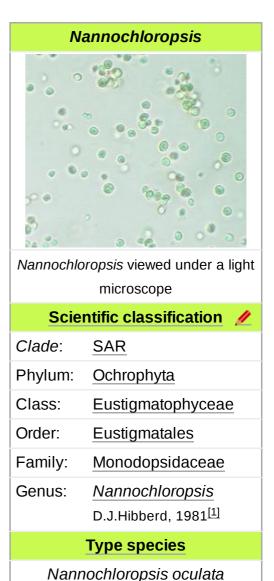
Nannochloropsis

Nannochloropsis is a genus of algae comprising six known species. The genus in the current taxonomic classification was first termed by Hibberd (1981). The species have mostly been known from the marine environment but also occur in fresh and brackish water. All of the species are small, nonmotile spheres which do not express any distinct morphological features that can be distinguished by either light or electron microscopy. The characterisation is mostly done by rbcL gene and 18S rRNA sequence analysis.

The algae of the <u>genus</u> *Nannochloropsis* differ from other related <u>microalgae</u> in that they have <u>chlorophyll a</u> and completely lack <u>chlorophyll b</u> and <u>chlorophyll c</u>. In addition they are able to build up a high concentrations of a range of pigments such as <u>astaxanthin</u>, <u>zeaxanthin</u> and <u>canthaxanthin</u>. They have a diameter of about 2 to 3 micrometers and a very simple <u>ultrastructure</u> with reduced structural elements compared to neighbouring taxa.

Nannochloropsis is considered a promising alga for industrial applications because of its ability to accumulate high levels of polyunsaturated fatty acids. [7][8] Moreover, it shows promising features that can allow genetic manipulation aimed at the genetic improvement of the current oleaginous strains. Various species of Nannochloropsis indeed are transfectable and there has been evidence that some strains are able to perform homologous recombination. [9] At the moment it is mainly used as an energyrich food source for fish larvae and rotifers. Nevertheless, it has raised growing interest also for the investigation of biofuel production photosynthetic organisms. from Nannochloropsis and biofuels). Nannochloropsis is actually in use as food additive for human nutrition and it is also served at



(Droop 1955) Hibberd 1981

Restaurant "A Poniente" of <u>El Puerto de Santa María</u> (<u>Cádiz</u>, <u>Spain</u>) close to the natural environment where *Nannochloropsis gaditana* was first isolated and still grows. [10] A 2020 study suggests it could be used for a highly performant, sustainable fish-free feed for farmed fish. [11][12]

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Species

The species currently recognised are:

- Nannochloropsis australis Fawley, Jameson & Fawley 2015
- Nannochloropsis gaditana Lubián 1982
- Nannochloropsis granulata Karlson & Potter 1996
- Nannochloropsis limnetica Krienitz et al. 2000
- Nannochloropsis oceanica Suda & Miyashita 2002
- Nannochloropsis oculata (Droop 1955) Hibberd 1981
- Nannochloropsis salina Hibberd 1981

Sequenced genomes

The scientific community has obtained the genomic sequence of different strains of *Nannochloropsis* belonging to two species: *N. gaditana* [13][14] and *N. oceanica*. [15][16] A genome portal (https://web.archive.org/web/20131029184338/http://www.nannochloropsis.org/) based on the *N. gaditana* B-31 (https://web.archive.org/web/20131029184338/http://www.nannochloropsis.org/) genome allows accessing much of the genomic information that concerns this micro-organism, moreover dedicated web pages are also available for the genomes of *N. gaditana* CCMP526 (http://nannochloropsis.genomeprojectsolutions-databases.com/) and *N. oceanica* CCMP1779 (https://web.archive.org/web/20131030101356/http://www.bmb.msu.edu/nannochloropsis.html).

The <u>genomes</u> of the sequenced *Nannochloropsis* <u>strains</u> were between 28.5 and 29 Mega bases long, they had high density of <u>genes</u>, reduced <u>intron</u> content, short intergenic regions^[13] and very limited presence of repetitive sequences. The genes of the two <u>species</u> share extended similarity.

The analysis of the <u>genomes</u> revealed that these <u>microalgae</u> have set of <u>genes</u> for the synthesis and incorporation in the <u>cell wall</u> of <u>cellulose</u> and sulfated fucans and that they are able to store carbon in polymers of β -1,3- and β -1,6-linked glucose called <u>chrysolaminarin</u>. An <u>NMR</u> analysis of whole algal cells which were cultivated in <u>autotrophic growth</u> reports evidence of the presence of <u>cellulose</u> in the cell wall and of mobile chrysolaminarin, probably accumulated in solution in vacuoles inside the cell.

