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Review on: Mechanism of sensing and responding to excess light by higher plants

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Abstract
Plants are the basis for the survival of living things in nature. They can prepare their own food through photosynthesis. Hence, they are the bottom of food chain. Photosynthesis is the process by which plants use the energy from sunlight to produce sugar, which converts into energy (ATP), with the action of chlorophyll. Sun light meets two very important needs of biological organisms. First, the sun light maintains the planet's surface temperature in a range suitable for life through the process of photosynthesis which produce energy that sustains life on earth. Second, sunlight also provides critical information about the environment information for proper plant development and the measurement of daylength that is used by plants to regulate movement. Plants absorb too much light more than they can actually use in photosynthesis. To prevent photo-oxidative/photo inhibition damage and to acclimate to changes in their environment, plants have evolved direct and indirect mechanisms for sensing and responding to excess light. Directly through photoreceptors such as Phytochromes, phototropin, neochrome, and cryptochrome relay signals for chloroplast movement and gene expression responses. Indirectly through biochemical and metabolic signals.

Keywords: light, photoinhibition, photosynthesis

Introduction
Life on earth ultimately depends on light energy derived from the sun (Taiz and Zeiger, 2002) [20]. It is the sole energy source of plants and therefore, one of the most important environmental factors influencing their development and physiology. Light condition influences germination to seedling development and flowering (Pfeiffer *et al*., 2016) [17]. The energy source of plants prepared by photosynthesis process on principal organ called leaf (Hopkins and Huner,2008; Woodson, 2016) [22]. Chloroplast is an incredible thermodynamic machine in higher plants and green algae, on which the reactions of photosynthesis occur. The chloroplast traps the radiant energy of sunlight and conserves some of it in a stable chemical form (Taiz and Zeiger, 2002; Hopkins and Huner, 2008) [20].

Higher plants have two types of photosystems. First, photosystem I (PSI, plastocyanin-ferredoxin oxidoreductase), located in the stroma lamella of thylakoid. Second, photosystem II (PSII, water-plastoquinone oxidoreductase), located on the stacked grana domain (Albertsson, 2001; Dekker and Boekema, 2005; Hopkins and Huner, 2008) [1, 8]. They are composed of a core complex and a peripheral antenna system, light harvesting complex I (LHCI) for PSI and light harvesting complex II (LHCII) for PSII, respectively. Photosystem II (PSII) of the photosynthetic apparatus has been identified as the engine of life. However, considering both the cooperative relation between photosystem II (PSII) and photosystem I (PSI) in photosynthesis and the key role of photosynthesis in the biosphere, we prefer to consider the two photosystems together, as the engine of life driven by the energy from sunlight (Pessarakli, 2001) [16]. The two photosynthetic machineries are damaged by the absorption of excess sunlight; and also limit photosynthetic activity, thereby affecting growth and productivity (Allorent *et al*., 2016) [2].

Plants often absorb too much light more than they can actually use during photosynthesis. Plants have evolved direct and indirect mechanisms for sensing and responding to excess light to prevent photo-oxidative/photo inhibition damage and to acclimate to changes in their environment. Directly through Photoreceptors such as phytochromes, phototropin, neochrome, and cryptochrome relay signals for chloroplast movement and gene expression responses, Indirectly through biochemical and metabolic signals.

plants have the mechanism and ability to develop anatomical, morphological, and physiological and biochemical alterations in response to different light intensities (Hopkins and Huner, 2009; Zhirong *et al*., 2008) [20, 25].

In this paper, the effect of excess light, the mechanism of plant how sensing and responding excess light and the response of plants to excess light will be reviewed.

Light

The physical nature of light

Johnson recognized more than 200 years ago, light is a form of radiant energy, a narrow band of energy within the continuous electromagnetic spectrum of radiation emitted by the sun. Light is defined by the range of wavelengths between 400 and approximately 700 nanometers capable of stimulating the receptors located in the retina of the human eye (Taiz and Zeiger, 2002; Hopkins and Huner, 2008) [20].

