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Coupling Proton Movement to ATP Synthesis in the Chloroplast ATP Synthase

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The chloroplast F_0F_1-ATP synthase-ATPase is a tiny rotary motor responsible for coupling ATP synthesis and hydrolysis to the light-driven electrochemical proton gradient. Reversible oxidation/reduction of a dithiol, located within a special regulatory domain of the γ subunit of the chloroplast F_1 enzyme, switches the enzyme between an inactive and an active state. This regulatory mechanism is unique to the ATP synthases of higher plants and its physiological significance lies in preventing nonproductive depletion of essential ATP pools in the dark. The three-dimensional structure of the chloroplast F_1 gamma subunit has not yet been solved. To examine the mechanism of dithiol regulation, a model of the chloroplast gamma subunit was obtained through segmental homology modeling based on the known structures of the mitochondrial and bacterial γ subunits, together with *de novo* construction of the unknown regulatory domain. The model has provided considerable insight into how the dithiol might modulate catalytic function. This has, in turn, suggested a mechanism by which rotation of subunits in F_0, the transmembrane proton channel portion of the enzyme, can be coupled, via the ε subunit, to rotation of the γ subunit of F_1 to achieve the 120° (or 90° + 30°) stepping action that is characteristic of F_1 γ subunit rotation.

KEY WORDS: Chloroplast F_0F_1 ATP synthase; dithiol regulation.

INTRODUCTION

The chloroplast ATP synthase is comprised of two physically separable parts, F_0 (coupling factor 0) which is an integral membrane-spanning proton channel, and F_1 (coupling factor 1) which is peripheral to the membrane and contains the catalytic site(s) for reversible ATP synthesis. The F_0 portion of the enzyme (CF_0) has four different subunit types, labeled I, II, III and IV, whereas chloroplast F_1 (CF_1) has five different subunit types labeled α to ε in order of decreasing molecular weight. The subunit stoichiometry is $I_1II_1III_{14}$ $IV_1\alpha_3\beta_3\gamma_1\delta_1\varepsilon_1$ (Richter, 2004).

Chloroplast F_1, like its mitochondrial and bacterial counterparts, is a tiny rotary motor that couples ATP hydrolysis to generate enough torque to drive rotation of large (1–2 μm) actin filaments (Sabert *et al*., 1996; Hisabori *et al*., 1999; Tucker *et al*., 2004; Noji *et al*., 1997; Yasuda *et al*., 2001; Mitome *et al*., 2004; Duncan *et al*., 1995; Soong *et al*., 2000; Tsunoda *et al*., 2000; Sambongi *et al*., 2000). The prevailing model for the structural organization of the CF_0F_1 complex is shown in Fig. 1. Subunits δ, II and IV together form a peripheral stalk which binds F_0 to F_1. This stalk is considered to act as a "stator" holding the α, β and I subunits still while the γ, ε and III subunits rotate. The ε subunit, and part of the γ subunit, together form a second, central stalk connected to the ring of *c* subunits. There are six nucleotide binding sites, one at each of the $\alpha\beta$ subunit interfaces about halfway along the vertical axis of the hexamer. Three of the sites are located primarily on the β subunits and are catalytic,

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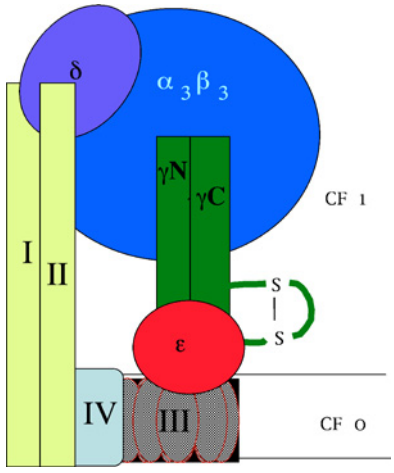

Fig. 1. Proposed structural organization of the chloroplast F_0F_1 ATP synthase. N- and C-terminal helices of the γ subunit extend into the $\alpha_3\beta_3$ hexamer and, together with the ε subunit, act as a rotating spindle.

the other three are noncatalytic and probably regulatory. The three-dimensional structure of the $\alpha_3\beta_3$ hexamer has been solved to a resolution of 3.2 Å(Groth and Pohl, 2000).