Comparison between the <u>lipid</u> metabolic genes of *N. gaditana* and of <u>red/green/brown algae</u> and <u>diatoms</u> provided some insights into the exemplary lipid production of *Nannochloropsis* cultures. The comparisons indeed highlighted the presence of an expanded repertoire of some of the <u>genes</u> involved in <u>TAG</u> assembly in *Nannochloropsis*. Numerous <u>TAG</u> lipases, which can affect <u>TAG</u> metabolism through either <u>TAG</u> degradation or <u>lipid</u> remodeling, were identified in *Nannochloropsis*, $\overline{[15]}$ many of them belonging to a <u>gene</u> family which seems to be exclusive of *Nannochloropsis*.

Analysis of the genomic data suggested the presence in both the two <u>species</u> of *Nannochloropsis* of <u>regulatory RNA</u> and in particular miRNA. [13][15]

Various <u>orthologs</u> of known blue light sensing proteins were found in the genomes of *Nannochloropsis* suggesting possible circadian regulation. [13][15]

A research community from Qingdao Institute of Bioenergy and Bioprocess Technology (QIBEBT [1] (htt p://www.singlecellcenter.org/en/index.aspx)), Chinese Academy of Sciences, sequenced and compared six Nannochloropsis genomes that include two N. oceanica strains (IMET1 and CCMP531) and one strain from each of four other recognized species: N. salina (CCMP537), N. gaditana (CCMP526, which was previously reported [14]), N. oculata (CCMP525) and N. granulata (CCMP529). They found that the six genomes share key oleaginous traits, such as the gene dose expansion of selected lipid biosynthesis genes compared to green algae Chlamydomonas. The most prominent example of gene dose expansion is Diacylglycerol acyltransferase (DGAT), which catalyzes the last step of triacylglycerol (TAG) synthesis. There are 13 DGAT genes in Nannochloropsis, representing the highest gene dose in known genomes.

Through a comprehensive phylogenetic analysis, researchers proposed that among the 11 DGAT-2s, one gene might originate from the <u>red algae</u> related secondary <u>endosymbiont</u>, four from <u>green algae</u> related <u>endosymbiont</u>, and the other six from the eukaryotic host genome. In addition, a large proportion (15.3%) of <u>TAG</u> biosynthesis related <u>genes</u> were acquired by *Nannochloropsis* via <u>horizontal gene transfer</u> (HGT) from <u>bacteria</u>. Therefore, multiple genome pooling and horizontal genetic exchange, together with selective <u>inheritance</u> of <u>lipid</u> synthesis genes and species-specific gene loss, have led to the enormous genetic apparatus for oleaginousness and the wide genomic divergence among present-day *Nannochloropsis* spp.

Accumulation of oil in nitrogen deprivation

When cultured in normal growth conditions in standard f/2 medium (http://www.ccap.ac.uk/media/docume nts/f2.pdf) supplemented with nitrogen, *Nannochloropsis* cells have an oil content of about 30% of their dry weight. This oil can be used to produce biodiesel. In order to produce biodiesel, the oil content of *Nannochloropsis* cultures must be increased. Fatty acid biosynthesis in N. oceanica was shown to be integrated with the regulation of the cholesterol biosynthetic pathway, suggesting new genetic engineering or chemical biology approaches for enhanced oil production in microalgae. On the other hand, various culturing conditions were observed to increase the average oil content per cell, supporting however only slow growth rates of the cultures (see the related section Nannochloropsis and biofuels), and decreasing the overall productivity. Among these conditions, nitrogen deprivation has been one of the most vastly studied. Studies have examined the behaviour of the cultures in nitrogen stress in various culturing set-ups, as well as the physiological and molecular response of the cells to nitrogen deprivation.

Various <u>strains</u> of *Nannochloropsis* were shown to accumulate up to 60–70% of their overall biomass as <u>lipids</u> in nitrogen limitation. [8][21] In this condition not only the amount of <u>lipids</u> changes, but also the composition. It was observed that <u>triacylglycerols</u> largely increase in nitrogen depletion while other <u>lipids</u>, mainly polar <u>glycerolipids</u>, free <u>fatty acids</u> and <u>diacylglycerols</u>, slightly decrease. The increase in <u>triacylglycerols</u> in nitrogen depletion is much larger than the decrease in the other <u>glycerolipids</u>, supporting the hypothesis that the cells actively synthesise new <u>triacylglycerols</u> rather than just transforming the existing lipids into triacylglycerols. [22]

While <u>triacylglycerols</u> accumulate and lipid droplets enlarge, other important morphological changes take place. The <u>chloroplasts</u> became smaller and the amount of lipids that are characteristic of the <u>photosynthetic membranes</u> decrease significantly. <u>Photosynthetic yield</u> decreases in the nitrogen depleted cells, but it is still sufficient to drive cell survival and growth. If <u>photosynthesis</u> is inhibited indeed, *Nannochloropsis* cells stop growing, indicating that they rely on <u>photosynthetic solar energy conversion</u> and not on stored <u>carbohydrates</u> or <u>lipids</u> as energy source. [22]

