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REVIEW

Photosynthetic efficiency in sun and shade plants

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Abstract

Photosynthesis is amongst the plant cell functions that are highly sensitive to any type of changes. Sun and shade conditions are prevalent in fields as well as dense forests. Dense forests face extreme sun and shade conditions, and plants adapt themselves accordingly. Sun flecks cause changes in plant metabolic processes. In the field, plants have to face high light intensity and survive under such conditions. Sun and shade type of plants develops a respective type of chloroplasts which help plants to survive and perform photosynthesis under adverse conditions. PSII and Rubisco behave differently under different sun and shade conditions. In this review, morphological, physiological, and biochemical changes under conditions of sun (high light) and shade (low light) on the process of photosynthesis, as well as the tolerance and adaptive mechanisms involved for the same, were summarized.

Additional key words: chlorophyll fluorescence; high light; low light; photosynthesis; shade; sun.

Introduction

Researchers have categorized plants into sun plants and shade plants. The perception of sun and shade plants has been used for plants that need high irradiance/light and intense shading to grow and complete their life cycle, respectively (Cuzzuol and Milanez 2012). Sunlight represents the energy source for photosynthesis and plant growth. Photosynthesis is the key factor that regulates plant growth and in turn the overall crop yield. Leaves are the main functional and productive unit of a plant. Light not only governs photosynthesis but also regulates the function and structure of the whole photosynthetic apparatus. Light-saturated rates of photosynthesis vary between sun (high light) and shade (low light) environments (Boardman 1977, Ojanguren *et al.* 2013). Plants modulate themselves according to fluctuating light conditions to attain utmost robustness (Li *et al.* 2014, Valladares and Niinemets 2008). In low light (LL), plants need to absorb sufficient light for photosynthesis. Under low light conditions, insufficient ATP is produced for carbon fixation and carbohydrate biosynthesis (Shao *et al.* 2014) leading to reduction in plant growth. In order to avoid this, plants growing under low light need to maximise light absorption. In high light (HL) condition, however, the problem is reversed, as plants need to maximise their PSII capacity for utilising abundant light energy available while at the same time to deal with excess

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Abbreviations: ABS – absorption; AOX – alternative oxidase ; APX – ascorbate peroxidise; CAT– catalase; CET – cyclic electron flow; Chl – chlorophyll; CP – chloroplast protein; Cyt *b*/*f* – cytochrome *b*/*f*; DHA – dehydroascorbate; DHAR – dehydroascorbate reductase; ETR – electron rate; F_0 – minimal fluorescence; F_m – maximal fluorescence; FQR – ferredoxin-plastoquinone reductase; g_s – stomatal conductance; HL – high light; LCP – light-compensation point; LL – low light; LSP – light-saturation point; LTR – long-term response; MDA – malondialdehyde; MDAR – monodehydroascorbate reductase; NPQ – nonphotochemical quenching; OJ, JI, IP – phases of Chl *a* fluorescence induction curve; PET – photosynthetic electron transport; *pgr* – proton gradient regulation mutant; pLHCII – phosphorylated LHCII; P_N – net CO_2 assimilation rates; POD – peroxidase; PQH_2 – plastoquinol; q_P – proportion of open PSII reaction centers; RC – reaction center; ROS – reactive oxygen species; SS – soluble sugars; SOD – superoxide dismutase; VDE – violaxanthin de-epoxidase; V_J – variable fluorescence at 2 ms; φ_{Po} –maximum quantum yield of PSII photochemistry; Ψ_{ET2o} – probability of electron transport from reduced Q_A to Q_B; Ψ_{RE1o} – probability of electron transport from the PSII to the PSI acceptor side; ZEP – zeaxanthin epoxidase.
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sunlight when photosynthetic capacity is exceeded. As a consequence, plants have evolved a variety of features that optimise light interception, absorption, and processing. According to the nature of light environment to which plants are exposed, either sun or shade leaves are exhibited by the plant. Leaves developed under sun or HL are small, thick with well-developed palisade tissue, higher stomatal density, and thin granal stacks as compared to shade leaves or LL (Jiang *et al.* 2011, Martins *et al.* 2014).

