

formed complexes with tungstate, the cells did not take them up in the experiments by Bellenger and colleagues. Furthermore, cells with low V concentrations rapidly took up siderophore–V complexes, but only if they also had low Mo concentrations. The Mo–nitrogenase is the most efficient version of the enzyme, explaining why uptake of the siderophore–V complex is suppressed when Mo is sufficiently available.

The strategy of producing siderophores to generate bioavailable metal complexes may be ancient, potentially having evolved under pressure from a low Mo environment in the Earth's early oceans¹². Plants, too, may rely on such strategies. Extractable pools of Mo in soil may be too low to supply plants with the Mo they need. Plants are known to facilitate their own uptake of Fe, manganese, and zinc by producing phytosiderophores¹³, though whether these influence Mo availability is not known. How important are siderophores for providing elements to nitrogen-fixing bacteria in natural systems, as opposed to the laboratory as in the study by Bellenger and colleagues? Might phytosiderophores promote Mo availability to plants?

The production of extracellular metal-scavenging compounds raises interesting ecological and evolutionary questions (Fig. 1). For example, Bellenger *et al.* found that excretion of azotochelin out-competes another

siderophore — desferrioxamine B — which is produced by a fungus. This is important because the complex of desferrioxamine B and vanadium cannot be taken up by *A. vinelandii*, so by sending its more effective scavenger protein into the environment, *A. vinelandii* helps promote its own uptake of V, and potentially reduces V uptake by the fungus. In this way, metal-scavenging compounds could mediate resource competition outside the cell, modulating the availability of limiting elements to competing organisms.

On the other hand, some siderophores form complexes that are available to numerous bacteria in the environment, such that 'cheaters' can evolve that take up the metal complexes without expending the resources to produce the siderophores themselves. As described earlier, plants produce their own phytosiderophores³, but plants can also cheat, taking up the siderophore–Fe complexes where the siderophore was produced by bacteria¹³. Because these metal-scavenging compounds are extracellular, they may or may not end up benefiting the organism that produced them. Production of siderophores thus provides an excellent model system for exploring competition and cooperation among microorganisms, and possibly even between plants and microorganisms¹⁴.

Nitrogen fixation is the major natural pathway for converting nitrogen into available forms, and is important because of widespread nitrogen limitation of plant

growth¹⁵. Limitation of nitrogen fixation by other elements, including Mo, has been empirically demonstrated¹⁶ and raises the possibility that terrestrial productivity is ultimately limited by one or several 'master' elements¹⁵.

As shown by Bellenger and colleagues, organisms engineer element cycling by secreting compounds into the environment to scavenge for rare metals, manipulating their geochemical environment, and providing yet another example of the footprint of biology on the earth system.

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OCEANOGRAPHY

Knock-on effect



DAVID M. LAWRENCE

Between the lush islands of Indonesia lies one of the bottlenecks of the global ocean circulation — the Indonesian throughflow, which connects the Pacific and Indian oceans. Over 80% of the water flowing from the Pacific to the

Indian Ocean in the low latitudes passes through a tiny 45-km-wide channel in the Makassar Strait, which separates the islands of Borneo and Sulawesi. Through this narrow passage, comparatively warm and fresh Pacific waters are delivered into the Indian Ocean and transported further westward, towards Africa.

In 1976–1977, the characteristics of the tropical Pacific background climate changed distinctly, first noticed because the large-scale climatic seesaw of the El Niño/Southern Oscillation became biased towards more El Niño-like conditions. The equatorial Pacific sea surface temperatures rose sharply, beyond expectations from global warming. At the same time, the easterly trade winds weakened.

Lana Wainwright at the University of Tasmania, Australia, and colleagues

suggest that these changes in the Pacific Ocean affected the Indian Ocean. According to their data analysis, the strength of the Indonesian throughflow was about 23% weaker after the 1976–1977 climate shift (*Geophys. Res. Lett.* **35**, L03604; 2008). As a result, the thermocline became shallower and cooler on the Indian Ocean side of the passage.

The origin of the Pacific climate shift in 1976–1977 is still a matter of debate, with natural variability and human-induced global warming both being considered as possible contributors. It is clear, however, that the change in the Pacific Ocean had an effect on the waters around it.

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