Light has properties of both particles and waves. A wave is characterized by a wavelength, denoted by the Greek letter lambda (λ), which is the distance between successive wave crests. The frequency, represented by the Greek letter nu (v), is the number of wave crests that pass an observer in a given time. A simple equation relates the wavelength, the frequency, and the speed of any wave: $c = \lambda v$ Where, c is the speed of the wave in the present case, the speed of light (3.0 x 10^8 ms–1). Light has a particle property called a photon, contains an amount of energy that is called a quantum. The energy content of light is depending on the wave length of light and it is not continuous but rather is delivered in these discrete packets, the quanta. The energy (E) of a photon depends on the frequency of the light according to a relation known as Planck's law: $E = hv$ where h is Planck's constant (6.626 x 10^{-34} J s) (Taiz and Zeiger, 2002) [20]. Only 700 nm to 400 nm wavelength range of light is photosynthetically-active radiation absorbed by plants. Hence, violent, blue and red light are absorbed and lighter blue, green and yellow light are reflected (Taiz and Zeiger, 2002) [20].

Table 1: Radiation color, wavelength and average energy.

Color	Wavelength range(nm)	Average Energy (kJ mol^{-1} protons
Ultraviolet 100-400		
UV-C	100-280	471
UV-B	280-320	399
UV-A	320-400	332
Visible 400-740		
Violet	400-425	290
Blue	425-490	274
Green	490-550	230
Yellow	550-585	212
Orange	585-640	196
Red	640-700	181
Far-red	700-740	166
Infrared	longer than 740	85

Source: (Hopkins and Huner, 2008)

