



The role of photosynthesis related pigments in light harvesting, photoprotection and enhancement of photosynthetic yield in plants

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Abstract

Photosynthetic pigments are an integral and vital part of all photosynthetic machinery and are present in different types and abundances throughout the photosynthetic apparatus. Chlorophyll, carotenoids and phycobilins are the prime photosynthetic pigments which facilitate efficient light absorption in plants, algae, and cyanobacteria. The chlorophyll family plays a vital role in light harvesting by absorbing light at different wavelengths and allowing photosynthetic organisms to adapt to different environments, either in the long-term or during transient changes in light. Carotenoids play diverse roles in photosynthesis, including light capture and as crucial antioxidants to reduce photodamage and photoinhibition. In the marine habitat, phycobilins capture a wide spectrum of light and have allowed cyanobacteria and red algae to colonise deep waters where other frequencies of light are attenuated by the water column. In this review, we discuss the potential strategies that photosynthetic pigments provide, coupled with development of molecular biological techniques, to improve crop yields through enhanced light harvesting, increased photoprotection and improved photosynthetic efficiency.

Keywords Anthocyanins · Carotenoids · Chlorophyll · Xanthophyll cycle · Nonphotochemical quenching · Phycobilins

Introduction

Photosynthesis is the process by which photosynthetic organisms utilize the energy from sunlight to assimilate CO₂ from the atmosphere and convert it into soluble carbohydrates, which are then used for plant growth (Bassham and Calvin 1960; Biel and Fomina 2015; Calvin and Benson 1948; Raines 2003). To meet global demand, the predicted requirement to increase crop yield, including the global

staples such as maize (*Zea mays*), wheat (*Triticum aestivum*) and soybean (*Glycine max*), is as much as 70–100% by 2050. This escalation is due to advancements in living standards and changing human diets as well as the heightened requirement for plant-based proteins for animal feed (FAO 2017; RSOL 2009; Tilman and Clark 2015; World-Bank 2008). Thus enhancement of photosynthetic efficiency is a crucial step to achieving these ends. Furthermore, given that current breeding approaches are no longer leading to significant genetic gains in yield (Ray et al. 2013, 2012), new approaches for increasing crop productivity such as manipulating photosynthesis related pigments to improve light capture and or photoprotection are called for.

Crop yield is the result of the cumulative photosynthetic rate during the growing season with the yield potential (maximal yield obtained) described as the maximum yield of plant growth under optimal healthy conditions (Evans and Fischer 1999). Yield potential is defined by three pivotal factors: (i) the capacity to capture light; (ii) the energy conversion efficiency also known as radiation use efficiency (RUE), which ultimately generates biomass and (iii) harvest index (HI), which is defined as the harvestable product in relation to total plant biomass (Reynolds et al.

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2009). Substantial increments in light capture and HI have been noted post green revolution and the introduction of dwarfing genes (Calderini et al. 1995; Gale and Yousefian 1985). The current focus for improving crop yields concentrates on enhancing RUE, which is defined by the photosynthetic rate and the efficiency at which light energy is converted to fixed carbon (Parry et al. 2011; Reynolds et al. 2009).

Several studies have reported that enhanced photosynthetic capacity can be achieved in leaves by increasing photosynthetic electron transport rates (Chida et al. 2007; Lopez-Calcano et al. 2020; Simkin et al. 2017b; Yadav et al. 2018), manipulating Calvin Benson Cycle (CBC) enzymes to increase energy conversion (Driever et al. 2017; Lefebvre et al. 2005; Lopez-Calcano et al. 2020; Simkin et al. 2015, 2017a, 2019; Raines et al. 2022), modifying photorespiration (López-Calcano et al. 2018; Simkin et al. 2017a; Timm et al. 2012), along with improving the kinetics of non-photochemical quenching (NPQ), a photoprotective mechanism employed by plants under high light stress, and the re-allocation of absorbed energy back into photosynthesis rather than being dissipated as heat (Glowacka et al. 2018; Kromdijk et al. 2016). Furthermore, recent studies have also suggested that increasing the photosynthetic capacity of non-foliar tissue such as fruits, stems and wheat ears could play a key role in improving yield (Simkin et al. 2020).

As outlined above, there is currently significant interest in manipulating photosynthetic processes to improve plant productivity, including efforts to maximize light harvesting and effective light use. At the core of this, are photosynthetic pigments, chlorophylls (Chl), carotenoids and/or phycobilins (in cyanobacteria), which play pivotal roles in both light harvesting and photoprotection of the photosynthetic apparatus and are therefore fundamental to our efforts to improve plant productivity (Mirkovic et al. 2017). In addition, pigments such as anthocyanins, though not being involved in light capture, act as photoprotectants, absorbing harmful UV rays, reducing photoinhibition and photodamage. Each pigment performs a specific function in the photosynthetic machinery and is also involved with its repair cycle (Croce and Van Amerongen 2014). This review focuses on the relative abundance and functions of pigments in the photosynthetic apparatus of photosynthetic organisms (plants, cyanobacteria, algae), and their contribution to the acclimation of these organisms to unique dynamic environments. In addition, we will highlight the potential use of these novel pigment to optimise light capture and thereby the overall carbon pool in planta to improve crop productivity, explored in a context of improving food production for a growing population (Simkin 2019; Simkin et al. 2019).

Chlorophylls in photosynthetic tissues

The Chlorophyll (Chl) family are essential pigments required by all photosynthetic organisms to absorb light energy and play a key role in acclimation to environments with a varied light spectra. The structure of Chl is similar to that of haemoglobin consisting of a cyclic tetrapyrrole ring, known as chlorin, which is linked to a central atom of magnesium instead of an iron-containing porphyrin compound (haeme) (Senge et al. 2014). The evolution of Chl has been unravelled to some extent via the stages of its biosynthetic pathway, which contains at least 17 steps with the earliest being identical to heme biosynthesis indicating the likelihood that these were adopted from this pathway (Beale 1999; Granick 1965). The later stages of Chl biosynthesis include (i) magnesium insertion and (ii) the formation of the characteristic ring structure (Raymond and Blankenship 2004).

Chlorophyll *a* (absorption maxima (λ_{\max}) 665 nm in 90% acetone) is found in the photosynthetic reaction centres (RC) and the light harvesting complexes and is the main collector of light energy (400–450 nm, 660–675 nm) transferred to the RC. The substitution of the formyl group at the chlorin ring of Chl *a* for a methyl or vinyl group leads to the formation of Chl *b*, Chl *c*, Chl *d*, and Chl *f* with differential spectral properties and variation in λ_{\max} (Chen and Blankenship 2011). Terrestrial plants only possess Chl *a* and Chl *b* (Kume et al. 2018), whereas marine organisms contain a wide range of Chl (*a*, *b*, *c1*, *c2*, *c3*, *d* and *f*) that enables them to adapt to the aquatic environment and variations in solar radiation (i.e., blue-green light) at different depths (Croce and Van Amerongen 2014; Kirk 2011) (see Fig. 1). All photosynthetic pigments eventually transfer absorbed light to Chl *a* (Fig. 2) in the RC and Chl *a* is the most abundant form of chlorophyll in terrestrial plants, present in both the light harvesting complexes and reaction centres of almost all organisms capable of oxygenic photosynthesis (Croce and Van Amerongen 2014). Higher plants, algae and prokaryotes contain different chlorophyll compositions often dictated by adaptation to their surrounding environment.

