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ATP SYNTHASE SUBUNITS: STRUCTURE AND ROLE IN PLANTS UNDER STRESS CONDITIONS

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Abstract

Mitochondrial F1F0 -ATP synthase is a vital enzymatic complex in energy metabolism that provides the cell with ATP. ATP synthase is composed of five complexes carry out which execute electron transport and ATP synthesis, vital processes of cellular oxidative phosphorylation. Complex V also known as the F1 F0 ATP synthase or ATPase is mainly involved in of production of ATP by phosphorylating ADP with electrochemical energy produced by the proton gradient across the inner membrane of mitochondria. Plant reproduction and survival are harmed by abiotic factors such as drought, salinity and high temperature. Previously genes of ATP synthase were to over express in stress conditions in plants. It was discovered that during abiotic stresses, such as high salts, drought, and cold, expression of the AtMtATP6 gene was high in *Arabidopsis*. In transgenic yeast and Arabidopsis plants, overexpression of the AtMtATP6 gene increased resistance to salts, drought, oxidative and cold stress. Antisense construct of ATP synthase transformed in various palnts exhibited diverse effects including decline in plant growth, impaired flowering as well as reduced plant vigor. Consequently, ATP synthase subunits gene is crucial for plant development and growth by providing cellular energy source to cell.

Key words: Drought, Salinity, Metabolism, Proton gradient, Biotic and abiotic stress, Oxidative, Cotton, Fiber, Chaperons.

Introduction

ATP (Adenosine- 5'-triphosphate) is a ubiquitous, energy rich molecule that plays important role in survival of living organisms. It is a crucial substrate and cofactor in many biochemical processes, and present in the all cells. ATP (Adenosine- 5'-triphosphate) is synthesized or hydrolyzed in the cells by ATP synthase. This enzyme produces ATP from its precursor ADP and cellular phosphate. The location of ATP synthase is cristae, thylakoid membrane, inner membrane of mitochondria and plasma membrane of bacteria (Devenish *et al*., 2008). The production of ATP through oxidative phosphorylation is usually thought to take place in mitochondria. On the other hand, in prokaryotes, the production of ATP takes place in plasma membrane because prokaryotes don't have mitochondria. ATP synthases are also permitted to reside in the chloroplast of plant cells. ATP synthases are identical in structure and procedure in all three compartments including chloroplast where light energy moves the electrons, allowing transmembrane transport of H^+ ions (McCarty *et al*., 2000). The most crucial chemical reaction for production of energy in living bodies is ATP synthesis. In oxidative phosphorylation, ATP synthase is the last enzyme which uses electrochemical energy to fuel ATP synthesis (Capaldi *et al*., 1994). One of the most common and abundant protein in all living things is ATP synthase that catalyzes amendable conversion of Adenosine- 5'-triphosphate to Adenosine- 5'-diphosphate and inorganic phosphate into ATP. Protein sequence analysis revealed that there is 60% conserved region in catalytic β subunit's amino-acid residues in plants, bacteria and mammals (Yoshida *et al*., 2001). Diverse forms of ATP synthases include V (vacuole), F (phosphorylation factor), E (extracellular) and P (proton), they all catalyzes the synthesis and hydrolysis of ATP. ATPases are classified according to their functional diversities. This enzyme has molecular weight of about 550 KDa and is multi subunit protein complex. Fifth phase of oxidative phosphorylation is known as F1F0 ATPase or Complex V (Jonckheere *et al*., 2012). The ATP synthase enzyme complex defined as small moieties consisting of two opposing rotary motors F1 and F0 which enable enzyme complex to perform either synthetic or hydrolytic activity. These two opposing behaviors must be effectively controlled in order for cells adapt to changing environmental situations. The production of ATP (Adenosine- 5'-triphosphate) in mitochondria is necessary for development and growth of plants. For plant growth and development, mitochondrial oxidative phosphorylation is needed throughout all developmental period (Chen *et al*., 2020). Major sub complexes of enzyme execute significant proton pumping and catalysis activities, correspondingly (Welch *et al*., 2011). In eukaryotes, structure of enzyme and composition of basic subunits are conserved and share resemblance with its bacterial homologues (Zancani *et al*., 2020). Catalytic head, which is made up of three dimers is located in the F1 region. F0 unit has a somewhat different structure in plants, when compared to yeast and humans; there is a significant difference (Li *et al*., 2010). Photons energy is delivered to plants via photosynthetic ETC, generates electrochemical gradient across membrane. ATP synthase phosphorylates ADP to produce ATP with energy provided by this electrochemical gradient. Mitochondria participate in photorespiration pathway, in C3 photosynthetic process, which increase the ratio of CO_2/O_2 and serves as sink for reprocessing excess chloroplast reducing power (Schwarzländer *et al*., 2012). So, mitochondrial F1F0 ATP synthase complex have a critical role in cellular energy metabolism. In inner mitochondrial membrane, transformation of electrochemical proton

