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Review on; Nature and 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. Sunlight helps to maintain the planet's surface temperature through photosynthesis, it is the process that plants use to change carbon dioxide (CO_2), and water (H_2O) through light energy using Rubisco enzyme into sugars which help to maintain plant growth, development through continuous supply of energy (ATP) on the leaf chlorophyll. On the other hand, sunlight also provides critical information about the environment information for proper plant development and the measurement of day length that is used by plants to regulate movement. Plants absorb too much light more than they can actually use in photosynthesis. To control photo-inhibition/photo-oxidative injury and adapt to their environmental conditions, all plants have developed different mechanisms to scenes and respond too much light stimuli directly and indirectly. Phytochromes, phototropin, neochrome, and cryptochrome dependent signals for chloroplast movement and gene expression responses are considered as direct sensing and responding mechanism through photoreceptors. Additionally, plants can sense excess light through biochemical and metabolic signals indirectly.

Keywords: Light, Photo inhibition, Photosynthesis.

I. INTRODUCTION

All living organism on our planet ultimately depends on light energy light energy derived from the sun (Taiz and Zeiger, 2002). The growth, development and physiology of higher plant influenced by light energy. Therefore, several of the core developmental decisions during the lifecycle of a plant from germination to seedling development and flowering are strongly influenced by light conditions (Pfeiffer *et al*., 2016). The energy source of plants prepared by photosynthesis process on principal organ called leaf (Hopkins and Huner,2008; Woodson, 2016). photosynthesis occurs not only in eukaryotic organisms such as green plants and green algae but also in prokaryotic organisms such as cyanobacteria and certain groups of bacteria. Chloroplast is an incredible thermodynamic machine present in eukaryotic organisms in which photosynthesis occur. It captures light energy of sunlight and produce energy and oxygen (Taiz and Zeiger, 2002; Hopkins and Huner,2008).

Higher plants have two types of photosystems (photosystem I and photosystem II). Photosystem I is located in the stroma and photosystem II located on grana. Among the two photosystem II considered as the engine of life, but both are cooperatively working together to produce energy (Albertsson, 2001; Pessarakli, 2001; Dekker and Boekema, 2005; Hopkins and Huner, 2008). Each photosystem has a core complex and a peripheral antenna system, light harvesting complex I (LHCI) for PSI and light harvesting complex II (LHCII) for PSII, respectively. Absorption of too much sunlight during photosynthesis can harm the two photosystems and hinder photosynthetic activity, thus affecting growth and productivity (Allorent *et al*., 2016).

Plants regularly assimilate a lot of light beyond what they can really use during photo synthesis. To avoid photo-oxidative/photo-inhibition hindrance and to adapt to changes in their environment, photosynthetic plants have a mechanism for detecting and reacting to overabundance of light during photosynthesis. Directly through Photoreceptors, for example, phytochromes, phototropin, neochrome, and cryptochrome depend signals for chloroplast movement and gene expression responses, Indirectly through biochemical and metabolic signals. plants have the machine and capacity to develop anatomical, morphological, and physiological and biochemical changes because of different light intensities(Hopkins and Huner, 2009; zhironget *al*., 2008).

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.

II. LIGHT

A. The physical nature of light

Johnson recognized more than 200 years ago, light is a type of radiant energy, a slight band of energy inside the continuous electromagnetic range of radiation emanated by the sun. Light is characterized by the variation of wavelengths between 400- 700 nanometers fit for stimulating the receptors situated in the retina of human eye (Taiz and Zeiger, 2002; Hopkins and Huner, 2008).

Light has particles and waves properties. 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. 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).

Table 1. Radiation color, wavelength and average energy.