Chl *b* (λ_{\max} ~ 450 nm; blue light) is only found in the antennae of the light harvesting complexes (Croce 2012; Kume et al. 2018). Chl *b* binding influences the protein levels in the antenna complexes and thereby the final size (truncated antenna with low Chl *b* levels) and composition of antenna. Therefore, Chl *b* has a critical role in the stacking of grana, harvesting light at lower light intensities as well as photoprotection (see Fig. 2) (Kume et al. 2018; Voitsekhovskaja and Tyutereva 2015). The ratios of Chl *a* to *b* have been shown to be variable dependent on environmental conditions, including light levels, nutrient

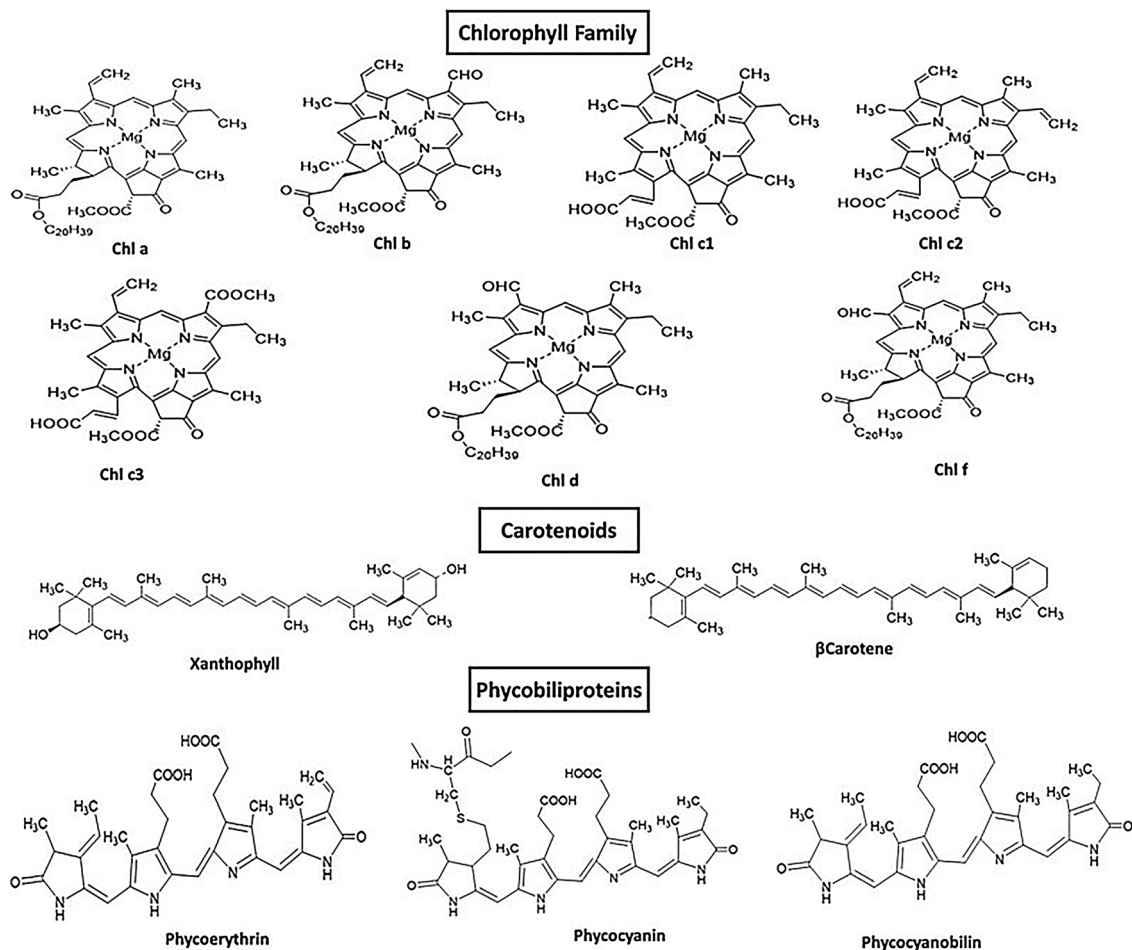


Fig. 1 Structural variation in photosynthetic pigments. The figure depicts the structural variation amongst photosynthetic pigments; Chlorophyll, Carotenoids and Phycobiliproteins, underpinning their absorption properties. The different side chains in the Chl family widen their absorption spectrum range for photosynthesis. Chl *a* absorbance is shifted to a red shift (longer wavelength), in case of Chl *d* (C_3 formyl substitution) and to an even longer wavelength in case of Chl *f* (C_2 formyl substitution) However, Chl *b* (C_7 formyl substi-

tion) switches the spectrum towards the blue shift (shorter wavelength). The structures of Chl *c1*, Chl *c2* and Chl *c3* differ from Chl *a* due to absence of a phytyl chain. Carotenoids are broadly classified into xanthophyll and carotene; with similarity in structure, except the presence of oxygen in xanthophylls. Phycobiliproteins differ in their spectral properties due to presence of open chain tetrapyrroles; chromophores; phycobilins

availability, stress linked to low temperature, desiccation, and stage of development (Violet-Chabrand et al. 2017; Esteban et al. 2015; Yamori 2016). A high Chl *a/b* ratio for example indicates greater acclimation to high light intensities and an enhancement in photosynthetic electron transport (Jin et al. 2016), whereas a low Chl *a/b* ratio indicates shade tolerance (Matsubara et al. 2012). Optimizing the balance between pigment composition and light capturing capacity of the plant is a potential strategy to increase photosynthetic efficiency and plant performance (Beckmann et al. 2009). For example, in green algae and plants downregulation of a gene responsible for Chl *a* to Chl *b* conversion (chlorophyllide *a* oxygenase (CAO)) reduced Chl *b* accumulation thereby increasing the Chl *a/b* ratio and enhancing the biomass production by 40% (Ayumi

Tanaka 1998; Czarnecki and Grimm 2012; Perrine et al. 2012) (see Fig. 3). Jin et al (2016) demonstrated that a reduction in the levels of the *High Photosynthetic Efficiency 1* gene reduced the total Chl content and lead to an increase in the Chl *a/b* ratio. This altered ratio of Chl *a/b* resulted in a moderately decreased antenna size that was optimal for enhanced light use efficiency. The fine tuning of the antenna size results in greater light penetration and distribution within the canopy due to a smaller antennae cross section, avoiding light saturation associated photodamage (requiring repair to restore efficiency) and wasteful dissipation of energy (Jin et al. 2016). Also, exposure to high light intensities activates photoprotective mechanisms, which in fluctuating light environments can drop photosynthetic efficiency (Ort and Melis 2011).

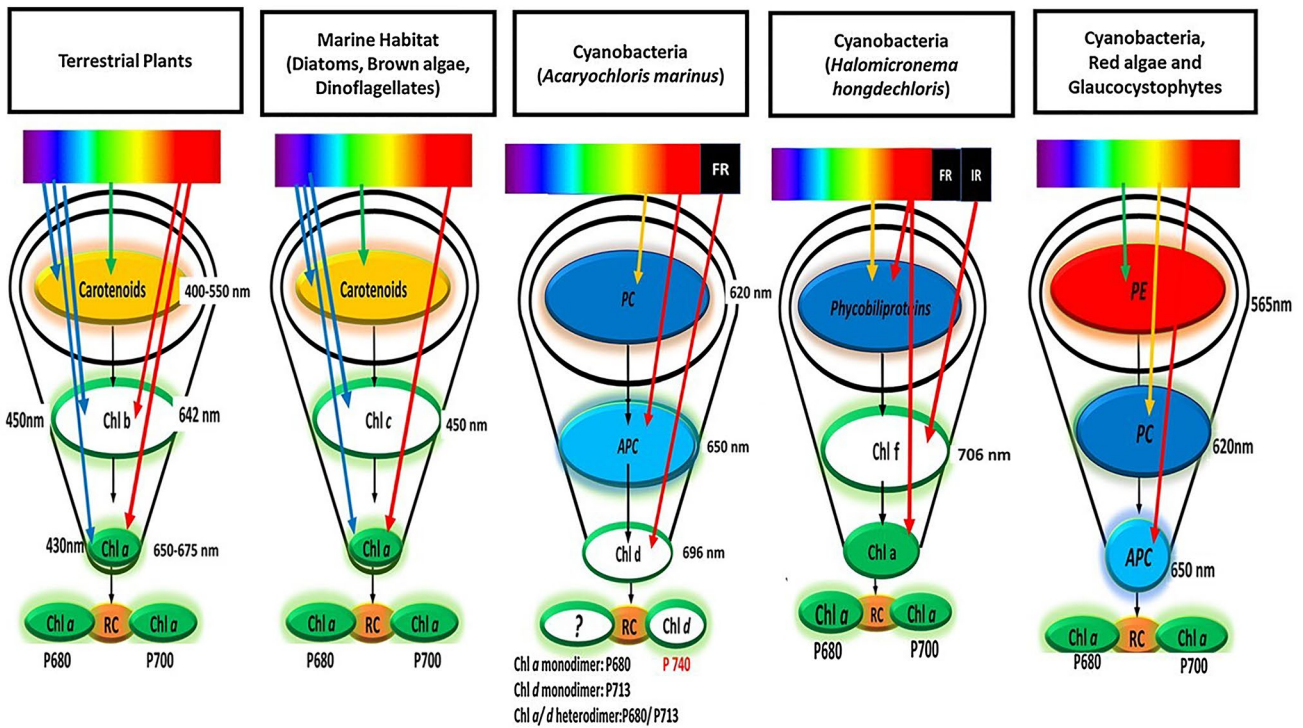


Fig. 2 Role of pigments in light capture and excitation energy transfer. The photosynthetic pigments in diverse phototrophs absorb a wide range of wavelength and facilitate photosynthesis in varied habitat. The figure depicts the flow of excitation energy (down-hill) to the RC received by chlorophyll P680 in PSII and P700 in PSI. In cyanobacteria *A. marinus*, the electron donor, Chl *d* absorbs Far Red (FR) light and transfers the energy to PSII (the constitution of PSII in