gradient into Adenosine- 5'-triphosphate catalyzed via membrane bound F1F0 ATP synthase (Geisler *et al*., 2012). The enzyme structure is very similar in both eukaryotic and prokaryotic species (Walker *et al*., 1984). F1Fo ATP synthase has extensively studied both in humans and animals. However in plant very little research on this crucial enzyme has been conducted. Plants are exposed to various biotic and abiotic environmental adverse conditions that result in the production of free radicals and reactive oxygen molecules (Fig. 1).

ROS can activate mitochondrial dysfunction stimulon genes, triggering mitochondrial retrograde regulation (De Clercq *et al*., 2013). Mitochondrial Dysfunction Stimulon (MDS) genes products like MGE1, OM66 and AOX1a are thought to aid in the repair of mitochondrial dysfunction. MDS genes including AOX1a and ANAC013 are induced when complex V is temporarily inhibited with oligomycin therapy (Clifton *et al*., 2005). Organisms required energy to carry out all of their daily activities. Consequently, mutations in ATP synthase subunits result in severe development abnormalities and in most cases, cause death in *Arabidopsis* (Kong *et al*., 2019). Deviations in all genes of mitochondria are linked with cytoplasmic male sterility (CMS)(Horn *et al*., 2014).

History of research into ATP synthase: In 1960, Efraim Racker and his colleagues extracted a soluble component from beef heart mitochondria and studied detailed structure and function of ATP synthase. They found a similar component of ATP synthase located in chloroplasts, demonstrating that the key function of ATP production in chloroplast and mitochondria are same. Peter Mitchell proposed the chemiosmosis hypothesis in 1961 (Mitchell, 1961), in which long-sought high-energy chemical intermediate connecting respiratory fuel oxidation and ATP production was stated to be an delusion. Alternatively, high-energy state based on protons' electrochemical potential across a membrane was proposed. As a result, a proton-translocating ATP synthase or hydrolyase was predicted for the putative ATP synthase. Biochemists at the time were unfamiliar with this hypothesis, and it was quite unpopular. In the absence of light, he forced pH incline across chloroplast membranes and detected ATP production. Yasuo Kagawa (Kagawa & Racker, 1971) pioneered the vesicle-reconstitution approach, resulted in the discovery of chemiosmotic mechanism. ATP production was catalyzed via vesicles carrying purified ATP synthase, which were driven by an artificially induced H+. The next step was to figure out how ATP synthase transfers energy between flow of proton at F0 and ATP production or splitting at F1. Binding change' mechanism introduced by Paul Boyer (Boyer, 1998) based on the kinetics of enzyme catalyzed exchange between H2O and ATP/Pi. As stated in this process, each of ATP synthase's three catalytic β-subunits switches between states with varying nucleotide affinities in a sequential manner (Gresser *et al*., 1982). This shift in binding affinity is linked to energy input or output but not to the chemical conversion of ATP production or splitting. Physical spinning of centrally placed γ-subunit was also considered by Boyer as a cause of sequential change (Gresser *et al*., 1982).

Structure of ATP synthase: ATP synthase protein complex is large protein complex ~500kDa with complex structure. It comprises membrane-embedded part, Fo central and side stalks and huge head piece. Fo part is involved in proton translocation and is surround to the inner mitochondrial membrane, while F1 part is hydrophilic catalytic domain and is present in mitochondrial matrix. F1 which is involved in oxidative phosphorylation was the first component identified and extracted from bovine heart mitochondria (McCarty, 1992). Fo component confers oligomycin immunity to hydrophilic F1. The structure of enzyme ATP synthase have resembles with arrangement of two motors with peripheral stator stalk and joint common shaft that stabilizes oligomycin sensitivity to soluble F1. Eight subunits 3α, 3β, γ, δ and ε make part F1 of the enzyme where subunit δ, γ and ε make to central stalk and hexameric ring with central cavity is formed by intermittent ordering of 3β and 3α (Fig. 2).