Color of light	Wavelength of light in (nm)	Energy produced by protonsin (kJ mol^{-1})
Ultraviolet light range 100-400		
UV-C	100-280	471
UV-B	280-320	399
UV-A	320-400	332
Visible light range 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	above 740	85

Source; (Hopkins and Huner, 2008)

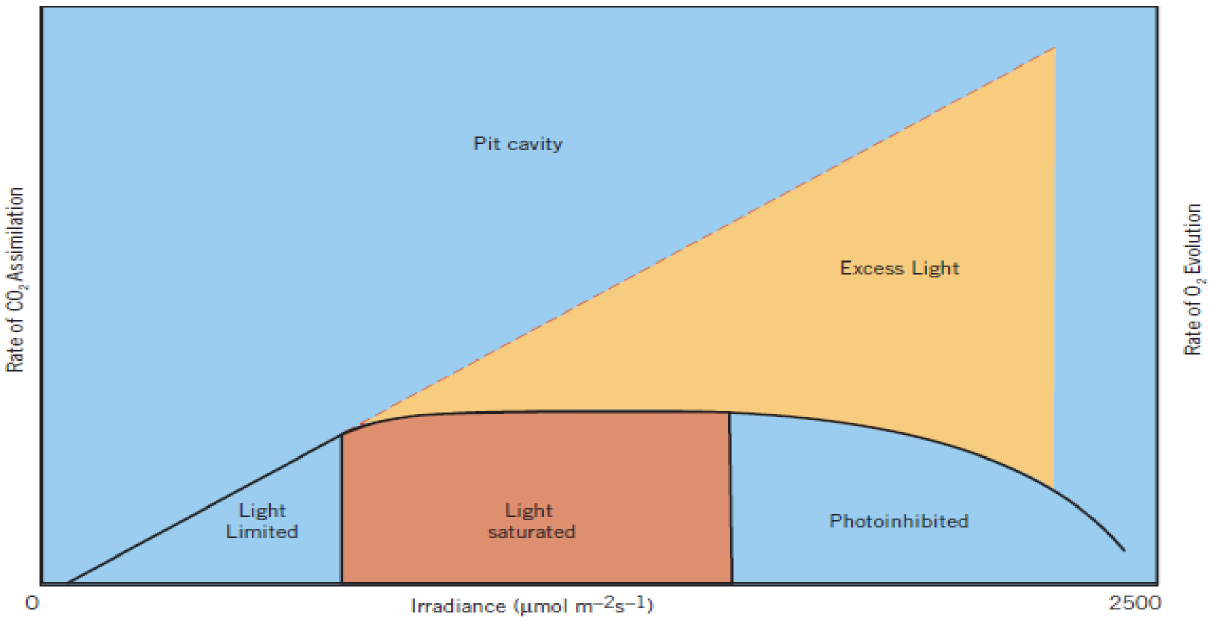
B. Importance of light

Living organisms in our planet are reliant on the photosynthetic change of light energy into chemical energy Sunlight is basic for any plants. Photosynthesis activities enhanced when the intensity of light increases, hence dry matter production increased until optimum level. Light is the sole source of energy of eukaryotic plants therefore, it influences growth, development and physiology (Taiz and Zeiger, 2002; Pfeiffer *et al*., 2016).

Plant pigments absorb light energy to produce ATP which is required for metabolic activities 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 in the chloroplast(Hopkins and Huner, 2008).

C. Effect of excess light

Photosynthesis activity is highly influenced many environmental factors. Among them radiant energy is the most regulating factor and therefore, the plant growth, survival, and adaptation (Zhang *et al*., 2003). Upon additional rises in light radiation, the rate of photosynthesis will not increase continuously rather stopped. This stage of photosynthesis is said to be light saturated, which indicated that, the Calvin Cycle is saturated through ATP and NADPH(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). The saturation level of light on maize plant is much higher than the other crop plants, because of this maize take advantage of higher light intensity (Li*et al*., 2005).



Adapted from; Hopkins and Norman, 2009.