In contrast to sun leaves, shade leaves have been reported to maximize light capture but lessen the costs of maintaining excess photosynthetic machinery. These leaves are thin and lighter and have a high specific leaf area. Shade leaves also show evidence of high chlorophyll (Chl) concentrations per unit leaf mass and low ATPase activities and Rubisco contents as compared to sun counterparts (Boardman 1977, Walters 2005, Niinemets 2007, Martins *et al.* 2013). A classic shade leaf is at risk of photoinhibition and damage from the high irradiance of sun flecks, while a classic sun leaf is ill-suited to shade conditions (Boardman 1977, Way and Pearcy 2012, Martins *et al.* 2013).

Light capture and its use by plants

The first step involved in photosynthesis is capture of light and absorption of photons by the photosynthetic apparatus followed by utilization and dissipation of captured photons. In plants, light capture varies with the size, angle, orientation, arrangement of the photosynthetic apparatus. Light capture and distribution is maintained in shade plants by larger leaves. Plants adapt a clever mechanism for optimum light capture and utilization in a sense that the smallest leaves are always present at the highest canopy, while the larger ones near the ground level. Plants also modify their leaf angle and orientation for maximum light usage. For this, many plants have vertical orientation during low sunlight conditions and receive less light during noon, when the intensities are very high, in order to protect themselves. Plants having horizontal orientation receive light for the whole day. Some plants do this to increase surface area, while others do it to escape from HL. *Oxalis oregano* is well known for its modification for bright and dull lights. During dull light, the plant has the capacity to capture sun light and in case the light intensity changes to bright light within few minutes it changes its horizontal leaf angle to a vertical one (Björkman and Powles 1981). Therefore, in nature, plants in rainforest have dual orientation in which vertical is present at the top, while horizontal at understorey. Another mechanism chosen by plants for amending light energy is modifications in leaf-surface characters. In this way, leaves can maintain maximum photosynthetic rates under a variety of light conditions. A number of plants have waxy coat and develop thick silver fibres on their leaf surface to avoid excessive light (Robinson *et al.* 1993).

A few plants modify their epidermal cells and modify the cells into lens-like structure thus increasing the light capturing and distributing area. Thus, these plants prevent light transmittance and excess reflection. Sometimes plants have mesophyll cells isobilaterally in order to enhance photosynthetic area (Brugnoli and Björkman 1992, Park *et al.* 1996). Thus, plants have evolved several mechanisms to protect themselves from excessive light. Plants maintain optimum photosynthesis under changing lights.

Once sun light has been intercepted by an assimilatory organ, photon absorption then depends on the extent and nature of light-absorbing pigments in the photosynthetic tissues. In terrestrial plants, the major light-absorbing pigments are chlorophylls (Chl) *a* and *b* plus a range of carotenoids, which act as accessory pigments. Compared to high-light plants, plants grown in LL tend to allocate relatively more resources to these light-harvesting pigments and their associated proteins than to Rubisco and other soluble proteins involved in CO_2 fixation. This shift in allocation of nitrogen-based resources can be accompanied by marked changes in leaf anatomy, especially depth of mesophyll tissue, and reflects a need for increased efficiency of light absorption when sun light is limited.

Effect of varied light intensities on plant growth and regulation

Growth and development of plants is regulated by phytohormones and signalling molecules associated with them. Plants could sense the variation in quality and quantity of light falling on them through a network of phytohormones and thus regulate their growth accordingly (Casal 2013, Kurepin and Pheris 2014). Sun and shade plants show alterations in leaf anatomy, leaf color, morphology, pigment content, and protein content (Björkman 1981, Atanasova *et al.* 2003). High content of carotenoids has been reported in sun leaves of mahogany (Gonçalves *et al.* 2001).