The central portion spins in respect to the surrounding piece and even though the rotor–stator relation is relatable, we will name the former the ‘rotor' and the later the ‘stator' for convenience. Dipping flow of protonvia Fo allows rotor to rotate when the magnitude of H+ is high. Thus, γε-subunits of F1 are rotated. Rotating motion of γ causes structure ofβ-subunit to alternate, allowing ATP to be produced. In reverse reaction, ATP catalysis in F1 causes rotor to rotate in opposite track and hence the Fo rotor to rotate in the other way. Proton pumping is then triggered and side stalk linking Fo stator and F1 stator keeps them from being tangled through central rotor in either circumstances.

Simplest version of ATP synthases is depicted by bacterial ATP synthase. ATP synthase in *E.coli* is made up of eight separate subunits. It is made up of a 380 kDa F1 water-soluble protein complex and Fo hydrophobic transmembrane piece. F1 section of the membrane can be removed in water after removing Mg2+ at deficient salt concentrations but Fo portion stays in membrane. However, by reintroducing Mg2+ (Fessenden & Racker, 1966), Fo and F1 can reconstruct into complete ATP synthase. The subunit architectures of ATP synthases have remained relatively unchanged throughout evolution yet there are notable differences between sources. The simplest form is bacterial ATP synthase, which consists of five subunits with stoichiometry of α3β3γ1δ1ε1 and transmembrane subunits of three types with stoichiometry of a1b2c10–14? Five (Foα), one (Foβ), and two (Foc) transmembrane helices.In the chloroplast and mitochondria, there are only minor structural differences in this enzyme. There are two isoforms of chloroplasts ATPase and 7-9 additional subunits in the mitochondria. Except for two types of Foβ homologue, chloroplast ATP synthase has identical subunit structure.At least six additional accessory subunits are found in mitochondrial ATP synthase. F1 β-subunits contain catalytic sites for ATP catalysis; however residues from α-subunits also play a role. Non catalytic nucleotide-binding site exists in the α-subunits, although its function is unknown. γ- and ε-subunits make up central stalk, while F1δ and Foβ2-subunits make up side stalk (Fig. 3).

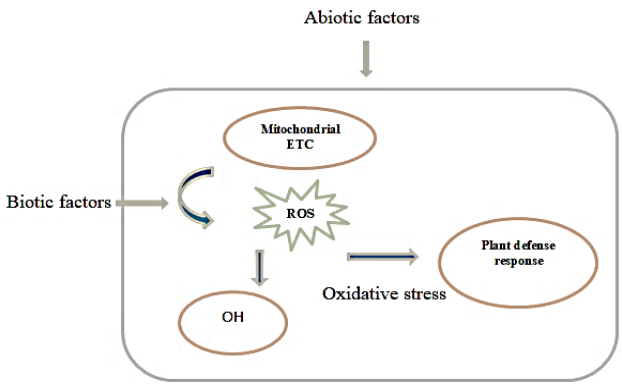

Fig. 1. Effect of biotic and abiotic stress on mETC and response of plants.

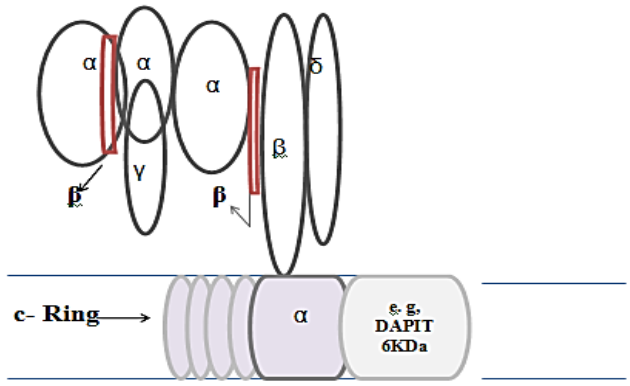

Fig. 2. Structural arrangement of ATP synthase subunits.