Nannochloropsis cultivated in normal growth condition and deprived of a nitrogen source continues growing for 4–5 days. The analysis of <u>gene expression</u> reveals that mechanisms for <u>nitrogen assimilation</u> and redistribution are activated in the cells in nitrogen scarcity and allow survival through a partial reorganisation of the <u>cellular metabolism</u>. The genes responsible for the incorporation of free <u>ammonium</u> into glutamate (L-glutamine + 2-oxoglutarate + NADPH + H⁺ $\leftarrow \rightarrow 2$ L-glutamate + NADP⁺) are up-

regulated . Their up-regulation increases the capability of the cells to assimilate minimal amount of <u>ammonium</u> eventually present in the medium and, more importantly, allows them to assimilate the intracellular ammonium that can be released by degradative processes. <u>Transcriptomic</u> data of nitrogendeprived *Nannochloropsis* cultures show that various <u>enzymes</u> responsible for degradative processes that release ammonium are indeed up regulated. Moreover, the expression of genes coding for proteins involved in controlled degradation of proteins increase, together with others involved in the formation of cytosolic sequestering vesicles used for degradation and recycling of cellular components. [13]

The machinery of gene expression of <u>chloroplast</u> and <u>mitochondrion</u> is down regulated in *Nannochloropsis* in response to nitrogen depletion. 13[14]

Corteggiani Carpinelli and coworkers (2013)^[13] report a complete analysis of the gene expression of *Nannochloropsis* cultures grown in normal conditions and nitrogen deprivation for 3 days and 6 days. Data on similar conditions were also collected by Radakovits et al. (2012)^[14] and Vieler et al. (2012).^[15] The all of this data show that genes involved in fatty acid and triacylglycerol biosynthesis are always abundant in the cells and their expression is not correlated with the amount of oil accumulated. Also the expression of the genes involved in triacylglycerols degradation is not significantly down-regulated as triacylglycerols accumulate. The general conclusion suggested by the experimental data is that *Nannochloropsis* constitutively produces triacylglycerols and that the metabolic reorganisation that follows nitrogen deprivation increases the flux of substrates through this pathway, which is in turn capable to sustain the increased metabolic flux. Corteggiani Carpinelli and coworkers (2013)^[13] advance the hypothesis that, in their experimental conditions, photosynthesis is the main energy source and the down-regulation of the metabolic activity of the mitochondrion is determinant in increasing the amount of substrates that enter the fatty acid biosynthetic pathway. If more precursors are available, more fatty acids are synthesised and as a consequence more triacylglycerols are produced and accumulated into the cells as oil droplets.

Dong et al. (2013)^[23] report a quantification of the abundance of various <u>proteins</u> in cultures of *Nannochloropsis* grown with a supplement of <u>CO2</u> and deprived of nitrogen. Despite the different experimental conditions, also the <u>proteomic</u> study seems to support the hypothesis that the accumulation of <u>triacylglycerols</u> is due to an increase of the metabolic flux through the <u>fatty acid biosynthetic pathway</u>. The authors advance the hypothesis that, in their experimental conditions, the degradation of <u>storage sugars</u> and the up-regulation of glycolysis are responsible for the increase of substrates through the pathway.

More recently Li and coworkers $(2014)^{[24]}$ collected extensive experimental data from cultures of *Nannochloropsis oculata* IMET1 grown in nitrogen sufficient and nitrogen depleted media. According to their analysis it is the <u>catabolism</u> of <u>carbohydrates</u> and <u>proteins</u> together with the <u>up-regulation</u> of genes assigned to various <u>pathways</u> (the cytosolic <u>glycolysis</u> pathway, which produces <u>pyruvate</u>; the PDHC bypass, which yields additional <u>acetyl-CoA</u>; and the coupling of <u>TCA</u> reactions with mitochondrial <u>poxidation</u>) that have to be claimed for increasing the supply of carbon precursors to the <u>fatty acidal biosynthetic pathway</u>. Nevertheless, the authors suggest that it isn't the increased synthesis of <u>fatty acidal biosynthetic pathway</u>. Nevertheless, the authors suggest that it is rather the <u>up-regulation</u> of genes involved in the <u>assembly of triacylglycerols</u> that determines the final oil concentration. In other words, under nitrogen depletion, it is the <u>up-regulation</u> of the <u>transcript</u> level of the key genes in <u>triacylglycerol assembly</u>, rather than those in fatty acids biosynthesis, that leads to accelerated triacylglycerol production.

In 2017, a study jointly funded by ExxonMobil and Synthetic Genomics achieved a breakthrough in lipid percentages in Nannochloropsis gaditana through applications of the CRISPR-Cas9 reverse-genetics pipeline and nitrogen starving—improving partitioning of total carbon to lipids from 20% (wild type) to 40-45% (mutant type). [25]

See also

- Microalgae
- Planktonic algae
- Nannochloropsis and biofuels
- Biofuel
- Sustainable aviation fuel
- Energy content of biofuel

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