Rotation of the γ subunit is driven in one direction by hydrolysis of ATP at the three catalytic sites. Rotation in the reverse direction is assumed to result from protons binding to acidic groups on the membrane-spanning III subunits, causing them to rotate unidirectionally with respect to subunits I, II and IV within the membrane. Rotation of the ring of III subunits in turn causes rotation of the γ subunit which imparts structural asymmetry to the catalytic sites in the F_1 moiety leading to binding and release of nucleotides at the catalytic sites (Oster and Wang, 2000). The ε subunit links the γ subunit to the subunit III ring (Schulenbrg *et al*., 1997; Capaldi and Schulenberg, 2000) to form the "drive shaft" of the motor. There are 14 subunit III monomers in the ring (Muller *et al*., 2001; Seelert *et al*., 2000) each with a critical acidic residue that is involved in proton transport. It is thought that each time a subunit III monomer is protonated the whole ring of III subunits advances through a small rotational step of $\sim 26^\circ$ (Oster and Wang, 2000). In contrast, the γ subunits appear to rotate in discrete 120° steps with possible 90° and 30° substeps (Yasuda *et al*., 2001; Hasler *et al*., 1998; Adachi *et al*., 2000). To couple the two rotating parts, the γ and ε subunits would be required to absorb several incremental rotational steps in the subunit III ring before contacts between $\gamma\varepsilon$ and the $\alpha_3\beta_3$ hexamer are released and the $\gamma\varepsilon$ drive-shaft rotates through a 120° step. A possible mechanism for achieving this energy transduction step is described in this report.

The γ and ε Subunits Regulate the Activity of the Chloroplast ATP Synthase

The chloroplast ATP synthase is unique among the ATP synthases in that it is a fully latent ATPase, requiring some form of activation for expression of significant rates of ATP hydrolysis. Activation of CF_1 that has been isolated from dark-adapted membranes can be achieved artificially in two ways: (a) reduction of a disulfide bond formed between Cys199 and Cys205 in the γ subunit, the only disulfide bond in the entire enzyme, using thiol reducing agents such as dithiothreitol (Arana and Vallejos, 1982; McCarty and Nalin, 1986); or (b) removal of the inhibitory ε subunit (Richter *et al*., 1984, 1985). These two activation mechanisms are interrelated. Reduction of the γ dithiol decreases the affinity of CF_1 for the ε subunit by more than twenty-fold (Soteropoulos *et al*., 1994). On the other hand, removal of ε from CF_1 significantly enhances the accessibility of the region containing the γ dithiol to thiol reagents and proteases (Richter *et al*., 1985; Moroney and McCarty, 1982; Schumann *et al*., 1985). The activations resulting from reduction of the γ dithiol and from ε removal are additive (Richter and McCarty, 1987a). Activation of the latent ATPase activity of CF_1 on the membrane is also achieved by reducing the γ dithiol either artificially by dithiothreitol, or under physiological conditions by the enzyme thioredoxin (Mills and Mitchell, 1982; Pick, 1983; Dann and McCarty, 1992). Efficient reduction of the γ disulfide of CF_0F_1, as well as induction and maintenance of the activated state of the enzyme, require the presence of a small transmembrane potential ($\Delta\mu H^+$) (Ketcham *et al*., 1984; Andreo *et al*., 1980; Ort and Oxborough, 1992).