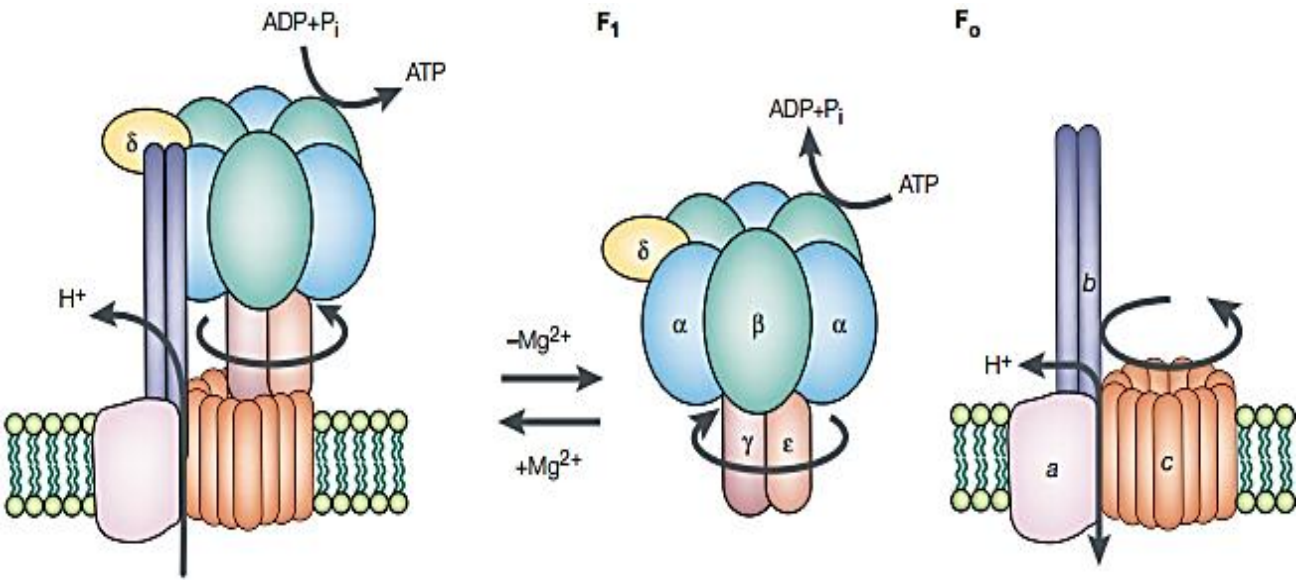

Fig. 3. Structure of ATP synthase complex. The figure shows that Mg2+ has major role in maintaining structural integrity of ATP synthase complex.

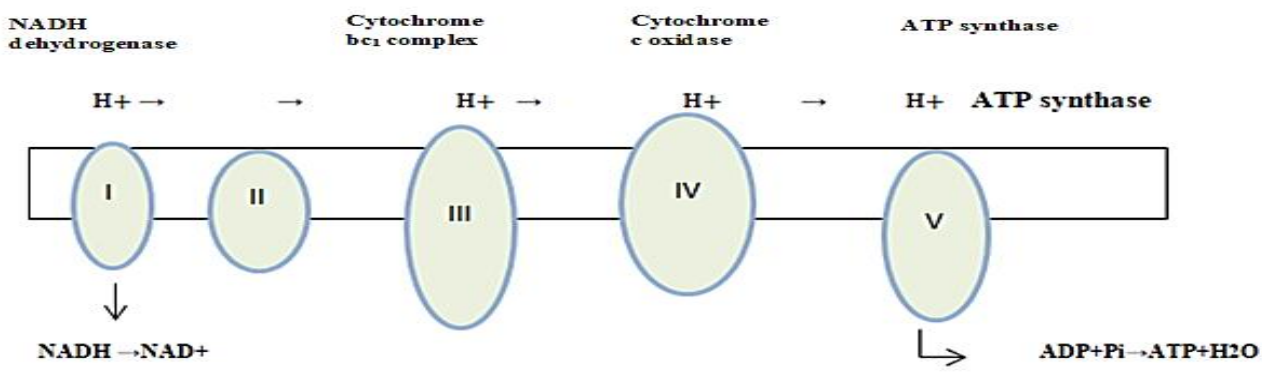

Fig. 4. Mitochondrial ETC and ATP synthase.