A. marinus has been debatable so far) whilst Chl *d* P740 replaces Chl *a* in PSI. In *Halomicronema hongdechloris* Chl *f* absorbs the infrared light (IR) and energy is transferred to PSII (P680) and PSI (P700) respectively. Most cyanobacteria and red algae have phycobiliproteins; Phycoerythrin (PE), Phycocyanin (PC) and Allophycocyanin (APC) which absorb a wide range of wavelength (green, orange, and red) thereby enhancing the light capture and photosynthetic efficiency

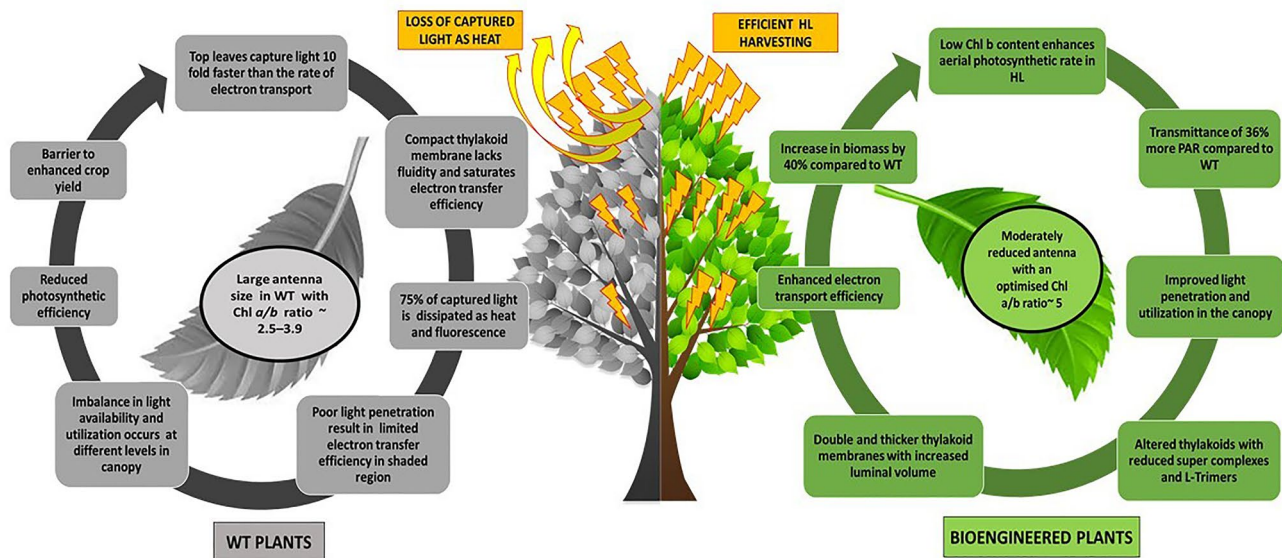


Fig. 3 Optimized Chl *a/b* ratio boost photosynthesis. The figure portrays the role of optimised Chl *a/b* ratio in bioengineered plants (and algae) in uplifting photosynthetic performance and crop yield as compared to WT (wild type). An efficient utilization of HL (high light)

supported by moderately reduced antenna size due to reduction in Chl *b* levels and an increase in Chl *a/b* ratio strikes a balance between the speed of light capture and its utilization

These authors have suggested that manipulating Chl *a/b* ratio would be a novel strategy for improving biomass production in plants (Jin et al. 2016). Furthermore, Friedland et al (2019) reported that the down regulation of CAO in transgenic *Camelina* plants reduced chlorophyll *b* levels resulting in an increase in the Chl *a/b* ratio and a reduction in the light harvesting antenna size. Plants with a smaller antenna size outperformed control plants in both greenhouse and field conditions achieving a 40% increase in biomass yield (Friedland et al. 2019). These authors then demonstrated that either a reduction or increase in antenna size from this new smaller antenna size reduce photosynthetic efficiency and tolerance to light stress (Friedland et al. 2019) (Fig. 3). Manipulating chlorophyll, *a/b* ratio and antenna size could therefore be a mechanism for manipulating photosynthesis and resource use efficiency dependent on the growing environment. For example, crops grown within commercial greenhouses, where light is highly regulated may benefit from a smaller antenna size compared to crops grown outside, as well as providing idiotypes for specific field locations. In addition to manipulation of the Chl *a/b* ratio and antenna sizes, balanced light absorption, and electron transport flow between the two photosystems are important for efficient and optimal photosynthesis, including carbon dioxide reduction and therefore could be a mechanism for manipulating photosynthesis and resource use efficiency depending on the growing environment.

In marine habitats, Chl *c*, Chl *a*, and carotenoids function together to harvest light (Garrido et al. 1995). Chl *c1*, *c2*, and *c3* are present in the antennae of organisms, including diatoms, brown algae and dinoflagellates inhabiting oceanic areas where light penetration is attenuated by the water column and organisms at shallower levels (Songaila et al. 2013). Structurally, Chl *c* differs from other chlorophylls *a* and *b* (Fig. 1) due to the presence of an unsaturated tetra pyrrole macrocycle and is therefore a magnesium-protochlorophyllide rather than a magnesium-chlorin (Budzikiewicz and Taraz 1971; Jeffrey 1989; Scheer 1991). However, Chl *c* is classed as a chlorophyll due to its light harvesting role and λ_{\max} at 450 nm (for review see (Zapata et al. 2006) and plays a vital role as an accessory pigment (Dougherty et al. 1970).

In the cyanobacteria *Acaryochloris marina*, which live in infra-red rich surroundings, the main photosynthetic pigment is Chl *d* (~97%), which differs in chemical structure, whereby the vinyl group of Chl *a* is replaced by a formyl group (Fig. 1) (Chen and Blankenship 2011; Miyashita et al. 1996, 2014; Renger and Schlodder 2008), resulting in shift of absorption maxima (red shift) towards longer wavelengths (λ_{\max} :710 nm). Chlorophyll *d* is found only in the RC of a few cyanobacteria that dwell in aquatic habitats (Kashiyaama et al. 2008; Mielke et al. 2011) (see Fig. 2). Chl *d* has enabled *A. marina* to adapt to occupy a niche with reduced

light availability at lower depths, due to higher energy light being absorbed by Chl *a* containing organism closer to the surface of the water. Along with Chl *d*, *A. marina* contains trace amounts of Chl *a* (located at key positions) (Miyashita et al. 2014; Renger and Schlodder 2008; Mimuro et al. 2004), with the exact amount present dependent on available light intensities (Mimuro et al. 2004). Similarly, cyanobacteria found living in stromatolites in near infra-red environments have been shown to contain a novel pigment; Chl *f* (λ_{\max} : 706 nm) (Chen et al. 2010; Gan et al. 2014; Miyashita et al. 2014). Chl *f* has a reported maximum absorbance of ~706 nm (in methanol) and has been assumed to have a purely light harvesting role (Fig. 2) (Chen and Blankenship 2011) (for detailed review on Chl *d* and Chl *f* see (Allakhverdiev et al. 2016). However, further work by Nürnberg et al (2018) demonstrated the involvement of Chl *f* in charge separation between photosystem I and II at 745 nm and Chl *f/d* at 727 nm, respectively. Chl *f* containing photosystems function ‘beyond the red limit’ absorbing light at > 760 nm and could therefore extend the photosynthetic absorption spectrum (Nürnberg et al. 2018).

