Endosymbiosis and chloroplasts

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Abstract. The present work deals with endosymbiosis and the appearance of the chloroplast as an organelle with an important role in the functioning of the plant eukaryotic cell and the biosphere. Endosymbiosis has played a crucial role in the evolution of eukaryotic cells, contributing to the complexity and diversity of life on Earth. The establishment of these symbiotic relationships has led to the emergence of more complex organisms with specialized cellular functions. The endosymbiotic theory proposes that chloroplasts and mitochondria, both organelles with their own genetic material, were once free-living bacteria that were engulfed by ancestral eukaryotic cells. Over time, a symbiotic relationship developed, with the engulfed bacteria evolving into the present-day chloroplasts and mitochondria. Chloroplasts play a central role in the energy metabolism of plants and algae. Through photosynthesis, they convert light energy into chemical energy, producing glucose and oxygen. This process is not only essential for the survival of plants but also has broader ecological implications by sustaining life on Earth through the production of oxygen and the base of the food chain. There is genetic polymorphism among chloroplasts of different plant species. Chloroplasts have their own DNA, which is separate from the nuclear DNA of the plant cell. This chloroplast DNA (cpDNA) is often used in studies of plant evolution and taxonomy because it is maternally inherited and evolves at a slower rate compared to nuclear DNA. While chloroplast DNA can reveal information about the evolutionary history of plants, it represents only a small portion of the overall genetic makeup of a plant. Combining chloroplast DNA data with nuclear DNA data and other molecular markers provides a more comprehensive understanding of plant evolution and diversity.

Key Words: function, organelle, photosynthesis, eukaryotic, plastid, plant cell, glucose.

Introduction. Organic matter began to be born and become abundant on Earth when the first photosynthetic pigments made their appearance. Subsequently, life, in its complexity, evolved, taking over and incorporating this function of photosynthetic pigments. The present work deals with endosymbiosis and the appearance of the chloroplast as an organelle with an important role in the functioning of the plant eukaryotic cell and the biosphere.

Endosymbiosis. Endosymbiosis is a biological phenomenon that involves one organism living inside another in a mutually beneficial relationship. This concept is particularly significant in the context of eukaryotic cells and their organelles, such as mitochondria and chloroplasts. The endosymbiotic theory, proposed by Lynn Margulis in the 1960s, suggests that certain organelles within eukaryotic cells originated as free-living bacteria that were engulfed by a host cell (Sato & Sato 2019). Over time, these engulfed bacteria formed a symbiotic relationship with the host cell, with both parties benefiting from the association. This theory is supported by several lines of evidence, including the structural similarities between certain organelles and free-living bacteria, as well as the presence of a double membrane in mitochondria and chloroplasts, which is characteristic of bacterial cells.

The most well-known example of endosymbiosis is the origin of mitochondria, which are responsible for energy production in eukaryotic cells. It is believed that mitochondria originated from aerobic bacteria that were engulfed by a primitive eukaryotic cell (Roger et al 2017). This endosymbiotic event allowed the host cell to harness the energy produced by the bacteria through aerobic respiration, providing a significant advantage in terms of ATP production (Sato 2020).

Similarly, chloroplasts, the organelles responsible for photosynthesis in plant cells, are thought to have originated from photosynthetic bacteria that were engulfed by a eukaryotic cell. This endosymbiotic event allowed the host cell to utilize sunlight to produce energy through photosynthesis (Sato 2020).

Endosymbiosis has played a crucial role in the evolution of eukaryotic cells, contributing to the complexity and diversity of life on Earth (Gabaldón 2021). The establishment of these symbiotic relationships has led to the emergence of more complex organisms with specialized cellular functions.

Chloroplasts. The chloroplast is a double-membraned organelle found in plant cells and some algae, containing chlorophyll pigments that capture light energy for photosynthesis, the process by which plants convert light into chemical energy to produce their own food.

Function. Chloroplasts are responsible for conducting photosynthesis, a process that converts light energy into chemical energy in the form of glucose. The physiological and biochemical functions of chloroplasts are intricately tied to this crucial process. We will present further the main functions of chloroplasts.

