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Orange Carotenoid Protein (OCP): A Key Player in Non-photochemical Quenching of Cyanobacteria under Fluctuating Light Condition

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Abstract

Fluctuating light condition poses major threat to photosynthetic organisms by evoking the production of reactive oxygen species (ROS). To endure the high irradiance level, plants and algae have evolved a photo-protective mechanism, referred as non-photochemical quenching (NPQ). This mechanism concerns with minimizing arrival of the excess excitation energy on reaction centers by dissipating surplus energy in form of harmless heat. Earlier cyanobacteria were not considered to capable of performing NPQ. Alternatively, state transition was supposed to be the major means that cyanobacteria preferably carried out to be protected under high light. Recently it was substantiated with evidence that these organisms can execute NPQ as a prominent photo-protective strategy. NPQ in cyanobacteria is mediated by a water soluble orange carotenoid protein (OCP) which is structurally and functionally modular. OCP consists of two domains (i) N-terminal domain (NTD) and (ii) C-terminal domain (CTD) with a single carotenoid as a chromophore spanning symmetrically in both domains. Blue-green or strong white light induces conversion of OCP from an inactive orange state (OCP^O) to active red state (OCP^R). Active form of OCP (OCP^R) binds to core of light harvesting antenna complex, phycobilisome (PBS), where it quenches fluorescence and assists in dissipation of excess energy by non-radiative pathway. Prior to prevent wasteful quenching of fluorescence under light starvation, another protein named fluorescence recovery protein (FRP) partakes in decoupling OCP^R from PBS and accelerates conversion of OCP^R state back to OCP^O state.

1. Introduction

In nature, variability in the light environment is very common which present photosynthetic organisms to confront frequent fluctuations of light intensity. Success of these phototrophs relies on how efficiently they adapt themselves in changing environmental conditions (Ruban, 2009). To cope up with frequently changing irradiance level in natural environment, plants and algae are equipped with several mechanisms to dissipate excess absorbed energy in form of harmless heat (Karapetyan, 2007; Gorbunov *et al*., 2011). Generally to counter this problem, one mechanism competes with fluorescence and further quenches it in form of non-photochemical way. Thus, this photo-protective mechanism is referred as non-photochemical quenching (NPQ).

Photosynthetic Organisms harness solar energy and transform it into chemical energy, later to be used to fuel the organisms activity. Although light is vital for photosynthesis, it can be devastating if photon energy captured by light harvesting antenna complex continues even after the saturation of photosynthetic electron transport. For example, if the energy of singlet excited molecules of antenna chlorophyll cannot be completely utilized by reaction centers, then this singlet state will form long lived triplet states. Excited chlorophyll triplets may interact with oxygen molecules and leads to the generation of potentially ruinous singlet oxygen (Morosinotto and Bassi, 2014). Singlet oxygen is highly reactive oxidizing molecule that can damage all classes of bio-molecules, including protein, lipid and DNA (Triantaphylidès and Havaux, 2009; Gorbunov *et al*., 2011; Cogdell and Gardiner, 2015) as well as also causes destruction of photosynthetic apparatus (Karapetyan, 2007).

Under excess light NPQ operates in different manner among most of the photosynthetic organisms. In plants and green algae, NPQ embrace membrane embedded chlorophyll containing light harvesting complex (LHC II) and sparked by drop in thylakoid lumen pH (Muller *et al*., 2001). Acidification of thylakoid lumen activates de-epoxidasae enzyme of xanthophyll cycle which entails oxidation of violaxanthin to zeaxanthin via an intermediate antheraxanthin (Demmig-Adams and Adams, 1996; Ort, 2001) and induces the protonation of PsbS, a subunit of photosystem II (PS II) that belongs to LHC super family (Li *et al*., 2000, 2004). PsbS is strongly perceptive to low pH (Morosinotto and Bassi, 2014) and it lacks chlorophyll and xanthophyll. All these processes engender conformational changes in LHC II that modifies the interaction between chlorophyll and carotenoids and eventually enhances the thermal dissipation of excess absorbed energy for preserving the integrity of PS II. Similar kind of photo-protective mechanism also occurs in many species of Bacillariophyceae, Chloromon-

adophyceae, Chrysophyceae, Euglenophyceae, Xanthophyceae and Dinophyceae that relies on light-stimulated conversion of diadinoxanthin to diatoxanthin (Gorbunov *et al*., 2011).

