



## REVIEW PAPER

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## Photosynthesis: Fundamentals and advances

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### Abstract

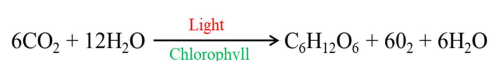
Photosynthesis is one of the most incomparable and meticulous metabolic processes that maximize the use of available light, carbon and nitrogen and minimizes the destructive effects of surplus light. Indeed, photosynthesis comprises of two major reactions that occur in separate parts in the chloroplast. The light reactions take place in the thylakoid membrane which generates ATP and NADPH while dark reactions (so called Calvin–Benson cycle) exploit these ATP and NADPH to reduce carbon CO<sub>2</sub> (carbon-di-oxide) to carbohydrates (CH<sub>2</sub>O) in the stroma of chloroplast. In plants various carbon fixation mechanisms are evolved naturally such as, less efficient C<sub>3</sub> carbon fixation having photorespiration, more efficient C<sub>4</sub> carbon fixation having cellular CO<sub>2</sub> pumping system for avoiding photorespiration and CAM (Crassulacean acid metabolism) carbon fixation for escaping transpiration during day. Besides plant proceeds different alternative sinks for carbon fixation under surplus light. Chlorophyll fluorescence is one of the most influential and advanced technique for studying photosystems health but on the other hand photo inhibition and ROS (reactive oxygen species) generation are unfortunate for photosystems during various stresses. However, photo inhibition and ROS generation are obligatory during stresses whereas chloroplastic antioxidants are accountable for ROS regulation in plant cells. These insight between fundamental and advance information on photosynthesis assist to switch less efficient C<sub>3</sub> rice to highly efficient C<sub>4</sub> rice development to feed the ever-increasing population in the globe. Therefore, this article reviews fundamental aspects of photosynthetic machineries, underlying physiological, biochemical and molecular mechanisms and highlighted the modern scientific achievements on C<sub>4</sub> rice development.

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## Introduction

Photosynthesis is a sequential biological progress through which plants convert light energy into chemical energy in the form of sugars, which is readily absorbed to operate various cellular functions (Rabinowitch, 1956; Gest, 2002). Photosynthesis occurs likely in several photoautotrophs (El-Sharkawy and Hesketh, 1965) through absorbing light energy by reaction centers (RCs) (Rabinowitch, 1956; Whitmarsh, 1999).

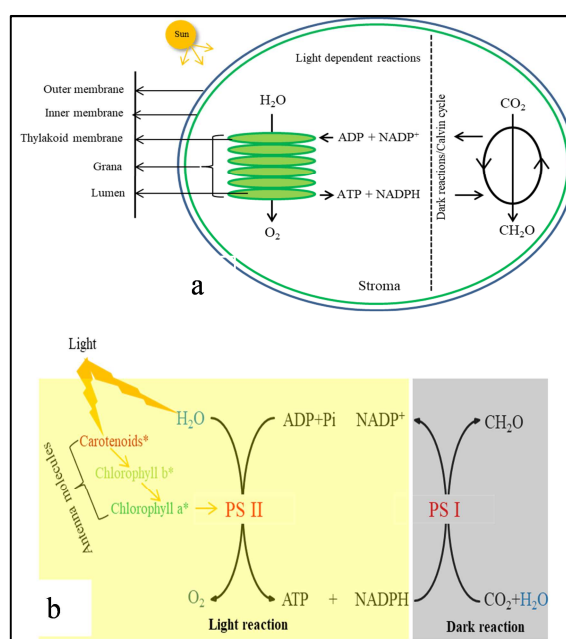
In plants, RCs are sited in the chloroplasts which are abundant in leaves, while in cyanobacteria they are localized in the plasmamembrane (Joyard *et al.*, 1991; Tavano and Donohue, 2006; Flores, 2008) therefore the prime organ of photosynthesis in plants is leaves (Reyes-Prieto *et al.*, 2007) that expose the maximum probable area to light (Hamlyn G. Jones, 1992). Each cell in the green tissue of leaves contains around 100 chloroplasts which are accountable for photosynthetic reactions (Reyes-Prieto *et al.*, 2007; Johnson, 2017). The fundamental reaction of photosynthesis is,



It consists of two major reactions; (i) light reaction where assimilatory energy is produced and (ii) dark reaction where assimilatory energy is consumed for reduction of carbon in producing carbohydrates. Photosynthesis is important for feeding the creatures but its efficiency greatly varies with  $\text{C}_3$ ,  $\text{C}_4$  and CAM (Crassulacean acid metabolism) plants. Photorespiration in  $\text{C}_3$  plants causes around 25% carbon loss while absence of this ham-fisted process in  $\text{C}_4$  and CAM there is no carbon loss occur. Nowadays scientists are trying to overcome photorespiration by introducing a maize-like ( $\text{C}_4$ ) photosynthetic pathway in  $\text{C}_3$  plants specially in rice which is anticipated to increase around 50% photosynthetic efficiency. So, it is foremost and crucial to have a clear sense about these enter processes. Therefore, this current flurry of work aims to present a well understanding about photosynthesis process and how to overcome carbon loss by fixing maize-like photosynthetic pathway.

## Fundamentals of photosynthesis

Life is almost incredible without photosynthesis as it bestows  $\text{O}_2$  to breathe and reduces mischievous  $\text{CO}_2$  for food ( $\text{CH}_2\text{O}$ ) through solar energy (Rabinowitch, 1956; Calvin, 1989; Whitmarsh, 1999). In this process,  $\text{O}_2$  derives from  $\text{H}_2\text{O}$  (Hill 1939) and chlorophyll primarily delivers electron ( $e^-$ ) to yield NADPH and ATP in presence of light (light reaction) (Raven *et al.*, 2005; Ziehe *et al.*, 2018; Onge, 2018) to meet up the demand for  $\text{CO}_2$  assimilation in dark reaction (Calvin-Benson cycle) (Calvin and Benson, 1948; Bassham *et al.*, 1950; Badger and Price, 2003).