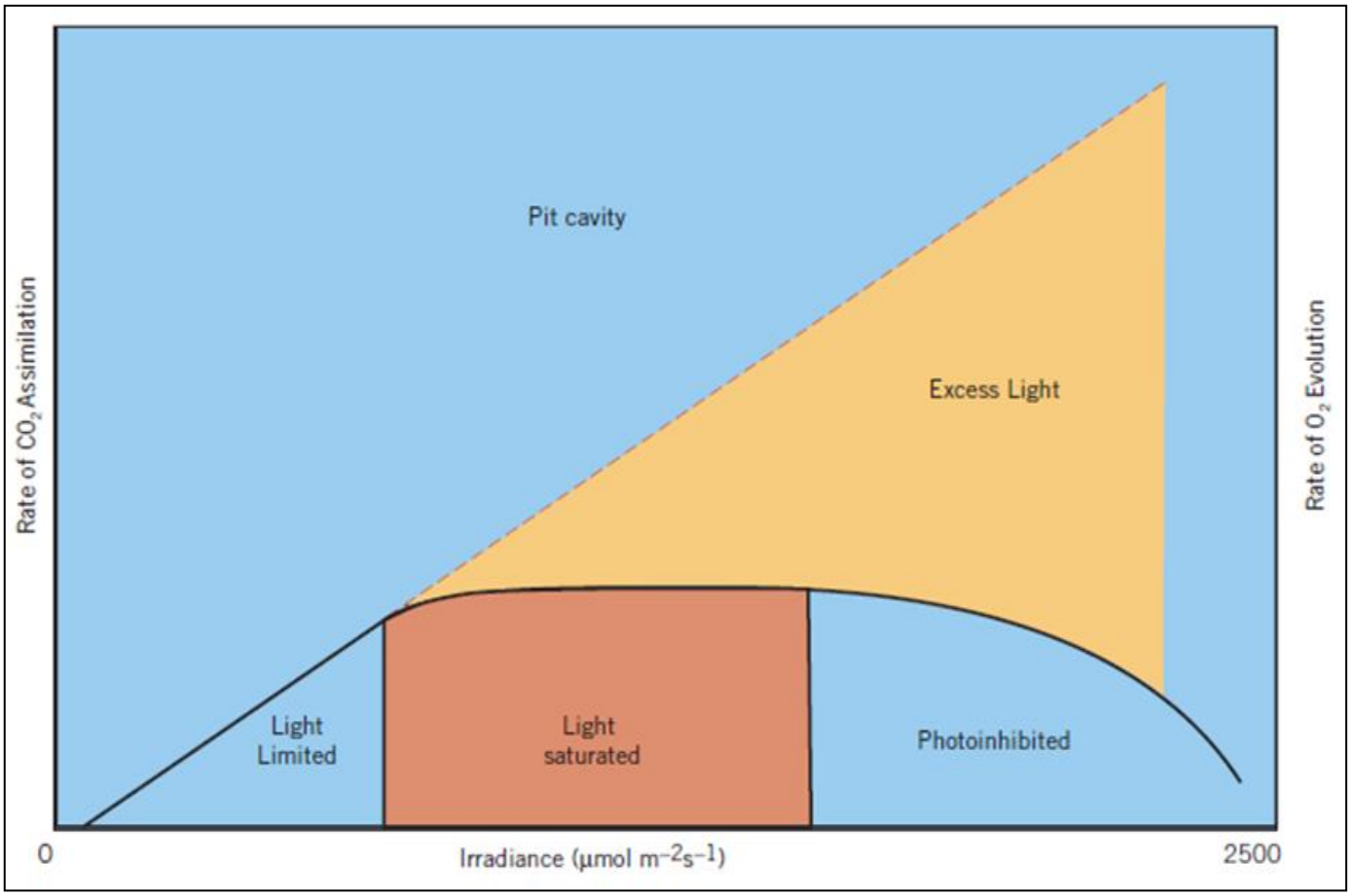
Importance of light

Life on earth is dependent on the photosynthetic conversion of light energy into chemical energy Sunlight is essential for any crop. Increasing amounts of light often increases dry matter production until optimum level. Light is the sole energy source of plants and therefore one of the most important environmental factors influencing their development and physiology (Taiz and Zeiger, 2002; Pfeiffer *et al*., 2016) [20, 17].

All pigments have a characteristic absorption spectrum that describes the efficiency of light absorption as a function of wavelength. When light is absorbed, the pigment becomes excited, or unstable. Light is very important because, in addition to using ATP (along with NADPH) for the reduction of CO2, a continual supply of ATP is required to support a variety of other metabolic activities in the chloroplast. These activities include amino acid, fatty acid, and starch biosynthesis, the synthesis of proteins in the stroma, and the transport of proteins and metabolites across the envelope membranes (Hopkins and Huner, 2008).

Effect of excess light

Plant survival, growth and adaptation significantly affected by solar radiation; regulates the photosynthesis (Zhang *et al*., 2003). The rate of photosynthesis is no longer a linear function of irradiance when there is an extended increase in irradiance, but rather levels off. At these higher light intensities, the rate of photosynthesis is said to be light saturated (figure 1). This means that the Calvin Cycle is saturated with ATP and NADPH which, in turn, means that Rubisco is saturated with one of its substrates, RuBP. The maximum light saturated rate is a measure of photosynthetic (Hopkins and Huner,2008). Light requirements of the plant vary with growth stages and from plant to plant. Plants are referred to as either high energy or low-energy plants, depending on the intensity of light they need (Zhirong *et al*., 2008) [25].



Adapted from; Hopkins and Norman, 2009.

Fig 1: A schematic light response curve for photosynthesis measured as either the rate of CO2 assimilation or the rate of O2 evolution. The area above the light response curve represents excess irradiance that is not used in photosynthesis.

