Role of Light in Plant Development

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Abstract

During the course of evolution, plants developed the capability of capturing and utilizing the solar radiation. These plants gained an evolutionary advantage over those that have not developed these traits. Light besides being an important source of energy also controls many developmental processes like photoperiodism, phototropism and photomorphogenesis of plant growth. Oxygen in the atmosphere is generally believed to come from light induced water-splitting that occurs in oxyphotosynthetic organisms catalysed by the oxygen evolving centre of photosystem II. To optimize both the roles of light, plants evolved complex system and the most established higher plants photoautotrophic mode of nutrition is responsible for establishing and sustaining the human civilization.

Key words: Light, Photoperiodism, Photomorphogenesis, Evolution, Subcellular level.

1. Introduction

Solar radiation is the most powerful and inexhaustible source of energy on the surface of the Earth. The solar electromagnetic energy reaching the Earth's surface surpasses the energy contributed by all the other sources by four to five orders of magnitude (Mauzerall, 1992). Light is electromagnetic radiation of wavelengths to which the human eye is sensitive (400 to 700 nm). A description of the light incident on a plant requires the characterization of its intensity (photon or energy irradiance), duration, quality (spectral composition), and direction (relative location of source and degree of scattering). Light is both a source of energy and a source of information for green plants. It is a source of energy for photosynthesis, and a source of information for photoperiodism (night/day length), phototropism (light direction), and photomorphogenesis (light quantity and quality).

Light is particularly important for photosynthetic plants as it is the main source of energy to carry on the physiological functions working and, consequently has an enormous influence on plant development (Thomas, 2006). The higher plants and algae have adopted several complex mechanisms to respond to light in a concerted way to gain an evolutionary advantage over other organisms that have not developed these traits, fixing 45-60 Pg-C/year (Cramer *et al*., 2001) or 6-8% of the atmospheric carbon content (Reeburg *et al*., 1997).

If this global primary production is converted to energy units (39.9 kJ.g C^{-1} assuming that all photosynthetic products are carbohydrates), 0.21 Wm^{-2} or 0.13% of light energy is converted into chemical energy stored in organic molecule still exceeds geothermal energy by at least one order of magnitude. As a consequence, photosynthesis directly or indirectly drives the biogeochemical cycles in all the existing ecosystems of the planet.

Plant response to light can be studied at different scales. At the subcellular level, the best characterized response is altered gene expression (Gilmartin *et al*., 1990), but other possible actions associated are transient changes in membrane permeability (Pike, 1976) and modulation of the activity of specific enzymes (Sibley and Anderson, 1989). All plants respond to shading and/or neighbours with increased stem elongation rates, increased area of individual leaves, altered shape of leaf blades, more horizontal leaf blades and more vertical stems, branches or tillers, increased apical dominance and changes in chemical composition (Aphalo, 2006). In canopy, either closed or sparse, plants adjust their growth and development in response to their sensing of neighboring vegetation. Another important response of plants to light quality is related to the timing of seed germination.

Light regulation is driven by different mechanisms in plants, but some are particularly important such as the redox (Buchanan and Balmer, 2005), photoreceptor-dependent, circadian clock (Dodd *et al*., 2005), and photoperiodic (Thomas and Vince-Pruce, 1997) regulatory systems. The evolution of photosynthesis was one of the most important events in the history of biology, because this process allowed biological energy production to be coupled to an inexhaustible solar energy (Fig. 1). By coupling a solar energy module with a biochemical module for CO_2 reduction, ancestral organisms eventually gained both energy and nutritional independence. The emergence of primary producers, and the eventual development of oxygenic photosynthesis, inevitably changed the trajectory of the evolution of life on Earth. Light-driven evolutions of plants on Earth have prompted

research into receptor-dependent and-independent physiological responses. This issue in relation with evolutionary development/significance is dealt extensively in this review paper in the light of recent advances.

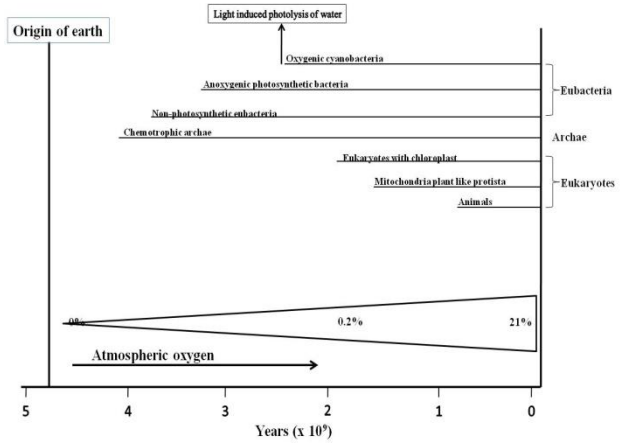

Fig. 1: Important events in the history of plant evolution

2. Dominance of Photo-autotrophs

During the evolution of life on the earth some of the organisms in their fight for existence were forced to evolve metabolic pathways which not only permitted them to assimilate external (exogenous) organic substances in a more rational pathway, but also allowed them to utilize other means of extracting energy from the environment and also for assimilating the simplest forms of carbon-containing compounds (Oparin, 1968). Of the various possibilities, utilization of solar light energy turned out to be the most rational. At that time, due to a number of processes taking place in the upper layers of the atmosphere (formation of the ozone layer), the photochemically most active radiation, the short ultraviolet ceased reaching the Earth's surface and the visible and near infrared spectral regions became the main source of photochemically active light energy. It is precisely to the light energy of these spectral regions, organisms had to adjust themselves during their transitions to the photoautotrophic mode of life.