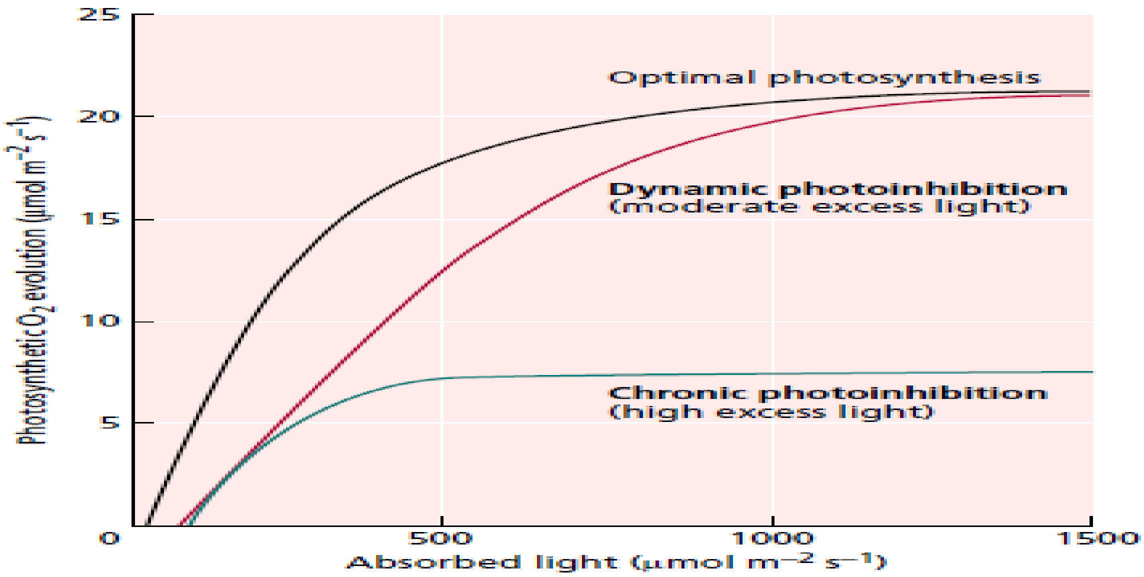
Figure1. A light response curve showing the effect of excess light on photosynthesis.

a. Photoinhibition

Plants vary in their light demand for growth and development. Reliant up on the intensity of light they required plants are classified as high energy and low-energy plants. photosynthetic productivity estimated either as moles of CO_2 acclimatized per photon consumed, or then again, moles of O_2 advanced per photon assimilated if photosynthesis is estimated as the pace of O_2 development (Figure 1). Upon additional increments in irradiance, the pace of photosynthesis activity is not increase linearly, but slightly levels off. At higher light intensities, the amount of photosynthesis is said to be light saturated. When the plant exposed to increasingly elevated degrees of overabundance light, Photo inhibition of photosynthesis happens. Accordingly, photo-inhibition could be reversible or irreversible (Zaman *et al*., 2004; Hopkins and Huner, 2008).

Ultraviolet light (UV) and visible light or their interaction causes photo inhibition of photosynthesis (Powles, 1984), when photosystem II (PSII) reaction center injured due to excess light induce severe damage to other components of the photosynthetic apparatus (Baker, 1996; Zaman *et al*., 2004).PSII reaction center is highly affected and susceptible to the injury, due to P680 very strong oxidation potential (Ruban, 2009). The elimination of a photosynthetic system by overabundance light prompts a stepwise inactivation of photosystem II (PSII). This light-reliant inactivation of PS II may either be quickly reversible or involve irreversible harm to the PS II reaction center proteins (D1), requiring once more *de novo* protein synthesis for fix (Michael *et al*, 1998).

The utilization of the quantum consumed by the leaf results in a hyperbolic response of photosynthesis to light. Higher than 80% of the consumed quantum can be consumed in photosynthesis when the intensity of light is low (less than 100 µmol.$m^{-2}s^{-1}$), on the other hand light intensity reaches 1000 µmol. $m^{-2}s^{-1}$ (50% of the full sunlight value) the maximum quantum efficiency in releasing O_2 andless than 25% of the absorbed quantum is consumed; finally, under full sunlight, consumption declines to 10% (figure 1.) (Alves*et al.*, 2002).Photo inhibition study on maize indicated that, the extent of inhibition was increased with increasing of the number between 4-20 plant population during afternoon (James et al., 1990).