In contrast to plants and eukaryotic algae, cyanobacteria follow a different mechanism of NPQ which involves a giant water soluble light harvesting complex, phycobilisome (PBS), bounded on surface of thylakoid membrane and a carotenoid as chromophore which is activated by strong light. Despite, differences in organization of light harvesting antenna complexes, carotenoids play a crucial role in plants as well as in cyanobacteria. Considering their light harvesting and photo-protective capability under fluctuating light condition, carotenoids are imperative for proper functioning of photosynthetic apparatus (Zakar *et al*., 2016). NPQ mechanism is studied exclusively in vascular plants for a long time, however a photo-protective mechanism in cyanobacteria uncovered in the mid late 1980s (Holt and Krogmann, 1981). Cyanobacteria were considered as incapable of performing NPQ for protecting their photosynthetic machinery under light saturating condition. Instead, state transition that involves redistribution of energy between Photosystem II (PS II) and Photosystem I (PS I), considered as major photo-protective mechanism to divert excess excitation flux away. Now several researches have clearly proved that cyanobacteria can also operate NPQ as one of important photo-protective strategies to deal with high light.

NPQ in cyanobacteria essentially require 3 basic components: (i) a distinct, large water soluble light harvesting complex, phycobilisome (PBS) (ii) An orange carotenoid protein (OCP) with a sensor that senses elevated light level and an effector that quenches excess fluorescence after interacting with PBS core and (iii) Fluorescence recovery protein (FRP) which helps in dissociation of OCP from PBS core (Shirshin *et al*., 2017).

This review gives an overview on understanding of structural and functional organization of PBS, OCP and FRP along with that it also focuses on how these tricomplex (PBS-OCP-FRP) interact and help in photoprotective energy dissipating mechanism in cyanobacteria.

2. What are the Fates of Excitation Energy Pumped into a Pigment Molecule?

On photo-excitation, chlorophyll or accessory pigments get boosted from its lowest energy state to higher potential energy state. At the time of returning to the ground state, these excited molecules can attain number of alternative pathway that incorporates photochemistry, fluorescence and non-photochemical process (Fig. 1). Theses pathways compete with each other. Any increase in one results in decrement of others. Likewise increase in either photochemistry or non-photochemical process accounts for slow fluorescence level down. Therefore, it is said that fluorescence is either photochemically or non-photochemically quenched. Under light starvation, light harvesting antenna complexes maximize the absorption of excitation energy by orienting chlorophylls molecule in precise configuration and minimize the energy loss in form of fluorescence and NPQ. Exposure of high light causes saturation of photochemistry and extra quanta energy concurrently leads to the activation of other pathways that assist in de-excitation of pigment molecules (El-Bissati *et al*., 2000; Bailey and Grossman, 2008).

3. How do the Light Harvesting Complexes Organized in Cyanobacteria?

Rapid and regular fluctuations in light intensities are very common that poses major challenge to photosynthetic organisms. To survive under light limiting condition photosynthetic organisms have developed scrupulous light harvesting antenna complexes that can help in absorbing excitation energy optimally. However, high light intensity can be very noxious for these organisms where light harvesting antenna complex captures energy even after the saturation of photochemistry. To avoid the potentially phototoxic effect of excess absorbed energy, cyanobacteria have evolved a strategy that regulates the flow of excitation energy to reaction centers (Sluchanko *et al*., 2017).

The mode of oxygenic photosynthesis committed by cyanobacteria is similar to plants and eukaryotic algae. However, organization and location of light harvesting antenna complexes that fuel the reaction centers are quite different. Plants and eukaryotic algae employ integral membrane light harvesting complexes that are capable of diffusing laterally across the thylakoid membrane. Whilst major light harvesting antenna complex in cyanobacteria is phycobilisome (PBS), a supramolecular complex of water soluble accessory pigments. PBS, in association with membrane embedded reaction center, are coated on surface of thylakoid membranes in form of regular arrays (Bryant *et al*., 1979; Karapetyan, 2007).