The physical attributes of the pigments involved in harvesting light were important contributing factors in the evolutionary selection of the chemicals used for photosynthesis (Blankenship and Hartman, 1998). Green algae and higher plants utilize chlorophylls (a and b) and a variety of carotenoids to capture light for photosynthesis (Glazer, 1980). The selective forces that drove the evolutionary selection of these pigments are unknown. Other pigments utilized by photosynthetic organisms, such as chlorophyll (Chl.) c, fucoxanthin and phycobilins, absorb light in all regions of the visible spectrum (Glazer, 1980), but such pigments are not utilized by green algae and higher plants. The physiological reasons that plants with green algae as progenitors were evolutionarily successful on land remain unknown (Fig. 1). Since plants evolved well before vision, there is probably no adaptive value in being 'green' with regard to co-evolution with animals; although vertebrate vision is most sensitive to green light. Insects do have innumerable co-evolutionary relations with plants, many of which are based on floral colour. Besides being important as a source of energy, light also controls many developmental processes of plant growth. The presumption is made that the photosynthetic pigments for energy collection were selected prior to light-sensing systems for development (Nishio, 2000).

Changes that need to take place before oxygenic photosynthesis could work include alternation in the energetics of pigments and redox reactions, the genesis of the oxygen evolution complex itself and the development of the ability to protect against the oxygen generated in the complex (Blankenship and Hartman, 1998). Studies have demonstrated that photosynthetic eukaryotes acquired photosynthetic properties through endosymbiosis with cyanobateria which ultimately became chloroplast (Gray, 1992) (Fig. 2).

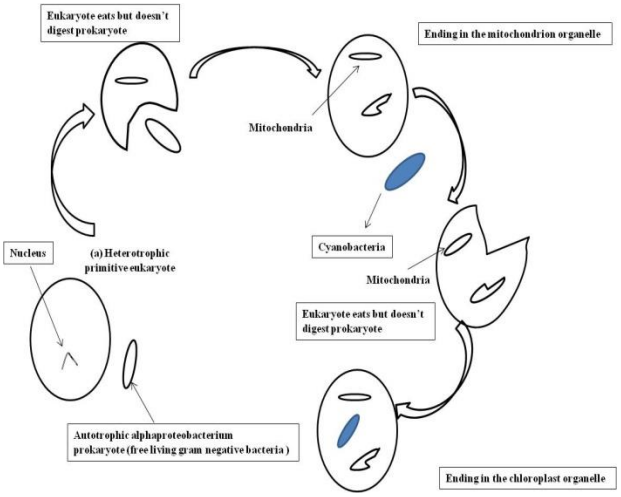

Fig. 2: The Endosymbiotic theory and origin of eukaryotic cells

This observation, coupled with the fact that no Mg-tetrapyrrole-based photosynthesis has been found in Archaea, supports the notion that photosynthesis is a bacterial derived process (Olson and Pierson, 1987). Process of endosymbiosis commenced when the eukaryote engulfed but did not digest an autotrophic bacterium, an autotroph that uses photosynthesis to acquire energy. The eukaryote then began a symbiotic relationship with it whereby the eukaryote provided protection and nutrients to the prokaryote, and in return the prokaryotic endosymbiont provided additional energy to its eukaryotic host through its respiratory cellular machinery. During the early events of evolution, photosynthetic pigments functioned mainly in the protection of primordial nucleic acids

and proteins from photochemical damage. Later, they assembled together with specific proteins to form primordial reaction centers that were adopted by DNA/protein based organisms and eventually evolved into the different current photosynthetic apparatuses. There are numerous photosynthetic processes that can harness the light energy for supporting life processes, but as per available literature, only oxygenic photosynthesis is capable to energize life by utilizing water as an electron donor (Blankenship and Hartman, 1998). It is generally believed that photosynthetic organisms developed the machine to oxidize water into oxygen and reducing equivalents. Nature had evolved the perfect solution of using solar energy to split water and thus provide the carbon fixation process of photosynthesis with an endless supply of reducing equivalents. It was this solution that is responsible for enormous amount of available biomass on this planet. Oxygen (O_2) is the byproduct of the water-splitting reaction and its release over the past two billion years or so, has not only created an oxygen enriched atmosphere but also established the ozone (O_3) layer in stratosphere needed to shield terrestrial life from harmful ultraviolet-B radiation. Photosystem II (PSII) use light to drive the oxidation of H_2O and reduction of quinones, Q_A and Q_B. Even purple and green non-sulphur bacteria have type II photosystems but they perform anoxygenic photosynthesis.

During the course of evolution, PSII has undergone some alteration on the e^- donor side that gave it the ability to oxidize water. PSII with its oxygen evolving complex (OEC) defines oxyphotosynthetic organisms, which included a phylogenetically wide range of organisms from prokaryotes (such as cyanobacteria and green oxyphotobacteria) to unicellular eukaryotes (such as red algae and green algae) and all multicellular plants. PSII is located in the photosynthetic membranes and contains pigment molecules that are needed to absorb solar energy to convert it into electrochemical potential energy. The attainable oxidizing potential is attributable to the presence of chlorophyll in the oxygenic photosystem whereas all anoxygenic phototrophs contain longer wavelength absorbing and therefore lower energy bacteriochlorophyll. An oxidizing potential of 1V of $P680^+$ helped in oxidizing water, with the help of a catalytic centre composed of four manganese atoms. Four photons are required to produce one oxygen molecule. Bacteriochlorophyll and chlorophyll as well as their epimers are isomeric to each other (Kobayashi *et al*., 1998). In fact, light induced isomerization of bacteriochlorophyll to chlorophyll (Beer-Romero *et al*., 1988). De Las Rivas *et al*. (2004) reported genome-wide analysis of the OEC extrinsic proteins, particularly PsbO, as a means to explore the evolution of the OEC from an ancestral oxyphotosynthetic bacterium to the OEC present in the chloroplast of eukaryotic algae and higher plants. Other extrinsic proteins include PsbP, PsbQ, PsbU. PsbP (23 kDa) and PsbQ (17 kDa) are found in higher plants and green algae, whereas PsbU (12 kDa) and Psb (cytochrome c550) are found in cyanobacteria and red algae. These extrinsic proteins optimize the availability of Ca^{2+} and Cl^- cofactors for water oxidation. The presence of PsbO in all known oxyphototrophs indicates that this protein could be the minimal element required for an adequate functioning of the water splitting system in PSII (De Las Rivas *et al*., 2004).