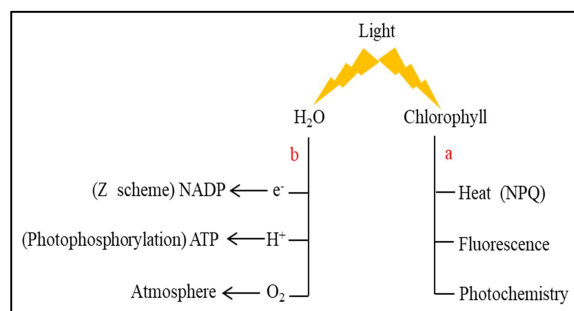


**Fig. 1. (a and b)** Fundamental mechanisms (light and dark reactions) of photosynthesis.

## Light reaction

Photosynthesis initiates with light reaction that takes place in the thylakoid membrane of chloroplast (Mullineaux, 1999; Tavano and Donohue, 2006; Ziehe *et al.*, 2018). Light reaction involves two light activated reactions, (a) photo-excitation of chlorophyll (Whatley and Allen, 1954; Green and Durnford, 1996; Allen and Forsberg, 2001; Chitnis, 2001) and (b) Photolysis of water or water oxidation that generates  $\text{H}^+$ ,  $e^-$  and  $\text{O}_2$  (Hill, 1939; Grossman *et al.*, 1995; Green and Durnford, 1996; Blankenship and Hartman, 1998; Asada, 1999; Tommos and Babcock, 1999; Haldrup *et al.*, 2001; Allen and Forsberg, 2001; Blankenship, 2002) (Fig. 2).

As these reactions depend on light, these are familiar as light reaction in which chlorophyll is primary and water is secondary electron donor (Campbell *et al.*, 2006; Onge, 2018).

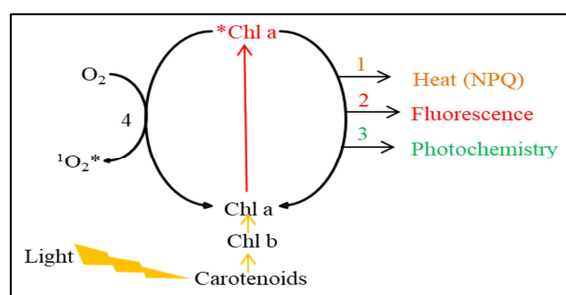


**Fig. 2.** An outline of light reaction.

#### Photo-excitation of chlorophyll

Once chlorophyll molecule (P680 in photosystem II and P700 in photosystem I) gets solar energy it becomes energy rich and excited (\*Chl) (Whatley and Allen, 1954; Allen and Forsberg, 2001) which ejects one electron and becomes oxidized with a positive charge that known as ionized or protonated chlorophyll (Chl<sup>+</sup>) (Grossman *et al.*, 1995; Green and Durnford, 1996; Barber *et al.*, 1999; Allen and Forsberg, 2001; Chitnis, 2001; Adams *et al.*, 2005).

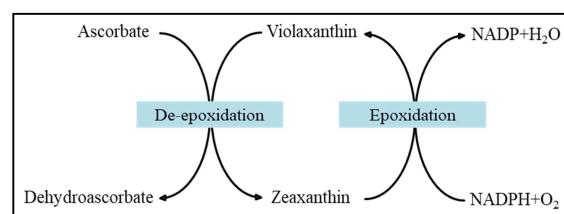
The \*Chl ease back to Chl<sup>+</sup> by four pathways: (1) emitting energy in the form of heat via violaxanthin-antheraxanthin-zeaxanthin (VAZ pathway) or xanthophylls cycle which is recognized as non-photochemical quenching (NPQ) or thermal heat dissipation. (Yamamoto *et al.*, 1962; Bilger and Bjorkman, 1990; Niyogi *et al.*, 1998, Niyogi, 1999, 2000); (2) in the form fluorescence light (F) (Adams *et al.*, 1990; Maxwell and Johnson, 2000; Rosenqvist and van Kooten, 2003; Earl and Ennahli, 2004; Baker, 2008); (3) photochemistry i.e. transmitting the energy across Photosystem II (PSII), the photosynthetic electron transport chain (PETC), and Photosystem I (PSI), resulting in the reduction of NADP<sup>+</sup> to NADPH (Grossman *et al.*, 1995; Fryer *et al.*, 1998; Allen and Forsberg, 2001; Ziehe *et al.*, 2018; Onge, 2018) and (4) shifting energy to molecular oxygen to form singlet oxygen (<sup>1</sup>O<sub>2</sub><sup>\*</sup>) (Krieger-Liszkay, 2005; Krieger-Liszkay *et al.*, 2008; Stephen *et al.*, 2010; Takagi *et al.*, 2016b).



**Fig. 3.** Fates of excited Chlorophyll.

#### Non-photochemical quenching (NPQ)/Heat dissipation

Heat dissipation occurs through xanthophyll cycle or VAZ pathway that comprises of violaxanthin, antheraxanthin, and zeaxanthin pigments (Müller *et al.*, 2001; Müller *et al.*, 2002; Horton and Ruban, 2005; Cazzaniga *et al.*, 2016). In moderate light conditions, violaxanthin is the most abundant pigment, whereas under high light, violaxanthin de-epoxidase and converts into zeaxanthin via antheraxanthin (an intermediate pigment), by this process plants eliminated more than 75% of absorbed photons (Yamamoto *et al.*, 1962; Bilger and Bjorkman, 1990; Pfündel and Bilger, 1994; Demming-Adams *et al.*, 1996; Demming-Adams *et al.*, 1998; Niyogi *et al.*, 1998, Niyogi, 2000; Horton and Ruban, 2005).



**Fig 4** VAZ/Xanthophyll cycle.

#### Chlorophyll fluorescence

The excited chlorophyll dissipates its energy through four fates i.e. photochemical quenching or charge separation (photosynthesis), non-photochemical quenching (NPQ), generating <sup>1</sup>O<sub>2</sub><sup>\*</sup>, and chlorophyll fluorescence (Yamamoto *et al.*, 1962; Adams *et al.*, 1990; Bilger and Bjorkman, 1990; Grossman *et al.*, 1995; Niyogi *et al.*, 1998; Fryer *et al.*, 1998; Asada, 1999; Niyogi, 2000; Maxwell and Johnson, 2000; Allen and Forsberg, 2001; Rosenqvist and van Kooten, 2003; Earl and Ennahli, 2004; Krieger-Liszkay, 2005; Baker, 2008; Stephen *et al.*, 2010; Ziehe *et al.*, 2018; Onge, 2018).