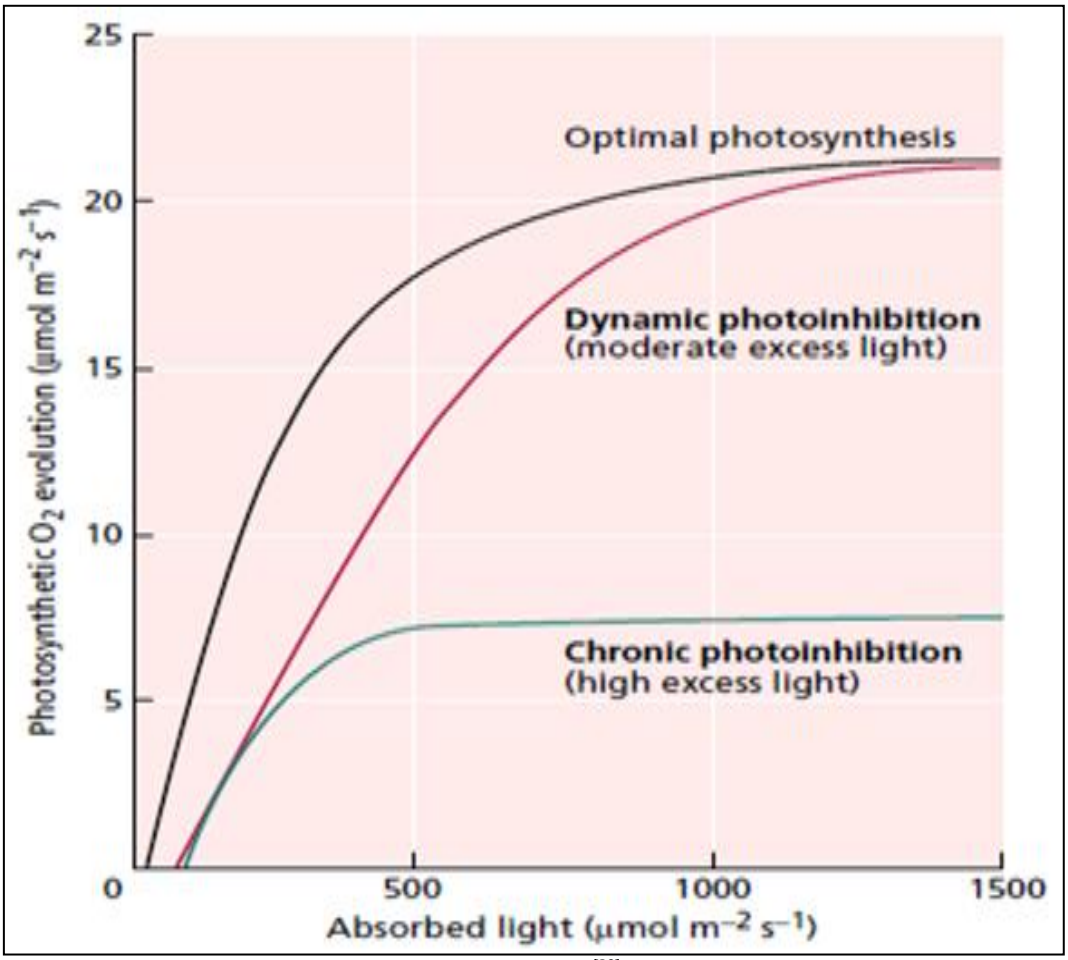
Photoinhibition

Plants differ in their light requirement for growth and development. Depending on the intensity of light they required plants are classified as high energy and low-energy plants. photosynthetic efficiency measured either as moles of CO_2 assimilated per photon absorbed, or alternatively, moles of O_2 evolved per photon absorbed if photosynthesis is measured as the rate of O_2 evolution (Figure 1). At these higher light intensities, the rate of photosynthesis is said to be light saturated (Hopkins and Huner, 2008). Photoinhibition of photosynthesis occurs when the plants are exposed to higher and higher levels of excess light, as a result the rate of photosynthesis productivity begins to decrease (Hopkins and Norman, 2009).