These novel marine pigments could potentially be exploited to engineer crops that can make greater use of light at a larger range of frequencies improving light capture, light use efficiency and growth rates. For example, the accumulation of Chl *d* in the lower leaves of a canopy could allow plants to harvest light at the lower canopy at wavelengths not being absorbed by Chl *a* containing leaves in the upper canopy (Chen and Blankenship 2011). This could prove invaluable to crops that grow in densely packed fields where higher energy shorter wavelengths are absorbed by the upper canopy leaving the lower leaves in shade and enriched in longer wavelengths. Such an approach would require a greater understanding of the changing patterns of metabolism in leaves in different parts of the canopy and may require an “inducible” approach in which chlorophyll ratios are manipulated at an individual leaf level depending on where that leaf is within the canopy at various developmental stages, as well as the density of crop planting. Furthermore, such an approach could be used to engineer crops to be cultivated in environments where non-artificial light may be attenuated by water such as in below-water greenhouses or engineered into crops i.e., seaweeds harvestable from the sea.

Fine tuning of chlorophyll for enhanced photosynthesis

Lowering of leaf absorptivity with attenuated levels of photosynthetic pigments such as chlorophyll resulting in small antenna size of the photosystems has been considered as an effective strategy under several trials to augment PSII

and electron transport efficiency (Gu et al. 2017; Pettigrew et al. 1989; Sobiechowska-Sasim et al. 2014; Sakowska et al. 2018; Slattery et al. 2017). Gu et al (2017) reported that rice mutants with lowered chlorophyll levels displayed uncompromised development of chloroplast with higher expression of thylakoid membrane protein genes (increased potential for electron transport in the chloroplast) and the protein genes involved in chlorophyll binding (suggesting smaller antenna size) thereby avoiding excessive absorption of light, resulting in increased PSII efficiency with improved carbon dioxide conductance and Rubisco activity (Gu et al. 2017). Furthermore, decreasing the chlorophyll content of sun exposed leaves is an effective approach which can be used to increase the total canopy photosynthesis via improved distribution of light in the canopy, reduced photoprotection related energy losses coupled with increased carbon fixation and PSII quantum yield (Ort et al. 2015a). In chlorophyll-deficient leaf mutants, higher light energy reaches the abaxial (under) side of the leaf (deeper penetration and even distribution) and the green and yellow light is not absorbed as it passes through the adaxial (upper) side due to reduced chlorophyll levels. In wild type (WT) green leaved plants, blue and red light is absorbed at the adaxial side of the leaf with only green photons reaching the chloroplasts on the abaxial side (Sakowska et al. 2018). These findings are supported by chlorophyll-deficient soybean isolines exhibiting higher penetration of PPFD (photosynthetic photon flux densities) into the canopy (Pettigrew et al. 1989) thereby indicating over investment in chlorophyll as soybean mutants with > 50% reduction in chlorophyll, exhibited higher leaf level photosynthesis and light use efficiency in comparison to the WT (Slattery et al. 2017). Taken together, this data indicate an effective strategy to relocate energy resources and nitrogen towards enhancing biochemical photosynthetic capacity (used otherwise in pigment protein) to enhance biomass and yield.

Exploring the introduction of phycobilins into higher plants

Phycobilins are open chain tetrapyrroles (see Fig. 1) and the main light harvesting system in cyanobacteria. They are also present in glaucocystophytes, red algae and some cryptomonads but are absent in green algae or in higher plants (Chakdar and Pabbi 2016; Tanaka et al. 2011). They belong to the class of accessory pigments that absorb light in the range of 520 and 670 nm and are particularly efficient absorbers of green (550 nm, not absorbed by Chl *a*), yellow (580 nm), orange (600 nm), and red light (620) (see Fig. 2). Unlike other photosynthetic pigments, phycobilins are bound to water-soluble proteins called phycobiliproteins with molecular masses of between 30 and 35 kDa. The pigment protein structures contain between 300 and

800 phycobilins and form phycobilisomes, which are about 40 nm in diameter (Nobel 2009). In red algae and cyanobacteria, these phycobilisomes are found associated with the lamellar membrane stromal surfaces and function as the primary accessory pigment.

In the water column, green light can penetrate much deeper and the absorption of this light by photosynthetic pigments such as phycobilins allows cyanobacteria and red algae to stay at greater depths (Sobiechowska-Sasim et al. 2014) compared to organisms that depend on Chl such as green algae, which are therefore confined to shallower waters (Blankenship 2002, 2014). Some shallow-water organisms also contain phycobilins that can capture yellow/red light. However, it should be noted, that even in these organism's photosynthesis still relies on Chl *a* and phycobilins efficiently transfer the absorbed light energy to Chl *a* for photosynthesis (Cho 1970; Liu et al. 2013).

Three types of pigment protein complexes form the phycobiliprotein family have been identified in photosynthetic organisms: (1) phycoerythrin/phycoerythrocyanin (PE/PEC); (2) phycocyanin (PC) and (3) allophycocyanin (APC) (Fig. 2). The reddish PE is soluble in aqueous solutions and absorbs green light (between 530 and 570 nm). PC and APC (appears bluish in colour) as PC absorbs orange and red light (610–660 nm; $\lambda_{\max} \sim 620$) whilst APC (consisting of two subunits of protein each binding one phycocyanobilin chromophore) absorbs red light ($\lambda_{\max} \sim 650$ nm) (Chakdar and Pabbi 2016). Multiple forms of these phycobiliproteins have been observed in both red algae and cyanobacteria.

Phycobilins are considered as weak chromophores as they are less stable and more flexible in terms of their structural configuration compared to chlorophylls. However, on binding with proteins, phycobilins gain stability thereby increasing their rate of light absorption and ultimately enhancing light harvesting capacity (Parson et al. 2003). In addition, during fluctuating light intensities, phycobilins carry out state transitions, which is an adaptive mechanism involving rapid physiological changes in which the light harvesting antenna move between the two photosystems to balance the excitation pressure between photosystem I (PSI) and photosystem II (PSII). During state 1 transition, PSI is predominantly excited thus favouring the association of major light harvesting antenna complexes to PS II. On the contrary, when the varying light regime favour PSII excitation (state 2) the mobile antenna complexes are linked to PSI (Allen and Forsberg 2001). The mobility of phycobilisomes has been documented to be essential during cyanobacterial state 1- state 2 transitions, which keeps a check on the extent and choice of excitation energy transfer to either photosystem I or II. In cyanobacteria it has been reported that state transitions take place at low light and help to maximize the productivity of absorbed light; however, these transitions are directed only towards maximum utilization of absorbed

light and do not protect the organism from photoinhibition (Mullineaux and Emlyn-Jones 2005). The addition of phycobilins to plant photosynthetic structures (wherein PSI and PSII compete for similar wavelengths) via biotechnological approaches could be a novel mechanism for widening the spectrum of light capture and optimize light use efficiency. Since, phycobilin pigments harvest light at different frequencies such plant manipulations could be exploited to grow crops in specific environments or to increase light harvesting by leaves lower down in the canopy structure where light intensity and spectra are altered. However, the impact of introducing foreign pigments into plant photosynthetic systems will impact on endogenous pigments and may prove problematic. Two of the more obvious problems in such a scenario could be (a) the architecture of green plant thylakoids being incompatible with phycobiliproteins-PSII association and (b) a major metabolic re-adjustment would be required to sustain the production of enough phycobiliproteins to have a significant impact on light harvesting. Such an option is complex and would require extensive research to determine if any benefit could be realised by such an endeavour.