Various studies have been conducted under sun and shade conditions in various food and crop plants during the last few years. Lichtenthaler *et al.* (1981) performed studies on radish plants under HL conditions and reported an increased cotyledon area growth, hypocotyl growth declined, while anthocyanin content of epidermal and subepidermal hypocotyl increased. Stomatal density of LL cotyledons was high due to reduced cotyledon area. This can be explained by the fact that in LL there is lower rate of photosynthesis resulting in lack of organic substrate, and also that reserve material is used for the growth in the

hypocotyl length. When HL study was performed on primary leaves of wheat seedlings, an enhanced dry mass, lower leaf surface and fresh mass were observed. HL leaves were much shorter than primary leaves of LL-grown wheat seedlings. Similar pattern was obtained for secondary leaf also under HL/LL conditions. Water content, when measured for HL-grown primary and secondary leaves, was found to decline with increasing days, while it remained constant for primary leaf under LL. Leaf blades of LL were thinner as compared to HL plants (Lichtenthaler *et al.* 1981). Mishra *et al.* (2012) have investigated effects on *Arabidopsis* under varied light conditions. With change in light intensities, leaf size and shape was changed. *Arabidopsis* plants with elongated petioles and less compact rosettes were observed as result of LL and these plants needed much more time to reach maturity. HL-grown plants had thicker and larger leaves (Mishra *et al.* 2012).

Effect of fluctuating light intensities on photosynthesis

In nature, plants and phytoplankton frequently face quick variations in light intensities or fluctuations. Light intensity received by plants is regulated by sun, angle of clouds, and leaf movements (Ganeteg *et al.* 2004, Hirth *et al.* 2013). Dense forests with closed canopies receive very much less light and thus its penetration as well as its capture is quite difficult for plants. Under such conditions, shade conditions are interrupted with small sun flecks (Allahverdiyeva *et al.* 2014). Sun flecks are the direct rays of sun light that passed through small gaps in a canopy for a small period of time, but contribute significantly to the total PFD available for photosynthesis to shade plants. Field conditions are totally different from the forest conditions. In a field, plants are constantly under changing light intensities during the whole day because of direct sun light. Changes in light intensity in seconds, minutes, and hours also cause changes in plant photosynthesis (Yamori *et al.* 2016). In order to maximize photosynthesis, plants resourcefully develop strategy through which they undergo short as well as long-term responses and acclimate themselves to fluctuating light intensities. Varied light intensities cause PSI and PSII excitation and disparity. This may take place under LL/shade, HL/sun conditions, during sun flecks or at higher and lower leaf canopies. Changes in light fluctuations may lead to state transition in both photosystems. This in turn is compensated by rearrangement of antenna structures in both photosystems so that plants can utilize captured light maximally (Wollman 2001, Allen 2003, Rochaix 2007). Plants attain this stability by sidewise (lateral) movement of LHCII of either PSI or PSII. This is achieved by the lateral movement of the so-called 'mobile pool' of LHCII, which can reversibly associate with either PSI or PSII. Recent findings have shown that the movement of the mobile LHCII fraction during state transitions occurs due to differences between the two photosystems in their relative affinities for LHCII and pLHCII (Lunde *et al.* 2000). Phosphorylation of LHCII leads to a decrease in its affinity for PSII and increased tendency to bind at a specific site on PSI.

To attain maximum photosynthesis in fluctuating light conditions in dense forests, plants undergo long-term response (LTR). This LTR maintains the photosynthesis in plants by regulating photosystem stoichiometry (Dietzel *et al.* 2008). It is reported that in most of the species active reduction of PQ pool and overexpression of PSI reaction centre genes, *psaA* and *psaB* (encoding for P700 appo-proteins), take place. Along with PSI, plants that adopt LTR also show overexpression of PSII reaction centre gene, *psbA* (encoding for D1 protein) (Pfannschmidt 2003). LTR is found to be responsible for several other physiological and molecular parameters other than modifications in PSII and PSI gene expression. Alterations in a Chl *a*/*b* ratio, steady-state Chl fluorescence, thylakoid protein phosphorylation, and structure of thylakoid membranes have been reported as a result of LTR (Bonardi *et al.* 2005, Tikkanen *et al.* 2006). Plants grown under PSI- specific and PSII-specific light showed less transitory starch in PSI-specific plants as compared to PSII-specific light, while no change was reported for fatty acid accumulation and total protein content (Bräutigam *et al.* 2009). Furthermore, metabolic profiling, performed on plants subjected to PSI–PSII light-quality shifts, indicates that a number of important organic acids and several amino acids, which are precursor metabolites of secondary metabolism, are co-regulated in opposite directions, depending on light conditions (Bräutigam *et al.* 2009). LTR helps plants to cope with adverse environmental conditions by maintaining primary photochemistry and normal regulation of electron transport system (Pesaresi *et al.* 2010). A comparison of sun and shade plants can be seen in Fig. 1.