These processes compete with each other, i.e., an augment in the efficiency of one will result in a decrease of the others. By measuring the fluorescence, photochemical quenching ( $q^P$ ) and non-photochemical quenching (NPQ) can be calculated (Murchie and Lawson, 2013; Terletskaia *et al.*, 2018; Guidi *et al.*, 2019; Terletskaia *et al.*, 2020). Indeed, chlorophyll fluorescence gives a rapid and non-destructive means of studying plants' photosynthetic performance (Adams *et al.*, 1990; Krause and Weis, 1991; Maxwell and Johnson, 2000; Baker, 2008; Bussotti *et al.*, 2020). Normally it is done with a pulse amplitude modulated (PAM) fluorometer. Usually the sample plants need to dark adjusted for at least 10-15 minutes prior to reading. This dark adjustment allows all the electrons in PSII passes through to the end of the electron chain, rendering all of the reaction centers open ( $Q_A$ ). Upon revealing to light,  $Q_A$  receives an electron and becomes  $Q_A^-$  thus the reaction center is termed to be 'closed' which leads to maximize fluorescence yield (Adams *et al.*, 1990; Maxwell and Johnson, 2000; Rosenqvist and van Kooten, 2003; Earl and Ennahli 2004; Baker, 2008).

As chlorophyll fluorescence is a fluent way for photo-biological research, the most useful parameters are crucial to discuss. Such as,

$F_0$ : Minimum fluorescence level in a dark adjusted leaf where photochemical quenching,  $q^P=1$  and non-photochemical quenching,  $q^N=0$ . In this case, PSII reaction center is open ( $Q_A$ ) for taking electron from pheophytin.

$F_m$ : Maximum fluorescence level where  $q^P=0$  and  $q^N=0$ . Here, the reaction center of PSII is closed ( $Q_A^-$ ) for taking electron from pheophytin.

$F_v$ : Variable fluorescence designated by  $F_m-F_0$ ; maximum variable Chl fluorescence occurs when all non-photochemical processes are at minimum.

$F_v/F_m$ : Quantum efficiency ( $\Phi_{PSII}$ ) or potential quantum yield of PSII in a dark adapted leaf.

$F_v/F_m$  is a key measuring tool for photosystems health determination. Typical the values of  $F_v/F_m$  for most

plant species ranges from 0.78–0.87 and values drop than that will be seen when the plants are subjected to stress. (Kitajima and Butler, 1975; Bjorkman and Demmig, 1987; Adams *et al.*, 1990; Johnson *et al.*, 1993; Adams and Demmig-Adams, 2004).

For example, an elevated  $F_v/F_m$  value of 0.854 suggests that the photosystems are running at 85.4% proficiency and indicates everything inside PSII is operating properly and specifically. On the other hand low  $F_v/F_m$  value of 0.628 suggests that the photosystems are running at 62.8% proficiency demonstrating the photosystems are most likely stressed and/or damaged.

#### *Photolysis of water or water oxidation*

Upon exposure to light photolysis of water takes place in the lumen of thylakoid membrane through water oxidation complex (WOC) and generates  $H^+$ ,  $e^-$  and  $O_2$  (Fig. 2) (Hill, 1939; Joliot *et al.*, 1969; Kok *et al.*, 1970; Blankenship and Hartman, 1998; Asada, 1999; Allen and Forsberg, 2001; Blankenship, 2002; Pushkar *et al.*, 2008).

The  $O_2$  expels to the environment and ATP synthase pumps  $H^+$  from lumen to stroma in order to generate ATP which is known as photophosphorylation (Arnon, 1956; Hoganson and Babcock, 1997; Haraux and Kouchkovsky, 1998; Stock *et al.*, 1999). Finally, the electron ( $e^-$ ) is terminated to NADPH travelling through the direction  $H_2O$ ---PSII---PQ---Cytchrome  $b_6f$ ---PC---PSI (Allen and Forsberg, 2001; Blankenship, 2002; Pushkar *et al.*, 2008). Here, the ATP and NADPH are collectively known as assimilatory power (Karplus *et al.*, 1991; Raven *et al.*, 2005; Ziehe *et al.*, 2018; Onge, 2018).

#### *Photophosphorylation*

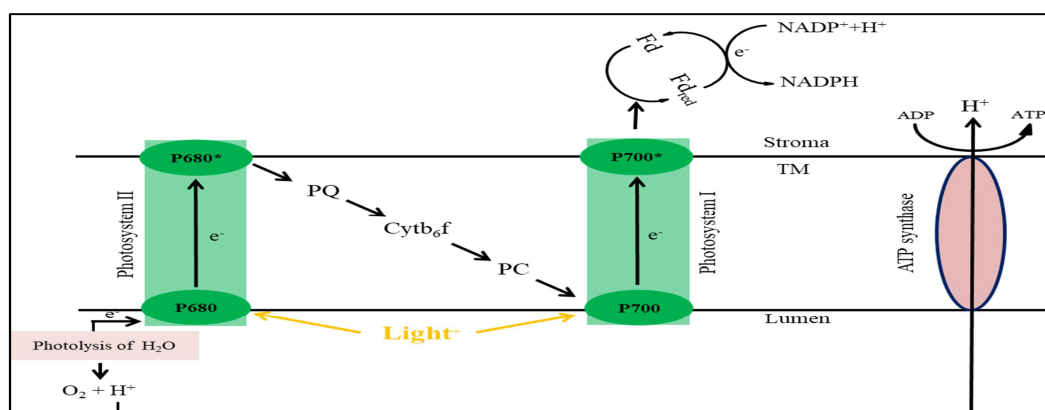
ATP forms due to a hydrogen ion ( $H^+$ ) gradient across the thylakoid membrane (Mitchell, 1966). Indeed, the energy that begins the synthesis of ATP derives from the 'osmosis' of protons through thylakoid membrane from lumen to stroma (Whatley and Allen, 1954; Arnon, 1956; Hoganson and Babcock, 1997; Haraux and Kouchkovsky, 1998; Stock *et al.*, 1999).

There are two types of photophosphorylation; (i) Non-cyclic and (ii) Cyclic photophosphorylation.