Role of ATP synthase in electron transport chain: Protons electrochemical potential supplied via ETC around chloroplast, mitochondria or membrane of bacteria gives energy for ATP generation (Senior *et al*., 2002). Cellular respiration mechanism has been extensively analyzed in mitochondria which use chemiosmosis to produce ATP. Mitochondria are main organelles which generate ATP. Prokaryotic species lack mitochondria, which are the primary organelles that produce ATP. They use chemiosmosis by photophosphorylation to produce ATP. Proton gradient, chemiosmosis and electron transport chain are all in sync with this mechanism which occurs across the inner membrane (Schäfer *et al*., 1999). Electron from oxidizable substrates and NADH move by ETC complexes in inner membrane of mitochondria which are arranged asymmetrically. The flow of electrons is followed by protons (H+) are transferred through the

membrane resulting in electric and chemical gradient. The proton motive force (PMF) is produced by electrochemical energy created by the deviation in concentration of proton and charge segregation around the inner membrane of mitochondria. Proton motive force drag ATP production by allowing back movement of protons into matrix by proton specific channels (F0) part of the enzyme (Nelson & Cox, 2008). Electron transport chain, which is made up of complex of four multi subunits, transfer the electrons sequentially to reduce O_2 to H_2O. Transfer of electrons is linked to displacement of vectorial proton into matrix by three of four complexes. Protons clump together in inner membrane of mitochondria forming electrochemical lean. The protons do not pass by inner membrane of mitochondria. As result, F0 enforce the protons to re-migrate into matrix, while F1 impel neurons to re-enter the matrix and ATP production is catalyzed by F1. Enzyme and electron transport chain work together to determine energy efficiency in plants, as well as cellular biosynthesis, growth, and development (Fig. 4).

From NADH dehydrogenase to cytochrome c, electrons are transported via coenzyme Q, cytochrome bc_1 complexand cytochrome c oxidase. Established incline of proton across inner mitochondrial membrane stimulates flow of protein in ATP synthase, which is required for synthesis of ATP. The structures are made up of cytochrome bc1 complex (Iwata *et al*., 1998), cytochrome c oxidase (Tsukihara *et al*., 1995), F1 component of ATP synthase (Gibbons *et al*., 2000) and F0 part of ATP synthase (Rastogi & Girvin, 1999).

Control of organellar ATP synthases: Demand for ATP and supply of respiration fuel and (in photosynthetic organisms, sunlight) for ATP synthesis fluctuate from one second to next in living cells. As the magnitude of H+ decreases, ATP synthase begins to hydrolyze ATP and activity of ATP synthase must be regulated to prevent wasteful ATP consumption. Disulphide bond among two cysteine residues in chloroplast specific additional region in γ-subunit regulates chloroplast ATP synthase production or cleavage. Chloroplasts decrease this disulphide bond via thioredoxin 87 when exposed to light and ATP synthase is triggered to produce ATP (Nalin & McCarty, 1984). Sulfhydryl's are oxidized to produce disulphide bond in the dark, which suppresses ATP hydrolysis activity. Binding of 9-kDa basic protein to mitochondrial ATP synthase inhibits its ATP hydrolytic function. Binding is dependent on existence of ATP-Mg and an acidic pH, both of which are unfavorable for ATP production. According to recent structural investigations, protein's non-inhibitory tetramer disassemble into inhibitory dimer as pH drops, connecting two ATP synthases by their F1 parts (Cabezón *et al*., 2000; Cabezon *et al*., 2000).

RNA editing in mitochondrial ATP1 mRNA: Role of RNA editing in ATP synthase recently have been discovered in energy generation. Lack of RNA editing in ATP synthase subunits induced cytoplasmic male sterility (Chase, 2007). Faulty editing sites can impair development of plants and interrupting with stress resistance by causing the encoded RNA to lose their function i.e. cytosine to Uracil editing at rp116-458 location is required for mitochondrial function and any change in this location produces defectiveseed phenotype in maize (Liu *et al*., 2013). Chloroplast RNA editing locations were found in *Gossypium hirsutum* and were predicted to impact 2-D and 3-D structure of protein (Jiang *et al*., 2012). During cotton fiber cell elongation, RNA editing in *GhATP1* at C1292 and C1415 locations is required for energy demands and failure of editing at sites C1292 and C1415 is associated with reduction in ATP synthase action (He *et al*., 2018). RNA editing changes have an effect on a variety of physiological functions involving CMS development, a condition in which male reproductive systems don't mature properly, resulting in little to no production of pollen (Carlsson *et al*., 2008). Low production of ATP synthase may result in lowering the level of ATP resulting cell death and ultimately in CMS. Real time PCR analsyis of five anther ATP synthase genes during tetrad development showed lower expression of four ATP synthase was associated with CMS in cotton (Kong *et al*., 2019). In mitochondrial genome of *Gossypium hirsutum*, 692 RNA editing sites have discovered through high throughput sequencing. Two crucial sites of editing found to be essential for connection among ATP synthase subunits α and β, leading in ATP accumulation and increased cell development in yeast, according to biochemical and genetic analyses.

