Carbon cycling: How much life has ever existed on Earth?

Michael A. Kipp[1,2]
[1]Division of Geological and Planetary Sciences, California Institute of Technology, Pasadena, CA, USA
[2]Division of Earth and Climate Sciences, Duke University, Durham, NC, USA
Correspondence: michael.kipp@duke.edu
https://doi.org/10.1016/j.cub.2023.09.041

Carbon has cycled through Earth's biosphere for billions of years. New work estimates that life has recycled the equivalent of almost 100 times the Earth's entire carbon reservoir through the biosphere. This highlights life's global impact, providing a benchmark for habitable planets.

What is life? This question evades a simple answer[1,2], but most biologists would at least agree that the metabolic core of life on Earth is reduction of inorganic carbon to organic matter, balanced by oxidation of another substrate. While organic carbon is found throughout the cosmos — including in meteorites[3], the building blocks of planets — biological carbon fixation is by far the dominant source of organic matter on Earth today. Furthermore, biological carbon fixation may have arisen very early in Earth's ~4.5-billion-year (Gyr) history[4]. In this issue of *Current Biology*, Crockford and colleagues[5] present a synthesis of biological carbon fixation through Earth history, thus quantifying the planetary impact of life.

Integrating productivity

Multiple terms are used to describe ecosystem productivity. Gross primary production (GPP) is the total carbon fixed into biomass by autotrophs. Net primary production (NPP) is GPP minus the carbon respired by autotrophs (typically ~half of GPP[6]). Of NPP, >99% is respired by heterotrophs, with only a miniscule fraction buried in sediments[6].

To quantify the amount of biomass ever created, one must integrate GPP over ~4.5 Gyr. Crockford and colleagues[5] undertook this gargantuan task, compiling theoretical constraints and proxy estimates of NPP and GPP from the literature. Before considering their results, it is worth examining the productivity constraints.

The literature agrees that chemoautotrophic and/or anoxygenic photoautotrophic metabolism dominated Earth's early history. Theoretical upper limits on the productivity of such a biosphere[7] inform this portion of the record, and their uncertainties do not significantly impact the results due to the low productivity in this interval.

Following the origin of oxygenic photosynthesis, cyanobacteria, eventually algae, and ultimately plants came to dominate productivity. Productivity constraints in these regimes are mostly geochemical. In particular, this compilation[5] rests heavily on work using mass-independent oxygen isotope signatures as a GPP proxy. This proxy requires assumptions about the sources of mineral-bound oxygen[8] (e.g., how much O in $CaSO_4$ came from O_2 *versus* H_2O) and the paleo-atmospheric concentration of oxygen-containing gases[9] (i.e., pO_2, pCO_2). These are poorly constrained in the Precambrian. Indeed, the greatest uncertainty in the compilation comes just after the Great Oxidation Event (GOE) and stems from our poor understanding of pO_2 at that time.

After the GOE, estimates are better constrained. The 'boring billion' — so-called for its unobtrusive carbon isotope record[10] — spans 1.8–0.8 Gyr. According to Crockford *et al.*, this interval represents ~3% of the carbon ever fixed by the biosphere, which indeed does not represent much of life's history. Productivity is then thought to have increased with the Cryogenian rise of eukaryotic algae[11], and again with the origin of vascular land plants, as well as with the Mesozoic phytoplankton revolution.

This compendium of productivity through time is rife with statistical curiosities for the Earth-history aficionado. For instance, because of increasing productivity, integrated organic matter production is strongly biased toward the present (Figure 1). It took >2 Gyr for life to cycle the equivalent of Earth's entire carbon reservoir through the biosphere once, but <200 Myr to happen again. Also, ~80% of all organic carbon has been fixed since the dawn of the Cambrian, despite comprising ~10% of Earth history. These numbers capture the plight of Precambrian paleobiologists, who face a needle-in-haystack search for microfossils due to not only the sparse geologic record, but also the low rate at which cells were produced. With this view we also see that global calamities — such as glaciations or bolide impacts — hardly impact integrated productivity due to their transience. If anything, as Crockford *et al.* note, such events have ultimately increased productivity by creating evolutionary opportunities.