Photosynthesis. The primary function of chloroplasts is to carry out photosynthesis, a complex series of biochemical reactions that use light energy to synthesize organic compounds from carbon dioxide and water. Chlorophyll, a green pigment present in chloroplasts, absorbs light energy and initiates the conversion of carbon dioxide and water into glucose and oxygen. This process is essential for the production of organic molecules that serve as energy sources for the plant and other organisms in the food chain.

Light absorption and pigment synthesis. Chloroplasts contain various pigments, including chlorophyll a and b, carotenoids, and xanthophylls (Ashenafi et al 2023). These pigments are involved in capturing different wavelengths of light during photosynthesis. The absorption of light by chlorophyll molecules initiates the energy conversion process, while other pigments help broaden the range of light absorption and protect the chloroplasts from excessive light damage.

Thylakoid membrane functions. Chloroplasts have an inner membrane system called thylakoids, which are organized into stacks known as grana. The thylakoid membranes house the pigments involved in the light-dependent reactions of photosynthesis. These reactions generate ATP (adenosine triphosphate) and NADPH (nicotinamide adenine dinucleotide phosphate), which are crucial energy carriers used in the subsequent dark reactions (Calvin cycle) to produce glucose (Anderson 1986; Staehelin & van der Staay 1996).

Starch synthesis. During times of excess glucose production (e.g., in the presence of abundant light), chloroplasts may convert some of the glucose into starch for storage. Starch serves as a reserve carbohydrate that can be mobilized when the plant requires additional energy (Nomura et al 1967).

Production of oxygen. In the process of photosynthesis, oxygen is produced as a byproduct when water molecules are split during the light-dependent reactions (Hill & Scarisbrick 1940). This oxygen is released into the atmosphere, contributing to the oxygen content of our planet.

Own DNA. Chloroplasts have their own DNA, separate from the nuclear DNA of the plant cell (Kang et al 2021). This characteristic is a remnant of the evolutionary origin of chloroplasts, which are believed to have originated from free-living cyanobacteria through a process called endosymbiosis.

The endosymbiotic theory proposes that chloroplasts and mitochondria, both organelles with their own genetic material, were once free-living bacteria that were engulfed by ancestral eukaryotic cells. Over time, a symbiotic relationship developed, with the engulfed bacteria evolving into the present-day chloroplasts and mitochondria.

The DNA in chloroplasts is typically a circular, double-stranded molecule, similar to bacterial DNA (Dobrogojski et al 2020; Kang et al 2021). It encodes a number of essential genes involved in the chloroplast's functions, including those related to photosynthesis. However, chloroplasts do not have the complete set of genes needed for their own maintenance and function; they rely on the host cell's nuclear DNA for the synthesis of many proteins and other components (Dobrogojski et al 2020; Kang et al 2021).

In most plants, chloroplast DNA is maternally inherited, meaning it is passed down from the mother plant to the offspring (Gastony & Yatskievych 1992). The presence of DNA in chloroplasts provides evidence supporting the endosymbiotic theory and reflects the evolutionary history of these organelles.

Chloroplasts are polymorphic. There is genetic polymorphism among chloroplasts of different plant species. Chloroplasts have their own DNA, which is separate from the nuclear DNA of the plant cell (Kang et al 2021). This chloroplast DNA (cpDNA) is often used in studies of plant evolution and taxonomy because it is maternally inherited and evolves at a slower rate compared to nuclear DNA (Gui et al 2020).

The genetic polymorphism in chloroplasts arises from variations in the sequence of nucleotides in the chloroplast genome (Gui et al 2020). These variations can include single nucleotide polymorphisms (SNPs), insertions, deletions, and other types of genetic changes (Abdullah et al 2021).

Researchers use chloroplast DNA markers to study the relationships between different plant species, populations, and individuals. Comparing the chloroplast DNA sequences allows scientists to infer evolutionary relationships, trace migration patterns, and understand the genetic diversity within and among plant populations (Li et al 2020).

Chloroplast DNA polymorphism is often employed in phylogenetic studies to reconstruct the evolutionary history of plant species. It can provide insights into the divergence and relationships between different plant taxa (Li et al 2020). The information derived from chloroplast DNA analysis is particularly valuable in plant systematics, conservation biology, and population genetics (Li et al 2020; Abdullah et al 2021).

While chloroplast DNA can reveal information about the evolutionary history of plants, it represents only a small portion of the overall genetic makeup of a plant. Combining chloroplast DNA data with nuclear DNA data and other molecular markers provides a more comprehensive understanding of plant evolution and diversity (Mu et al 2020).

