patch size (15), one would need the equivalent of 1 million SOIREE or SOFeX experiments to transfer downward a POC flux at 100 m that is equivalent to 30% of the carbon released annually as a result of human activities (1 million  $\times$  2000 tons POC export = 30% of annual carbon input of 6.5 billion tons). It would scale up to a region of  $10^9$  km<sup>2</sup>—more than an order of magnitude larger than the entire area of the Southern Ocean (defined as waters south of 50°S).

Fertilization experiments have not yet been performed over sufficiently long times to observe the termination of the polar iron-induced blooms. Recent modeling studies indicate that slow growth rates in polar waters, combined with physical dilution of phytoplankton cells, may limit aggregation and export (16). Larger scale or longer term experiments might mimic more closely the possible POC flux of commercial-scale applications or be more readily extrapolated to records of past global climate. The latter show that dust (and hence iron) input to the Southern Ocean is associated with cooler temperatures and lower atmospheric CO<sub>2</sub> concentrations (5).

The oceans have already taken up some 100,000 million tons of anthropogenic CO<sub>2</sub> (17). The resulting changes to ocean chemistry, ecology, and climate are already upon us. Thus, exploring regulation of the ocean's biological pump by iron supply is strongly warranted. However, ocean iron fertilization may not be a cheap and attractive option if impacts on carbon export and sequestration are as low as observed to date. Until we can adequately answer the basic questions regarding the viability of this particular mitigation strategy, overarching concerns regarding ecological consequences, verification issues, time scales of carbon sequestration, and possible unintended feedbacks cannot begin to be addressed.

## References

1. S. W. Chisholm *et al.*, *Science* **294**, 309 (2001).
2. K. S. Johnson, D. M. Karl, *Science* **296**, 467 (2002).
3. M. G. Lawrence, *Science* **297**, 1993 (2002).
4. Q. Schlermeier, *Nature* **421**, 109 (2003).
5. J. H. Martin, *Paleoceanography* **5**, 1 (1990).
6. P. Boyd *et al.*, *Nature* **407**, 695 (2000).
7. V. Smetacek, *US JCOFS News* **11**(1), 11 (2001).
8. K. Coale *et al.*, *Eos* **83** (fall meeting suppl.), abstract OS22D-01 (2002).
9. M. A. Charette, K. O. Buesseler, *Geochem. Geophys. Geosyst.* **1**, 2000GC000069 (2000).
10. S. D. Nodder *et al.*, *Geophys. Res. Lett.* **28**, 2409 (2001).
11. K. O. Buesseler *et al.*, *Eos* **83** (fall meeting suppl.), abstract OS22D-09 (2002).
12. M. R. Abbott *et al.*, *Deep-Sea Res. II* **48**, 3891 (2001).
13. W. G. Sunda, S. A. Huntsman, *Mar. Chem.* **50**, 189 (1995).
14. M. Markels Jr., R. T. Barber, 220th ACS Annual Meeting, Symposium on CO<sub>2</sub> Capture, Washington, DC, 20 to 24 August 2000.
15. J. R. Ledwell, A. J. Watson, C. S. Law, *J. Geophys. Res.* **103**, 21499 (1998).
16. P. W. Boyd, G. A. Jackson, A. Waite, *Geophys. Res. Lett.* **29**, 36-1 (2002).
17. R. A. Feely *et al.*, *Oceanogr. Soc.* **14**, 18 (2001).

## PLANETARY SCIENCE

# Peering into Stardust

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The smallest components of the Milky Way—the (sub)micrometer-sized grains of “stardust”—may provide crucial insights into star and planet formation. Most interstellar dust is thought to form in the ejecta of red giants or supernovae (1). Stardust locks in the characteristics of its stellar birthplace, particularly its anomalous isotopic composition, which is often used to identify presolar grains in solar system materials. But as may be concluded

from the study by Messenger *et al.* on page 105 of this issue (2), isotopically anomalous stardust particles may not be the only presolar grains in the solar system.

Some 15 years ago, Anders and co-workers (3) isolated the first genuine stardust grains from meteorites. Searching for the carrier of noble gas isotopic anomalies in meteorites, they “burned the haystack to find the needle.” Removing all material except for a few very resistant compounds, they localized the isotopic anomalies in nanometer-sized diamond stardust grains. Analogous procedures following the trail of different noble gas anomalies led to the isolation of other stardust components, including SiC and graphite grains. In each case, the presolar nature of the grains was

established by their anomalous isotopic composition, not only in the trapped noble gases but essentially in all elements.

Messenger *et al.* (2) now report the results of another technique to find stardust. Instead of searching for a needle, they study the haystack itself. They thus overcome one of the key drawbacks of the technique of Anders and co-workers: the removal of silicates. Astronomical studies show that a major fraction of interstellar dust is in the form of small silicates rather than carbonaceous grains.

In their study, Messenger *et al.* mapped the oxygen isotope composition of micrometer-sized interplanetary dust particles (IDPs) with a NanoSIMS (SIMS, Scanning Ion Microprobe Spectrometer). In that way, they were able to identify isotopically anomalous silicate stardust grains. Once identified, various techniques can be brought to bear on these isolated mineral stardust grains to determine their composition, mineralogy, and textural relationship with their environments.

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