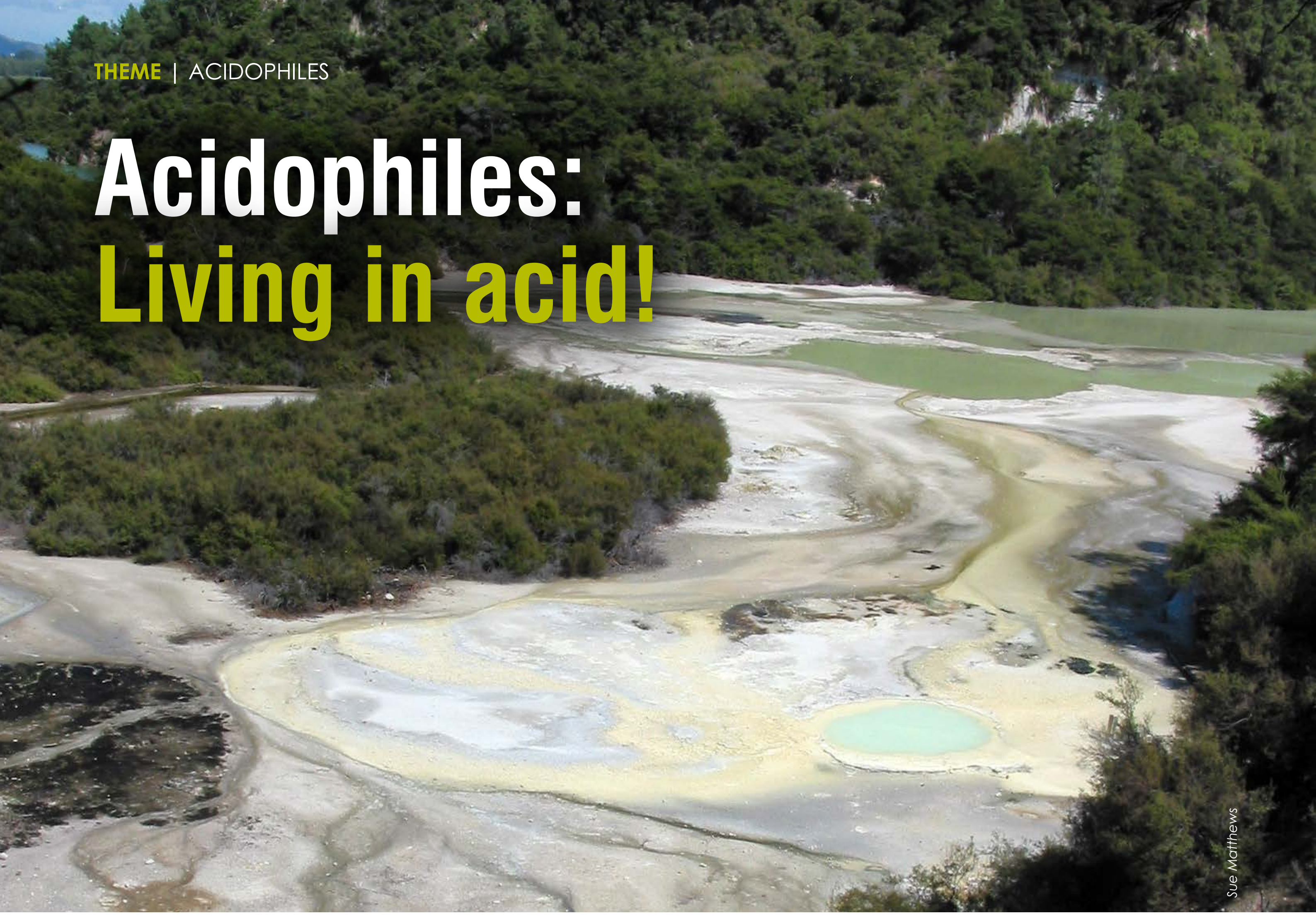
Acidophiles: Living in acid!



Sue Matthews

Don Cowan gives an overview of microorganisms adapted to acidic environments

The world has many acidic environments, some man-made but most natural. The best known of the former would be acid mine drainage (AMD), the product of acid-releasing oxidation processes when mineral deposits are exposed to air as a result of mining activities. The pH of AMD can vary widely but is mostly between 2 and 6. Given that most terrestrial organisms are not adapted to living in even mild acid, AMD can have a devastating effect on local vegetation, as well as on aquatic life in contaminated surface waters, such as rivers and wetlands.

Of the natural acidic environments, the human stomach is probably the best known. The human gut, which includes the stomach, small intestine and colon, is home to a vast array of different microorganisms, but only the stomach is an acidic environment, normally with a pH range between 1 and 3. In the stomach, relatively few microbial taxa persist, represented by the genera *Streptococcus*, *Staphylococcus* and *Lactobacillus*. These organisms are mostly beneficial, and *Lactobacillus* is a well-known probiotic. Not all gut bacteria are beneficial, however: the gram-negative spiral bacterium, *Helicobacter pylori*, is the causative agent of chronic gastritis and peptic ulcers.