Photoinhibition of photosynthesis can be caused by ultraviolet light (UV), by visible light (V) and by the interaction of both (Powles, 1984), when light-induced damage to the PSII reaction center, then more severe radical-induced damage to other components of the photosynthetic apparatus (Baker, 1996) [4].

The use of the quantum absorbed by the leaf results in a hyperbolic response of photosynthesis to light. Under low-intensity light (less than 100 µmol.$m^{-2}s^{-1}$), more than 80% of the absorbed quantum can be used in photosynthesis, according to the maximum quantum efficiency in releasing O_2 when light intensity approaches 1000 µmol. $m^{-2}s^{-1}$ (50% of the full sunlight value), less than 25% of the absorbed quantum is used; and, under full sunlight, utilization decreases to 10% (figure 1.) (Alves *et al*., 2002) [3].

The reaction center of the PSII is more susceptible to the damage, because of a very strong oxidation potential of the P680. The powerful oxidant P680+ will inevitably oxidize the nearest pigments and amino acids, causing their degradation and the subsequent D1 degradation (Ruban, 2009). Reduction of photosynthesis due to excess light leads to a stepwise inactivation of photosystem II (PSII). There is consistent *in vivo* evidence that the major site of photoinhibition is located in PSII (Krause, 1988) cited in (Zaman *et al*., 2004). Inactivation of PS II may either be rapidly reversible or entail irreversible damage to core PS II reaction center proteins (D1), requiring *de novo* protein synthesis for repair (Prasil *et al*., 1992) cited in (Michael *et al*, 1998) [14].



Source: After Osmond (1994) cited in Taiz and Zeiger (2002) [20].

Fig 2: levels of photoinhibition. There are two level of photoinhibition.

Dynamic photoinhibition;
Quantum efficiency decreases (contrast the slopes of the curves in above, but the maximum photosynthetic rate remains unchanged. It is caused by the diversion of absorbed light energy towards heat dissipation hence the decrease in quantum efficiency; which is often temporary, and quantum efficiency can return to its initial higher value when photon flux decreases below saturation levels (figure 2) (Hopkins and Huner, 2008).

Chronic photoinhibition
It results from exposure to high levels of excess light that damage the photosynthetic system and decrease both quantum efficiency and maximum photosynthetic rate. It is associated with damage and replacement of the D1 protein from the reaction center of PSII. The damage effect is long lasting and persisting for weeks or months as compared to dynamic photoinhibition (figure 2) (Taiz and Zeiger, 2002) [20].

Photooxidation
PSII reaction centers exhibit an inherent life time. The D1 polypeptide of PSII reaction centers exhibits the fastest turnover rate of any plant protein. The D1 polypeptide is degraded and resynthesized in the time span of approximately 30 minutes. Shorten the time to absorb the necessary photons to cause the degradation of D1. PSII reaction center is irreversibly damaged due to photooxidation (Hopkins and Huner, 2008).

Mechanism of sensing and responding of excess light
To prevent photo-oxidative/photoinhibition damage and to acclimate to changes in their environment, photosynthetic organisms have evolved direct and indirect mechanisms for sensing and responding to excess light. On the other hand, plants can indirectly sense excess light through biochemical and metabolic signals can be transduced into local responses within chloroplasts, into changes in nuclear gene expression via retrograde signaling pathways, or even into systemic responses, all of which are associated with photo acclimation (Zhirong *et al*., 2008) [25].

Direct sensing
No significant advances toward the identification of blue light photoreceptors were made until the early 1990s. Nowadays, identification of mutants for key blue-light responses, and the subsequent isolation of the relevant gene for phototropism and the inhibition of stem elongation. There are four photoreceptors associated with blue-light responses: phytocrome, cryptochromes, phototropins, and zeaxanthin (Franklin and Whitelam, 2007; Briggs and Christie, 2002; Zeiger *et al*., 2002) [6].