The regulatory γ dithiol is unique to higher plants and is located in an extra domain (the dithiol domain) that is present only in the γ subunit of CF_1 from higher plants. This domain is comprised of approximately 40 amino acids (196 to 242) and is highly conserved among plant species (Richter, 2004). The dithiol domain in the chloroplast F_1 has apparently evolved to provide an effective mechanism of switching the enzyme "on" and "off" via the reduction and oxidation respectively of the critically-placed dithiol.

The switch of the enzyme from the inactive to the active state results in a change in the conformation of the ε subunit. This change was first detected using polyclonal antibodies raised against the isolated ε subunit (Richter and McCarty, 1987). With purified CF_1, the antibodies strip off the ε subunit and activate the ATPase activity. On the membrane, however, the antibodies are unable to reach their target sites on ε until the membranes are supplied with a light-induced $\Delta\mu H^+$. The light-driven

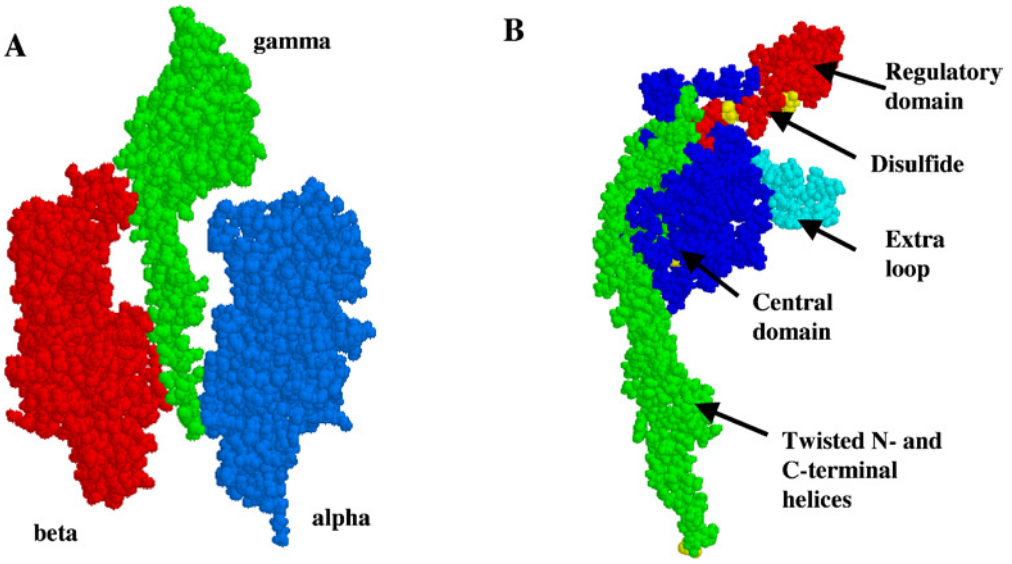

Fig. 2. Homology model of the γ subunit of CF_1. (A). cross-section through the mitochondrial F_1 (Menz *et al*., 2000) showing the γ subunit in green. (B). Homology model of the CF_1 γ subunit indicating the regulatory domain (*red*) containing the dithiol cysteines (*yellow*), the extra loop (*cyan*) and the central domain (*blue*).

shift in ε conformation exposes it to the antibodies which bind and remove it from the membranes. The resulting ε-less CF_0F_1 actively hydrolyzes ATP but the membranes are uncoupled and unable to synthesize ATP. Addition of fresh ε to the antibody-treated membranes reverses these effects. It was thus proposed that the ε subunit oscillates between two (at least) bound conformational states either as part of an activation/inactivation mechanism and/or as part of the catalytic cycle (Richter and Gao, 1996).