From inorganic to organic. The transformation of inorganic matter into organic matter on Earth primarily occurs through the process of photosynthesis, which is carried out by certain autotrophic organisms, particularly plants, algae, and some bacteria. We describe further a brief overview of how this transformation takes place.

Light absorption. Photosynthesis begins with the absorption of sunlight by pigments, primarily chlorophyll, located in the chloroplasts of plant cells and certain types of bacteria. These pigments are capable of capturing light energy.

Water uptake and splitting. In the light-dependent reactions of photosynthesis, water molecules are taken up by the plant or algal cells (Renger 2012). The energy from sunlight is used to split water molecules into oxygen, hydrogen ions (protons), and electrons. This process is known as photolysis.

$$2H_2O + 4\text{photons} \rightarrow 4H^+ + 4e^- + O_2$$

ATP and NADPH production. The electrons and protons generated during the photolysis process are used to produce ATP (adenosine triphosphate) and NADPH (nicotinamide adenine dinucleotide phosphate) in the thylakoid membranes of the chloroplasts. These molecules serve as energy carriers for the subsequent steps of photosynthesis (Noctor & Foyer 1998).

Carbon dioxide fixation. In the light-independent reactions (Calvin cycle) of photosynthesis, carbon dioxide (CO_2) from the atmosphere is captured and fixed into organic molecules. This process is facilitated by the enzyme ribulose-1,5-bisphosphate carboxylase/oxygenase (RuBisCO). The carbon fixation results in the formation of three-carbon compounds, which are then used to synthesize sugars and other organic molecules (Iñiguez et al 2021).

$$3CO_2 + 9ATP + 6N\ ADPH + 6H^+ \rightarrow C_3H_6O_3(sugar) + 9ADP + 8Pi + 6N\ ADP^+$$

Sugar synthesis. The three-carbon compounds produced in the Calvin cycle are used to synthesize sugars (such as glucose) and other organic compounds. These sugars serve as the primary source of energy for the plant or alga and can also be used for growth and storage (Van Dingenen e al 2016). The overall chemical equation for photosynthesis is:

$$6CO_2 + 6H_2O + \text{light energy} \rightarrow C_6H_{12}O_6 + 6O_2$$

This equation illustrates how inorganic carbon dioxide and water are converted into organic glucose and oxygen in the presence of light energy.

Photosynthesis is the key process by which inorganic matter (carbon dioxide and water) is transformed into organic matter (sugars and other organic compounds) by capturing and utilizing light energy. This process is fundamental to the energy flow in ecosystems and sustains life on Earth by providing the foundation of the food chain.

Conclusions. Endosymbiosis has played a crucial role in the evolution of eukaryotic cells, contributing to the complexity and diversity of life on Earth. The establishment of these symbiotic relationships has led to the emergence of more complex organisms with specialized cellular functions. The endosymbiotic theory proposes that chloroplasts and mitochondria, both organelles with their own genetic material, were once free-living bacteria that were engulfed by ancestral eukaryotic cells. Over time, a symbiotic relationship developed, with the engulfed bacteria evolving into the present-day chloroplasts and mitochondria. Chloroplasts play a central role in the energy metabolism of plants and algae. Through photosynthesis, they convert light energy into chemical energy, producing glucose and oxygen. This process is not only essential for the survival of plants but also has broader ecological implications by sustaining life on Earth through the production of oxygen and the base of the food chain. There is genetic polymorphism among chloroplasts of different plant species. Chloroplasts have their own DNA, which is separate from the nuclear DNA of the plant cell. This chloroplast DNA (cpDNA) is often used in studies of plant evolution and taxonomy because it is maternally inherited and evolves at a slower rate compared to nuclear DNA. While chloroplast DNA can reveal information about the evolutionary history of plants, it represents only a small portion of the overall genetic makeup of a plant. Combining chloroplast DNA data with nuclear DNA data and other molecular markers provides a more comprehensive understanding of plant evolution and diversity.

Conflict of interest. The authors declare no conflict of interest.

References

Abdullah, Mehmood F., Shahzadi I., Ali Z., Islam M., Naeem M., Mirza B., Lockhart P. J., Ahmed I., Waheed M. T., 2021 Correlations among oligonucleotide repeats, nucleotide substitutions, and insertion-deletion mutations in chloroplast genomes of plant family Malvaceae. Journal of Systematics and Evolution 59(2):388-402.