Pioneered work on PBS was performed by Gantt and Cori in 1969 in red alga *Porphyridium cruentum* and later discovered in many cyanobacteria. PBS consists of two substructures named, the rod and core. These substructures contain trimers and hexamers of pigment phycobiliproteins (PBPs) along with non-pigmented linker polypeptides that act as stabilizer in the complex. PBPs are composed of α and β subunits (in

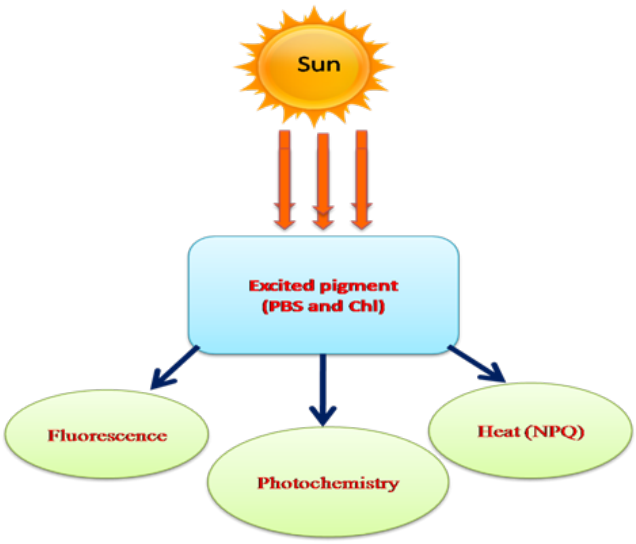

Fig. 1: Alternative pathways adopted by excited pigment molecules in cyanobacteria. After energy absorption, pigment molecules get promoted from their ground state to excited state. Excited state is extremely unstable so it quickly returns back again to its ground state and releases energy. The released energy can acquire number of different routes, including photochemistry, fluorescence and NPQ.

some phycoerythrin a special γ subunit can also be found) that bear covalently attached open chain tetrapyroles termed as phycobilins.

On the basis of pigment composition and their spectral properties PBPs are divided into the four groups: (i) phycocyanin (PC absorption maxima ~ 620nm), (ii) phycoerythrin (PE absorption maxima ~ 560nm), (iii) phycoerythrocyanin (PEC absorption maxima ~ 595nm) and (iv) allophycocyanin (APC absorption maxima ~ 650nm). The rod can consists of PC and PE, although few cyanobacteria exclusively consists of only PC e.g. *Synechocystis* sp. PCC 6803, while core specifically contains APC. The non-pigmented linker polypeptides (not shown in figure) are one of the important components of PBS that is critical for organizing PBPs arrays into rod and core substructures and giving it final touch in form of highly efficient light harvesting complexes. The PE and PC of rod absorb excitation energy efficiently and transfer them to APC core of PBS. These harvested excitation energy finally migrates from core to the reaction center of PS II (Liu *et al*., 2005; Bailey and Grossman, 2008; Saer and Blankenship, 2017).

According to a recent structural model proposed by Liu *et al*. (2013), PBS transfers excitation energy to both PS I and PS II by acquiring a mega-complex like structure with both reaction centers (Liu *et al*., 2013) (Fig. 2).

4. Regulation of Photo-Protective Response in Cyanobacteria

To accommodate under high light condition photosynthetic organisms have developed several strategies. Regulation of these strategies is critical to maintain the photosynthetic efficiency by minimizing photo-destruction. NPQ of fluorescence is one of the important strategies to rapidly dissipate excess excitation energy in form of heat. Molecular mechanism involved in this type of quenching is different in plants, eukaryotic algae and cyanobacteria. In contrast to pH-triggered NPQ in higher plants and eukaryotic algae, cyanobacteria requires OCP as well as fluorescence recovery protein (FRP) for photo-protection in form of NPQ in cyanobacteria.