Energy supply via photosynthesis was thus superimposed on a pre-established set of primary metabolic reaction based on energy generation from oxidation of chemical compounds present in the environment (chemiautotrophs) and formation and turnover of carbohydrates as a means to channel energy flux and carbon into specific biosynthetic pathways. Inherent limitations in the ability of photosynthesizing organism to channel the use of light-generated reducing equivalents directly into synthesis of specific compounds may reflect the evolutionary history (Gust *et al*., 2008). Photosystem I (PSI) operates at a quantum yield of 1.0. This efficiency is unmatched by any other biological or chemical system and denotes that each captured photon succeeds in exciting an electron in the reaction center of PS I (Nelson and Yocum, 2006). Two separate one electron photooxidation events in the P700 reaction center of PSI are required for the reduction of $NADP^+$ to NADPH with the final steps being mediated by the soluble electron carrier ferredoxin and by ferredoxin NADP-oxidoreductase (Mulo, 2011). The pH gradient formed over the thylakoid membrane by light driven electron transport through photosystem II (PS II) and then PS I is utilized for ATP formation. Photosynthetic carbon fixation at the expense of NADPH and ATP enables synthesis of complex organic molecules. The light driven electron transfer reactions are optimized through evolution. The evolutionary ancestor(s) of reaction centers is not known. Xiong and Bauer (2002) have suggested that reaction centers (and light harvesting proteins) are descendents from Cytochrome b (Cyt. b), a broadly distinguished heme-binding protein, which could provide a connection between respiratory and light driven electron transport. Alternatively, Mulkidjanian and Junge (1997) suggested that reaction centers evolved from proteins that provided photoprotection from ultraviolet radiation by absorption rather than dissipation of this excess energy.

3. Physiological Responses to Light and its Evolutionary Significance

Plants possess two types of photoreceptors: photosynthetic pigments that harvest light for photosynthesis, and photosensory receptors that regulate non-photosynthetic light responses.

Photomorphogenesis, i.e. control of plant form by ambient light conditions, mediated by a set of photoreceptors. Photoreceptors are the molecules that function at the interface between organism and environment. Plants rely heavily on these receptors that absorb maximally in the blue (400-500 nm) and in the red and far-red (600-800 nm) regions of the visible spectrum. This may reflect the utility of these particular pigments to serve as reliable indicators of ecologically significant fluctuations in the light environment. Light scattering by clouds leads to a slight increase in blue light (Smith, 1982). Thus, blue light receptors might have particular utility for fundamental processes, such as early seedling development and the perception of time and season.

Contrary to this, light scattering within a stem is greater for short wavelengths and there are steeper gradients of blue than of red light in a stem irradiated with unilateral light (Hart, 1988). In autotrophic plants, light provides circadian and seasonal information, used to mediate the induction and inhibition of flowering and bud dormancy, the opening and closing of stomata and flowers (Mathews, 2006).

Phytochromes are among the most important environmental receptor/sensor in plants and they regulate numerous aspects of plant growth and development from germination to floral induction (Chen *et al*., 2004). Being photoreceptors of red and far-red light, they perceive signals of seed burial, competition from a vegetative canopy (Mathews, 2006). Phytochrome evolution in land plants is marked by a series of gene duplications that have led to independently evolving and functionally distinct lines (Mathews and Sharrock, 1997). Gene duplications are considered to be a significant force in gene evolution (Wagner, 2001) and may also play a significant role in speciation (Lynch and Conery, 2000). A duplication preceding the origin of seed plants resulted in two distinct lines that persist in all extant seed plants. Phylogenetic analysis suggest that subsequent duplications occurred in each of lines, leading to the four major forms found in angiosperms, phytochrome A, B, C and E (phy A-C and E), encoded by *PHYA-C* and *E* (Mathews and Sharrock, 1997). *PHYA* and *PHYC* form one duplicate pair; *PHYB* and *PHYE* form a second duplicate pair.

Cryptochrome, a blue light receptor with action spectra comprising two peaks, one in the UV-A light region (~320-400 nm), and the other with fine structures in the blue light region (~400-500 nm) (Senger, 1984). It was so called because blue light responses appeared prevalent in cryptogams and the molecular nature of blue light receptors was cryptic in nature. An early phylogenetic analysis suggested that ancestral cryptochrome genes may have emerged before the divergence of eukaryotes and prokaryotes (Kanai *et al*., 1997). Sequence comparison reveals that the mammalian and fly cryptochromes are more closely related to (6-4) photolyases including the *Arabidopsis* (6-4) photolyases than they are to the plant cryptochromes (Cashmore *et al*., 1999). It confirms that the plant and animal cryptochromes are likely to have arisen from independent evolutionary events. Thus, the cryptochromes represent an example of repeated evolution, a special case of convergent evolution in which a new genetic function arises independently in two different lineages from orthologous (or paralogous) genes (Cseke *et al*., 1998). Absence of cryptochromes in eubacteria and archaebacteria, prompted to speculate that the first cryptochromes-the progenitors of the plant cryptochromes evolved soon after the origin of eukaryotic organisms.

It has been proposed that at least four gene duplication events may have occurred in evolution to give rise to present day photolyases and cryptochromes (Todo, 1999). The first gene duplication produced the ancestral type I CPD photolyase and type II CPD photolyases. The ancestral type I photolyase gene duplicated again to become the present day type I photolyase and the progenitor of cryptochrome/6-4 photolyase. One copy evolved to become the present day cryptochromes in higher plants, whereas the other copy duplicated again to give rise to the 6-4 photolyases as well the cryptochromes in animal lineage (Lin and Shalitin, 2003).