An evolving cast of characters

This record also quantifies the number of times life has rolled the dice during gene replication. Crockford *et al.* show that biological productivity is not constant. Molecular clocks aiming to temporally constrain past events should therefore account for such changes. Coupled to uncertain calibrations[12], this further highlights the limitations of molecular clocks as time-tellers, though these issues don't impede the authors' ability to reconstruct relative sequences of evolutionary events.

A possible implication of this analysis is that evolution was inefficient in Earth's early history since fewer reproductive events occurred per year. Indeed, under a constant mutation rate, evolutionary innovations would arise at a rate proportional to productivity. However, natural selection is the interplay between genetic drift and environmental opportunity. Using similar estimates of mutation rate, genome size and

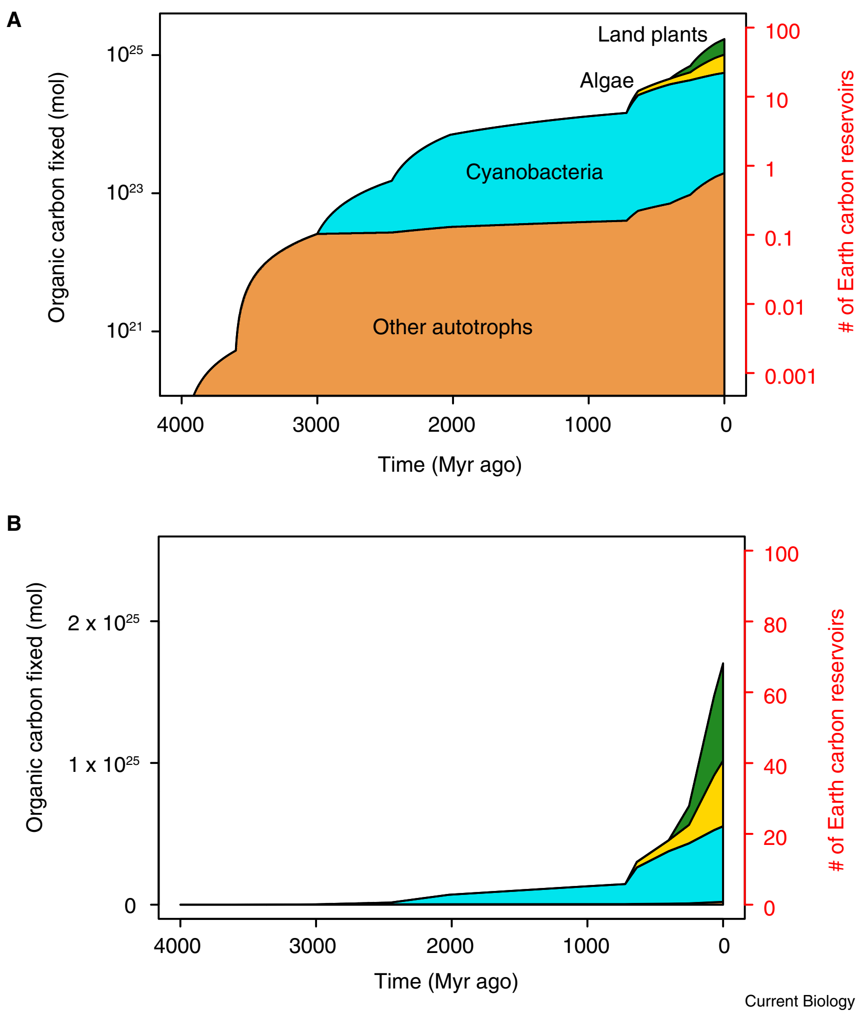

Figure 1. Total carbon fixed by life on Earth.
Same plot shown in (A) log scale and (B) linear scale. The biosphere has cycled ~67× Earth's total carbon reservoir, with most of that occurring in the last few hundred million years.

population size (~productivity), others have inferred that evolution has always proceeded rapidly relative to the pace of environmental change[13]. Crockford *et al.* challenge that notion, at least for Earth's early history. Further work quantifying adaptation rates under changing productivity and environmental conditions would better elucidate the timetable of evolution.

Regardless of precise rates, the dominant primary producers on Earth indeed changed over time. Cyanobacteria are the most ancient oxygenic photosynthesizers, and likely dominated GPP until the rise of algae. Algae were, in turn, superseded by plants. Importantly, these shifts were not merely displacements of prior dominant phototrophs, but also increases in total productivity. As a result, despite their more recent origins, algae and plants have cumulatively fixed comparable amounts of carbon to cyanobacteria. Still, due to differences in cellular architecture and life cycle, cyanobacteria have dominated Earth in terms of cell numbers.

