BIOGEOCHEMISTRY

Fixing forests

The uneven distribution of biological nitrogen fixation in terrestrial ecosystems has yet to be explained. Latitudinal gradients in temperature and phosphorus may hold the answer.

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Like the ancient mariner surrounded by sea water unfit to drink — "water, water, everywhere, nor any drop to drink" — living organisms are bathed in an atmosphere of nitrogen, but not in a form that most can assimilate. Nitrogen is needed to synthesize the amino acids and enzymes essential for life, but only a few taxa of bacteria have evolved the capacity to convert atmospheric dinitrogen gas, N_2, into assimilable forms of nitrogen, a process known as biological nitrogen fixation. Some of these nitrogen-fixing bacteria live independently in soils, but others have co-evolved with a select few taxa of higher plants, mostly in the legume family, to form symbioses that support nitrogen fixation in specialized compartments, or nodules, within roots. The global distribution of these nitrogen-fixing plants in terrestrial ecosystems is highly uneven, and has generally eluded explanation by ecosystem models. Houlton and co-workers[1] show that a framework that incorporates latitudinal gradients in temperature and phosphorous can account for the distribution of terrestrial nitrogen fixers in mature forests across the globe.

In aquatic ecosystems, nitrogen-fixing bacteria generally respond to the presence or absence of available nitrogen as theory predicts: when nitrogen is limiting, nitrogen-fixing bacteria (mostly a specialized group known as cyanobacteria) have a competitive advantage and increase in abundance, and when the limitations are relieved, they lose their advantage and decrease in number. Salinity and micronutrients may complicate the story in aquatic ecosystems, but the situation in forest ecosystems is much more complex. Here, trees with a capacity for nitrogen fixation are most numerous in lowland tropical forests, where soils are already rich in plant-available nitrogen. Why nitrogen-fixation would confer a competitive advantage in nitrogen-rich regions, and why it would not be more common in temperate and boreal forests, where the growth of trees is strongly limited by nitrogen, is not clear.

Figure 1 Modelled mean distribution of nitrogen-fixing trees across the globe. Modelled estimates were generated using a biogeochemical model that incorporates latitudinal gradients in temperature, phosphorous and other resources[1]. The coloured regions reflect the mean estimate for mature forest ecosystems. Estimates do not consider disturbance, land use change or secondary succession. Regions in black were not considered in the analysis. The latitudinal gradient in the abundance of nitrogen-fixing trees is qualitatively corroborated by their real-world distribution in mature non-disturbed forests. This figure is based on model simulations presented by Houlton *et al.*[1]; The authors thank Scott Morford for preparing the figure.

Reducing molecular N_2 is hungry work, and bacterial nitrogen fixers that form a symbiosis with plants derive their energy from the photosynthates, or sugars, supplied by the plant. When the growing season for these plants is short, as in high latitudes, the diversion of an already limited energy supply to nitrogen fixers may be too steep a price to pay for the nitrogen that is gained. Add to this the temperature-dependency of the nitrogen-fixing enzyme nitrogenase, and it becomes less certain whether nitrogen fixation in the boreal and temperate forests that typify higher latitudes would be advantageous.

Conversely, in lowland tropical forests, conditions for photosynthesis and nitrogenase activity are generally more favourable, and although their soils are rich in nitrogen, they tend to be poor in biologically available forms of phosphorus. It is this phosphorus limitation that Houlton *et al.* suggest might provide an explanation for the curiously high abundance of nitrogen-fixing trees in these regions. Phosphorus in many lowland tropical ecosystems is bound up with old, highly weathered soil minerals and organic matter. Plants and microorganisms are able to liberate some of this phosphorus by exuding phosphatase enzymes that breakdown organic matter. Crucially, the synthesis of these enzymes requires large amounts of nitrogen. Thus nitrogen fixation in tropical forests may confer a competitive advantage to trees by facilitating the uptake of phosphorus.

Houlton and colleagues provide empirical evidence for both the universality of the relationship between temperature and nitrogenase activity, and the stimulation of phosphatase activity by nitrogen-fixing plants. Using this framework they generate a biogeochemical model that predicts rather accurately the distribution of nitrogen-fixing trees in mature forests across the globe. Model runs excluding the influence of either temperature or phosphorus availability were unable to explain the current distribution of nitrogen-fixing trees. Thus the conceptual framework put forward by Houlton and colleagues reveals how biogeochemical and biophysical limitations interact with the advantages and disadvantages of nitrogen fixation to determine the distribution of nitrogen fixers across the globe.