Source; After Osmond (1994) cited in Taiz and Zeiger (2002).

Figure 2. photoinhibition of photosynthesis light–response curve

There are two level of photoinhibition.

Dynamic Photoinhibition

The maximum amount of photosynthetic rate is not changed, hence quantum effectiveness declines. It is brought by the change of absorbed light energy in the direction of heat dissipation, this reduction is often impermanent, and quantum efficiency can come back to its early higher value when photon flux declines below saturation levels (figure 2).

Chronic /Irreversible/ photoinhibition

This results from the introduction of too much levels of excess light that harm the photosynthetic system and reduction of both quantum efficiency and maximum photosynthetic rate. It is related with damage and replacement of the D1 protein from the PSII reaction center. The injury consequence is continuous and persisting for weeks or months as compared to dynamic photoinhibition (Taiz and Zeiger, 2002).

III. MECHANISM OF SENSING EXCESS LIGHT

Photoinhibition injury and to adjust to changes in their situation, photosynthetic plants have developed direct and indirect sensing mechanisms to much light intensities. Photoreceptors, for example, phytochromes, phototropin, neochrome, and cryptochrome can detect and react abundance of light directly and relay signs for chloroplast movement and gene expression responses. Therefore, plants can indirectly sense abundance of light using biochemical and metabolic signals can be transduced into local responses within chloroplasts, all of which are related with light adaptation (zhirong*et al*., 2008).

A. Direct sensing

Plants have four photoreceptors related to blue-light responses such as zeaxanthin, phytocrome, cryptochromes and phototropins. No critical advances toward the distinguishing of blue light photoreceptors were made until 1990s.Phototropism and the inhibition of stem elongation, advancement caused from the identification of mutants for important blue-light responses, and the successive isolation of the appropriate gene.(Franklin and Whitelam, 2007; Briggs and Christie, 2002; Zeiger *et al*., 2002).

i. Phytochromes

Phytochromes are blue protein pigment with a with an atomic mass of around 125 kDa (kilodaltons). Seeds of plants sensing the light condition and control germination by red and far-red light through phytochrome. Phytochromes can present in two stable states those are; red light absorbing form (Pr) with a captivation maximum at about 665 nm wavelength and far-red light captivating form (Pfr) with its absorption maximum at 730 nm wavelength. Phytochromes change their sedentary state during night, Pr, which captivates red light this leads to convert to the active state. The active Pfr phytochrome absorbs far-red wavelengths; captivation of FR converts the Pfr back to Pr, therefore, the higher the R:FR ratio, the higher the Pr: P total ratio (Franklin and Whitelam, 2007). This impact is known as reversibility

Various light reactions are intervened by phytochromes (zhirong*et al*., 2008). Phytochromes facilitated responses classified into three modes of action based on their light exposure necessities; the first is high irradiance responses (HIR), second low fluence responses (LFR) (light intensity between 1 µmol m^{-2} and 1,000 µmol m^{-2}), and thirdly very low fluence responses (VLFR). Study on seed germination identified very low fluence responses (occur at photon doses as low as 0.1 nmol m^{-2}) which seeds do not germinate in darkness, nevertheless for which germination can be induced by enormously (Zervoudakis et al., 2012; Hopkins and Huner, 2008).

ii. Phototropin

Most plant have faced light induced movements such as chloroplast movement, phototropism, leaf expansion, and stomatal opening. This event is controlled by phototropins receptors. Study on newly isolated *Arabidopsis* mutants like *nph1* (*n*on-*p*hototropic *h*ypocotyl) reduced in blue light–dependent phototropism of the hypocotyl has provided valued information. This mutant has been found to be genetically independent of the *hy4* (*cry1*) mutant(Briggs and Christie, 2002).