Published structures of the mitochondrial (Menz *et al*., 2001; Gibbons *et al*., 2000) and bacterial (Uhlin *et al*., 1997; Wilkens and Capaldi, 1998, Hausrath *et al*., 1999; Rodgers and Wilco, 2000) F_1 γ and ε subunits have identified two potential conformational states of the ε subunit. The structures of the γ subunits are very similar to each other, both are comprised of very long N- and C-terminal α helices that extend through the center of the $\alpha_3\beta_3$ hexamer plus a third compact globular domain that connects the N- and C-terminal helices, located on the outside of the $\alpha_3\beta_3$ hexamer as indicated in the cross-section of the mitochondrial F_1 shown in Fig. 2. The mitochondrial and *E. coli* ε subunits are also very similar in their tertiary structures, having two domains, an N-terminal β barrel and a helix-turn-helix C-terminus. The position of the ε subunit, however, is markedly different in the two structures. In the *E. coli* complex the central axis of the β barrel of ε is roughly parallel to the N- and C-terminal helices of the γ subunit. The C-terminal helices of the ε subunit are wound around the γ subunit, extending upwards where they would be expected to come in contact with the base of the $\alpha_3\beta_3$ hexamer. In stark contrast, in the mitochondrial complex the central axis of the β barrel of ε is roughly perpendicular to the N- and C-terminal helices of the γ subunit and the C-terminal helices of the ε subunit are flattened against the side of the β barrel, about 40 Å away from the base of the $\alpha_3\beta_3$ hexamer. It has been suggested that the different conformations represent two different states between which the ε subunit oscillates, acting as a "ratchet," limiting the reverse reaction of ATP hydrolysis under conditions in which the transmembrane potential is limiting (Tsunoda *et al*., 2001). Cross-linking studies in the *E. coli* F_1 have provided evidence for this mechanism (Schulenberg *et al*., 1997; Tsunoda *et al*., 2001; Bulygin *et al*., 2004).

Fluorescence distance mapping studies (Richter *et al*., 1985) indicated that the CF_1 ε subunit is located at the base of the $\alpha_3\beta_3$ hexamer, sandwiched between the catalytic subunits and the membrane and in close association with the γ subunit. It thus occupies a position similar to that found in the *E. coli* and mitochiondrial enzymes. The conformational change that occurs in the ε subunit upon reduction of the γ dithiol and generation of a transmembrane potential (Richter and McCarty, 1987; Komatsu-Takaki, 1992; Johnson and McCarty, 2002)