As far as mature forests go, this framework of interacting multiple resource limitations makes sense, and it joins a growing number of recent studies that emphasize the influence of nitrogen–phosphorus interactions on ecosystem functioning[2,3]. However, several important details await incorporation. First, the framework does not attempt to explain the distribution of nitrogen-fixing shrubs and herbs, which can play an important role in ecosystems at all latitudes. Second, the framework only addresses symbiotic nitrogen fixation, but recent studies provide intriguing evidence that nitrogen fixation by free-living soil bacteria[4,5] and cyanobacteria[6] may be quantitatively important in some ecosystems. The activity of these free-living nitrogen fixers increases on the addition of phosphorus and in the presence of phosphorus-rich leaf litter[4,5], providing more evidence for nitrogen–phosphorus linkages, and also highlighting the need for an improved understanding of competition for phosphorus in soils. Houlton and colleagues use their model to demonstrate that the advantages of symbiotic nitrogen fixation are lost if all competitors for soil phosphorus benefit from the phosphatase exuded by roots of nitrogen-fixing trees. Given that competition for phosphorus between roots of fixing and non-fixing species, mycorrhizae, free-living nitrogen-fixing bacteria and other soil organisms is poorly understood, we can't yet determine the fate of this phosphorus.

Furthermore, the presence of tree species capable of symbiotic nitrogen fixation is not always a reliable indicator of the presence of nitrogen-fixing nodules; hence the abundance of leguminous trees in some regions of the lowland tropics may not reflect biological nitrogen fixation[7]. Finally, secondary succession (where shrubs and small trees colonize previously disturbed patches of forest) is not completely addressed by this new framework. Nitrogen is often lost from mature forests following disturbance, which should confer a competitive advantage to symbiotic nitrogen-fixing species. But although this often appears to be the case in temperate zones, it is less clear whether symbiotic nitrogen fixation plays an important role in the secondary succession of boreal and tropical forests[3,6].

Frameworks are, of course, meant to be built on. A unified conceptual framework that also encompasses free-living nitrogen fixation, non-tree nitrogen-fixing symbioses, root competition, nodulation and secondary forest succession would provide a more satisfying structure for understanding the distribution of terrestrial nitrogen fixation. But in the meantime, the insights of Houlton and colleagues lay a much needed foundation for future research into the conundrum of terrestrial nitrogen fixation.

References

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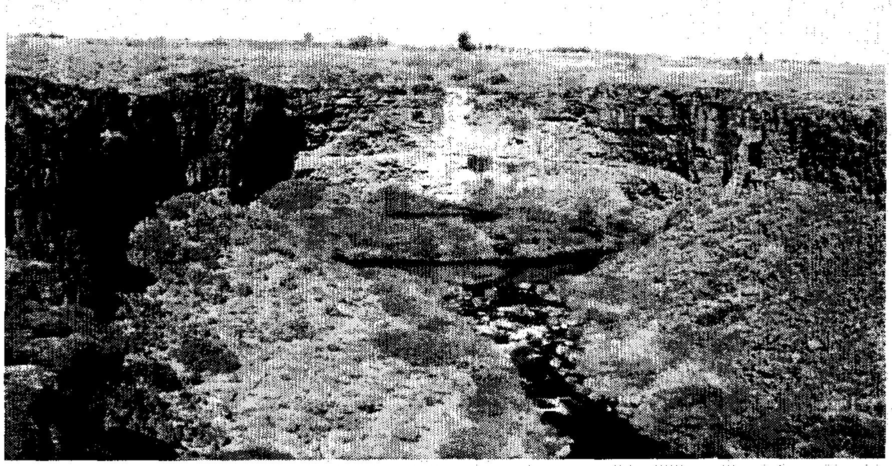
GEOMORPHOLOGY

Sculpted by a megaflood



Not all canyons are created equal. Steep canyons with amphitheatre-shaped heads are thought to result from the activity of groundwater, on the basis of studies of such features that developed in sand, for example in the Florida Panhandle. In such settings, groundwater emerges in springs and can destabilize slopes. Growth of the canyon is achieved not by surface flow, such as in a river, but by the retreat of canyon heads by periodic toppling of material that could have been softened by groundwater.

But when amphitheatre-headed canyons are carved in hard rock, the possibility that surface water was involved cannot be discounted. Michael Lamb of the University of California at Berkeley and his colleagues focused on the Box Canyon in Idaho, USA (*Science* **320,** 1067–1070; 2008). The location is ideal to investigate the ways in which water shapes the Earth's surface, because the canyon seemed a perfect example of groundwater-aided carving: a spring originates at its head and provides almost all of the water that flows in this canyon and there is no surface drainage upstream of the canyon head.

But the researchers found heaps of boulders near the canyon head, which are usually associated with pools of water that assemble under waterfalls, and they discovered scour marks made by surface water extending upstream from the rim of the canyon. In addition, hydraulic calculations suggest that the water flow in the present stream is grossly insufficient to carve a canyon of this size. Something far more powerful would be needed and groundwater-related erosion is not a viable candidate to provide that force.

The most likely process for the formation of Box Canyon is an immense flood. Such a surge would have had to persist for between about a month and six months, eroding the canyon rapidly headward and transporting the resulting debris out of the canyon. Exposure ages of the rocks suggest that the canyon formed tens of thousands of years ago. The flood is unlikely to have resulted from heavy rainfall because precipitation in this area was probably quite low at the time, just as it is now.

Similarly shaped canyons have been found in volcanic terrains on Mars. Landforms like Box Canyon that go back to brief periods of catastrophic flooding may be more suitable terrestrial analogues for these martian canyons than amphitheatre-headed canyons formed by groundwater activity in sand.

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