## 3.4. The power of unicellular primary producers

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Marine phytoplankton, including cyanobacteria and microalgae, dominates primary production across two thirds of the earth's surface, sustaining virtually all marine life and exerting a fundamental control over global climate through carbon sequestration into the deep ocean. These unicellular photoautotrophs are responsible for roughly 50% of global net primary production, which is equivalent to producing 50 gigatons of organic carbon (C) per year (about 140 million t per day). Phytoplankton produce a massive amount of organic C despite representing only 1% to 2% of the photosynthetic biomass on earth, thus reflecting their extraordinarily high turnover rate. Almost all of the phytoplankton standing right now in the world's oceans will be consumed and produced again in a week or less. Unlike terrestrial ecosystems, where plant biomass dominates the landscape (imagine a lush rainforest), the living seascape is dominated by heterotrophic microorganisms, including bacteria, protozoans, ciliates and tiny crustaceans, whose global biomass exceeds the biomass of marine primary producers by up to five times (Bar-On et al. 2018). This inverted biomass distribution pattern is one of the most prominent hallmarks of ocean plankton ecosystems, which rely on the activity of heterotrophic microorganisms to continually recycle photosynthetic biomass and replenish fast-growing phytoplankton with essential nutrients. This close coupling between microbial primary producers and recyclers forms the so-called microbial food web (Azam and Malfatti 2007), which

keeps ocean plankton ecosystems close to steady state. However, in some cases, ocean currents, continental runoff and dust storms, among other events, bring new nutrients to the surface, boosting primary productivity and moving plankton ecosystems away from the steady state. Because marine primary production incorporates roughly 6.6 moles of carbon dioxide  $(CO_2)$ for every mole of nitrogen, the input of new nutrients into the sunlit layer of the ocean reduces the concentration of dissolved CO<sub>2</sub> in surface waters. The resulting "new" primary production (to differentiate it from the "recycled" primary production) takes heterotrophs by surprise and they cannot instantly consume the excess primary production. As a result, a large fraction of this "new" primary production ends up being exported to the depths of the ocean. This phenomenon, called the biological C pump, generates a CO<sub>2</sub> deficit on the ocean surface, which is offset by the absorption of CO<sub>2</sub> from the atmosphere. In this way, the ocean's biological pump helps mitigate the greenhouse effect and cool the earth's climate.

Understanding the ecological and biogeochemical functioning of plankton ecosystems is key to harnessing the power of unicellular primary producers in order to develop solutions that help address some of the current challenges facing our society, such as global warming and food shortages. Because many of these solutions require the natural processes to be accelerated, before explaining how these microscopic primary producers could contribute to this global effort, let us start by illustrating here how they impacted the earth system in the geological past. The ultimate goal is to condense into decades/ centuries the changes that nature took hundreds of thousands of years to achieve.

## The powerful plankton

Two mechanisms are thought to have increased the ocean's biological potential to boost primary production, fuelling marine food webs and reducing the concentration of CO<sub>2</sub> in the atmosphere. The first one involves an increase in the oceanic inventory of inorganic nutrients. Because primary production in many oceanic regions is limited by the availability of essential nutrients, such as nitrogen, phosphorus and iron, an increase in nutrient input into the ocean will have boosted global ocean primary production, as well as the fraction of primary production transferred to upper trophic levels and exported to the depths. The second mechanism has to do with changes in the stoichiometry of the phytoplankton biomass and detrital fractions in comparison with that described by Alfred C. Redfield, who found that the ratio between carbon (C), nitrogen (N) and phosphorus (P) is a nearly constant 106:16:1 throughout the world's oceans in both phytoplankton biomass and in dissolved nutrient pools. An increase in these elemental ratios would involve an increase in the amount of C exported per unit of N or P entering the surface ocean. There is evidence that these two mechanisms have acted in the geological past (Falkowski 2012), by i) increasing marine export production, ii) promoting the formation of vast deposits of oil and gas, and iii) helping cool the earth's climate.

## The prospect of algaculture

Our deep understanding of marine ecosystems gives us, as marine scientists, the ability to invent smart solutions to address some of today's most pressing social and environmental challenges. For centuries, conventional agriculture has struggled to prevent the collapse of food crops, which are often ruined by pests and diseases. Decades of agricultural research have enabled the development of crop protection measures that have resulted in previously unthinkable crop yields. For example, corn yield (i.e. corn production per unit of land used) has increased five-fold over the last 80 years, thanks to some extent to breakthroughs in pest management (Figure 1). Unicellular primary producers are three to four times more efficient than terrestrial plants at converting sunlight energy into biomass and can achieve biomass production yields that are up to one order of magnitude higher (Figure 1). However, their use as a sustainable source of feedstock for human food, animal feed or biofuels remains untapped. Algaculture or phycoculture, hereinafter the cultivation of cyanobacteria and microalgae using wastewater or seawater, has incredible potential to become an important source of biomass for the future, as well as an efficient sink of CO<sub>2</sub> from industrial flue gases (Araújo et al. 2021). However, the large-scale implementation of algaculture suffers from the same problems that conventional agriculture has faced for centuries. As discussed in the opening paragraph, hetero-

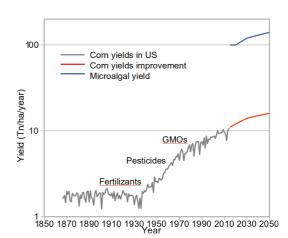


Figure 1. Average maize yields in the United States from 1866–2014, based on data from the United States Department of Agriculture (USDA) and the UN Food and Agriculture Organization. The yields remained relatively flat until the 1930s. In the period since 1940, yields have increased more than five-fold thanks to irrigation, fertilizers, improved pest management and genetically-modified organisms. Microalgae biomass production yields are one order of magnitude higher than current maize yields and are expected to increase substantially as the currently underdeveloped algaculture technology improves strain productivity and pest resistance.

trophic microorganisms can take over plankton communities in a matter of days, leading to the failure/collapse of biomass production systems. Furthermore, cyanobacteria and microalgae have enormous nutritional (fertilizer) needs, which hinder the global expansion of algaculture for mass production of low-price commodities such as food, feeds and biofuels. Protecting microalgal crops from biological consumption, pests and diseases and finding ways to re-supply nutrients and  $CO_2$  in order to enhance, respectively, biomass production and the biological capture of C are critical to make algaculture truly sustainable and profitable in the coming decades.

The advent of new technologies, such as genomics, has enabled marine scientists to gain a deeper understanding of how unicellular primary producers thrive, die and decay in natural plankton ecosystems (Pedrós-Alió 2006). This knowledge provides us with extremely valuable information for exploring ways to accelerate natural processes and help i) provide a sustainable source of biomass for food and biofuels and ii) reduce atmospheric  $CO_2$  emitted from burning fossil fuels by capturing it in the form of refractory organic compounds, just as nature has been doing since the origin of oxygenic pho-

tosynthesis about 2.5 billion years ago. Just as agriculture represented a momentous change in the history of humanity and of our planet, the expansion of algaculture is called to play a crucial role in the evolution of our society towards a more habitable future planet.

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