Life's imprint on Earth's surface

Having tallied the who, where, and when of biological carbon fixation, we can consider its environmental impacts. A first question is: how much organic matter has been preserved in sediments? If the biosphere was perfectly efficient in recycling its products, there would be no secular impact on Earth's surface chemistry. However, as noted above, a small fraction of NPP escapes respiration and accumulates in sedimentary rocks. This buried organic carbon leaves behind a stoichiometric equivalent of byproducts, allowing life to shape the chemistry of Earth's surface.

Of the many potential byproducts of autotrophy, none has had a greater impact than O_2. The timing of the origin of oxygenic photosynthesis is debated, with estimates ranging from >3.8 to 2.4 Gyr ago[14,15]. Crockford *et al.* demonstrate that this >1 Gyr uncertainty has little impact on the amount of O_2 ever produced, since early biological O_2 production was muted. In other words, while the field debates whether atmospheric oxygenation was caused by declining O_2 sinks after an early appearance of oxygenic photosynthesis[14] or increasing O_2 sources after a late appearance[15], as long as oxygenic photosynthesis appears, Earth becomes oxygenated. This is the distinction we care about when considering the prevalence of oxygenated Earth-like planets elsewhere in our galaxy.

This compilation also informs our understanding of a long-studied archive of biological O_2 production: the carbon isotopic composition of carbonate sediments[16]. Crockford *et al.* note that according to their compilation, a face-value reading of the carbon isotope record would imply unphysical rates of organic matter burial (>100% of NPP). This is in line with other recent work[17,18], which has inferred that organic burial efficiency was higher in the Precambrian, but also the carbon isotope record does not reflect organic burial in the canonical fashion. Together with concerns about the preservation and representativeness of the carbon isotope record[19], this deals another blow to a long-time favorite archive of Earth's evolution, but corroborates the notion of efficient organic matter burial on early Earth.

Looking ahead

The authors close by considering the future of life on Earth. It is thought that solar brightening will induce a runaway greenhouse ~2 Gyr from now[20]. Furthermore, as this brightening drives a pCO_2 decline via the silicate weathering feedback, plant photosynthesis may become impossible in only ~1 Gyr[20]. Considering life's ~4 Gyr history, most of Earth's habitable lifetime has passed. However, given historically high rates of current productivity, we may in fact only be at the halfway point of total carbon ever fixed on our planet. In other words, a lot can still happen! From the extinction of the dinosaurs to the present, ~13% of all carbon has been fixed. If ~8× that much carbon moves through the biosphere in the next 1–2 Gyr, there will surely be new evolutionary sagas similarly astounding to those we study in the fossil record.

Finally, we can zoom out to an astrobiological context. Earth may ultimately cycle the equivalent of its entire carbon reservoir through the biosphere 100–200× over 5–6 Gyr. The other terrestrial planets in our Solar System have had shorter habitable windows, if at all. If life arose on Venus or Mars, how productive might it have been? In the vast cosmic arena, there are perhaps planets that live fast & die young, while others are slow & steady. Where does Earth sit on this spectrum? Moreover, we could define a new parameter, ''gross stellar system production'', as the sum of GPP on all planets orbiting a star. Some stars may host a handful of productive worlds, while others are dominated by a single living planet. As we search for life beyond Earth, this type of quantitative framework may help to compare planetary ecosystems both near and far.

DECLARATION OF INTERESTS

The author declares no competing interests.