Role of carotenoids in light harvesting and photoprotection

Carotenoids are yellow-orange-coloured chromophores (Fig. 1) that absorb light in the range of 400–550 nm. They are found in all photosynthetic organisms (Sankari et al. 2018) where they carry out multiple important biological functions, including (i) stabilisation of lipid membranes (Gruszecki and Strzałka 2005; Havaux 1998) and the assembly of lipid protein structures (i.e. fibrils) (Deruere et al. 1994; Simkin et al. 2004a, 2007b), (ii) photosynthetic light harvesting and, (iii) protecting the photosystems from photo radiation related oxidative damage often attributed to reactive oxygen species (ROS) (Frank and Cogdell 1996; Hashimoto et al. 2016; Ledford and Niyogi 2005). Apart from their protective role, carotenoids also act as key regulatory molecules in both photosynthetic and non-photosynthetic organisms (Blankenship 2010). For example, carotenoids are cleaved by enzymes such as CCDs (carotenoid cleavage dioxygenases) and NCED's (9-cis-epoxy carotenoid dioxygenases) and the products act as precursors for the generation of vital primary and secondary metabolites, including the phytohormones abscisic acid (Parry et al. 1990; Qin and Zeevaart 1999; Tan et al. 2003; Simkin 2021) and strigolactones (Booker et al. 2004; Lopez-Obando et al. 2015; Schwartz et al. 2004; Snowden et al. 2005; Vogel et al. 2010) as well as important flavours and aroma compounds, in fruit pericarp, flowers and seeds (Auldridge et al. 2006a, 2006b; Giberti et al. 2019; Rubio et al. 2008; Schwartz et al.

2001; Simkin et al. 2010, 2004c, 2004b). These carotenoid-derived flavour and aroma compounds are valuable products in foods, flowers (Lin et al. 2002; Mahattanatawee et al. 2005), wine (Winterhalter and Gök 2013), Kentucky bourbon (Poisson and Schieberle 2008), cosmetic and spice industries (Bouvier et al. 2003a, 2003b).

Carotenoids are multifunctional and play an indispensable role in absorption of light in the blue-green zone (Hashimoto et al. 2016), transferring energy to Chl, (see Fig. 2) thereby increasing the spectrum of light collected by the light harvesting complex (Domonkos et al. 2013). Carotenoids also participate in the assembly of photosystems enhancing the functions of the photosynthetic apparatus and are engaged in regulating the expression of various genes via the by-products of oxidation (Ramel et al. 2012). Carotenoids aid in quenching of excess energy (Fig. 5) when light absorption is greater than can be utilized by the photosystems as it may initiate damaging Chl triplet formation (see Xanthophyll (ZAV) and Lutein (LxL) cycles below) (Krieger-Liszky et al. 2008). This protective function of carotenoids related with the antenna/light harvesting complex and the RC is so crucial that any obstruction in carotenoid biosynthesis is lethal to all photosynthetic organisms (Josse et al. 2000; Sandmann 1989; Simkin et al. 2000).

High light (HL) stress intensifies production of ROS (Fryer et al. 2002), which can prove to be destructive to plant lipids, proteins, nucleic acids and pigments. The lipids present in the thylakoid membrane are abundant in polyunsaturated fatty acids which are highly prone to oxidation by ROS resulting in lipid hydroperoxides initiating chain reactions which can ultimately demolish the chloroplast membrane (de Bianchi et al. 2010). When the light absorption by the plant is more than its photosynthetic capacity, dissipation of the excess energy is required or it may cause damage to the photosystems (particularly the D1 protein) reducing photosynthetic capacity, a process known as photoinhibition (Fig. 5). Under extreme conditions of stress, the rate of photoinhibition increases if the rate at which photodamage occurs in PSII exceeds its repair rate (Takahashi and Badger 2011) (see Fig. 5). Certain carotenoids are responsible for quenching ROS as well as directly quenching triplet Chl, which is a major source of singlet oxygen. For example, β -carotene (β -car) has been reported in the core complex of photosystems where it quenches triplet Chls and singlet oxygen (Cazzaniga et al. 2016). Zeaxanthin (Z), a xanthophyll pigment, is found bound to the antenna proteins in the light harvesting complexes or free in thylakoids. It has been reported that this free pool of Z is capable of quenching excited Chl molecules, (Havaux et al. 2007) and its antioxidant capacity is enhanced when it is bound to proteins in the light harvesting centre (Dall'Osto et al. 2010). Moreover, the free pool of Z, acts as an antioxidant in a synergistic manner with tocopherol and showcases its photoprotective property

in the lipids of the thylakoid membrane by removal of singlet oxygen species (Johnson et al. 2008, 2007; Johnson and Ruban 2010). Lutein, another xanthophyll carotenoid, also plays an active role as a photo protectant and has been reported to be the most important xanthophyll stabilizing the light harvesting complexes (Dall'Osto et al. 2007).

The Xanthophyll (Zeaxanthin) cycle and non-photochemical quenching

As mentioned above, photosynthetic organisms are able to adjust the size of the light harvesting antennae as a moderate to long-term acclimation to growth light environment (Walters 2005), however, irradiance also changes on much shorter time scales, seconds to hours, and therefore many photosynthetic organisms employ mechanisms to dissipate absorbed light energy that is greater than can be used for photosynthesis. This process is known as non-photochemical quenching (NPQ), in which singlet-excited chlorophylls are

quenched and the energy is dissipated as heat (Müller et al. 2001). The major form of NPQ is the pH or energy dependent component termed qE (Fig. 4), which relies on both the xanthophyll cycle (VAZ cycle) and the protein PsbS (Niyogi et al. 2004). This major quenching component is brought about by acidification of the thylakoid lumen (see below), which occurs as a result of electron transport (Baker 2008) and results in the activation of violaxanthin de-epoxidase catalysing the conversion of violaxanthin (V) [via antheraxanthin (A) to zeaxanthin (Z) (Jahns et al. 2009)].

The interconversion of zeaxanthin (Z) and violaxanthin (V) (via antheraxanthin (A)) known as the 'VAZ cycle' (Jahns et al. 2009) is dependent on the enzymes violaxanthin de-epoxidase (VDE) (Demmig-Adams and Adams III 1996; Farber et al. 1997; Ruban et al. 1994; Woitsch and Romer 2003) and zeaxanthin epoxidase (ZEP) (Demmig-Adams and Adams III 1996; Esteban et al. 2015) (see Fig. 4). The rapid changes in the VAZ cycle regulates light energy conversion protecting the photosynthetic machinery and is an essential process for plastid acclimation to fluctuating light

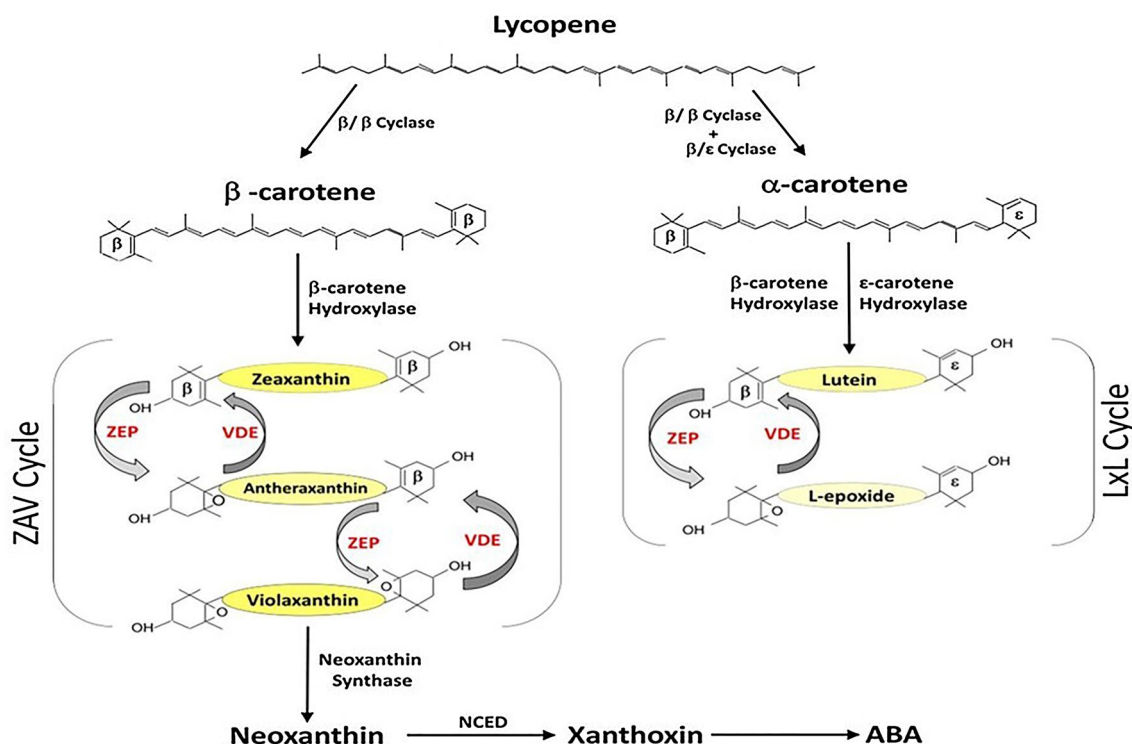


Fig. 4 Pathways of xanthophyll biosynthesis representing Xanthophyll (ZAV) and the Lutein (LxL) cycles. Lycopene β -cyclase (β/β -cyclase) introduces two β -rings to the ends of the Lycopene carbon chain forming β -carotene. α -carotene is formed by the addition of a β -ring and ϵ -ring respectively to lycopene by Lycopene β -cyclase and Lycopene ϵ -cyclase, respectively. The hydroxylation of the β - and ϵ -rings of β -carotene and α -carotene results in the formation of oxygenated carotenoids. β -carotene is converted to zeaxanthin by the action of β -carotene hydroxylase and the β -rings of α -carotene is