Phototropins are paralogous members of the same family of blue-light photoreceptors (Briggs and Christie, 2002). Phototropins probably arose early in plant evolution and have been conserved over subsequent episodes of diversification. Genes homologous to PHOT1 and NPH3 have been found in a broad assemblage of plants including algae, mosses, ferns, dicots and monocots (Briggs and Olney, 2001). Similarly, genes homologous to PHOT2 have been found in ferns, monocots and dicots. It is likely that one or the other phototropins represents the product of an ancient gene duplication event in a common ancestor of ferns (*Adiantum*) and flowering plants (Briggs, 2001).

Nishio (2000) demonstrated role of green light in carbon fixation within leaves and showed that it drives carbon fixation deep within leaves. Both the palisade mesophyll (PM) and spongy mesophyll (SM) contribute significantly to carbon fixation (Nishio *et al*., 1993). However, the maximum carbon fixation across a spinach leaf occurred not at the top of the leaf, where light is maximum (Cui *et al*., 1991). The light absorption is mainly due to chlorophyll whereas the pattern of fixation across the leaves is due to the distribution of *Rubisco* (Nishio *et al*., 1993).

The quantum yield of photosynthesis, calculated per absorbed light quanta, drops at the red end of the absorption spectrum of leaves and green algae (Emerson and Lewis, 1943). The photosynthetic apparatus of higher plants must be highly adaptable

to large changes in quantum flux (Ort and Baker, 1988). In heterogeneous environment, the ability of a genotype to develop different phenotypes in response to environmental cues of future selective condition may be an important performance trait. If such phenotypic plasticity results in accurate matching of phenotype to the environment, it may result in high relative fitness across the range of ecological conditions, which an organism experiences.

3.1. Chloroplast accumulation

Chloroplasts are the primary photosynthetic apparatus of plants, and their intracellular distribution depends on environmental factors, especially the availability and quality of light. During photorelocation, the chloroplasts situate along the periclinal cell walls, optimizing their potential to harvest sufficient sunlight for optimal photosynthesis under low light conditions. Under high light, the chloroplasts move away from the periclinal walls and toward the anticlinal walls, minimizing potential photodamage. Two cytoskeletal systems, actin filaments and microtubules, are critical for organelle movement and positioning. In plant cells, organelle movement appears to depend more on actin filament than on microtubules, and actin filaments have been shown to be involved in the movement of chloroplasts (Kandasamy and Meagher, 1999), mitochondria (van Gestel *et al*., 2002), nuclei (Chytilova *et al*., 2000), peroxisomes, the endoplasmic reticulum, and the Golgi body (Boevink *et al*., 1998). Pharmological studies have also revealed that the motility system for light-induced chloroplast movements in angiosperms uses the actin cytoskeleton (Mathur *et al*., 2002). For example, addition of cytochalasin and latrumulin disrupts chloroplast movements, whereas colchicine does not, implicating actin and not microtubules to be the candidate cytoskeletal network (Tlalka and Gabrys, 1993).

Phototropins control the movement of chloroplasts in response to different light intensities (Wada *et al*., 2003). This functionality results in two separate phases: chloroplast accumulation and chloroplast avoidance, appear to employ phototropin 1 (phot1) and phototropin 2 (phot2), respectively, likely as a consequence of their light sensitivities (Sakai *et al*., 2001). Under low light conditions, phot1 and phot2 induce chloroplast accumulation movement to the upper cell surface to promote light capture for photosynthesis (Sakai *et al*., 2001). Phot1 is more sensitive than phot2 in activating chloroplast accumulation movement, as phot2 activity requires a higher light threshold (Sakai *et al*., 2001). In high light conditions, chloroplasts move away from the site of irradiation (Wada *et al*., 2003).

Arabidopsis mutants impaired in blue-light induced chloroplast movements have also provided insights into the signaling events acting downstream of phototropin receptor activation. Oikawa *et al*. (2003) identified the components involved in chloroplast movement in *Arabidopsis* and observed that the mutations in a gene encoding the photoreceptor mediate the high light-induced chloroplast avoidance movement. They isolated additional *Arabidopsis* mutants showing aberrant chloroplast positioning (termed chloroplast unusual positioning [Chup]) encodes a novel 112-KD protein. *Chup1* mutants exhibit different chloroplast positioning in which chloroplasts are accumulated at the bottom of the palisade cells, in contrast to wild type (Oikawa *et al*., 2003). CHUP1 provides the ability to target a given fluorescent protein (GFP) into the chloroplast envelope (Oikawa *et al*., 2003), indicating that CHUP1 may function at the periphery of the chloroplast outer membrane.

Irrespective of the exact nature of the motility system involved in BL-induced chloroplast movements, rearrangements of the actin cytoskeleton as well as myosin function can be regulated by calcium (Ca^{2+}) concentrations within the cell (Staiger, 2000). Light induced chloroplast movements can be affected by altering cytosolic Ca^{2+} levels (Sato *et al*., 2001). It has been shown that phot1 and phot2, which are bound to the plasma membrane (Sakamoto and Briggs, 2002), mediate BL-induced increases in cytosolic Ca^{2+} in *Arabidopsis* mesophyll cells (Stoelzle *et al*., 2003). The phot mediated Ca^{+2} influx is fluence dependent. At fluence rates between 0.1 and 50 μmol m^{-2} s^{-1}, phot1 induces Ca^{2+} influx from the apoplast through a channel within the plasma membrane. At fluence rates between 1 and 250 μmol m^{-2} s^{-1}, phot2 mediates Ca^{2+} influx through plasma membrane bound channels as well as release of Ca^{2+} from internal stores via a phospholipase C-mediated phosphoinositide signaling pathway (Harada *et al*., 2003).

Mutations in locus, J-DOMAIN PROTEIN REQUIRED FOR CHLOROPLAST ACCUMULATION RESPONSE 1 (JAC1) impaired chloroplast accumulation responses but have a normal avoidance response (Suetsugu *et al*., 2005). Similarly, the plastid movement impaired mutant *pmi1* exhibits severely attenuated chloroplast movements under both low and high light intensities (DeBlasio *et al*., 2005), indicating that PMI1 is required for both chloroplast accumulation and avoidance movement (Luesse *et al*., 2006).