iii. Cryptochrome

Cryptochromes are found widely in eukaryotes which is demonstrated to be associated with blue-light morphogenetic responses including stem elongation inhibition, including cell elongation, leaf expansion, gene expression and photoperiodic flowering. Cryptochromes work along with red- and far-red wavebands captivating phytochromes (Lin, 2005). *Arabidopsis CRY1* gene is one of the first identified cryptochrome gene. Recently, research on blue light photoreceptors CRY1 and CRY2 genes indicated that blue light inhibition of hypocotyl elongation (Taiz and Zeiger, 2002).

iv. Carotenoid accumulation

Different studies on different plants showed that, light energy play a great role in the introduction of carotenogenic gene expression through the change of etioplasts to chloroplasts (de-etiolation) and during fruit and flower development and it function as antioxidant. The abundance of excess light induced excess accumulation of carotenoid. It plays an important role in inhibiting photosynthesis activities from the poisonous effect of over-excitation (Luca, 2012).

v. Zeaxanthin and Lutein accumulation

Excess light induced the binding and accumulation of zeaxanthin (and its structural isomer Lutein) to specific proteins which enhancing excess light protection by controlling the yield of possibly hazardous chlorophyll-excited states *in vivo* and stopping the production of singlet oxygen (Barbara et al., 2020).

Plants have protection mechanism from too much light excitation energy, from these xanthophylls cycle of chloroplasts. In this cycle there are three co three mechanisms. Therefore, xanthophyll cycle is one which helps to protect plant from excess light. Plants required much light such as *Vicia faba*, zeaxanthin accumulation in the mesophyll starts around 200 µmol m^{-2} s^{-1}, and zeaxanthin accumulation is not detected in both early morning or late afternoon(Zeiger *et al*. 2002).

B. Indirect sensing

i. Biochemical signal

Plant cells are reactive to many stimuli, the first is the chemical signals from their surroundings. The plasm membrane sense different biochemical signs through specific receptor molecules which impact the cell and its surrounding. and these receptors are the suitable for the transfer of biochemical signals to the internal part of the cell to respond. The receptors of the stimuli are part of membrane crossing receptors, thus includes histidine kinase sensors, tyrosine kinase receptors, and G-protein coupled receptors(Hopkins and Huner,2008).

ii. Metabolic signal

The variability of the environmental condition due to light stress can be primarily respond by metabolic processes. The light intensity absorbed by the plant disturbs the active linkage of metabolites as well as the gene expression and proteins help our understanding of the controlling mechanisms at work throughout photosynthesis activities of the plant (Davis *et al*., 2013).

When the plant exposed to excess light environment the metabolic activity is incapable to use the energy (ATP)produced by charge departure in photosynthesis, the proton gradient leads to increase pH in the thylakoids, finally violaxanthin changed to zeaxanthin. Zeaxanthin accumulation is responsible for dissipation of energy as heat. When excess energy is not dissipated in xanthophyll cycle (i.e. universal in photosynthetic organisms), this problem makes photosystem II reaction center photosynthetically inactive. In most plant this process is reversible or slower (Demmig and Adams, 1996).

IV. PLANTS RESPONSE TO EXCESS LIGHT

Higher plants have diverse number of light quality and intensity response mechanism to wide range of developmental response. This response is regulated by the collaborative performance of phytochrome and cryptochrome (Hopkins and Huner, 2008).

A. Photo protection and photo inactivation

During photosynthesis the light response curve shows saturation kinetics. Photosynthesis starts to reduced when plants are exposed to too much light intensity (Hopkins and Huner,2008).Under low light environment the rate of CO2 consumption increases in increasing manner with an increase in light interception, thus leads to increase the levels of ATP and NADPH for the regeneration of RuBP(Taiz and Zeiger, 2002).

Research result indicated that, plants are different in their response to different level of light conditions. Hence, plants having low light requirement (shade loving) face reversible damage due to exposure of the plant to full sun light. Study showed that, leaves during sun light condition the rate of photosynthesis reduced from 40W $m^{-2}$to 12% with 2h to 400 W m^{-2} while the corresponding decrease for shade leaves was 45%. This phenomenon is termed as photoinhibition (Osmond *et al*., 1999).