hydroxylated by β CHY then the ϵ -ring is hydroxylated by ϵ -carotene hydroxylase to form lutein. Zeaxanthin epoxidase (ZEP) catalyses the epoxidation of the two hydroxylated β -rings of zeaxanthin in two steps to generate antheraxanthin and violaxanthin. In high light, violaxanthin is converted back to zeaxanthin by the activity of violaxanthin de-epoxidase (VDE). These two enzymes are also capable of epoxidating and de-epoxidating the β -rings of Lutein to form Lutein epoxide

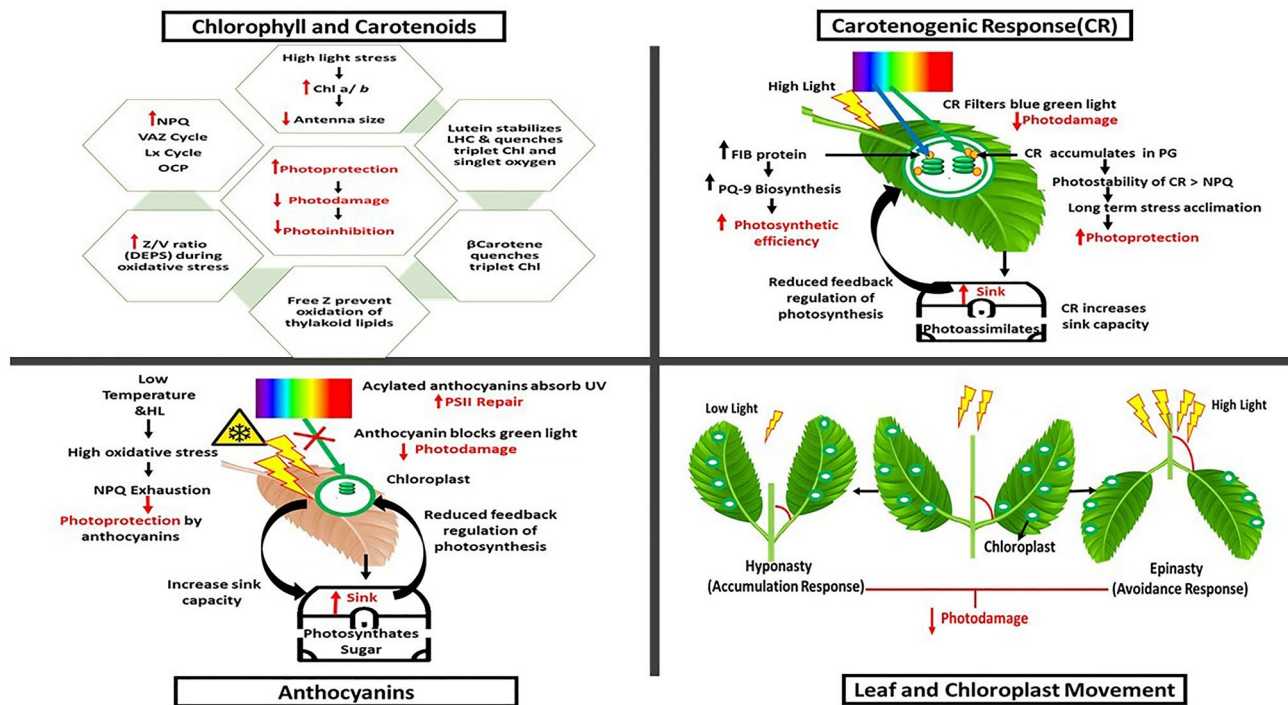


Fig. 5 Defence mechanisms of photosynthetic pigments as stress busters. The figure illustrates the pathways initiated by pigments as photo protectants in response to environmental stress thereby reducing photoinhibition which curtails photosynthetic efficiency. The role

of chlorophyll, carotenoids, carotenogenic response (CR), anthocyanin, chloroplast, and leaf movements in curbing the rate of photodamage, promoting PSII repair and thereby attenuating photoinhibition has been described

(Hieber et al. 2000; Latowski et al. 2000, 2011). Environmental stress (high light, wounding, cold, drought and salt stress), which may lead to increased ROS formation due to saturation of photosynthetic electron transport induces Z formation. For example, drought increases zeaxanthin levels in *Araure 4*, *Rice cv*, elevating DEPS by 40% (Pieters and El Souki 2005), which has also been shown in *Talinum triangulare* (Pieters et al. 2003) and coffee (Simkin et al. 2007a, 2008). Speeding up or changing components of the xanthophyll cycle could enhance productivity by increasing the photosynthetic efficiency based on the inverse relationship between NPQ and photosynthesis (e.g., (Kromdijk et al. 2016) see below).

Transmembrane pH differences, activates NPQ by protonation of carboxylic acid residues of the PSII antennae protein PsbS, and the enzymatic de-epoxidation of violaxanthin to zeaxanthin (Sacharz et al. 2017). Proteins like PsbS and Light Harvesting Complex Stress Related 3 (LhcSR3) function as stress sensors and play a crucial role in the initiation of NPQ. Correa-Galvis et al (2016) demonstrated that high light-induced PsbS and LhcSR3 accumulation triggered NPQ in *C. reinhardtii* and these authors further proposed the crucial role of PsbS in activation of NPQ by promoting conformational changes essential for activating LHCSR3-dependent quenching in the antenna of photosystem II.

Unlike PsbS, LhcSR3 is a pigment binding protein, which binds xanthophylls V, Z, L along with Chl *a* and Chl *b*. It accumulates in periods of high light intensity and quenches Chl molecules in the excited state and is essential for energy quenching (qE) in *C. reinhardtii* (Bonente et al. 2011; Girolomoni et al. 2019). Moreover, this protein facilitates lutein radical cation formation, which further aids in the process of dissipating excess energy (Ballottari et al. 2016).

In a recently published study on bioengineered tobacco plants, Kromdijk et al (2016) revealed that the over expression of VDE, and ZEP, to augment xanthophyll cycle kinetics, and escalating the amount of the PsbS protein, for sensing pH in the lumen, directly contributed to faster NPQ relaxation and quicker retrieval of CO₂ fixation after a period of high light intensity (Kromdijk et al. 2016). These findings showed that CO₂ fixation, ribulose biphosphate regeneration capacity (J_{max}) and maximum carboxylation capacity (V_{max}) could be improved upon. Speeding up plant recovery to fluctuating environments in field conditions also resulted in an increase in biomass by 14 to 20% (Kromdijk et al. 2016). These data indicate that the faster activation and relaxation of NPQ can be exploited to improve plant productivity and yield potential. In yet another study in transgenic tobacco plants, an increased PsbS expression was found to reduce stomatal opening, with water loss curtailed by 25%

per carbon dioxide assimilated (Glowacka et al. 2018). In contrast to the results reported in tobacco, recent results in *Arabidopsis thaliana* have shown that the overexpression of VDE, ZEP and the PsbS proteins did not lead to increased productivity but to impaired biomass accumulation (García-Molina and Leister 2020). These contradictory results between tobacco and *Arabidopsis* are a further indication that the limitations and control of NPQ may be species dependent and identification of specific targeted manipulations for different crop plants needs to be carried out to obtain consistent results providing consistent increases in yield in different growing environments. However, these data provide a route for improving crop productivity through the manipulation of NPQ and could be exploited to study a variety of crops to determine the impact on crop yield. Such manipulations may also be beneficial in crop plants grown in environments where high light and future high temperatures could curtail biomass/grain yield of conventional crops.