3.2. Stomatal opening

Stomata regulate the uptake of CO_2 with loss of water vapour. The functioning of stomata is based on a proper control of the turgor pressure in guard cells, which in pairs surround the stomatal pores. The opening and closing of stomata is important for gas-exchange processes leading to photosynthesis and is affected by both light and hormones (Schroeder *et al*., 2001). Control of the guard cell

aperture is regulated largely through the flow of potassium ions regulated by the action of H^+-ATPase. Stomatal guard cells of the *phot1 phot2* double mutant fail to extrude protons in response to blue-light treatment (Kinoshita *et al*., 2001). Proton extrusion is essential for stomatal opening and involves activation of the plasma membrane H^+-ATPase (Dietrich *et al*., 2001). Activation of the guard cell H^+-ATPase involves phosphorylation of the H^+-ATPase and 14-3-3 protein upon autophosphorylation (Kinoshita *et al*., 2003) specifically, 14-3-3 binding to *Vicia faba* phot1 requires phosphorylation of Ser^{358} situated between LOV1 and LOV2, which is equivalent to Ser^{325} of oat phot1 that is phosphorylated in response to intermediate fluencies of blue light (Salomon *et al*., 2000). The autophosphorylated form is in an active state and dephosphorylation of the Ser residues stops the signaling. As seen in rcn1 mutant, inhibition of the dephosphorylation of phot2 enhances stomatal opening. Dephosphorylation of the phot2 is catalyzed by PP2A (Tseng and Briggs, 2010). The phosphatase that catalyzes the phot1 dephosphorylation is unknown. The immediate downstream component or the substrate for the phototropin kinase has not been identified in guard cells. Then, the signal might be transmitted to a regulatory subunit of protein phosphatase 1 (PP1) and modulate the catalytic subunit of PP1, which acts as a positive regulator for stomatal opening (Takemiya *et al*., 2006).

The signal ultimately activates the plasma membrane H^+-ATPase by the phosphorylation of a Thr residue in the C-terminus with a subsequent binding of a 14-3-3 protein (Shimzaki *et al*., 2007). The activated H^+-ATPase transports H^+ across the membrane and increases the inside-negative electrical potential, driving the K^+ which facilitates the water influx into the guard cells, leading to an increase of turgor pressure and stomatal opening (Shimzaki *et al*., 2007). The leaves of young *phot1 phot2* double mutants grown in white light were observed to be smaller than those of wild-type plants and *phot* single mutants and curled downward (leaf epinasty) suggesting a redundant role for phototropins in regulating leaf expansion (Sakamoto and Briggs, 2002).

3.3. De-etiolation

De-etiolation is the major developmental switch of young seedlings emerging from the darkness under soil and becoming exposed to light. De-etiolation is characterized by several morphological changes, including hypocotyl's growth arrest, cotyledon expansion and chloroplast development. Light inhibits hypocotyl elongation, but stimulates cotyledon expansion and conversion of etioplasts to chloroplasts (Nemhauser and Chory, 2002). Genetic analyses of *Arabidopsis* mutations impaired in the de-etiolation responses revealed that many genes such as COP1, SPA1, HY5/HYH, HFR1, PP7, SUB1, SHB1, BIT1, OBP3, HRB1 and ATAB2 have been found to participate in cryptochrome regulation of de-etiolation (Hong *et al*., 2008). Also, the isolation of mutants deficient in cryptochromes 1 and 2 (*cry 1* and *cry 2*) has revealed roles for these photoreceptors throughout seedling development.

Overexpression of CRY1 is responsible for hypersensitive blue-light inhibition of hypocotyl elongation, resulting in shorter hypocotyls and dwarf seedlings in continuous blue light (Lin *et al*., 1998). It seems that the function of CRY2 in de-etiolation is limited to low intensities of blue light (<10 μmole m^{-2} s^{-1}), probably due to faster turnover of the CRY2 protein under higher fluence rates of blue light (Lin *et al*., 1998). The *cry1cry2* double mutant exhibited a more pronounced long hypocotyl phenotype when grown in continuous blue light than the cry1 or cry2 monogenic mutant, suggesting a partially redundant function of the two cryptochromes in this response (Mockler *et al*., 1999). The cellular mechanism behind the blue light and CRY-dependent growth inhibition has also been extensively studied (Spalding, 2000). It was proposed that cryptochromes activate anion channels, leading to PM depolarization and inhibition of cell elongation (Spalding, 2000). It was found that nuclear-localized CRY1 is responsible for both hypocotyl inhibition and membrane depolarization (Wu and Spalding, 2007). Membrane depolarization associated with nuclear CRY-1 occurs within seconds after illumination thus suggesting a mechanism faster than that which usually takes by regulation of transcription.

Etiolation is visualized as a specialized development pathway that is used to delay development in the dark or under low light conditions (McNellis and Deng, 1995). Etiolated seedlings of angiosperms require a light signal to de-etiolate, or to develop into a compact, green seedling with fully expanded seed leaves. Phytochrome null mutants of *Arabidopsis*, tomato and rice demonstrate that phyA induces seedling de-etiolation in response of continuous far-red light (FRc) via a far-red high irradiance response (Takano *et al*., 2001). Canopy shade in FR-enriched because chlorophyll strongly absorbs R; thus, in dense shade phyA induces de-etiolation. Conversely, open sunlight is R-enriched, and in these habitats, phyB induces de-etiolation. FRc suppresses phyB-mediated de-etiolation and Rc suppresses phyA-mediated de-etiolation (McCormac *et al*., 1992).

3.4. Shade avoidance

There is also growing evidence for quantitative genetic variation in plasticity to light quality, crowding and vegetation shade both within and between natural plant populations, suggesting the evolutionary potential for adaptive evolution (Skálová and Krahulec, 1992). Evolution within the phytochrome family appears to be faster than other

plant nuclear genes (Kehoe and Grossman, 1996). When grown in close proximity to one another, constraints on photosynthetic productivity can lead to competition between individuals for light. Plants have therefore evolved two principle adaptive strategies to enhance their survival in such situations, shade tolerance and shade avoidance. Plants perceive the presence of neighboring vegetation as a reduction in the ratio of red to far-red wavelengths in the light reflected from, or transmitted through green tissues.