REFERENCES

1. Schrodinger, E. (1951). What Is Life? The Physical Aspect of the Living Cell (Cambridge, UK: Cambridge University Press).
2. Margulis, L., and Sagan, D. (2000). What Is Life? (Berkeley and Los Angeles, CA: University of California Press).
3. Botta, O., and Bada, J.L. (2002). Extraterrestrial organic compounds in meteorites. Surv. Geophys. *23*, 411–467.
4. Arndt, N.T., and Nisbet, E.G. (2012). Processes on the young Earth and the habitats of early life. Annu. Rev. Earth Planet. Sci. *40*, 521–549.
5. Crockford, P.W., Bar On, Y.M., Ward, L.M., Milo, R., and Halevy, I. (2023). The geologic history of primary productivity. Curr. Biol. *33*, 4741–4750.
6. Schlesinger, W.H., and Bernhardt, E.S. (2013). Biogeochemistry: An Analysis of Global Change (Waltham, MA: Academic Press).
7. Ward, L.M., Rasmussen, B., and Fischer, W.W. (2019). Primary productivity was limited by electron donors prior to the advent of oxygenic photosynthesis. J. Geophys. Res. Biogeosciences *124*, 211–226.
8. Cao, X., and Bao, H. (2021). Small triple oxygen isotope variations in sulfate: Mechanisms and applications. Rev. Mineral. Geochem. *86*, 463–488.
9. Killingsworth, B.A., Cartigny, P., Hayles, J.A., Thomazo, C., Sansjofre, P., Pasquier, V., Lalonde, S.V., and Philippot, P. (2022). Towards a holistic sulfate-water-O_2 triple oxygen isotope systematics. Chem. Geol. *588*, 120678.
10. Buick, R., Des Marais, D.J., and Knoll, A.H. (1995). Stable isotopic compositions of carbonates from the Mesoproterozoic Bangemall Group, northwestern Australia. Chem. Geol. *123*, 153–171.
11. Brocks, J.J., Jarrett, A.J.M., Sirantoine, E., Hallmann, C., Hoshino, Y., and Liyanage, T. (2017). The rise of algae in Cryogenian oceans and the emergence of animals. Nature *548*, 578–581.
12. Graur, D., and Martin, W. (2004). Reading the entrails of chickens: molecular timescales of evolution and the illusion of precision. Trends Genet. *20*, 80–86.
13. Knoll, A.H., and Nowak, M.A. (2017). The timetable of evolution. Sci. Adv. *3*, e1603076.
14. Buick, R. (2008). When did oxygenic photosynthesis evolve? Philos. Trans. R. Soc. B Biol. Sci. *363*, 2731–2743.
15. Fischer, W.W., Hemp, J., and Johnson, J.E. (2016). Evolution of oxygenic photosynthesis. Annu. Rev. Earth Planet. Sci. *44*, 647–683.
16. Schidlowski, M. (2001). Carbon isotopes as biogeochemical recorders of life over 3.8 Ga of Earth history: evolution of a concept. Precambrian Res. *106*, 117–134.
17. Kipp, M.A., Krissansen-Totton, J., and Catling, D.C. (2021). High organic burial efficiency is required to explain mass balance in Earth's early carbon cycle. Glob. Biogeochem. Cycles *35*, e2020GB006707.
18. Krissansen-Totton, J., Kipp, M.A., and Catling, D.C. (2021). Carbon cycle inverse modeling suggests large changes in fractional organic burial are consistent with the carbon isotope record and may have contributed to the rise of oxygen. Geobiology *19*, 342–363.
19. Hodgskiss, M.S., Crockford, P.W., and Turchyn, A.V. (2023). Deconstructing the Lomagundi-Jatuli carbon isotope excursion. Annu. Rev. Earth Planet. Sci. *51*, 301–330.
20. Caldeira, K., and Kasting, J.F. (1992). The life span of the biosphere revisited. Nature *360*, 721–723.

Carnivorous plants: Unlocking the secrets of peristome geometry in pitcher plants

Kenji Fukushima
Department for Molecular Plant-Physiology and Biophysics - Botany I, University of Würzburg, Julius-von-Sachs-Institute for Biosciences, Würzburg, Germany
Correspondence: kenji.fukushima@uni-wuerzburg.de
https://doi.org/10.1016/j.cub.2023.09.056

A recent study employs computational models to explore the functional morphology of carnivorous trapping pitchers in *Nepenthes*. Focusing on the peristome, the study uncovers new dimensions in form–function relationships, offering theoretical insights into the role of complex trap morphology.

The marvels of evolutionary biology extend beyond iconic examples like Darwin's finches[1]. The pitcher plant genus *Nepenthes* presents what is likely an as-yet-undescribed case of adaptive radiation (Figure 1A–D). These carnivorous plants have transformed leaves, originally specialized for photosynthesis, into trapping pitchers that provide nutritional benefits[2,3], showcasing some of the most complex leaf shapes in flowering plants[4]. With 183 accepted species, the genus exhibits a diverse array of specialized pitcher shapes, each featuring a unique peristome, a slippery rim crucial for effective trapping[5].