4.1. Orange Carotenoid Protein (OCP)

In 1981, David Krogmann and colleagues discovered a water soluble carotenoid binding protein in crude extract of cyanobacteria and purified it from three different species named *Arthrospira*, *Aphanizomenon* and *Microcystis* (Holt and Krogmann, 1981). In 1997, by taking the reference of first sequenced cyanobacteria, the Krogmann group described that *slr1963* gene in *Synechocystis* sp PCC 6803, codes for orange carotenoid protein (OCP) (Wu and Krogmann, 1997). Later in 2003, OCP was crystallized from *Arthrospira maxima* and its structure was proposed (Kerfeld *et al*., 2003).

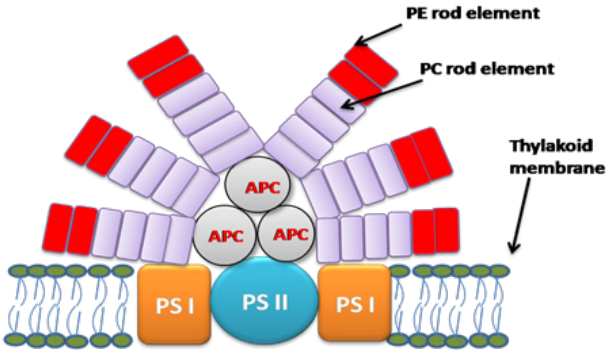

Fig. 2: Structural model of "mega-complex" containing PBS associates with both PS I and PS II. PS I is coloured yellow, PS II: sky blue, APC: grey, PC: light purple and PE: red. (Model adopted from Saer and Blankenship, 2017).

OCP is a 35 kDa water soluble and only known protein that harbours carotenoid as chromophore. According to proposed crystallized structure, OCP comprises two discrete structural domains (i) 18 kDa all helical N-terminal domain (NTD) and (ii) a mixed α-helical/β-sheet containing C-terminal domain (CTD) (Kirlovsky and Kerfeld, 2016; Bao *et al*., 2017; Kerfeld *et al*., 2017; Sluchanko *et al*., 2017).

NTD is specific to only cyanobacteria whereas CTD, a member of nuclear transport factor-2 (NTF-2) is common in prokaryotes and eukaryotes (Kirlovsky and Kerfeld, 2016; Kerfeld *et al*., 2017). Both domains are associated by a flexible linker of 25 a.a. but recently it has been seen that linker is not mandatory to connect two domains of OCP (Moldenhauer *et al*., 2018; Sluchanko *et al*., 2017). OCP acquires a compact globular structure, which is stabilized by inter-domain interaction at major interface including highly conserved R155 (NTD) / E244 (CTD) salt bridge. The second minor interface between two domains is stabilized by a hydrophobic bond between α-A helix within N-terminal extension (NTE) of NTD and several β-sheet of CTD (Sluchanko *et al*., 2017). Both domains of OCP encapsulate a single keto-carotenoid (Lu *et al*., 2016) that stretches into NTD and CTD almost completely, only 4% exposed to hydrophobic environment (Sluchanko *et al*., 2017) (Fig. 3A). Purified OCP from different cyanobacteria shows that it can bind to different kind of keto-carotenoids (3'-hydroxy-echineone, echineone, canthaxanthin, myxoxanthin etc) (Fig. 3C). The 4- keto oxygen play pivotal role to form carotenoid-protein specific interactions (H-bond) with two conserved residues Y201 and W288 within CTD. Hydrgen-bonds formed between carotenoid and conserved residues of CTD are critical for photoactivity. It has been proved practically that substitution with zeaxanthin which lacks carbonyl group can diminish photoactivity of OCP (Punginelli *et al*., 2009).

Under light limiting condition, OCP remains in their orange form (OCP^O) and the water soluble phycobilisome complex (PBS) functions efficiently to maximize the light absorption. When excitation energy (blue-green light) exceeds the optimum, it saturates the reaction centers. Concomitantly, excess energy switches inactive orange form of OCP (OCP^O) to the active red form (OCP^R) which is a shorter variant of OCP (Cogdell and Gardiner, 2015). In 2003, Kerfeld showed, although both OCP^O and OCP^R have ability to quench singlet oxygen but OCP^R comparatively quenches with faster rate. OCP^R was purified in 1981 by Krogmann and colleagues from several cyanobacteria (Holt and Krogmann, 1981). Subsequent researches showed that OCP^R is actually a proteolytic fragment of OCP which carries most of the NTD portion along with complete carotenoid but lacks CTD entirely (Wu and Krogmann, 1997).