Abiotic stresses: Abiotic stresses pose significant challenges to all living species but plants face greater challenges because they cannot move as easily as other organisms. Higher plants more susceptible to environmental challenges like freezing temperatures and high salt stress (Suda *et al*., 2009). Two main abiotic stresses like drought and salt stress pose a serious threat to the world's food supply (Nevo & Chen, 2010). Plants react to stresses at a cellular and molecular level and also at physiological and biochemical levels to keep them to survive. Abiotic stresses reduced development and productivity of plants. Stress inducible genes produce enzymes that make several osmoprotectants like chaperons, antifreeze proteins, detoxifying enzymes and late embryogenesis abundant proteins which may be especially guarding against these stresses. Gene products which are included in signal transduction pathway and expression of gene include various enzymes, transcription factors and protein kinases. Signal transduction pathways including mitogen activated protein kinase has been studied under osmotic/oxidative stress.

Role of ATP synthase subunits under environmental stresses: Isolation and characterization of Mitochondrial ATP synthase gene have been done in *Arabidopsis* (Kruft *et al*., 2001), potato (Jänsch *et al*., 1996), spinach (Hamasur & Glaser, 1992) and rice (Heazlewood *et al*.,

2003). Earlier research has mostly focused on identifying F1 subunit, with some of associated genes from organisms have been sequenced. The action of *MtATP synthase* subunits gene to stress have been examined in some research. According to (Sweetlove *et al*., 2002), oxidative stress substantially reduced the expression of *MtATP synthase* α and β subunits genes in *Arabidopsis*. The oxidants H2O2 and paraquat also reduced AtMtATP6 gene expression. As a result, oxidative stress is most expected to harm the subunits of ATP synthase. According to (Zhang *et al*., 2006), gene expression in RMtATP6 created through osmotic and salinity stress. RMtATP gene overexpressed which displayed improved resistance against salinity stress from NaCl and $NaHCO_3$ in transgenic tobacco. Environmental stresses like salt, cold and drought stress was observed to stimulate expression of AtMATP6 gene. Furthermore, AtMtATP gene overexpression in *Arabidopsis* and yeast improved tolerance to oxidative, salt and cold stress. These findings indicate that AtMtATP6 gene is implicated in environmental stress response. Role of Plant mitochondrial ATP synthase subunits in physiological processes and stress responses are summarized in Table 1.

Cold and heat stress: Low temperature condition above freezing temperatures causes F-ATP synthase activity to decline, resulting in a drop in the ADP/O ratio and ATP production. Compared to the other mETC components, this enzyme is more severely inhibited by low temperature (Rurek *et al*., 2018). Alternative an oxidase enzyme is induced and activated in plants as a unique physiological response to cold (Rurek *et al*., 2018, Vanlerberghe, 2020), however this complex continued proton transport still allows for a little amount of ATP generation. At high temperature adenylate limitation and variations in the substrate supply become the limiting variables.

According to a study done on curds of *Brassica oleracea* var. *botrytis*, transcriptome and proteomic profiles are affected differently by cold and warm climatic conditions. Specifically, the proteome profiling only found significant effects at elevated temperatures, when F-ATP synthase subunit b expression was increased and subunit α expression was decreased, exhibiting a completely different behaviour from cold stress. When normal conditions restored, the component remained under-expressed, reducing the stability of F-ATP synthase and compromising its assembly during the recovery phase following heat stress. As a result, both during the heat treatments and the recovery stage, the enzymatic activity was reduced (Rurek *et al*., 2015). One of the subumit of ATP synthase, ATPd has found to involve in normal plant development, and depicts its crucial role in tolerance to high temperature condition (Liu *et al*., 2013).

It was proposed that the increased need for ATP during heat stress causes the overexpression of certain subunits, favoring the construction of F-ATP synthase complexes, which are nevertheless unstable during the subsequent recovery phase (Rurek *et al*., 2018).