B. Light harvesting antennae size reduction

Excess light induces the reduction in the size of light harvesting complex antennae, number of reaction centers and the ratio of the two photosystems. They are the result of transcriptional and translational instruction of the proteins preparation of specific complexes (Taiz and Zeiger, 2002).

C. Chloroplast movement activation

Plant leaves have different mechanism which can change the arrangement of organelles with in the cell; particularly they change their chloroplasts in order to control light absorption and control excess light damage. Due to blue-light responses the action of chloroplast movement shows “three finger” structural arrangement. When the light interception is too minimum chloroplasts grouped at the bottom and upper exteriors of the mesophyll cells, there fore this helps the plant to receive maximum light required by the plant. On the other hand, when plants are exposed to strong sunlight condition, the chloroplasts move to the cell surfaces that are parallel to the light interception direction, so plant reduce the amount of light absorbed (Zervoudakis *et al*., 2012). Both photoprotection and photo inactivation can be measured by sensing the light emanated by photosystem II, where water is split to produce protons and electric charge (Osmond *et al*., 1999).

D. Stem elongation inhibition

Stem elongation is highly hindered by blue light. It is the important morphogenetic response of the plant starting from seedling emergence from the soil. On the other hand, the plant growing under dark condition induces elongated stem of seedlings.The reduction of stem elongation of etiolated plant mostly caused by the change of the red and far-red absorbing forms of phytochrome, respectively. (Taiz and Zeiger, 2002). Plants growing under dark condition acclimatizes to grow under excess light condition which leads to stunted growth, it is called de-etiolation. This process leads to some different morphological variations that are broadly used as indicators of the adaptation of light sensing and responding mechanism ability of the plant (Hopkins and Huner, 2008).Research on stem elongation indicated that, far-red light exposed plant seedlings showed stunted growth (Nikolaus *et al*.,2012).

E. Photoperiodism

Higher plants have different response to the time exposed to light and darkness, which is called photoperiodism. Accordingly, plants are classified as short-day (SD), long-day (LD), and day-neutral (DN) plants depending on the light requirement (Hopkins and Huner, 2008). The demand of light duration may be explained qualitatively or quantitatively explained. Mostly flowering plant requires suitable light exposure duration to set flower, therefore some plants such as wheat, barley, oat and other small cereal flowers when the season has short night. On the other hand, plants like maize and soybean having long maturity time requires longer night time to set flower (Borthwick and Hendricks, 1960).(Hopkins and Huner, 2008).

F. Phototropism

It is morphogenetic response which occurs in both monocots and dicots when grows under dark conditions. Additionally, it can also exist when the plants are exposed for un equal light distribution environment (Taiz and Zeiger, 2002).Plant growth and development pattern altered by morphogenetic responses of phytochrome and cryptochrome through blue- light response (Hopkins and Huner, 2008). This blue light induces the directional growth and development towards (or away in some conditions) the light direction, this condition is known as phototropism. Phototropism occurred on many plant species and highly occurred on plants having high light requirement, including fungi, ferns, and higher plants(Taiz and Zeiger, 2002).

G. Chloroplast gene activation

Plants have advanced a D1 (which is a single chloroplast gene which codes the D1 polypeptide called *psbA*) repair cycle which keeps excess light injury to PSII. Plants have developed different mechanism ones the injury happens on D1 polypeptide to aid degradation by protein phosphorylation through the process of proteolysis. Then, the *psb A*gene is transcribed and translated using the chloroplastic transcriptional and translational machinery with the succeeding accumulation of a new D1 polypeptide(Hopkins and Huner, 2008).

V. 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 excess light above they can actually use during photosynthesis. This excess light causes photo inhibition, reduction in light harvesting complex, activated chloroplast, inhibited stem elongation; photoperiodism and phototropism responses. Photosystem II reaction center has damaged significantly during excess light exposure. Hence, it is responsible for photo inhibition. They have their own mechanism for sensing too much light through directly and indirectly and responding through their photoreceptors. Directly, through chloroplast movement and gene expression responses and indirectly through biochemical and metabolic signals.

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