#### *Non-cyclic photophosphorylation/linear electron transport pathway*

Non-cyclic photophosphorylation involves linear electron movement i.e. electron derives from  $H_2O$  and ends to NADPH via PSII---PQ---Cytochrome  $b_6f$ ---PC---PSI

which looks like a 'Z-fashion' of electron flow. During PETC,  $H^+$  is pumped from lumen to stroma and generates ATP (Whatley and Allen, 1954; Arnon, 1956; Fajer *et al.*, 1977; Hoganson and Babcock, 1997; Haraux and Kouchkovsky, 1998; Asada, 1999; Stock *et al.*, 1999; Haldrup *et al.*, 2001; Allen and Forsberg, 2001; Blankenship, 2002; Takagi *et al.*, 2017a; Takagi and Miyake, 2018).



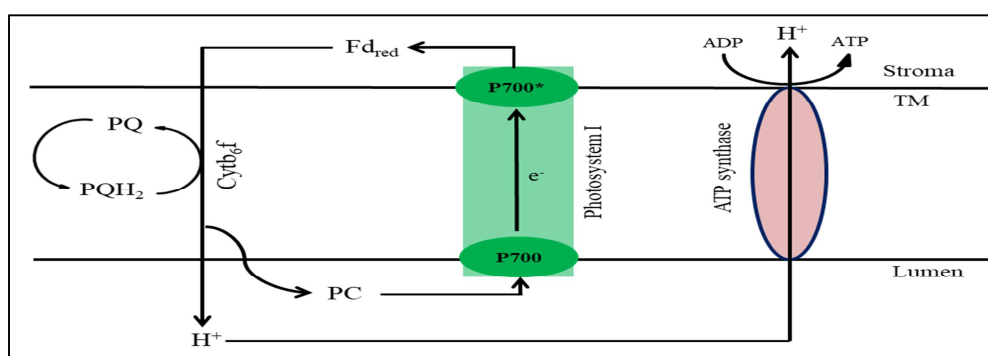
**Fig 5** Z-Scheme/Z fashion/non-cyclic electron flow.

#### *Cyclic photophosphorylation*

Here electron moves cyclically through PSI---Cytochrome  $b_6f$  complex---PC---PSI i.e. the initial electron donor and final electron acceptor is PSI (Asada, 1999; Allen and Forsberg, 2001; Blankenship, 2002; Pushkar *et al.*, 2008; Munekage *et al.*, 2016). In case of cyclic electron flow around PSI, the reduced ferredoxin ( $Fd_{red}$ ) transfers electron to plastoquinone (PQ) pool which is known as electron shuttling. Later on, when PQ shifts electron to Cyt  $b_6f$  complex, two protons ( $H^+$ ) from stroma are added to PQ and becomes  $PQH_2$ . Here, Q cycle is accountable for transferring protons from stroma to lumen. However, a lack of PQ can impede the operation of the Q-cycle

(Mitchell, 1966) and suppress electron transport in Cyt $b_6f$  complex. Finally, the luminal protons are pumped to stroma and generate ATP (Whatley and Allen, 1954; Arnon, 1956; Hoganson and Babcock, 1997; Stock *et al.*, 1999). Cyclic photophosphorylation has crucial role on photosynthesis (Suorsa, 2015).

Normally, photosynthesis requires 3ATP/2NADPH ratio whereas the linear electron flow is capable to support only 2.57ATP/2NADPH, offers the Q-cycle (Cyclic photophosphorylation) mandatorily runs in chloroplasts (Rich and Bendall, 1981; Rich, 1988; Sacksteder *et al.*, 2000) which covers at least 17% proton deficiency.



**Fig. 6.** Cyclic photophosphorylation.



### Photoinhibition

Photo inhibition is light-induced injury of oxygen evolution, electron-transport activity of PSII thus in photosynthetic capacity of plant, algae or cyanobacteria (Aro *et al.*, 1993, 1993; Baker, 1996; Murata *et al.*, 2007; Murata *et al.*, 2012). Among the two photosystems, PSII is more sensitive to light which is termed as light-induced damage of PSII (Kok, 1956; Jegerschoeld *et al.*, 1990; Aro *et al.*, 1993; Adams *et al.*, 2005).

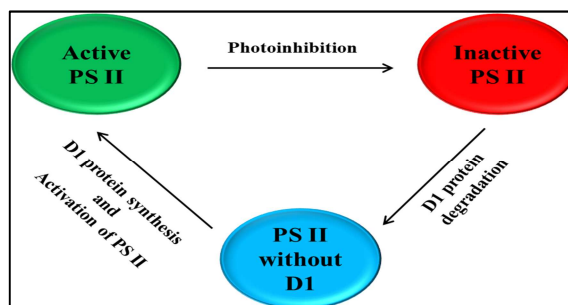
### Acceptor side photoinhibition

Strong light lowers the plastoquinone (PQ) pool, which leads to protonation and double reduction of the  $Q_A$  electron acceptor of Photosystem II, consequently  $Q_A$  do not function in electron transport system. The double reduction of the PQ acceptor ( $Q_A^{2-}$ ) leads to the formation of primary radical pair  $P680^+Pheo^-$ , subsequently the formation of  $P680$  in the triplet excited state, which reacts with  $O_2$  to form the highly toxic singlet oxygen ( $^1O_2$ ) (Jung and Kim, 1990; Krieger-Liszka *et al.*, 2008) causing acceptor-side inhibition of PSII electron transport (Jegerschoeld *et al.*, 1990; Vass *et al.*, 1992; Aro *et al.*, 1993; Tyystjärvi and Aro, 1996; Tyystjärvi, 2008).