The photosynthetic pigments (chlorophylls and carotenoids) absorb light over most of the visible spectrum. Radiation in the FR region is, however, photosynthetically ineffective and very poorly absorbed. Daylight reflected from, or transmitted through, chlorophyllous vegetation is therefore relatively enriched in far-red wavelengths, generally displaying a R: FR ratio of between 0.09-0.7 (Smith, 1982). Changes in R: FR ratio is detected by plants as a change in the relative proportions of Pr and Pfr. Phytochrome-mediated shade avoidance is a model for the functional significance of physiological adaptation to environmental signals, giving ecologists and evolutionary biologists a control on the evolution on phenotypic plasticity.

3.5. Circadian clock

Plants use internal receptors to anticipate upcoming seasonal changes and accordingly adjust their physiology and development. This circadian system contains three main parts: input, central oscillator and output. The central oscillator generates an oscillation with a period of approximately 24 h, based on negative feedback loops formed by the clock genes and proteins and it regulates the expression of genes through the output pathways. On the other side of the system, light signals absorbed by photoreceptors reach the central oscillator through the input pathways and synchronize its phase to the actual periodic environmental changes. The circadian clock timekeeper is a major regulator of plant gene expression.

The rotational movement of the earth determines a 24 h repetitive signal that is exploited by all photosynthetic organism, fungi and animal to precede external signals and provide a physiological advantage (Dodd *et al*., 2005). The system is so precise and critical that in cyanobacteria three proteins, two modulators (kaiA and kaiB) and the kinase/phosphatase kaiC, in the presence of ATP, can maintain a self-perpetuating clock with ~24 h of autophosphorylation/dephosphorylation cycles when isolated *in vitro*, thus, in organisms that evolved very early, such as some cyanobacteria, the capacity was present to set time independently of transcriptional inputs (Nakashima *et al*., 2008).

Transcription factors that activate photosynthetic genes are degraded during the night. This signal involves active proteasome-dependent protein degradation through a direct photoreceptor control. In *Arabidopsis*, PHYA, B, D, E, CRY1 and CRY2 photoreceptors have been shown to play a role in resetting the circadian clock (Devlin and Kay, 2000). CRY1 and CRY2 are involved in the blue light input to the central oscillator, PHYA alone is responsible for detecting far-red light, whereas PHYB, D and E function in red light signaling to the clock. It has also been shown that the expression of phytochromes and cryptochromes is under the control of the circadian clock itself (Tóth *et al*., 2001).

The *Arabidopsis* circadian clock comprises of multiple feedback regulations centered on two MYB transcription factors, CIRCADIAN CLOCK-ASSOCIATED 1 (CCA1) and LATE ELONGATED HYPOCOTYL 1 (LHY) (Harmer, 2009). CCA1 and LHY concomitantly suppress the expression of the other clock genes with afternoon to evening peaks, such as PRR5, TIMING OF CAB EXPRESSION (TOC1), CCA1 HIKIN EXPEDITION (CHE), GIGANTEA (G1), LUXARRHYTHMO (LUX), and EARLY FLOWERING (ELF4) (Farré *et al*., 2005). PRR9, PRR7 and PRR5 proteins are expressed throughout the day. They physically associate with the CCA1 and LHY promoters and repress their transcription (Nakamichi *et al*., 2010). As CCA1 and LHY protein levels decrease, CCA1/LHY-dependent repression fades away, facilitating accumulation of the evening lock gene transcripts. The direct role of the CONSTITUTIVE PHOTOMORPHOGENIC 1 gene product COP1, an E3 ring finger-type ubiquitin ligase, in the control of flowering through the direct regulation of CONSTANS (CO) stability has been described (Jang *et al*., 2008). CO is the central in all plants analyzed because it co-ordinates light and clock inputs in leaves to trigger the expression of FLOWERING LOCUST (FT) whose protein and possibly its mRNA, can move from the phloem to the meristem. The CO-FT module is conserved in all known plants, but the final outputs of the signal diverge; whereas in *Arabidopsis thaliana*, a facultative long day (LD) plant, CO promotes the expression of FT under long day condition (Suárez-López *et al*., 2001) in a short day (SD) plant, rice, the signals are different and CO is a repressor in non-inductive long days (Hayama *et al*., 2003).

Cell elongation occurs at a particular time of the night due to the gibberellin (GA)-dependent effect of DELLA protein on basic helix-loop-helix (bHLH) transcription factors of the PHYTOHROME INTERACTION (PIF) protein family (de Lucas *et al*., 2008). An interesting link between flowering and DELLA proteins, connected to both ethylene and GA signaling (Achard *et al*., 2007), but these proteins appear only in vascular plants and not in algae, so this mechanism is not as evolutionary conserved as photoperiodic signaling.

3.6. Phototropism

To perceive light efficiently for photosynthesis, plants involve various phototrophic responses at the organ, cell and organelle levels. It is well established that plants respond well to the direction of light (Briggs and Christie, 2002). The bending of plant stem towards or away from a light stimulus (termed phototropism) is primarily mediated by blue light detected by the phototropin family of photoreceptors. The identification of an *Arabidopsis* mutant impaired in hypocotyl phototropic curvature led to the cloning and characterization of the first phototropin gene (PHOT1). Originally designated *nph1* (non-phototropic hypocotyl), mutants failed to grow towards a low intensity blue light stimulus (Liscum and Briggs, 1995). The subsequent observations revealed *phot1* mutants to retain phototropic responsiveness to high irradiance blue light (Sakai *et al*., 2001). Studies using *cry1cry2* double mutants revealed no impairment of phototropism, confirming the unique role of phototropins in mediating this response (Lascéve *et al*., 1999).