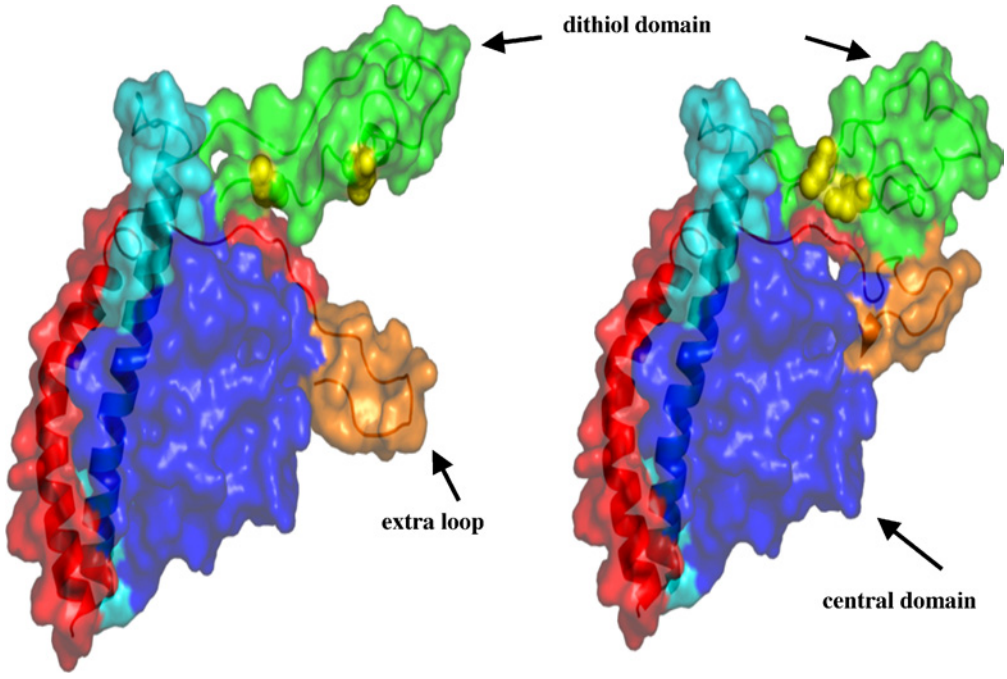

Fig. 3. Modeled structure of the CF_1 γ segment protruding from the $\alpha_3\beta_3$ hexamer shown with the dithiol domain (green) in the open and closed configurations. The C-terminal helix is colored cyan, the N-terminal helix is colored red. The dithiol cysteines are colored yellow.

indicate that it also may ratchet between similar conformational states during ATP synthesis.

A Homology Model of the Chloroplast γ Subunit Suggests a Mechanism for Dithiol Regulation

A possible explanation of how the redox state of the dithiol modulates catalytic function at such a large distance from the catalytic sites was recently proposed (Richter, 2004) wherein it was suggested that dithiol oxidation restricts a relative inter-domain movement within the γ subunit that is an essential step in the catalytic cycle. To examine which domains of the γ subunit may be involved in this process we have constructed a homology model of the CF_1 γ subunit based on its sequence homology with the mitochondrial and bacterial γ subunits. The overall structures of the smaller subunits of F_0F_1 complexes from different sources, although exhibiting low direct sequence homology, are expected to be very similar, especially in view of their critical roles in coupling proton movement to ATP synthesis and hydrolysis. Indeed, a high degree of structural conservation was confirmed by the striking similarities of the three-dimensional structures of the mitochondrial and bacterial subunits (Menz *et al*., 2001; Gibbons *et al*., 2000; Uhlin *et al*., 1997; Wilkens and Capaldi, 1998; Hausrath *et al*., 1999; Rodgers and Wilco, 2000).

The program MODELLER was used to create three-dimensional models of five segments of γ, 1–61; 83–107; 112–160; 163–196 and 242–322. The program CHARMM was used to generate the remaining four loops *de novo*. The final model, shown in Fig. 2 (*right*), was energy minimized using CHARMM and the results indicated a reasonable fit to the homologous structures. For comparison, the structure of the γ subunit in a cross-section of the mitochondrial F_1 is shown in Fig. 2 (*left*). Apart from two segments, the dithiol domain (*colored red*) and a short extra loop near the N-terminus (*colored cyan*) that are unique to the chloroplast γ subunit, the final model deviated little from the homologous mitochondrial subunit structure as expected. The γ model suggests that the regulatory domain of CF_1 γ (*colored green*) is connected to the main central domain by a flexible hinge region near one end of the twisted helical pair formed by the N- and C-terminal helical elements of γ (colored red and cyan).

Dynamic simulations of the γ structure, using a combination of CHARMM and the Replica Exchange components of the Multiscale Modeling Tools for Structure Biology (MMTSB), suggested that the dithiol domain may adopt a range of conformations. The two structures shown in Fig. 3 were chosen from the approximately

