Minireview

The chloroplast genes encoding subunits of the H+-ATP synthase

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Abstract. Three C_{F1} and three C_{F0} subunits of the chloroplast H+-ATP synthase are encoded on the chloroplast genome. The chloroplast atp genes are organized as two operons in plants but not in the green alga, Chlamydomonas reinhardtii. The atpBE or \( \alpha \) operon shows a relatively simple organisation and transcription pattern, while the atpHFA or \( \beta \) operon is transcribed into a large variety of mRNAs. The atp genes are related to those of cyanobacteria and, more distantly, to those of non-photosynthetic bacteria such as \( E. coli \), suggesting a common origin of most \( F_{t}F_{0} \) ATP synthase subunits. Both the chloroplast and cyanobacterial ATP synthases have four \( F_{0} \) subunits, not three as in the \( E. coli \) complex. The proton pore of the \( CF_{0} \) is proposed to be formed by the interaction of subunits III and IV.

1. Introduction

H+-ATP synthase is essential for electron transport and photophosphorylation during photosynthesis. It has an \( F_{t}F_{0} \) structure analogous to the proton-translocating ATP synthases of bacteria and mitochondria, that is, a hydrophobic sector (\( CF_{0} \)) within the thylakoid membrane and a hydrophilic moiety (\( CF_{1} \)) protruding into the stroma. The complex couples the phosphorylation of ADP with the transmembrane proton gradient generated during light-driven electron transport. The catalytic site for ATP synthesis is located on the CF_{1} portion while the CF_{0} subunits act as a proton channel for translocation of protons across the thylakoid membrane. A number of authors have reviewed the structure and function of the chloroplast ATP synthase complex and its subunits over recent years (Shavit 1980, Nelson 1981, Strotmann and Bickel-Sandkötter 1984, Merchant and Selman 1985).

Like other multimeric complexes of the chloroplast thylakoids, the ATP synthase is the product of the two genetic systems. Some subunits are encoded and synthesised in the chloroplast, while the remainder are encoded
in the nucleus, synthesised in the cytosol and transported into the organelle (Herrmann et al. 1985). This review covers the organisation, expression and evolution of the chloroplast atp genes encoding six subunits of the ATP synthase.

2. E. coli ATP synthase

Before discussing the chloroplast ATP synthase and atp genes, it is necessary to first briefly examine the ATP synthase of E. coli because of the wealth of genetic, biochemical and molecular data on this complex (Futai and Kanazawa 1980, Cross 1981, Dunn and Heppel 1981, Fillingame 1981, Senior and Wise 1983, Hoppe and Sebald 1984). Although there are fundamental differences between chloroplasts and E. coli in the mechanism by which the enzymes are regulated, in particular with respect to light activation of CF1CF0, they appear to be very similar in structure and catalytic mechanism.

E. coli F1F0 is composed of eight different types of polypeptides, five in the F1 factor (α, β, γ, δ, and ε) and three in F0 (α1, β2, and c6-10), with the stoichiometry believed to be as indicated (Foster and Fillingame 1982, Hoppe and Sebald 1984). The subunits are encoded by the unc or atp operon, and the DNA sequence of this region has been completely determined (Kanazawa and Futai 1982, Walker et al. 1984). The operon carries a single gene for each subunit, with the order of genes encoding subunits as follows: uncI, a, c, b, δ, α, γ, β, ε where the first gene (uncI or atpl) encodes a polypeptide of unknown function. Thus the genes for the F0 and F1 subunits are clustered respectively at the 5' and 3' ends of the operon.

The operon is transcribed off a single promotor upstream of uncI although a second weak promotor may exist within the uncI gene (Walker et al. 1984). Mechanisms involving differential translation initiation or elongation have been proposed to account for the different subunit stoichiometries required in the complex (Walker et al. 1984). Proof of translational control has been obtained by identification of a sequence involved in enhancement of translation initiation of the gene for subunit c (McCarthy et al. 1985). Conflicting data exist on the assembly pathway of the complex, in particular whether the F0 and F1 sectors can assemble independently or not (Cox et al. 1981, Aris et al. 1985).

The functions of the individual subunits, particularly those of F1, have been intensively studied (Futai and Kanazawa 1980, Dunn and Heppel 1981, Senior and Wise 1983, Walker et al. 1984). The α and β subunits carry the binding sites for adenine nucleotides, and with the γ subunit form the...