The Lutein epoxide cycle and non-photochemical quenching

Lutein (L) performs vital functions in plants, ranging from enhancing the stability of antenna proteins (Jahns et al. 2001), light harvesting through excitation energy transfer to Chl (Matsubara et al. 2009), Chl triplet state quenching in LHClI (Standfuss et al. 2005) and superfluous energy dissipation (NPQ) (Li et al. 2009). García-Plazaola et al (2007) proposed that accumulation of L (by conversion of lutein epoxide (Lx) to L) in the light harvesting complex converts this highly efficient light harvesting system into a system for energy dissipation (García-Plazaola et al. 2007) (Fig. 4). The induction of NPQ by L, as with the other protective carotenoids including VAZ, is brought about by a decrease in lumen pH. This is usually induced by photosynthetic electron transport at high light intensities and can also be attributed to increased cyclic electron flow (Armbruster et al. 2017) or can be driven by a decline in chloroplast ATPase proton conductance due to a reduction in the utilization of ATP by for example reduced Calvin cycle activity (Kanazawa and Kramer 2002; Takizawa et al. 2008). The LxL cycle was originally described in green tomato fruit by Rabinowitch et al. (Rabinowitch et al. 1975) and was identified later in photosynthetic stems of *Cuscuta reflexa* (Bungard et al. 1999). Functional Lx has been shown in several unrelated taxa, but it is reported to be an exclusive characteristic of woody plants (García-Plazaola et al. 2004), however, elevated rates of Lx have also been found in *Cucumis sativus* L (Esteban et al. 2009a, 2009b). As stated by Dall'Osto et al (2006), L is more efficient than V in terms of quenching of triplet states of Chl. Lx often accumulates in older shaded leaves, which are obscured from intense light by the higher

canopy (Dall'Osto et al. 2006). At low temperatures, the Lx cycle is operational and furthermore, the binding of lutein to Early Light-Induced Protein accumulating in the plant due to stress, results in increased lutein concentration (Verhoeven 2014). Lx has also been shown to co-localise with V in shade leaves of *Inga* (Matsubara et al. 2007, 2005). It has previously been suggested that this co-localisation indicates that Lx probably will be equivalent to V both structurally and functionally (García-Plazaola et al. 2007). Under high light, VDE enzyme which in addition to de-epoxylating V in the VAZ cycle, also de-epoxylates the Lx β -ring (see Fig. 4) (Goss 2003; Yamamoto and Higashi 1978), converting Lx back to L. The conversion of L to Lx by the epoxidation of the β -ring of L is most likely carried out by the enzyme ZEP (García-Plazaola et al. 2007). It should be noted that the epoxidation of L is extremely slow due to the low affinity of ZEP for L.

Identifying variants of ZEP and VDE with a greater affinity for L and Lx offers the possibility of engineering plants with a higher functioning LxL cycle, which complements and supplements the VAZ cycle increasing the efficiency of NPQ. This strategy would be effective since VAZ and LxL are two kinetically distinct cycles. On exposure to high light, L (formed by conversion of Lx to L) replaces Lx in the light harvesting complexes therefore taking the place of A + Z in light harvesting complexes; (Matsubara et al. 2007) to “lock in” a potential for higher NPQ in the dark thereby reducing PSII photochemical efficiency (Jia et al. 2013).

The precursor for the formation of L is α -car, which interestingly has been found to accumulate at the expense of β -car in the leaves and green fruit of a number of plant species including carrot (Koch and Goldman 2005), coffee (Simkin et al. 2010, 2008) and many shade-grown or shade-tolerant plants (Demmig-Adams 1998; Demmig-Adams and Adams III 1992; Matsubara et al. 2009; Siefermann-Harms 1994; Thayer and Björkman 1990). It has previously been suggested that α -car may substitute β -car molecules required for the assembly of photosystem II complex under certain conditions (Simkin et al. 2008) and this additional accumulation of α -car may be required to stabilise the pool of L for plants where the Lx cycle may have greater importance. Improving the Lx cycle in plants where the VAZ cycle predominates has the potential to offer either a greater degree of protection to plants exposed to high light or more flexibility dependent on the available pool of carotenoids.

Carotenoid binding proteins

In addition to the role of pigments in light harvesting and photoprotection, the role of pigment binding protein in plants and cyanobacteria must be discussed. In plants, Fibrillins (FIB/FBN/FIN), also known as chloroplast drought

stress-related proteins; for review see (Simkin et al. 2004a; Singh et al. 2010; Singh and McNellis 2011), and Orange Carotenoid Proteins (OCP) found in cyanobacteria play important roles in photoprotection.

FIBs have been identified as carotenoid associated proteins (Simkin et al. 2004a; Vishnevetsky et al. 1999) and are present in all photosynthetic organisms ranging from cyanobacteria to higher plants. FIBs have been shown to be a major structural protein involved in biotic/abiotic stresses, pathogenic infection, high salt, high light, exposure to ozone or drought (Simkin et al. 2004a, 2007b, 2008; Singh et al. 2010; Singh and McNellis 2011; Youssef et al. 2010; Ariizumi et al. 2014; Langenkämper et al. 2001; Rey et al. 2000; Jiang et al. 2020). FIB levels have also been correlated with a reduction in photoinhibition (Fig. 5) under high light, and FIB expression has been shown to be regulated by ABA indicating that FIB plays a role in abscisic acid-mediated photoprotection in *Arabidopsis* (Yang et al. 2006) and FIB accumulated linked response to the production of ROS in plastids. It has been reported that FIB are structural components required for the biosynthesis of plastoquinone-9 (PQ-9) (Kim et al. 2015). PQ-9 is the most common form of plastoquinone, an isoprenoid molecule involved in the transport of electrons between the Cytochrome *b₆f* complex and PSII in the light-dependent reactions of photosynthesis. Transgenic plants with reduced Fibrillin levels had less PQ-9 resulting in lower photosynthetic performance and a slower growth rate compared to control plants (Kim et al. 2015). In tobacco, over-expression of pepper fibrillin resulted in enhanced development and accelerated flowering when grown under HL proposing that fibrillin-related proteins play a vital role in plant development in relation to environmental and light stresses (Rey et al. 2000).

In cyanobacteria, NPQ relies on the light absorption (in the blue-green spectrum) by a protein which binds carotenoids; the Orange carotenoid protein (OCP) (Kirilovsky 2007). OCP binds a single non-covalently bound ketocarotenoid (3'-hydroxyzeaxanthin) (Holt and Krogmann 1981; Kerfeld 2004a, b; Wilson et al. 2006; Wu and Krogmann 1997) and plays a dual role as a photoreceptor and a facilitator of energy dissipation, modulating the extent of energy that arrives at the phycobilisome (Wilson et al. 2006). Upon illumination, OCP undertakes a reversible structural change from the secure 'orange' form to the active 'bright red' form and binds itself to the phycobilisome core, dissipating 80% of its excitations as heat before they reach to the RC (Kirilovsky and Kerfeld 2012). This photoprotective mechanism is essential for the adaptation of cyanobacteria to light-induced stress. No similar mechanism currently exists or functions in plant chloroplasts. The genetic introduction of such a mechanism has the potential to improve plant responses to stress/high light and therefore enhance productivity. Due to the complexity of this system, and the

key role played by ketocarotenoids, which are not found in plants, further research is required to comprehend the protein carotenoid association and whether such a mechanism could be functional and beneficial in higher plant chloroplasts. Attempts have already been made in this direction by Andreoni et al (2017) who evaluated the possibility of controlling the energy transfer pathway in response to light intensity by bioengineering OCP in an artificially designed antenna model (Andreoni et al. 2017).