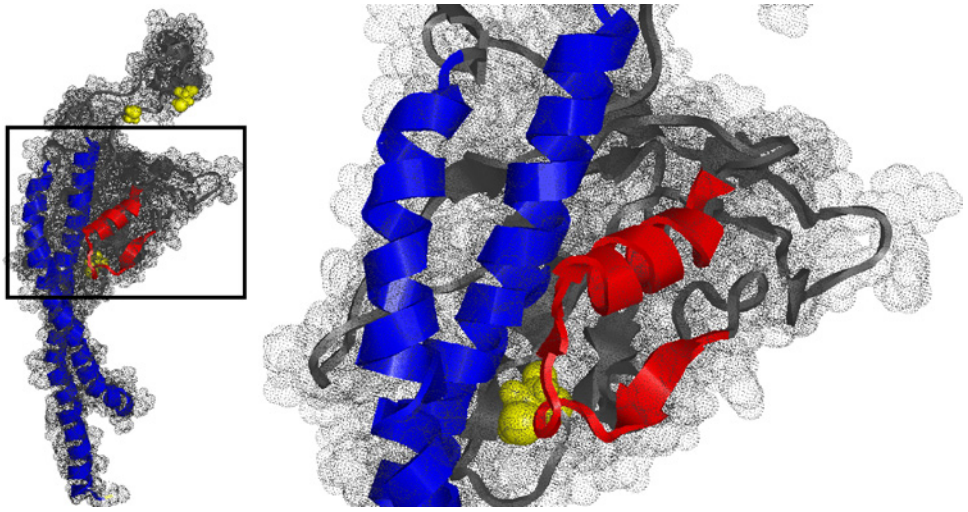

Fig. 4. Location of Cys89 in the CF_1 γ subunit. Left: Cys89 is located in the central domain of γ shown in the boxed segment; Right: Expanded view of the central domain showing Cys89 (*space-filled in yellow*) sandwiched between the central domain of γ and the twisted helical pair formed by the N- and C-terminal helices.

10,000 simulated structures because they were those in which the dithiol sulfhydryls were found to be either furthest apart or closest together. The model implies that dithiol oxidation induces the domain to assume a more compact structure that is accompanied by a downward or closing motion bringing it into close association with the central domain of γ, in particular with the short extra loop (colored brown) that is also unique to the chloroplast enzyme and is an extension of the N-terminal helical element. A change from a less ordered to a more ordered, rigid structure upon dithiol oxidation would explain why the γ subunit exhibits a shift in apparent molecular weight during gel electrophoresis following dithiol oxidation (Ketcham *et al*., 1984).

The position of the γ dithiol domain in the modeled structure, when considered together with known effects of dithiol reduction and oxidation, suggests that closing this domain blocks or impedes a relative movement of domains within the γ subunit that is required for catalysis. A hint as to which parts of γ move relative to each other is indicated by the location of cysteine 89 in the modeled γ structure as highlighted in Fig. 4. Cys89 is buried within the CF_0F_1 complex but becomes exposed to the medium following generation of a light-driven $\Delta\mu H^+$ (Dann and McCarty, 1992; Ketcham *et al*., 1984; Andreo *et al*., 1980; Moroney *et al*., 1984). This could be achieved by partial rotation of the twisted helical pair that is formed by the N- and C-termini (shown in blue in Fig. 4) relative to the central domain (shown in red and gray). The fact that blocking such a movement inhibits catalysis suggests that it is an essential step in the catalytic cycle as suggested previously (Richter, 2004). This intriguing possibility has far reaching implications for the mechanism of proton-coupled catalysis. First, it implies that a partial domain rotation within the γ subunit is an essential step in the rotational process. Secondly, it provides a plausible explanation of how rotational strain that is generated by proton-driven rotation of the ring of Subunit III molecules within the CF_0 segment may be absorbed within the γ subunit during the coupling process. That is, rotation of the γ subunit through 120° may be a two-step process involving partial rotation of domains within the γ subunit.

To test the structural requirements for regulation by the dithiol domain, several mutant γ subunits have been constructed and assembled with the native $\alpha_3\beta_3$ hexamer isolated from CF_1 as described elsewhere (Gao *et al*., 1995). The mutations included deletion of different parts of the dithiol domain including a mutation in which the entire domain between residues 197 and 240 was deleted. All of the mutants exhibited normal catalytic activity with the exception that none responded to thiol oxidizing or reducing conditions. As expected, therefore, the dithiol domain is only required for regulation and not for normal catalytic function. In another mutation, glycine at position 196 in the γ subunit was substituted for valine. The modeled structure suggests that Gly196 may act as a hinge residue about which the dithiol domain moves up-and-down. In support of this function, and of the structural model, substitution of this residue with the bulkier side chain of valine also abolished the redox regulation of catalysis (unpublished experiments).