Phytochromes

Phytochromes are blue protein pigment with a molecular mass of about 125 kDa (kilodaltons). They are involved in the sensing of the light environment by seeds, and the control of germination by red and far-red light was one of earliest phytochrome-mediated responses. Phytochromes can exist in two stable states. They are red-light absorbing form (Pr) and far-red light absorbing form (Pfr) with an absorption maximum at around 665 nm and 730nm wavelength, respectively. The R:FR ratio received determines the ratio between active and inactive forms of phytochrome. In darkness, phytochromes revert to their inactive state, Pr, which absorbs red light. When the inactive Pr absorbs red light, it converts to the active, Pfr, state. The active Pfr phytochrome absorbs far-red wavelengths; absorption of FR converts the Pfr back to Pr, thus the higher the R:FR ratio, the higher the Pr:Ptotal ratio (Franklin and Whitelam, 2007).

The responses mediated by phytochromes have been classified into three modes of action depending on their light exposure requirements: high irradiance responses (HIR), low fluence responses (LFR), and very low fluence responses (VLFR). VLFR has been reported in seeds that do not germinate in darkness but for which germination can be induced by extremely (Zervoudakis *et al*., 2012; Hopkins and Huner, 2008) [23].

Diverse light responses are mediated by phytochromes. Study on phytochrome mediated responses; stimulated by light doses between 1 µmol m^{-2} (equivalent to a 0.1 second exposure of light under a dense plant canopy, or under a few millimeters of soil) and 1,000 µmol m^{-2} (one second of broad daylight). These responses are called low fluence responses (LFRs). Phytochrome-mediated responses that are triggered by the dimmest light are called very low fluence responses (VLFR) and occur at photon doses as low as 0.1 nmol m^{-2} (Zhirong *et al*., 2008) [25].

Phototropin

Phototropins are receptors of blue light, which regulate photo induced movement in plants. Photo induced movement includes chloroplast movement, phototropism, leaf expansion, and stomatal opening.

Some recently isolated *Arabidopsis* mutants impaired in blue light–dependent phototropism of the hypocotyl have provided valuable information about cellular events preceding bending. One of these mutants, the *nph1* (*n*on-*p*hototropic *h*ypocotyl) mutant has been found to be genetically independent of the *hy4* (*cry1*) mutant. The *nph1* mutant lacks a phototropic response in the hypocotyl but has normal blue light–stimulated inhibition of hypocotyl elongation, while *hy4* has the converse phenotype. Recently the *nph1* gene was renamed *phot1*, and the protein it encodes was named phototropin (Briggs and Christie, 2002) [6].

Cryptochrome

Cryptochromes are shown to be involved in photo morphogenetic responses, such as cell elongation, stem elongation inhibition, leaf expansion, and entrainment of the circadian clock, gene expression, and photoperiodic flowering. Cryptochromes function together with red- and far-red wavebands absorbing phytochromes (Lin, 2002.). The *hy4* mutant of *Arabidopsis* lacks the blue light–stimulated inhibition of hypocotyl elongation. As a result of this genetic defect, *hy4* plants show an elongated hypocotyl when irradiated with blue light and was proposed to be a blue-light photoreceptor mediating the inhibition of stem elongation (Fitter and Hay, 2002) [9].

More recent studies indicate that the blue light photoreceptors CRY1 and CRY2 are involved in blue light inhibition of hypocotyl elongation (Taiz and Zeiger, 2002) [20].

Carotenoid accumulation

Carotenoid accumulation increases when plants are exposed to excess lite conditions. It plays a key role in protecting photosynthesis from the toxic effect of over-excitation (Luca, 2012) [13].