### Donor side photoinhibition

Water donates electron to  $P680^+$  to produce  $P680$  (So-called donor side). Photo damage to PSII occurs by two successive steps: (i) light-dependent destruction of the Mn cluster of the oxygen-evolving complex which comprises of 4 Mn, one Ca and one Cl atom (Tyystjärvi and Aro, 1996; Sauer and Yachandra, 2004) and (ii) inactivation of the PSII RCs by light (Ohnishi *et al.*, 2005). Water gives electron to highly-oxidizing  $P680^+$  (Hill, 1939) but inhibition of electron donation to the  $P680$  RCs expands the lifetime of  $P680^+$ , which is believed to cause donor-side inhibition, deactivation of PSII electron transport system and polypeptide damage of D1 protein (Callahan *et al.*, 1986; Hakala *et al.*, 2005; Ohnishi *et al.*, 2005). Therefore, on the electron donor side of PSII, photo-oxidized  $P680$  ( $P680^+$ ) oxidizes  $H_2O$  with the evolution of  $O_2$  through the help of the oxygen-evolving complex (Tyystjärvi, 2008; Nathan and Wolfgang, 2015). In addition, the

low pH in the lumen of thylakoid membrane suppresses the electron transport from  $H_2O$  to  $P680$  in PSII (Krieger-Liszka, 2005). Thus, the long-lived  $P680^+$  deactivates WOC seriously. This photoinhibited PSII RCs are continuously restored via degradation and synthesis of the D1 protein within several hours (Yokthongwattana and Melis, 2008; Kok, 1956) (Fig. 7).



**Fig. 7.** Rebuild the photosynthetic reaction center of PSII via degradation and synthesis of the D1 protein.

Photo inhibition to PSI occurs when the supply of electrons from PSII exceeds its capacity (Tikkanen and Grebe, 2018; Shimakawa and Miyake, 2018) that makes a dysfunction in the  $[4Fe-4S]$  clusters on the acceptor side of PSI (Mehler, 1951; Satoh, 1970; Inoue *et al.*, 1986; Asada, 2006; Sonoike, 2011; Rutherford *et al.*, 2012). PSI photo inhibition scarcely happens in comparison with PSII photo inhibition because PSI is less frequently damaged due to a very effective photo protection mechanism (ROS detoxification system) which can avert photo inhibition (Gururani *et al.*, 2015). But in contrast to PSII, the damaged PSI takes a long time (days or weeks) to completely recover (Zivcak *et al.*, 2015b). Therefore, PSI photo inhibition is a lethal for oxygenic photoautotrophs.

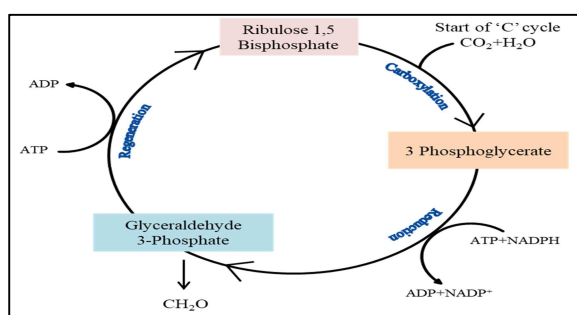
### Photo protection

Plants are fortified with diversified photo protective approaches to prevent photo inhibition (Anderson *et al.*, 1997; Adams *et al.*, 2005; Jung and Niyogi, 2008; Bailey and Grossman, 2008; Johnson *et al.*, 2011.). First of all, plants can protect themselves from excess light by avoiding absorption of the light. Plants use varied photo receptors to detect the light intensity, direction and duration that have capability to shift chloroplasts within the cell (chloroplast avoidance) and reduce antenna size (antenna size reduction)

from the surplus light thus reducing the detrimental consequences (Galvão and Fankhauser, 2015). Second, plants can lessen the amount of absorbed energy by thermal dissipation (NPQ) through xanthophyll cycle or VAZ pathway (Horton and Ruban, 2005; Müller *et al.*, 2001). Third, plants transfer electrons through alternative pathways (other than  $\text{CO}_2$ ) to alleviate excitation pressure (Asada, 1999; Ort, 2001). Fourth, plants have antioxidants (Table 1) defense system to detoxify ROS (Bartley and Scolnik, 1995; Smirnov, 2000; Zheng *et al.*, 2019; Tahjib-Ul-Arif *et al.*, 2020) and fifth, plants produce a diversity of secondary metabolites favorable for their survival and protection from excess light (Zheng *et al.*, 2019).

#### Dark reaction

Light is not obligatory for the accomplishment of dark reaction. The NADPH and ATP which are generated by light reaction consumed at dark reaction to reduce  $\text{CO}_2$  to  $\text{CH}_2\text{O}$  via a series of biochemical reactions such as (i) carboxylation, during which  $\text{CO}_2$  is allied to ribulose 1,5 biphosphate; (ii) reduction, during which carbohydrate is formed with the cost of the photo chemically derived ATP and NADPH; and (iii) regeneration, which re-forms ribulose 1,5-biphosphate as further  $\text{CO}_2$  receiver (Calvin and Benson, 1948; Bassham *et al.*, 1950).

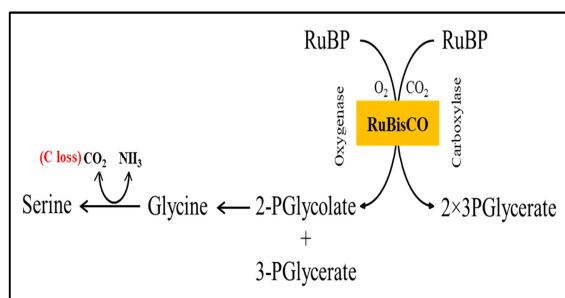


**Fig. 8.** Dark reaction or Calvin cycle or  $\text{C}_3$  cycle.

#### $\text{C}_3$ photosynthesis and photorespiration

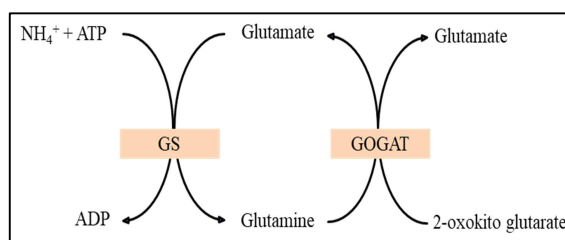
Competitive inhibition of carboxylase activity of RuBisCO leads to enhance its oxygenase activity (Fig. 9), which is known as photorespiration (Sharkey, 1988; Chen and Spreitzer, 1992; Griffiths, 2006; Leegood, 2007; Jones *et al.*, 2013). Actually, photorespiration reduces the efficiency of  $\text{CO}_2$