Table 1. Role of Plant mitochondrial ATP synthase subunits in physiological processes and stress responses (Zancani *et al*., 2020).

	Species	Modification	Effect	Reference
α (ATP1)	Sunflower, radish-rapeseed cybrids, sugar beet, stem mustard	Gene rearrangement	CMS	Senda *et al*., 1993; Yang *et al*., 2009; Yu *et al*., 2001; Wu *et al*., 2011
	Arabidopsis	mRNA editing	Slow growth and delayed development	Hammani *et al*., 2011
	Cotton	mRNA editing	Fibre cell elongation	He *et al*., 2018
β (ATP2)	Rice	Low temperature stress	Enhanced expression	Gammulla *et al*., 2011; Neilson *et al*., 2011
	Arabidopsis	Decrease of expression (anti-*atp*3	Seedling death, slow growth	Robison *et al*., 2009
γ (ATP3)	Sunflower	Low temperature stress	Increase in protein abundance in chilling-sensitive cv. Decrease in protein abundance in chilling-tolerant	Balbuena *et al*., 2011
	Wheat	Decrease in abundance	CMS	Wang *et al*., 2015
δ (ATP16)	Rice	Osmotic and salt stresses	Increase in abundance (tolerance to stress)	Zhang *et al*., 2006
a (ATP6)	Pepper	Gene rearrangement (Ψ*atp6-2*)	CMS	Li *et al*., 2013

Oxidative stress: Oxidative metabolism rises in response to different stresses that affect the plant mitochondria, due to changes in flow of electron in mETC. Numerous forms of stresses cause plant mitochondria to increase in oxidative metabolism allowing modification in the flow of electrons in the mETC and results in abrupt increase in respiration known as an "oxidative burst." Reactive oxygen species are produced, primarily at Complex I and III, as a result of the buildup of reduced intermediates with unpaired electrons (Jacoby *et al*., 2018). These events have a detrimental effect on F-ATP synthase in *Arabidopsis*, where the degradation of subunits and d has been connected to the stimulation of protease activity (Sweetlove *et al*., 2002). The subunit of the F-ATP synthase appears to be particularly vulnerable to various oxidative agents, as shown by the existence of its degradation byproducts produced by ATP-dependent protease activity. The F-ATP synthase, on the other hand, is still capable of supporting the metabolic responses during oxidative stress despite subunit loss. Despite the injection of H2O2, there is still some mitochondrial respiratory activity, which supports this view (Sweetlove *et al*., 2002).

Salt stress: Studies on *Mesembryanthemum crystallinum* demonstrated the dual nature of this halophytic plant's responses to saline stress, which can result in both osmotic alteration and an ionic unbalance (Tran *et al*., 2019). This characteristic is unique to halophytic plants and has been shown to depend on the ionic action to increase ATP synthesis. Due to their high fitness in salty circumstances and even a rise in biomass at NaCl concentrations as low as 100 mM, these highly adapted plants demonstrate an increase in ATP content in the presence of NaCl up to 300 mM. Similar outcomes were observed when NaCl treatments were applied to wheat, where a high salt content boosted F-ATP synthase activity.Even though multiple overlapping elements might increase respiratory rates under stress, similar results have been discovered in the case of NaCl treatments in wheat, where a high salt concentration enhanced F-ATP synthase activity (Jacoby *et al*., 2016). On the other hand, given that different effects of salt have been demonstrated on the various isoforms, this stimulation is hardly explained by an increase in the quantity of F-ATP synthase subunits (Jacoby *et al*., 2016).

Conclusion

ATP synthase is critical component of a systematic and conservative approach to energetic metabolism in various organisms. It is amazing that enzyme ATP synthase may have an auto regulatory mechanism capable of transitioning from energy synthesis to energy dispersion, provoking the cell death, last being a critical method for triggering pro apoptotic passage which is triggered under a variety of physiological and stress challenges e.g. salinity stress. Environmental stresses pose significant challenges to plant growth and production. Various signaling pathways regulate nuclear gene expression in stressful situations. Signals can control gene expression, which in turn controls protein expression. Mitochondria are vital cellular components that produce the energy required for plant development. Plant mitochondrial genes that encode for mitochondrial protein complexes, these are impacted by many kinds of RNA processing entailing RNA editing. This comprehensive study can help to provides information about structure and diverse function of ATP synthase gene in plant for energy generation and abiotic stresses.

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