On a landscape scale, geothermal areas around the world typically have extensive acid-water streams and pools. These are mostly dominated by sulphuric acid, produced when reduced sulphur carried to the surface from the deep subsurface comes in contact with atmospheric oxygen and undergoes chemical and/or microbiological oxidation. Often the reduced sulphur is in the form of hydrogen sulphide (H_2S), which is why hydrothermal areas always smell of rotten eggs! The reaction can be described as follows:

$$H_2S + 2O_2 \rightarrow 2H^+ + SO_4^{2-}$$

The hot springs and geysers of such hydrothermal areas are created by the mixing of upwelled, superheated subterranean water with cold surface water to yield temperatures ranging from boiling to ambient.

Life at low pH

Many organisms have adapted to live comfortably in acidic environments. Such organisms are termed 'acidophiles', meaning acid-loving, and most of them are microorganisms – bacteria, fungi and archaea. At the more extreme end of the environmental acid scale (<pH 3), virtually all acidophiles are prokaryotes, being either bacteria or archaea. Two of the commonest acidophiles, found in acid mine drainage and natural acid springs, are the bacterial species *Acidithiobacillus ferrooxidans* and *Leptospirillum ferrooxidans*. Both have the ability to grow chemoautotrophically on ferrous irons (Fe^{2+}) and elemental sulphur (S_0). In other words, they acquire energy from the oxidation of Fe^{2+} or S_0 and use the energy to drive CO_2 fixation.

'Thermoacidophiles' are bacteria and archaea that have adapted to live in environments of both low pH and high temperature, a combination of extreme environmental factors that should impose huge stresses on microbial

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A boiling, acidic mud-pool at Whakarewarewa thermal area in New Zealand belches hydrogen sulphide.

survival. Nevertheless, organisms such as *Sulfolobus solfataricus* grow best at 80°C and between pH 2 and 4. The current leaders in the 'most acidophilic organism on Earth' competition are members of the genus *Picrophilus*, which can grow at a pH of −0.06 and a temperature of 60°C.

Comparatively little is known of low-temperature, or 'psychrophilic', acidophiles. *Acidithiobacillus*-like organisms have been reported from High Arctic soils, but cold acid niches are much less common on Earth than hot acid niches.

Survival strategies

Low pH is generally considered to be very damaging to biological molecules (many proteins denature at low pH, which is why lemon juice is used to 'cook' raw fish). The ability of acidophiles to thrive under such conditions suggests that these organisms have adapted structurally and physiologically to withstand high acid levels.

Several decades of research have uncovered some fascinating examples of such adaptation. Firstly, the cytoplasm of acidophilic microorganisms is not at equilibrium with the external environment. The internal pH of these organisms is often at near-neutrality. To achieve this, the cells have to expend a lot of energy to constantly pump protons out of the cell. Secondly, acidophiles have adapted the cytoplasmic membrane – the critically important barrier between the external environment and the sensitive cytoplasmic contents – to be resistant to acid. Their cytoplasmic membranes contain a lipopolysaccharide-type material called lipoglycan, which consists of an unusual tetra-ether lipid monolayer membrane annotated with mannose and glucose, rather than the normal ester-linked bilayer membranes of most organisms.

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Yellowstone National Park in the United States contains more than 10 000 hydrothermal features. Sulphur Caldron is one of the most acidic hot springs, with a pH of approximately 1–2. In June 2016 a young man planning to take an illegal 'spa bath' in an area closed to tourists died after falling into a hot acid pool. When a rescue team returned to recover his body the following day, no remains could be found, so it was presumed he had dissolved overnight!

Acidophiles and biotechnology

A number of acidophiles, particularly thermoacidophiles, have biotechnological applications. For example, in the field of biohydrometallurgy they allow high-value minerals such as gold, uranium and copper to be recovered from sulphidic ores. Basically, the thermoacidophilic microorganisms degrade the mineral sulphides, releasing the high-value minerals as soluble ions or metal particles that can then be separated out.

Heap-leaching involves spraying ore piles containing natural populations of acidophilic microorganisms with acidic water so that the leachate draining from the base of the pile can be collected and the solubilised mineral recovered. The process is commonly applied around the world, while some ore-rich countries have established more specialised stirred-tank reactor systems, often operating at high temperatures with populations of the thermoacidophilic archaea *Sulfolobus* and/or *Acidianus*.

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Bacteria in this acidic slimes dam in the Zambian copperbelt could potentially be used to recover valuable metals in waste ores, a process known as biohydrometallurgy.

To their credit, South African researchers and companies have been leaders in the development and commercial implementation of such technology. At Stellenbosch University Professor Doug Rawlings, who sadly passed away in May 2020, was an international leader in the development of biomining processes using the moderate acidophile *Acidithiobacillus*. This organism has the added advantage of exhibiting a very high resistance to the toxic anions of arsenic. This is particularly important because gold-bearing arsenopyrite ores are common but very difficult to process biologically due to the high arsenic content. The development of high-temperature biohydrometallurgical processes is continuing at the University of Cape Town's Centre for Bioprocess Engineering Research, under the leadership of Professor Sue Harrison.

Prof. Don Cowan is the director of the Genomics Research Institute and the Centre for Microbial Ecology and Genomics at the University of Pretoria. He was raised and educated in New Zealand, which is well known for its geothermal waters.