assimilation and thus yield of  $\text{C}_3$  plants such as rice, wheat, soybean, potato etc. In  $\text{C}_3$  plants, both the  $\text{C}_3$  (Photosynthetic Carbon Reduction) and  $\text{C}_2$  (Photosynthetic Carbon Oxidation) cycle occurs in mesophyll cells during day time. Inhibition of carboxylase activity of RuBisCO generates 1 molecule of phosphoglycolate ( $\text{PG}=\text{2C}$ ; the  $\text{C}_2$  cycle) and 1 molecule of PGA ( $3\text{C}$ ) (Igamberdiev, 2015). This chloroplastic PG converts to glyoxylate by oxidation in peroxisomes and finally it converts into glycine (Wingler *et al.*, 1999; Eisenhut *et al.*, 2008; South *et al.*, 2019). In mitochondria, 2 molecule of glycine ( $2 \times 2\text{C}$ ) is converted to 1 molecule of serine ( $3\text{C}$ ) by liberating  $\text{CO}_2$  and  $\text{NH}_3$  (Sharkey, 1988; Rachmilevitch *et al.*, 2004). By this process 25% assimilatory carbons are lost and consequently remarkable yield loss observe in  $\text{C}_3$  plants (Griffiths, 2006; Leegood, 2007; Jones *et al.*, 2013).



**Fig. 9.** Competitive inhibition of  $\text{CO}_2$  fixation and photorespiration.

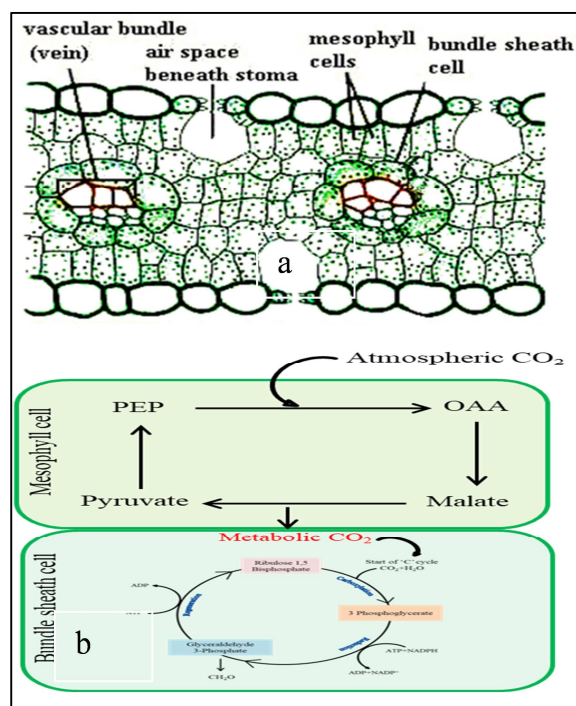
The photo respiratory  $\text{NH}_3$  is lethal for plants and it essentials to be detoxified or re-assimilated for plant's survival (Rachmilevitch *et al.*, 2004). In plants glutamine synthetase-glutamate synthase (GS-GOGAT) mediated cycle (Fig. 10) is accountable for the detoxification or re-assimilation of photo respiratory  $\text{NH}_3$  (Miflin and Lea, 1976; Hossain *et al.*, 2012).



**Fig. 10.** Re-assimilation of photorespiratory  $\text{NH}_3$  by GS-GOGAT cycle.

### C<sub>4</sub> Photosynthesis

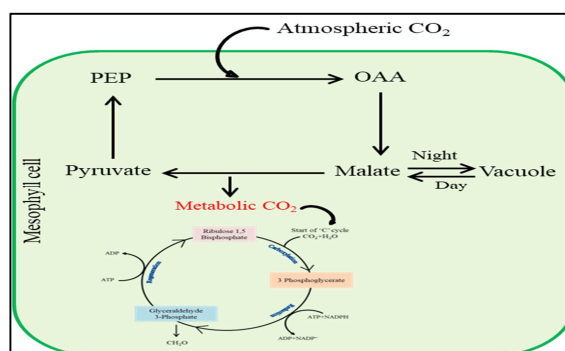
Photorespiration occurs when plants take O<sub>2</sub> and release CO<sub>2</sub> instead of taking CO<sub>2</sub> and releasing O<sub>2</sub> (Sharkey, 1988; Griffiths, 2006; Jones *et al.*, 2013). To escape photorespiration, C<sub>4</sub> plants (maize, millet, sugarcane, sorghum) evolve a special CO<sub>2</sub> fixation mechanism (von Caemmerer and Furbank, 2003; Sage, 2004; von Caemmerer *et al.*, 2017; Schluter and Weber, 2020). In C<sub>4</sub> plants RuBisCO activity occurs in bundle sheath cells instead of mesophyll cells which are familiar as Kranz anatomy (Ehleringer *et al.*, 1991; Sage and Sage, 2009; Hermida Carrera *et al.*, 2016; Bellasio and Lundgren, 2016) (Fig. 11a and b). Therefore, RuBisCO continuously gets high concentrated or metabolic CO<sub>2</sub> that ensures its carboxylase activity, therefore higher yield. Alternatively oxygenase activity of RuBisCO is suppressed so there is negligible or no photorespiration in C<sub>4</sub> plants (von Caemmerer and Furbank, 2003). That is why, C<sub>4</sub> species are more efficient at carbon assimilation than C<sub>3</sub> species, and in addition they present high water use efficiency, better nitrogen use efficiency, extreme temperature tolerance and increased yield (Evans *et al.*, 2008; Hibberd *et al.*, 2008; Kellogg, 2013; Bellasio, 2017).



**Fig. 11. (a)** Kranz anatomy in C<sub>4</sub> plants and **(b)** mechanism to avoid photorespiration in C<sub>4</sub> plants.

### Crassulacean acid metabolism (CAM) Photosynthesis

An exceptional pathway for carbon reduction is evolved in arid plants which are known as CAM (Bonner and Bonner, 1948; Ting, 1985; Bastide *et al.*, 1993; Cushman, 2001). CAM plant opens its stomata at night and closes during day. This adjustment helps the CAM plants to conserve moisture during the day time (Chu *et al.*, 1990; Ranson and Thomas, 1960; Lüttge, 2004; Forseth, 2010). At night, CAM plants take CO<sub>2</sub> through open stomata and fix CO<sub>2</sub> the similar way as C<sub>4</sub> plants do but they store the malic acid (malate) in vacuole (Fioretto and Alfani, 1988; Keeley, 1998; Keeley and Rundel, 2003; Martin *et al.*, 2005). During day time, CAM plants use that malate as their source of CO<sub>2</sub> for Calvin cycle (Bonner and Bonner, 1948; Guralnick and Jackson, 2001; Lüttge, 2004; Forseth, 2010; Hultine *et al.*, 2019).