Thus, OCP undergoes blue-green light-triggered domain dissociation which plays critical role in converting inactive

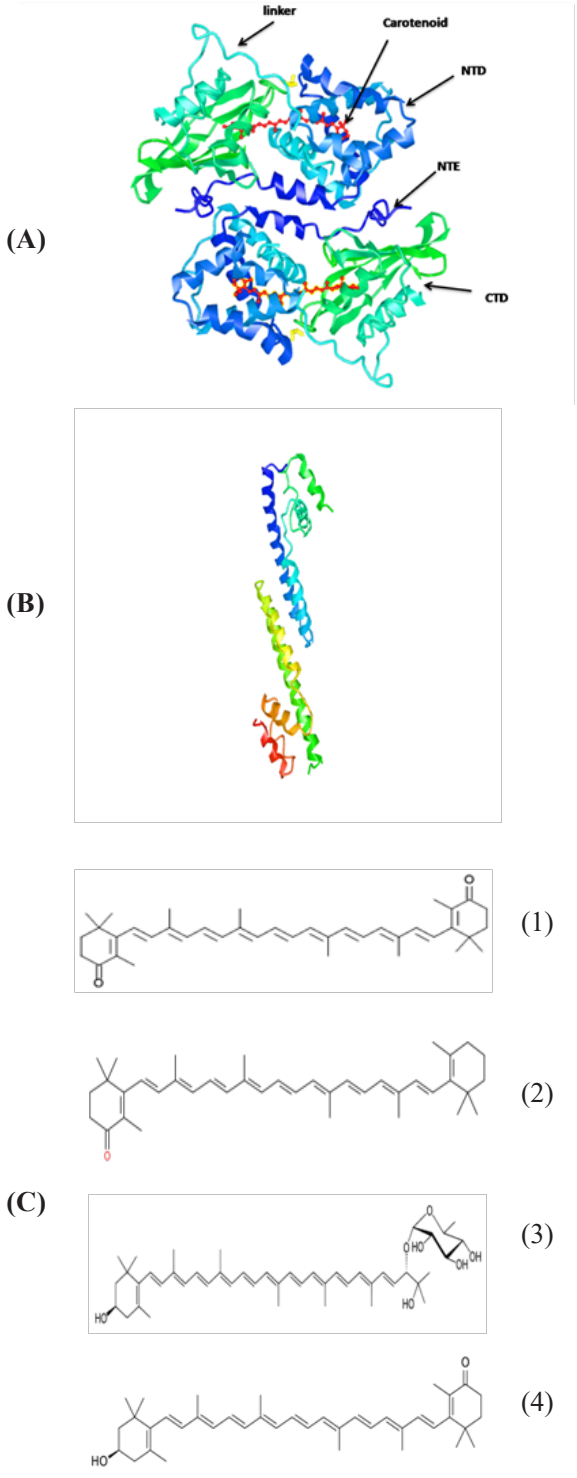

Fig. 3: The structure of OCP and FRP: (A) OCP^O dimer: NTD coloured in blue, CTD in green and carotenoid is shown as red stick (https://www.ncbi.nlm.nih.gov/Structure/pdb/3MG1) (B) FRP: active dimeric form (https://www.ncbi.nlm.nih.gov/Structure/pdb/4JDX) (C) List of carotenoids that can interact with OCP 1. Canthaxanthin 2. Echineone 3. Myxoxanthophyll 4. 3-Hydroxy echineone.

orange form of OCP (OCP^O) to the active red form (OCP^R) and sets the non-photochemical quenching (NPQ) mechanism platform in cyanobacteria.

4.2. Fluorescence Recovery Protein (FRP)

After the discovery of OCP (a gene product of *slr1963* of *Synechocystis*) by Krogmann groups, it was discovered that *slr1963* gene is consistently associated with a second open reading frame (Boulay *et al.,* 2010), termed as fluorescence recovery protein (FRP), which is crucial for regulation of OCP-mediated fluorescence quenching in cyanobacteria. In *Synechocystis* two oligomeric and conformational state of FRP has been crystallized one is active dimer, a compact fold of helix which interacts with CTD of OCP (Fig. 3B) and another one is inactive tetramer, an extended α-helix with a small helical cap that is a storage form of protein. These both form of FRP are interconvertible. Although the structure of FRP is now known but how they interact with OCP is still ambiguous.

