

How large are chloroplasts?

Plants and algae contain other membrane-bound organelles besides their mitochondria. Further, like the mitochondria, these chloroplasts play a key role in the energy economy of the cells that harbor them. Chloroplasts are less well known than their mitochondrial counterparts, though they are significantly larger and have a key role in producing the reduced compounds that store energy which is then broken down in mitochondria. Chloroplasts in vascular plants range from being football to lens shaped and as shown in Figure 1, have a characteristic diameter of $\approx 4\text{--}6$ microns (BNID 104982,107012), with a mean volume (for corn seedling) of $\approx 20\text{ }\mu\text{m}^3$ (BNID 106536). In algae they can also be cup-shaped, tubular or even form elaborate networks, paralleling the morphological diversity found in mitochondria.

Chloroplasts have the pivotal role in the biosphere of carrying out the chemical transformations linking the inorganic world (CO_2) to the organic world (carbohydrates). This feat of chemical transformation enables the storage of the fleeting sun's energy in carbohydrates and transient energy currencies such as ATP and NADPH for extended periods of time. Those same carbon compounds also serve to build all the cell biomass as a result of downstream metabolic transformations.

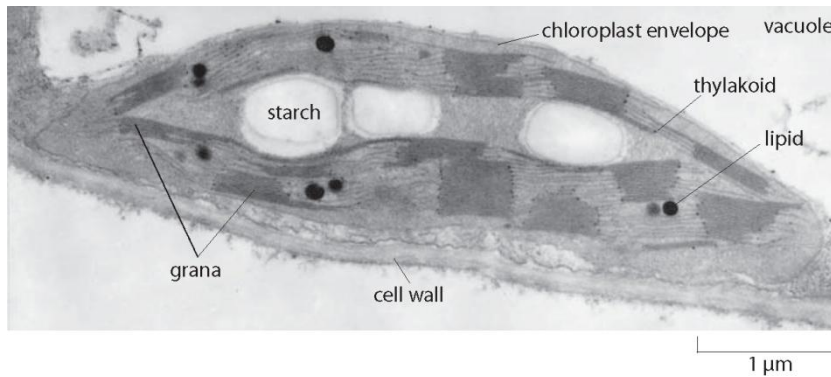
Though chloroplasts are many times larger than most bacteria, in their composition they can be much more homogenous, as required by their functional role which centers on carbon fixation. The interior of a chloroplast is made up of stacks of membranes, in some ways analogous to the membranes seen in the rod cells found in the visual systems of animals like us. The many membranes that make up a chloroplast are fully packed with the apparatus of light capture, photosystems and related complexes. The rest of the organelle is packed almost fully with one dominant protein species, namely, Rubisco, the protein serving to fix CO_2 and which is the slowest in the Calvin-Benson-Bassham carbon fixation pathway.

The number of chloroplasts per cell varies significantly between organisms and even within a given species can change significantly depending upon growth conditions. In the model algae *Chlamydomonas reinhardtii* there is only one prominent cup shaped chloroplast per cell whereas in a typical mesophyll cell from plants such as *Arabidopsis* and wheat there are about 100 chloroplasts per cell (BNID 107030, 107027, 107029). Each chloroplast has tens to hundreds of copies (BNID 107105, 107107, 107108) of the chloroplast genome which is $\approx 100\text{ kbp}$ in length (BNID 105918).

Much evidence points to the idea that chloroplasts originated in a process of endosymbiosis, i.e. they were originally free living cells - probably photosynthetic cyanobacteria - that were engulfed (or enslaved) a billion years ago (BNID 107041) by cells that have become their new hosts. With time these originally distinct cells forged a tight collaboration in which most genes transferred from the engulfed cell to the host nucleus, in much the same way that the mitochondrial genome obtained its tiny size. From genomes that probably originally contained over 3000 genes only about 130 genes remain in the chloroplasts of contemporary plants (BNID 106553, 106554).

These processes of engulfment followed by adaptation can still be observed today. Through a process known as kleptoplasty, different organisms ranging from dinoflagellates to sea slugs are able to digest algae while keeping the chloroplasts of these algae intact. These captured plastids are kept

functional for months and are used to “solar power” these organisms. Not only the act of engulfing but also the longer process of adaptation between the host and the organelle can be observed. In a recent paper (Huang et al. Nature 2003) it was determined that in one out of ~10,000 pollen grains a reporter gene is transferred from the chloroplast to the nuclear genome (BNID 103096). How can such a low value be assessed reliably? A drug resistance gene that can only function in the nucleus was incorporated into the chloroplasts of tobacco plants. Pollen from these plants was used to pollinate normal plants. 250,000 seeds were screened and 16 showed resistance to the drug. Now here is the catch. Chloroplast genomes are transferred only through the mother. The pollen has only nuclear genes. The only way for the resistance gene to arrive through the pollen was shown to be through infiltration from the chloroplast genome into the nuclear genome. Measuring the rate of this process gives some insight into how genomes of organelles can be so small. It leaves open the



question of what is the selective advantage of transferring the genomic information from the organelle's DNA to the central cell repository in the nucleus.

Figure 1: Electron micrograph of a chloroplast. There are usually about 40-60 grana stacks per chloroplast (107013), covering 50-70% of the thylakoid membrane surface (107016), with a single stack diameter of 0.3-0.6 [μm](#) (106014). (From MBOC)

How many photons does it take to make a cyanobacterium?

Autotrophs are those organisms that are able to make a living without resorting to preexisting organic compounds and as such, are the primary producers of organic matter on planet Earth. One of the most amazing autotrophic lifestyles involves the use of inorganic carbon in the form of CO_2 and the synthesis of organic carbons using light as the energy input, the phenomenon known as photosynthesis. Chemoautotrophs make a similar performance, though in their case, the energy source is not light from the sun, but some other terrestrial energy source such as a thermal vent in the ocean or a reduced inorganic compound such as molecular hydrogen or ferrous iron.