Anthocyanins

Anthocyanins are polyphenolic pigments found throughout the plant kingdom. In plants, anthocyanins play a number of critical roles in reproduction, attracting pollinators/seed dispersers and in protection against various stresses, both abiotic and biotic (Siva 2007). Foliar anthocyanins (AnCs) are abundant in juvenile and senescing leaves; however, their distribution varies amongst species. Anthocyanins are generally stored in the vacuole in or just below the adaxial epidermis, although under certain circumstances AnCs accumulate in cell vacuoles of the abaxial epidermis, palisade and spongy mesophyll where they are involved in photoprotection (Steyn et al. 2002; Chalker-Scott 1999; Hughes and Smith 2007; Hughes and Lev-Yadun 2015; Pietrini et al. 2002). AnCs play an active role in preventing photoinhibition and photodamage by quenching of excess solar radiation when the existing photoprotective mechanisms for quenching of excess energy in plants are completely exhausted during periods of extreme oxidative stress; particularly high light, extreme temperatures, elevated UV, drought, high soil salinity and nutrient deficiency (Chalker-Scott 1999; Steyn et al. 2002). Though the functionality of AnCs in leaves is debatable, in the epidermal layers they have been shown to absorb blue light (Chalker-Scott 1999; Feild et al. 2001) and it has been suggested that the photoprotective function of AnCs largely depends on this ability and to a lesser degree the absorption of red photons (Gould et al. 2018; Jordheim et al. 2016; Tattini et al. 2014). AnCs also act as sinks for excessive photosynthates generated due to light saturation and thus support photosynthesis by limiting feedback regulation of photosynthesis due to escalated production of photoassimilates. In a recent study by Piccolo et al (2020), AnCs were found to limit the accumulation of sugar (hexoses) in the cytosol by directing the excessive sugar into the vacuole. These researches emphasized on the sugar buffering role of AnCs which attenuated the sugar supported regulation of photosynthesis (Piccolo et al. 2020) (Fig. 5). Furthermore, AnCs, play a role in slowing down the rate of senescence and acting as metal chelating agents and sunscreens (acylated anthocyanins absorb UV) (Solovchenko and Merzlyak 2008; Merzlyak et al. 2008). Manipulation of

AnCs levels could be used to adapt plants to extreme light environments where other mechanisms for photoprotection may be overwhelmed, and/or delaying senescence increasing the photosynthetic lifespan of leaves to improve yield.

Other strategies to harvest light and avoid photodamage: chloroplast and leaf movement

Other strategies in line with avoidance of photodamage include mobility of the leaf where the leaf lamina aligns itself parallel to the light direction (paraheliotropism) (Pastenes et al. 2005) and movement of the chloroplast (Haupt and Scheuerlein 1990; Kasahara et al. 2002) (Fig. 5).

Chloroplast movement, also referred to as chloroplast photo relocation, is essential for plant adaptation to changing light conditions and allows plants to maximise photosynthetic efficiency whilst avoiding photodamage of chloroplasts (Kasahara et al. 2002). In the case of the ‘avoidance response’, relocation of chloroplasts away from the strong light helps to minimise photodamage and in the case of the ‘accumulation response’ they move towards weak light to optimise light use for photosynthesis (Wada and Kong 2011). These responses are vital for plants below a canopy where strong winds can rapidly change the environment from high light to dark shade, requiring plants to adapt quickly to these new norms and the requirements of chloroplasts to move down for photoprotection or up for optimal photosynthesis (Wada and Kong 2011). Chloroplast movements are regulated by phototropins (phot), which are blue light receptors (Christie 2007; Kodama et al. 2008; Komatsu et al. 2014). *phot 2* mediates the avoidance response whilst the accumulation response is facilitated by *phot 1* and *phot 2* (Kong et al., 2012; Suetsugu and Wada, 2012). The research findings using *phot2* mutant plants, in contrast to wild type, demonstrated that *phot2* mutant plants could not withstand the pressures of light fluctuations (Gotoh et al. 2018). Thereby the avoidance response plays a photoprotective role in plants experiencing sudden and extreme light fluctuations. These movements also protect chloroplast pigments from exposure to damaging light levels. Moreover, amongst the photosynthetic pigments the xanthophyll lipids have been speculated for their role in chloroplast movements initiated by blue light as the VAZ cycle pigments have been reported to be altered with a 40-fold increase in the levels of zeaxanthin. Also, the *cis* and *trans* photo isomers of zeaxanthin have been suggested to trigger the chloroplast mobility under the influence of blue light (Tlačka et al. 1999).

The positioning of the leaves in the plant have been observed to play a role in phototropism as the leaves positioned perpendicular to light will absorb more light as compared to leaves placed in a parallel orientation (Lovelock

et al. 1992). Therefore, variations in the leaf angle have been suggested to be an indicator of leaf movements in plants due to fluctuating light intensities. As per a recent study on soya bean plant, under high light conditions an increase in the leaf angle (epinasty) was observed due to the reduction in the angle between the stem and the abaxial leaf petiole (Feng et al. 2019). Thereby suggesting a parallel orientation of the leaf to the incident light of high intensity and protecting the plant from photodamage. On the contrary, leaf movements reported as a result of low light is an upward movement called hyponasty (increased angle between the stem and the abaxial leaf petiole) to capture more photons under limited light conditions (Pharis and King 1985) (Fig. 5). This leaf movement has been observed to vary amongst crop species and is regulated by cryptochromes and phytochromes (Millenaar et al. 2009). The variations in light intensities also affect the leaf anatomy as an increase in leaf thickness due to enhanced cell growth of palisade and spongy tissues has been reported under high light exposure (Fan et al. 2018). Whilst large cell gaps and reduced cellular development has been reported in leaves exposed to low light intensities (Kalve et al. 2014).

Conclusions

Enhancing crop yield to meet the global demand is challenging in these unprecedented times, therefore, enhancing the efficiency of the photosynthetic machinery, through genetic manipulation of the Calvin Benson cycle, photorespiration and photosynthetic electron transport (see for review (Ort et al. 2015b; Simkin 2019; Raines et al. 2022; Simkin et al. 2019)), coupled with the development of biotechnological tools (i.e. new vectors Exposito-Rodriguez et al. 2017; Engler et al. 2008) and promoters (Alotaibi et al. 2018; Mukherjee et al. 2015) have been key targets. Furthermore, novel pathways have been discovered and new targets identified to increase the efficiency of the photosynthetic machinery by optimizing the levels of photosynthetic pigment levels in the chloroplast, which could be exploited to enhance quantum efficiency and increase yield to meet the global demands for food security. The large variety of pigments with different absorption spectra offer the potential to engineer plants for specific environments or improve plant productivity by widening the spectra of light harvested and increasing the overall quantity of useable light. In combination with an enhanced ability to dissipate excess energy, prevent photodamage, stimulate repair and shorten the period of photoinhibition, photosynthetic pigments exhibit tremendous potential to boost the photosynthetic efficiency in diverse environments. Engineering of photosynthetic pigments in plants targeting specific environments would improve the survival potential,

coupled with enhanced biomass production. Furthermore, several current studies have demonstrated that photons of far-red light (701–750 nm) interplay with photons with a shorter wavelength to enhance leaf photosynthetic efficiency (Zhen and Bugbee 2020) indicating that improvements to far-red light interception could also have the potential to improve light use efficiencies and yield.

In addition, development of unique photosynthetic systems may open up the possibilities of designing plants for unique environments and new growing situations, including vertical farms, Antarctic greenhouse (Bamsey et al. 2015) and new non-terrestrial environments, such as space travel (Poulet et al. 2014), where plants would be exposed to different light intensities including a mix of artificial and natural light; or on the surface of Mars, where light levels are approximately 43% of those on Earth. Work to design and operate greenhouses in extreme environments, such as the Arthur Clarke Mars Greenhouse (Giroux et al. 2006; Bamsey et al. 2009) and the Lunar greenhouse design (Zeidler et al. 2017) are ongoing, but it may be necessary to ‘genetically’ acclimate new plant varieties to be productive in an essentially low light environment. Furthermore, extra-terrestrial environments also have high UV levels and as previously shown acylated anthocyanins absorb UV, offering a further potential mechanism of protecting plants in such environments. Manipulating photosynthetic pigment composition may offer opportunities to design crops for specific needs. This review has provided a background to various pigment protein complexes and introduced the scope to explore photosynthetic pigments towards enhancing biomass production. This area of research requires more study to fully benefit from the availability of chlorophylls and accessory pigments found in nature.

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Code availability Not applicable.

Declarations

Conflict of interest The authors have no conflicts of interest to declare that are relevant to the content of this article.

Ethical approval The authors declare that this article does not contain any research with human or animal subjects.

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