4.3. Mechanism of OCP-mediated quenching

In plants and eukaryotic algae NPQ occurs at light harvesting chlorophyll antenna complex which is embedded in thylakoid membrane. In light starvation these complexes optimize the light capturing efficiency to utilize essentially every photon. Upon exposure to intense light pH of lumen decreases which switches these antenna complex from light capturing state to photo-protective state by activating xanthophylls cycle. This cycle includes conversion of violaxanthin to zeaxanthin in high light stress. Accumulation of zeaxanthin is imperative because it acts as an effective quencher of excited chlorophyll molecule.

In contrast to pH-induced NPQ in plants and eukaryotic algae, cyanobacteria possess a simple OCP-mediated NPQ mechanism that occurs on the water-soluble light harvesting antenna complex present peripheral to thylakoid membrane (Kirlovsky, 2015). Upon induction by blue-green light or strong white light conformational change occurs in OCP which causes conversion of inactive OCP^O to an active OCP^R form, by dissociating both domains of OCP^O (Wilson *et al*., 2008). Conversion of OCP^O to an active OCP^R form become possible after breakage of salt bridge at R155-E244, major interface between two domains and separation of NTE from CTD at minor interface which subsequently allow the dissociation of two domains of OCP (Sluchanko *et al*., 2017). Once OCP^R is formed it acquires the ability to bind with PBS. After interaction between positively charged R155 exposed on NTD surface and negative surface charges on PBS core, OCP^R gets stabilized (Bao *et al*., 2017) and subsequently facilitates the efficient quenching of fluorescence from excited PBS core. It has been proposed that excess excitation energy migrates from bilin pigments of PBS to carotenoid chromophore of OCP^R for de-excitation of antenna (Tian *et al*., 2012). This process seems as if OCP^R closes the tap at the end of light harvesting antenna complex to minimize the flow of energy to the PS II (reaction center) which protects photosynthetic machinery from photo-damage. Beside these changes light also induces the translocation of carotenoid 12 Å deeper from CTD to NTD. Shifting of carotenoid is critical in the sense that it brings the carotenoid closure to bilin pigment of PBS core (Leverenz *et al*., 2015).

OCP^R is metastable and in dark condition can revert back to inactive OCP^O form. FRP a second protein which discovered as a second reading frame consistently present with the gene that codes for OCP, assists this reversion. FRP remains active in dimer form and gets ability to bind with CTD of active state of OCP (OCP^R) (Lu *et al*., 2016). In active OCP state, NTD and CTD both domains get separated which allows NTD to binds