Photoautotrophs refer to the sum total of those organisms that take energy from sunlight and convert it into organic compounds that can be oxidized. The most familiar examples are the plants that surround us in our forests and gardens. However, the overall synthetic budget goes well beyond that coming from plants and includes algae and a variety of microscopic organisms including single-celled eukaryotes (protists) and a whole range of prokaryotes such as cyanobacteria (formerly known as blue-green algae).

However, we shouldn't forget that the majority of the Earth's surface is covered by water and photosynthesis in these great aqueous reservoirs is a significant fraction of the total. Interestingly, aquatic photosynthesis is largely performed by organisms so small they are not visible to the naked eye. Despite their macroscopic invisibility, these organisms are responsible for fixing ≈ 50 gigatons (BNID 102936, 10^{39} CO_2 molecules) of carbon every year. This accounts for about one half of the total primary productivity on earth (BNID 102937) but the vast majority of this fixed carbon is soon returned to the atmosphere following rapid viral attacks, planktonic grazing and respiration (BNID 102947). The process of transforming inorganic carbon into the building blocks of the organic world occurs through the process of carbon fixation, where the energy from about 10 photons is used in order to convert CO_2 into a carbohydrate, $(\text{CH}_2\text{O})_n$. The H is donated by water as an electron donor which is thus transformed into oxygen. The process of oxygenic photosynthesis was invented about 3 billion years ago and transformed our atmosphere from one with practically no oxygen to one where abundant oxygen allows the existence of animals like us. Much of the carbon fixation happens in small organelles like those shown in figure 1 and known as carboxysomes that are home to an army of molecules which perform the carbon fixation process through a key carboxylating enzyme, Rubisco, the most abundant protein in the biosphere (about 5 kg of it for every person on earth (BNID 103827)).

From an order of magnitude perspective, it suffices to think of a cyanobacterium as similar in chemical composition to a conventional bacterium, which means that it takes roughly 10^{10} carbons (see vignette on elemental composition of cell) to supply the building materials for a new cyanobacterium with a volume of 1 micron^3 as depicted in figure 2. Given that it requires roughly ten photons to fix a carbon atom, this implies roughly 10^{11} photons are absorbed to fix those 10^{10} carbons. This carbon fixation is carried out by roughly 10^4 Rubisco monomers within a given cyanobacterium. What about the energy required for other cellular processes such as amino acid polymerization into proteins and keeping the membrane potential maintained to drive a multitude of coupled reactions? For bacteria these energetic requirements were estimated to be on the order of 10^{10} ATP (BNID XX). Given that a photon can be used to produce more than one ATP equivalent

(through extruding protons or electron storage in NADPH) we find that the burden of carbon fixation is dominant over these other biosynthetic and maintenance tasks.

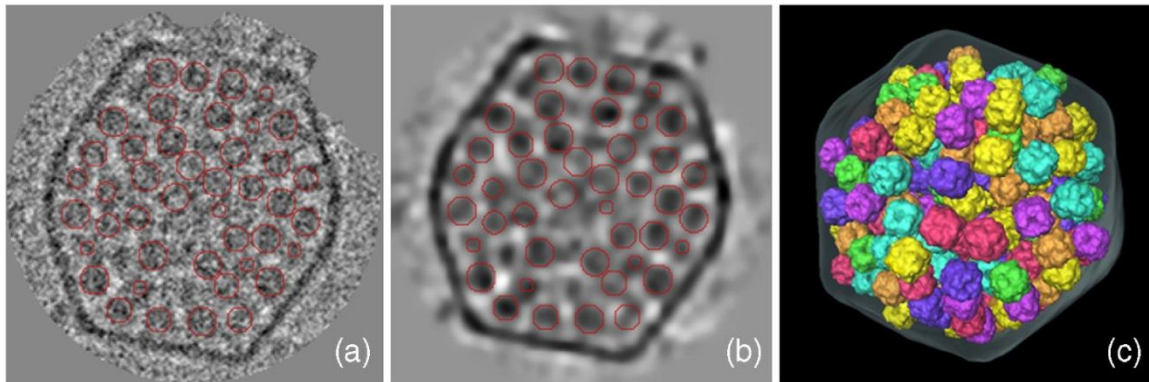


Figure 1: The structure of carboxysomes and the Rubisco octamers occupying them. The sizes of individual carboxysomes in this organism (*Synechococcus* Strain WH8102) varied from 114 nm to 137 nm, and were approximately icosahedral. There are on average ≈ 250 Rubisco octamers per carboxysome, organized into three to four concentric layers. (Adapted from: Jensen, Journal of Molecular Biology, Volume 372, Issue 3, 21 September 2007, Pages 764-773)

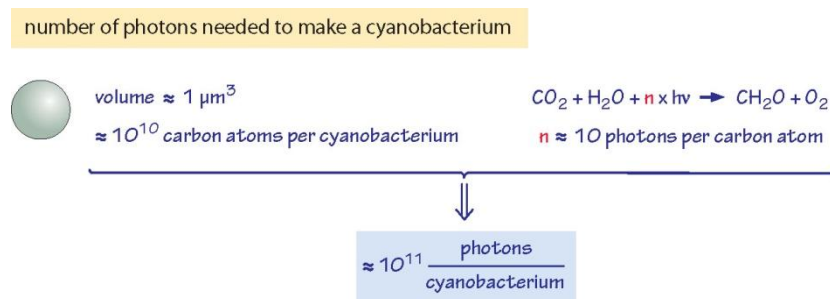


Figure 2: Order of magnitude estimation of the number of photons required to build a cyanobacterium.