4. Light Regulated Gene Expression

Several previous studies revealed that light causes a large-scale reorganization of chromatin during the floral transition in *Arabidopsis* (Tessadori *et al*., 2007) and that the presence or absence of light results in distinct gene expression profiles during the development of *Arabidopsis* seedlings (Ma *et al*., 2001). The discovery of light-regulated transcription factors (such as HY5, HYH and PIF3) and their binding sites (light responsive cis-elements) provided the first sign about its molecular mechanisms (Holm *et al*., 2002). The most extensively studied light responsive genes are those encoding the small subunit of ribulose-1, 5-bisphosphate carboxylase-oxygenase (rbcS) and chlorophyll a/b binding proteins (cab) (Dean *et al*., 1989). Transcription of the photosynthesis-associated nuclear genes from higher plants is activated by light receptors and its molecular mechanism has interesting evolutionary aspects. The transcription of photosynthesis associated nuclear gene (PhANG) in monocotyledonous and dicotyledonous plants are profoundly affected by light but the PhANG promoters in conifers, ferns and mosses are either light insensitive or weakly photosensitive (Quail, 1994). The G-box elements of rbc, chs and Lhcb1 are not homologous but only similar because they have different evolutionary origins. Three types of chlorophyll a/b proteins are found in the major light harvesting complex of photosystem II, encoded by *Lhcb1, Lhcb2, Lhcb3* (Grossman *et al*., 1995). Most *Lhcb* promoters that have been functionally analyzed are from the *Lhcb1* gene family and typically lack introns. In *Lhcb1* genes from dicotyledons, a Light Responsive Element (LRE) is located in the proximal promoter region of these genes. This LRE is characterized by three conserved GATA motifs spaced by 2 and 6 bp, respectively, which are located between CCAAT and TATA boxes (Mitra *et al*., 1989).

Genes upregulated under supplementary far-red grown plants are HOMEOBOX FROM ARABIDOPSIS THALIANA 4 (HAT4), which encodes a homeobox leucine zipper protein and PIF3-LIKE 1(PIL1), which encodes a bHLH. The promotion of hypocotyl elongation by far-red light added to white light background is largely mediated by phyB and antagonized by phyA. Far-red light reduces the proportion of phyB in its active form but activates the HIR mode of phyA. A large number of genes whose expression is upregulated by far-red light through phyB and down-regulated through phyA encode auxin-related proteins (Devlin *et al*., 2003). This includes several auxin regulated transcription factors such as INDOLEACETIC ACID-INDUCED PROTEIN 1 (IAA1), IAA19, as well as protein involved in auxin transport, PIN-FORMED-3 (PIN3) and PIN7. HAT2 is up-regualted by far-red light via phyB and downregulated by far-red light via phyA. Gibberellins, brassinosteroids and ethylene have been proposed to mediate and modulate the response to low red to far-red ratios (Pierik *et al*., 2004). This is in consistent with the observation that genes encoding proteins involved in gibberellins and ethylene biosynthesis (GIBBERELLIN 20 OXIDASE, 1-AMINO CYCLOPROPANE-1-CARBOXYL ACID SYNTHASE), gibberellin signaling (GIBBERELLIN INSENSITIVE, GAI), as well as brassinosteroids receptor BRASSINO-STEROID-INSENSITIVE 1(BRI1), are also regulated by reductions in the red to far-red ratios (Devlin *et al*., 2003). Changes in hormone levels or signaling activity ultimately modulate cell elongation through changes in cell wall extensibility leading to elongated stems and petioles in low red to far-red treated plants. Several genes encoding proteins that mediate cell wall loosening, such as pectin-esterases and expansions are upregulated by reduction in the red to far-red ratio (Devlin *et al*., 2003).

5. Redox and Evolution

Light-driven redox signaling is extremely important for plants as it coordinates, among other functions, whole metabolic rearrangements from starch-consuming catabolic reactions of the night phase to the light-driven anabolic synthesis during the day (Dietz, 2003). This regulatory level seems to have emerged very early in the evolution of photosynthetic organisms because a complex redox control system is already present in cyanobacteria (Li and Sherman, 2000). These types of signals may well belong to the earliest evolved controls since they prevent uncontrolled scenarios in energy availability, utilization and also its exchange. More complex aspects of redox control of physiology

through regulation of gene expression developed with the evolution of higher plants. All reducing power in plant cells ultimately originates from the light-driven electron transfer from water to $NADP^+$, which is performed by the photosynthetic machinery situated in the chloroplasts.

The evolution of oxygenic photosynthesis provided abundant oxygen and facilitated the elaboration of reactions involving O_2, particularly aerobic respiration. Almost all life is based on the essential energy exchange reactions of photosynthesis and respiration. The evolution of photosystem II first allowed use of the very high electrochemical (E_{M7}= +815 mV) of the O_2/H_2O redox couple. The light-driven chemistry of photosynthesis consists of a series of redox steps involving structural components or functionally coupled pools of redox-active compounds, such as thioredoxin (TRX), ascorbate and glutathione. Changes in the redox state of these components regulate the expression of both plastome- and nuclear encoded chloroplast protein.

This redox information co-ordinates expression in both compartments (Allen and Pfannschmidt, 2000). Significant advances have been made in our understanding of the composition, structure, assembly and regulation of the major photosynthetic complexes, PSII, PSI with their associated antenna systems, Cyt.b_6f and ATP synthase. Atomic resolution structures of PSII, PSI (Amunts *et al*., 2007), Cyt. b_6f (Smith *et al*., 2004) have been determined and provided new insights into the electron transfer routes within these complexes. They contain multiple subunits, pigments and redox co-factors and are synthesized through co-ordinate action of the nuclear and chloroplast genetic systems (Eberhard *et al*., 2008). Thus, some of the photosynthetic subunits are encoded by chloroplast genes and translated on chloroplast ribosomes while others are encoded by nuclear genes, synthesized on cytoplasmic ribosomes and imported into the chloroplast where they are assembled, together with their chloroplast encoded partners into functional complexes. This dual genetic origin of photosynthetic proteins requires a complex regulatory network for their co-ordinated expression and highlights the reasons behind the maintenance of this plastid genetic system during evolution. Allen (1993) proposed that plastid genomes have been maintained because of the dependence of their expression on the redox state of the electron transport chain. The localization of these two systems within the same cellular compartment would allow for rapid adjustments of gene expression to changes in environmental cues.