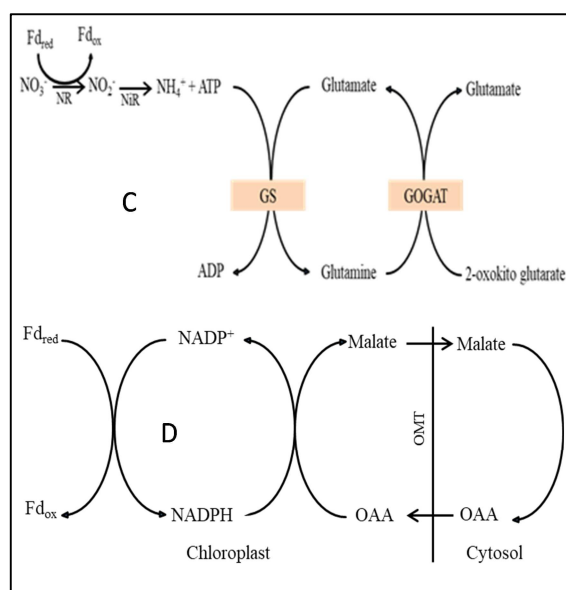
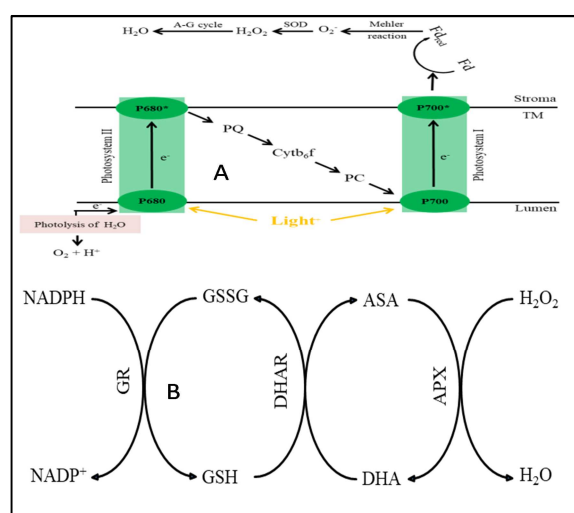
**Fig. 12.** Mechanism for avoiding transpiration in CAM plants.

### Competition among the alternative sinks during carbon reaction

Photosynthetic carbon metabolism provides the foremost sink for NADPH and ATP produced in light reaction (Tommos and Babcock, 1999; Asada, 1999, 2000; Haldrup *et al.*, 2001; Allen and Forsberg, 2001; Blankenship, 2002; Raven *et al.*, 2005; Ziehe *et al.*, 2018; Onge, 2018). On the other hand CO<sub>2</sub> is the major sink for electrons mainly in the linear electron transport system (Calvin and Benson, 1948; Bassham *et al.*, 1950; Badger and Price, 2003). But, this route is highly competitive since there are some alternative acceptors/routes of electron. Generally, in plants there are three major alternative routes of electron such as (i) Mehler-type O<sub>2</sub> reduction at the acceptor side of PSI, followed by ascorbate peroxidase reaction



(pseudocyclic electron transport/water–water cycle) (Mehler, 1951; Fryer *et al.*, 1998; Asada, 1999, 2000; Clarke and Johnson, 2001; Polash *et al.*, 2019); (ii) nitrite reduction which might consume up to about one tenth of the number of quanta used in photosynthetic C-metabolism (Guerrero *et al.*, 1981; Robinson, 1988, 1990); and (iii) the ‘malate valve’ that plays a significant role as a poisoning mechanism to adjust the ATP/NADPH ratio in the stroma (Ebbighausen *et al.*, 1987; Heineke *et al.*, 1991; Fridlyand *et al.*, 1998; Scheibe *et al.*, 2005; Selinski and Scheibe, 2019).



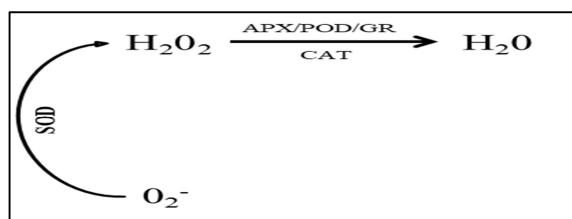
**Fig. 13.** (a) Mehler-type O<sub>2</sub> reduction at PSI, followed by (b) ascorbate-gultathion cycle, (c) nitrite reduction and (d) malate valve.

### Chloroplastic Antioxidants

Chloroplast is one of the most potential generators of Reactive Oxygen Species (ROS), such as O<sub>2</sub><sup>•-</sup>, H<sub>2</sub>O<sub>2</sub>, <sup>•</sup>OH and <sup>1</sup>O<sub>2</sub> (Asada, 2000; Muller *et al.*, 2001; Jung and Niyogi, 2008). To minimize oxidative damage carried out by ROS, chloroplast is naturally equipped with antioxidant defense systems.