The C-Terminus of the ε Subunit may Act by Blocking Inter-Domain Movement within the γ Subunit

A number of studies (Cruz *et al*., 1995; Dong *et al*., 2005; Nowak *et al*., 2002; Nowak and McCarty, 2004; Konno *et al*., 2004; Shi *et al*., 2001) have examined the structural requirements for the coupling and inhibitory functions of the ε subunit in the chloroplast and bacterial F_0F_1 complexes. The last 45 C-terminal amino acids of the chloroplast ε subunit are not necessary for coupling the $\Delta\mu H$ to ATP synthesis but are required for inhibition of the unwanted ATP hydrolysis (Cruz *et al*., 1995; Dong *et al*., 2005; Nowak and McCarty, 2004). In contrast, removal of as few as five residues from the N-terminus results in loss of both functions (Shi *et al*., 2001). It thus appears that the C-terminal domain is specifically involved in blocking ATP hydrolysis. Studies of amino acid accessibility (Komatsu-Takaki, 1992) and antibody interactions (Richter and McCarty, 1987; Johnson and McCarty, 2002) have shown that the C-terminus of ε moves in response to membrane energization. Epsilon cross-linking in CF_1 (Schulenberg *et al*., 1997) and bacterial F_1 (Tsunoda *et al*., 2001; Bulygin *et al*., 2004) and single molecule fluorescence (Diez *et al*., 2004) studies in the bacterial enzyme have indicated that the ε subunit remains tightly associated with F_1 during ATP synthesis, indicating that ε movement is localized to specific interactions within the complex and that ε does not dissociate during activation and catalysis. Assuming that the CF_1 ε occupies a similar conformation to that of the *E. coli* ε subunit (Richter, 2004; Ort and Oxborough, 1992), then its β-barrel domain would bind to the twisted helical element of the γ subunit on the side opposite to that of the dithiol domain where it would also form a close interaction with the ring of Subunit III molecules in the F_0 segment. This orientation is supported by fluorescence distance measurements (Richter *et al*., 1985). Again by analogy to the *E. coli* ε the C-terminal helical arm of CF_1 ε would wrap around the regulatory and central domains of the γ subunit reaching up towards the $\alpha_3\beta_3$ ring. Thus the C-terminal arm would provide stability to the closed conformational state of the γ regulatory domain, keeping the enzyme in a latent, inactive state. The C-terminus of ε may also interact with the $\alpha_3\beta_3$ hexamer to provide additional stabilization to the inactive conformation (Gibbons *et al*., 2000).

In this scenario, formation of a light-induced $\Delta\mu H^+$ would force the ε subunit, via its attachment to the Subunit III ring, to partially rotate, pulling with it the twisted helical domain of the γ subunit and causing a transient separation of this domain from the central domain of γ. The strain induced by ε rotation would cause the C-terminal helical arm of ε to release from its tight interaction with the regulatory and central domains of γ, destabilizing the interdomain associations within the gamma subunit resulting in an upward movement of the γ regulatory domain. Thus the enzyme would be activated. Reduction of the γ dithiol would facilitate this process, stabilizing the open conformation and helping to maintain the activated state. It would also explain why, in the presence of a $\Delta\mu H^+$, the γ dithiol region becomes hypersensitive to trypsin and more responsive to thiol reducing agents (Moroney and McCarty, 1982; Ketcham *et al*., 1984).

In summary, the newly constructed three dimensional model of the chloroplast F_1 γ subunit has provided a working model as well as considerable insight into how the proton-driven rotation of the $\gamma\varepsilon$ spindle element in the F_1 rotary motor can simultaneously lead to activation of the catalytic activity of the enzyme and coupling of proton transport to ATP synthesis. The γ model, as well as the proposed mechanism of regulation, can be readily tested using a variety of biochemical and biophysical approaches.

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