In plants, a role in flowering time for molecules involved in redox control, such as glutathione, salicylic acid and ascorbic acid, has also been proposed (Barth *et al*., 2006).

6. The "Darker" Side of Light

An oxygenic photoautotrophic organisms, require light for life; however, when environmental conditions prevent the maintenance of a high capacity for photosynthetic and photorespiratory carbon metabolism to utilize absorbed light, the likelihood for the photosynthetic generation of biologically damaging molecules including reduced and excited species of oxygen, peroxides, radicals and triplet state excited pigments increase (Asada, 1996). The quality of the light in natural environments can vary over several orders of magnitude and on a time scale that ranges from seconds to seasons. Because light is such an important environment parameter, plants have evolved numerous biochemical and developmental responses to light that help to optimize photosynthesis and growth. For example, plants rely on photoreceptors such as phytochrome for shade avoidance responses.

Some plants are able to adjust their capacity for harvesting sunlight through leaf and chloroplast movements. During long-term acclimation to changes in light intensity many plants regulate the size of their light harvesting pigment antennae through changes in gene expression and/or proteolysis. Large antennae are necessary for efficient light capture in limiting light, but they can be a liability when light is abundant or excessive. On a daily as well as seasonal basis most plants receive more sunlight than they can actually use for photosynthesis. Under these circumstances, regulation of light harvesting is necessary to balance the absorption and utilization of light energy, thereby minimizing the potential for photo-oxidative damage. Besides, adjusting light absorption, algae and higher plants have ways of getting rid of excess light energy by protective non-photochemical mechanisms that quench excited-singlet chlorophylls (Chl.) and harmlessly dissipate excess excitation energy as heat.

Absorption of sunlight for photosynthesis is accomplished by light-harvesting pigment-protein complexes (LHCs) that are associated with reaction centers. Light absorption results in singlet-state excitation of a Chlorophyll a molecule (1Chl*), which can return to the ground state via one of several pathways. Excitation energy can be re-emitted as chlorophyll fluorescence, it can be transferred to reaction centres and used to drive photochemistry, it can be de-excited by thermal dissipation process (NPQ), or it can decay via the triplet state (3 Chl*). 3Chl* can transfer energy to ground-state O_2 to generate singlet O_2 ($^1O_2$*), an extremely damaging reactive oxygen species.

Several mechanisms for regulating the photosynthetic light reaction have evolved and the fact that all photosynthetic organisms have photo-protective processes, operating in different ways and over varying timescales, suggests that they are

essential for survival. Feedback de-excitation (FDE), also called the qE -or energy-dependent component of non-photochemical quenching (NPQ), is a photo protective process of crucial importance for the plant. Psbs, a 22 kDa protein of the LHC superfamily, is necessary for the functioning of FDE (Li *et al*., 2000). Shortly after an increase in light intensity, plants reduce the excitation pressure on photosystem II (PS II) by inducing FDE, changing the conformation of the photosynthetic antennae from an "energy transfer state" to a "quenched state", allowing excess energy to be dissipated as heat. Plants lacking FDE through mutations in the Psbs gene show no marked phenotypic deviations from their respective wild-type in controlled growth chamber conditions (Li *et al*., 2000), but exhibit reductions in fitness when grown under fluctuating light or field conditions (Külheim *et al*., 2002). Other short-term responses to increases in light intensities include increases in cyclic electron transfer rates, activation of the Calvin cycle and photorespiration. Long-term responses include reductions in effective light intensities by thickening and tilting of leaves, accumulation of anthocyanins and movement of the chloroplasts.

7. Skotomorphogenesis

Seedlings kept in darkness adopt a development in which allocation of resource is typically directed toward hypocotyl elongation at the expense of cotyledon and root development. Rapid and exaggerated elongation of the hypocotyls provides a means for the seedling to seek light. Thus, the terrestrial flowering plants have evolved a developmental strategy termed skotomorphogenesis (etiolated, heteromorphic growth), whereby post-germinative seedlings emerging from buried seeds grow vigorously upward in the subterranean darkness toward the soil surface. Upon reaching the surface, the etilated growth is redirected by light toward the familiar photomorphogenic pattern of fully green plants. The developmental transition is termed de-etiolation and involves coordinate inhibition of hypocotyl elongation, unfolding of the apical hook, separation and expansion of the cotyledons and chlorophyll accumulation. In darkness, skotomorphogenesis is achieved by the active repression of the genes that would lead to de-etiolation and photomorphogenic development. This process is regulated by the COP1-SPA1 E3 ligase complex that targets transcription factors like HY5 for degradation by the proteasome (Osterlund *et al*., 2000). Leivar *et al*. (2008) illustrated how the balance between skotomorphogenesis and photo-morphogenesis is achieved during seedling establishment in *Arabidopsis*. Central to this process are the phytochrome interacting factor (PIF) trabscription factors, key modulators of the dark, etiolated states.

Photomorphogenesis and skotomorphogenesis can be distinguished not only on the level of the organism but also in intracellular morphogenesis of organelles. In the presence of light a protoplast develops into a green mature chloroplast whereas development in darkness follows a different strategy leading to an etioplast. Brassinosteroids are required to maintain the skotomorphogenesis pattern in darkness (Li *et al*., 1996) and brassinosteroid synthesis enzymes are downregulated in 6-day old light grown compared to dark grown seedlings. Seedlings grown for 6 days under red (600-700 nm), blue (400-700 nm) or far-red light (700-800 nm) display largely similar transcriptome patterns when compared to darkness (Ma *et al*., 2001).

Intriguing speculation is required to gain indepth knowledge on role of light in evolving plant's energy capturing and developmental processes. Light also played an indirect role by changing the external conditions.

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