**Table 1.** Role of chloroplastic antioxidants to reduce the oxidative damage carried out by ROS.

SL	Antioxidant	Roles	References
1	Catotenoides	i. Light harvesting via singlet state energy transfer ii. Photo protection via the quenching of chlorophyll (3Chl) triplet states iii. Singlet oxygen scavenging iv. Excess energy dissipation v. Structure stabilization	Frank and Cogdell, 1993; Frank and Cogdell, 1996; Baroli and Niyogi, 2000; Cazzaniga <i>et al.</i> , 2016
2	Tocopherols	i. Scavenge singlet oxygen ( <sup>1</sup> O <sub>2</sub> )	Fryer, 1992; Niyogi, 1999; Munne-Bosch and Alegre, 2002; Foyer <i>et al.</i> , 2008
3	Ascorbate-peroxidase (APXs)	i. It can remove ROS directly by acting as a cofactor of ascorbate peroxidases in the elimination of H <sub>2</sub> O <sub>2</sub> ii. It also acts as a cofactor of violaxanthin de-epoxidase in the xanthophyll cycle	Smirnoff, 2000, Conklin, 2001; Muller-Moule <i>et al.</i> , 2002; Tahjib-Ul-Arif <i>et al.</i> , 2019
4	Superoxide dismutase (SOD)	i. SOD commences the process of ROS detoxification by converting super oxide to hydrogen peroxide	Alscher <i>et al.</i> , 2002, Jalali-e-Emam <i>et al.</i> , 2011; Sohag <i>et al.</i> , 2020
5	Catalase (CAT)	i. CAT converts hydrogen peroxide into oxygen and water to remove the peroxide in plants	Tahjib-Ul-Arif <i>et al.</i> , 2019; Tahjib-Ul-Arif <i>et al.</i> , 2020
6	Glutathion	i. in the absence of an enzyme, glutathione is able to interact rapidly with free radicals such as superoxide and the hydroxyl radical	Alscher, 1989; Noctor and Foyer, 1998; Polle, 2001; Foyer <i>et al.</i> , 2005
7	Anthocyanin	i. Photo protection ii. ROS detoxification	Zheng <i>et al.</i> , 2019



**Fig. 14.** Antioxidant regulation in chloroplast for the detoxification of ROS.

#### *C<sub>4</sub> rice development through modification of photosynthesis*

The C<sub>4</sub> rice consortium is attempting to fix a maize-like photosynthetic pathway to overcome its yield barrier and to introduce “climate-smart” rice which will yield more under rising temperature and decreasing water availability (Rizal *et al.*, 2012; von Caemmerer *et al.*, 2012; Bellasio, 2017; Wang *et al.*, 2017; Ermakova *et al.*, 2020). ‘C<sub>4</sub>’ characters into rice is anticipated to increase around 50% photosynthetic efficiency, improve nitrogen and water use efficiency (von Caemmerer *et al.*, 2012; Bellasio and Farquhar, 2019).

#### *Evolutionary change*

C<sub>3</sub> species + anatomical change + biochemical change + fine tuning = C<sub>4</sub> species

#### *Anatomical Change*

##### *Development of Kranz anatomy*

Improve the number and size of chloroplast in bundle sheath cells of rice leaf (Matsuoka *et al.*, 1994; Nomura *et al.*, 2005; Wang *et al.*, 2013; Wang *et al.*, 2016; Reeves *et al.*, 2017; Sedelnikova *et al.*, 2018; Lin *et al.*, 2020).

##### *Alternation of metabolism*

In addition to the core C<sub>4</sub> enzymes viz. CA, PEPC, PPDK, NADP-MDH and NADP-ME, C<sub>4</sub> pathway also needs enclosure of metabolite transporters for oxaloacetate, malate, triosephosphate and pyruvate to give increased transport capacity for the C<sub>4</sub> cycle intermediates so that the Calvin cycle can role efficiently (Chen *et al.*, 2001; Weber and von. Caemmerer, 2010; Danila *et al.*, 2018).

#### *Biochemical Change*

##### *Single-cell model or mesophyll cells only*

Decreasing in expression of CA in chloroplast and GDC (glycine decarboxylase) assist to reduce

photorespiration. It is predicted that single cell C<sub>4</sub> system could be faster to install in C<sub>3</sub> plants (Miyao *et al.*, 2011). To introduce single cell C<sub>4</sub>-like pathway, mesophyll cells is made to capture and release CO<sub>2</sub> in the manner that takes place in *Hydrilla verticillata* (Ku *et al.*, 1999; Fukayama *et al.*, 2001; Tsuchida *et al.*, 2001; Taniguchi *et al.*, 2008).

Sage and Sage, (2009) revealed that chlorenchyma structure in rice and related *Oryza* species has adaptation to scavenge photo-respired CO<sub>2</sub> and to enhance the diffusive conductance of CO<sub>2</sub>.

#### *Double-cell model*

Double cell model involves the alteration in mesophyll cells by (i) decreasing the activity of Calvin cycle and photorespiration, (ii) demoting the expression of RuBisCO and GDC (iii) stimulating the expression of CA, PEPC in cytosol and PPDK, NADP-MDH in chloroplast and in Bundle sheath cells by (i) introducing of Calvin cycle activity, (ii) stimulating the expression of RuBisCO, GDC, PEP-CK, NADP-ME (Monson and Rawsthorne, 2000; Häusler *et al.*, 2002; Danila *et al.*, 2018).

#### *Metabolic Engineering and Omic approach for C<sub>4</sub> rice development*

It implies development of mechanism that fruitfully capture the photo-respired CO<sub>2</sub> to the site of photosynthesis by transferring the *Escherichia coli* glycolate catabolic pathway to chloroplasts in which glycolate in chloroplast expects to convert glycerate directly (Matsuoka *et al.*, 2001; Kebeish *et al.*, 2007; Furbank *et al.*, 2009). However, it could be a question that does the use of bacterial gene is apt for C<sub>4</sub> rice engineering. Characterization of specific transporters such as OMT1 (2-oxoglutarate/malate transporter), DiT2 (dicarboxylate transporter 2), PPT1 (PEP/phosphate transporter), MEP (mesophyll envelop protein), TPT (triose-phosphate phosphate translocator) through proteomics in maize bundle sheath and mesophyll cells and then transfer into rice variety will assist in C<sub>4</sub> rice development (Hibberd *et al.*, 2008; Hudson *et al.*, 2013; Lyu *et al.*, 2020, Zamani-Nour *et al.*, 2020).

## Conclusion

The low yield of  $C_3$  plants are partly related to an alteration in the nitrogen supply especially through the grain filling period, early senescence of leaves and inherent inadequacy of  $C_3$  photosynthesis. Therefore, introductions of  $C_4$  traits into  $C_3$  rice will break the current stagnation by boosting up the photosynthetic proficiency along with increasing nitrogen and water use efficiency. Hence, evolving the  $C_4$  pathway into a  $C_3$  rice plant needs perfect understanding on the fundamental aspects of photosynthetic machinery and its regulation for efficient manipulation of anatomical, physiological and biochemical traits.

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