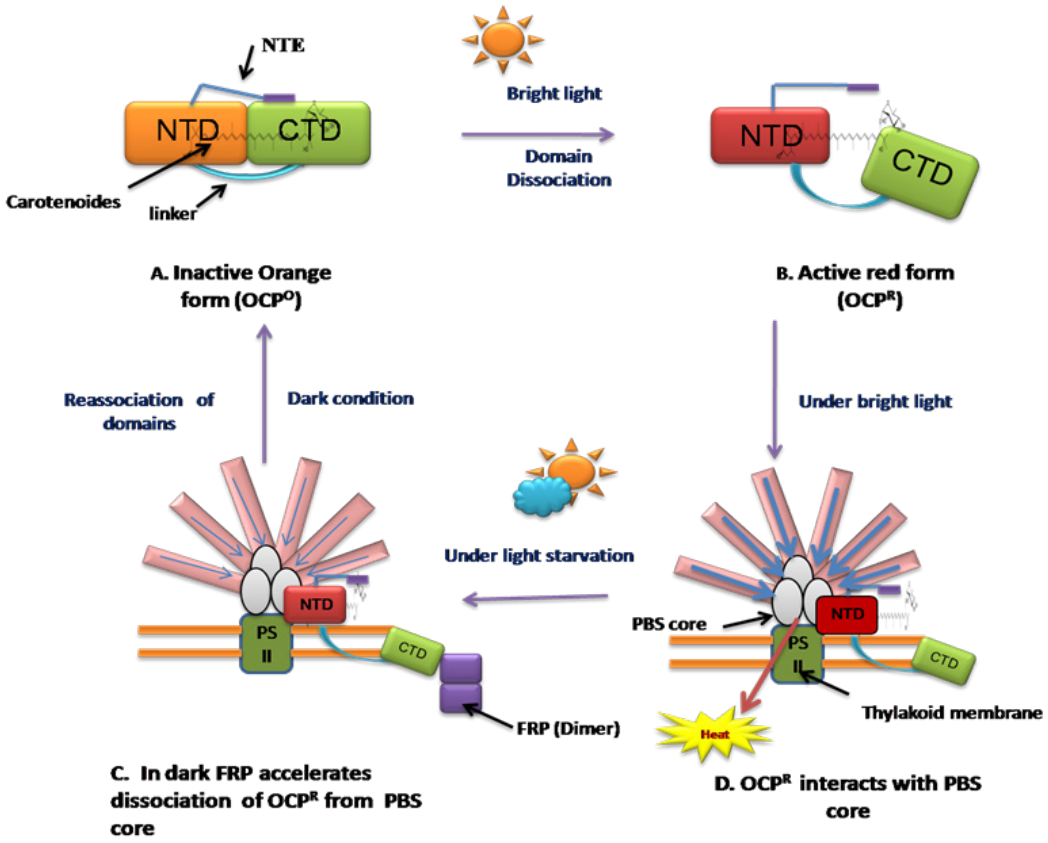

Fig. 4: Mechanism of OCP-mediated NPQ mechanism in cyanobacteria: **A** and **B**. Upon light absorption conformational change occurs in OCP that leads to the conversion of inactive OCP^O to an active OCP^R form **C.** Activated OCP^R binds to PBS core and facilitates the thermal dissipation of extra energy in form of heat **D.** In dark condition a second protein FRP binds to the CTD of OCP^R and accelerates its conversion back to inactivated form of OCP (OCP^O).

with PBS, whilst CTD hangs freely via inter-domain linker. FRP binds with freely mobile CTD and turns off the quenching of fluorescence by decoupling OCP^R from PBS core (Sutter *et al*., 2013). Site-directed mutagenesis and native Mass Spectrometry techniques have shown that head region of FRP can only bind with CTD. This binding at CTD causes changes in FRP conformation which helps in bridging both domains of OCP again (Lu *et al*., 2016). Prior to avoid wasteful quenching of fluorescence under light saturating condition, FRP plays a crucial role by helping the accumulation of absorbed photon at the antenna complex. Therefore, it is termed as fluorescence recovery protein (FRP) (Fig. 4). It is anticipated that FRP functions transiently by sensing fluctuating light condition , but still it is not clearly known whether FRP functions are regulated by environmental conditions or not. Moreover, how FRP interacts with PBS, what are the molecular mechanisms which facilitate their binding is under investigation.

5. Conclusions

We conclude that orange carotenoid protein (OCP) is essential for effectuating NPQ in cyanobacteria. Generally OCP that comprises two strongly allied domains: NTD and CTD, occurs in two different states one is inactive orange state (OCP^O) and second is active red form (OCP^R). NTD of OCP is common in OCP^O and OCP^R both. Under dark and light limiting condition both domains of OCP remains intact and does not involve in energy dissipating mechanism. It is being considered that blue-green or strong white light is necessary to break the hydrogen bonds and hydrophobic which joins these two domains together. Once OCP induced by light, both domains get separated and OCP come out in form OCP^R. Further OCP^R interacts with PBS core and helps in dissipating surfeit energy. To recover the capacity of antenna for maximizing light absorption under light limiting condition, the FRP decouples OCP^R from PBS and returns OCP^R back to OCP^O form.

Although a lot of research has been done the structural and functional organization of PBS, OCP and FRP but still complete scenario of cyanobacterial NPQ mechanism is ambiguous. Furthermore, how FRP binds to CTD and carry out recovery of fluorescence will be the matter of future research.

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