Zeaxanthin and Lutein accumulation

Excess light induced the binding and accumulation of zeaxanthin (and its structural isomer Lutein) to specific proteins which enhancing photoprotection by modulating the yield of potentially dangerous chlorophyll-excited states *in vivo* and preventing the production of singlet oxygen (Barbara *et al*., 2020) [5].

xanthophyll cycle of chloroplasts, which protects photosynthetic pigments from excess excitation energy through zeaxanthin. Changes in guard cells in zeaxanthin content as a function of incident radiation are distinctly different from the changes in mesophyll cells. Study on Faba bean (*Visa faba*) indicated that, zeaxanthin accumulation in the mesophyll begins at about 200 µmol m^{-2} s^{-1} in sun plants. and there is no detectable zeaxanthin in the early morning or late afternoon. In contrast, following the incident solar radiation at the leaf surface throughout the day; zeaxanthin content in guard cells increased, and it is linearly proportional to incident photon fluxes in the early morning and late afternoon. Guard cell has sensory transduction and not carbon fixation the function (Zeiger *et al*. 2002).

Indirect sensing

Biochemical signal

Plant cells are responsive to various stimuli, primarily chemical ligands from their environments. Specific receptor molecules in the plasma membrane detect the different biochemical signals that impact the cell, and these receptors are the conduits for transmission of this information to the cell interior for action. Signal transduction receptors and many specific receptors are the major classes of receptors. The decrease in lumen pH in excessive light activates the inter conversion of specific xanthophyll pigments (oxygenated carotenoids) that are mostly bound to LHC proteins (Hopkins and Huner,2008).

Metabolic signal

It the basis of cellular functions and one of the first cellular components to respond to stress related changes in environmental conditions. Harvested light intensity affects the dynamic networks of metabolites as well as the expression of genes and proteins aids our understanding of

the regulatory mechanisms at work during photosynthesis (Davis *et al*., 2013) [7].

If metabolic activity is unable to utilize the ATP generated by charge separation in photosynthesis, a proton gradient builds up, causing a rise in pH in the thylakoids and the conversion of violaxanthin to zeaxanthin; it is responsible for dissipation of energy as heat. When excess energy is not dissipated in xanthophyll cycle (i.e. universal in photosynthetic organisms), it can cause photoinactivation of the photosystem II reaction center. Photoinactivation is slower and reversible process, and there is an immediate loss of photosynthetic competence and a direct cost of the repair. This xanthophyll cycle seems to be common in photosynthetic organisms (Demmig and Adams, 1996). Detecting the fluorescence emitted by photosystem II, where water is split generating protons and electric charge helps to quantify photoprotection and photoinactivation can be quantified by (Osmond *et al*., 1999).

Plants response to excess light

Phytochrome and cryptochrome act both jointly and independently to regulate a wide range of developmental responses. Whole plant responses to spectral light quality and irradiance are numerous (Hopkins and Huner, 2008).

Photo protection and photo inactivation

The light response curve for photosynthesis exhibits saturation kinetics in all plants. If plants continue to be exposed for excess light, the rate of photosynthesis begins to decrease (Hopkins and Huner,2008). The rate of CO2 assimilation increases linearly with an increase in irradiance under low irradiance conditions. This is to be expected since more absorbed light means higher rates of electron transport which resulting increasing levels of ATP and NADPH for the regeneration of RuBP (Taiz and Zeiger, 2002) [20]. Research result indicates, high irradiance is a relative term. Mostly shade plants suffer reversible damage when grown in full sunshine. In sun leaves, photosynthesis at 40W m^{-2} was reduced by 12% by prior exposure for 2 h to 400 W m^{-2} whereas the corresponding reduction for shade leaves was 45%. This effect is known as photoinhibition (Osmond *et al*., 1999).

Reduction in light harvesting antennae size

Excess light induces the reduction in light harvesting complex antennae size, the PSI to PSII ratio, and the total number of reaction centers and light harvesting antennae are the result of transcriptional and translational regulation of the proteins making up these specific complexes (Taiz and Zeiger, 2002) [20].

Activated chloroplast movement.