Anderson J. M., 1986 Photoregulation of the composition, function, and structure of thylakoid membranes. Annual Review of Plant Physiology 37(1):93-136.

Ashenafi E. L., Nyman M. C., Shelley J. T., Mattson N. S., 2023 Spectral properties and stability of selected carotenoid and chlorophyll compounds in different solvent systems. Food Chemistry Advances 2:100178.

Dobrogojski J., Adamiec M., Luciński R., 2020 The chloroplast genome: a review. Acta Physiologiae Plantarum 42:1-13.

Gabaldón T., 2021 Origin and early evolution of the eukaryotic cell. Annual Review of Microbiology 75:631-647.
Gastony G. J., Yatskievych G., 1992 Maternal inheritance of the chloroplast and mitochondrial genomes in cheilanthoid ferns. American Journal of Botany 79(6):716-722.
Gui L., Jiang S., Xie D., Yu L., Huang Y., Zhang Z., Liu Y., 2020 Analysis of complete chloroplast genomes of Curcuma and the contribution to phylogeny and adaptive evolution. Gene 732:144355.
Hill R., Scarisbrick R., 1940 Production of oxygen by illuminated chloroplasts. Nature 146(3689):61-62.
Iñiguez C., Aguiló-Nicolau P., Galmés J., 2021 Improving photosynthesis through the enhancement of Rubisco carboxylation capacity. Biochemical Society Transactions 49(5):2007-2019.
Kang B. C., Bae S. J., Lee S., Lee J. S., Kim A., Lee H., Baek G., Seo H., Kim J., Kim J. S., 2021 Chloroplast and mitochondrial DNA editing in plants. Nature Plants 7(7):899-905.
Li D. M., Ye Y. J., Xu Y. C., Liu J. M., Zhu G. F., 2020 Complete chloroplast genomes of *Zingiber montanum* and *Zingiber zerumbet*: Genome structure, comparative and phylogenetic analyses. PLoS One 15(7):e0236590.
Mu X. Y., Tong L., Sun M., Zhu Y. X., Wen J., Lin Q. W., Liu B., 2020 Phylogeny and divergence time estimation of the walnut family (Juglandaceae) based on nuclear RAD-Seq and chloroplast genome data. Molecular Phylogenetics and Evolution 147:106802.
Noctor G., Foyer C. H., 1998 A re-evaluation of the ATP: NADPH budget during C3 photosynthesis: a contribution from nitrate assimilation and its associated respiratory activity? Journal of Experimental Botany 49(329):1895-1908.
Nomura T., Nakayama N., Murata T., Akazawa T., 1967 Biosynthesis of starch in chloroplasts. Plant Physiology 42(3):327-332.
Renger G., 2012 Photosynthetic water splitting: Apparatus and mechanism. In: Photosynthesis. Advances in photosynthesis and respiration. Eaton-Rye J., Tripathy B., Sharkey T. (eds), vol 34, Springer, Dordrecht, https://doi.org/10.1007/978-94-007-1579-0_17
Roger A. J., Muñoz-Gómez S. A., Kamikawa R., 2017 The origin and diversification of mitochondria. Current Biology 27(21):R1177-R1192.
Sato N., 2020 Endosymbiotic theories of organelles revisited: retrospects and prospects. Springer Nature.
Sato N., Sato N., 2019 Re-evaluation of the initial ideas of Lynn Margulis. Endosymbiotic Theories of Organelles Revisited: Retrospects and Prospects, pp. 45-72.
Staehelin L. A., van der Staay G. W. M., 1996 Structure, composition, functional organization and dynamic properties of thylakoid membranes. In: Oxygenic photosynthesis: The light reactions. Ort D. R., Yocum C. F., Heichel I. F. (eds), Advances in Photosynthesis and Respiration, vol 4, Springer, Dordrecht, https://doi.org/10.1007/0-306-48127-8_2
Van Dingenen J., De Milde L., Vermeersch M., Maleux K., De Rycke R., De Bruyne M., Storme V., Gonzalez N., Dhondt S., Inze D., 2016 Chloroplasts are central players in sugar-induced leaf growth. Plant Physiology 171(1):590-605.

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