Plant leaves can alter the intracellular distribution of their chloroplasts to control light absorption and prevent photodamage. When incident radiation is weak, chloroplasts gather at the upper and lower surfaces of the mesophyll cells (the "accumulation" response), thus maximizing light absorption. Under strong light, the chloroplasts move to the cell surfaces that are parallel to the incident light (the "avoidance" response), thus minimizing light absorption (Zervoudakis *et al*., 2012) [23].

Stem elongation inhibition

Blue light rapidly inhibits stem elongation. It is a key morphogenetic response of the seedling emerging from the soil surface. On the other hand, the stems of seedlings growing in the dark elongate very rapidly. The conversion of Pr to Pfr (the red- and far red–absorbing forms of phytochrome, respectively) in etiolated seedlings causes a phytochrome-dependent, sharp decrease in elongation rates (Taiz and Zeiger, 2002) [20]. De-etiolation is the process switching from heterotrophic to phototrophic metabolism. It is a process under control of both phytochromes and cryptochromes. This change is an indicators of a plant's light-sensing ability. During de-etiolation, the hypocotyl's (embryonic stem) rate of growth is reduced (Hopkins and Huner, 2008). Research on stem elongation indicated that, the stem elongation response to far-red light incident on the stem measured under laboratory conditions can be shown to have a very short lag (of the order of minutes in small seedlings) but continue for some time after the end of the stimulus (Nikolaus *et al*., 2012) [15].

Photoperiodism

Photoperiodism is a response to the duration and timing of light and dark periods (Taiz and Zeiger, 2002) [20]. There are three basic photoperiodic response types: short-day (SD) plants, long-day (LD) plants, and day-neutral (DN) plants. A photoperiod requirement may be qualitative, in which case the requirement is absolute, or quantitative, in which case the favorable photoperiod merely hastens the response. The distinction between LD plants and SD plants is based on their response to day lengths greater than or shorter than the critical day length. The absolute critical day length varies from one species to another and the critical day length for a LD plant may be shorter than the critical day length for a SD plant (Hopkins and Huner, 2008).

Phototropism

It is morphogenetic response is particularly dramatic in dark-grown seedlings of both monocots and dicots. It can also be observed when a seedling is exposed to two unequally bright light sources, a condition that can occur in nature (Taiz and Zeiger, 2002) [20]. the phototropic blue-light response is distinct from the blue-light responses mediated by phytochrome and cryptochrome Phytochrome and cryptochrome responses are morphogenetic responses—they alter the *pattern* of growth and development (Hopkins and Huner, 2008). Blue Light Stimulates Directional growth toward (or in special circumstances away from) the light, is called phototropism. It can be observed in fungi, ferns, and higher plants (Taiz and Zeiger, 2002) [20].

Chloroplast gene activation

Plants exhibit a single chloroplast gene that encodes the D1 polypeptide called *psbA*. Plants have evolved a D1 repair cycle which repairs photodamage to PSII. When the D1 polypeptide is damaged, it is marked for degradation by protein phosphorylation. This phosphorylation results in partially disassembled PSII and the D1 polypeptide is degraded by proteolysis. Subsequently, the *psbA* gene is transcribed and translated using the chloroplastic transcriptional and translational machinery with the

subsequent accumulation of a new D1 polypeptide (Hopkins and Huner, 2008).

Conclusion

Plant growth and development depending on soil, water, oxygen and light. Each factor has its own limit for normal activities of plants. Naturally, plants often absorb too much light above they can actually use in photosynthesis. This excess light causes photo inhibition, reduction in light harvesting complex, activated chloroplast, inhibited stem elongation, photoperiodism and phototropism responses. They have the mechanism for sensing and responding to excess light through their photoreceptors. Photosystem II (PS II) reaction centers is highly affected by excessive light exposure on plant photosynthesis, which is responsible for photoinhibition. Plants sense the excess light respond the presence of excess light directly through relay signals for chloroplast movement and gene expression responses and indirectly through biochemical and metabolic signals. After all, anatomical, morphological, physiological and biochemical alterations in response to different light intensities.

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