SUN	SHADE
➢High photosynthetic capacity	➢Low photosynthetic capacity
➢Higher Chl *a*/*b* ratio	➢Lower Chl *a*/*b* ratio
➢Lower level of LHC Chl *a*/*b* proteins (LHC II)	➢Higher level of LHC Chl *a*/*b* proteins (LHC II)
➢Low stacking degree of thylakoid	➢High stacking degree of thylakoid
➢Proportion of PSII RC more	➢Proportion of PSII RC less
➢Higher PSII Connectivity	➢ PSII Connectivity low
➢High PSII quantum efficiency	➢Low PSII quantum efficiency
➢Number of RC more	➢Number of RC less
➢Normal/high oxygen evolution capacity	➢Reduced oxygen evolution capacity
➢Higher electron transport	➢Decrease electron transport
➢Net CO_2 assimilation rate low	➢Net CO_2 assimilation rate high
➢Small PSII antenna size	➢Large PSII antenna size
➢Cyt *b*/*f* complex more	➢Cyt *b*/*f* complex less
➢ATP synthase level, ATPase activity and Rubisco activity high	➢ATP synthase level, ATPase activity and Rubisco activity low

Fig. 1. Effect of sun and shade on photosynthesis.

Changes in chloroplast ultrastructure under varied light intensities

Chloroplasts are the sole organelles responsible for the process of photosynthesis. HL and sun leaves have sun-type chloroplasts that are adapted to enhanced photosynthetic light conversion. Sun-type chloroplasts are characterized by increased photosynthetic efficacy per leaf area and Chl *a*/*b* ratio, more grana stacks with few thylakoids per granum, lamellar material very much less in starch-free stroma part of chloroplasts with enlarged starch grains, while light-harvesting Chl *a*-*b* proteins are present at a very low amounts with a reduced degree of stacking of thylakoid membranes (Lichtenthaler *et al.* 1981, 1984; Sarijeva *et al.* 2007). In contrast to sun-type chloroplasts, shade-type chloroplasts are riffled up with thylakoid membranes arranged in high grana stacks. The shade chloroplasts possess fewer grana stacks per chloroplast, but many thylakoids per granum/stack, no starch, and a significantly higher stacking degree of thylakoids than that of the sun-type chloroplasts. Width of grana stacks is larger in shade-type chloroplasts. These broader grana mainly invest in pigment antenna (Boardman 1977, Lichtenthaler *et al.* 1984, Meier and Lichtenthaler 1981). The increased extent of stacking is due to increased abundance of LHCII and an associated non-specific "Velcro effect" (Jia *et al.* 2012). It is reported that the chloroplasts of maize mesophyll cells, which are capable of forming grana stacks, also show this light adaptation response of chloroplasts, but they do not contain starch. The chloroplasts of the bundle sheet cells are free of grana and exhibit either large starch grains (HL-maize) or no starch (LL-maize) (Lichtenthaler *et al.* 1981, Sarijeva *et al.* 2007).

Effect of light fluctuations on light reactions

Plants live under different light conditions and acclimate to these conditions for their survival. Plants exhibit two varied growth responses depending upon the light conditions: first, strong-light growth response as found at HL and second, weak-light growth response in LL conditions. This ability of plants and chloroplasts to adapt to light is the basic growth response, which is associated with specific changes in the morphology, physiology, biochemistry, and structure of leaves and chloroplasts (Lichtenthaler *et al.* 1981). Based on leaf area, sun leaves also exhibit lower Chl content with higher quantities of electron transfer carriers and Rubisco (Anderson 1986, Marchiori *et al.* 2014). Also sun leaves have enhanced photosynthetic capacity per leaf area (Li *et al.* 2014). Leaves undergo many changes such as alterations in organization and/or abundance of protein complexes in the thylakoid membranes (Timperio *et al.* 2012) for acclimatization to light intensities. Under LL conditions, the content of PSII, ATP synthase, cytochrome *b*/*f* (Cyt *b*/*f*) complex, and components of the Calvin-Benson cycle, especially Rubisco, was lesser in pea leaves (Leong and Anderson 1984a,b). At the same time, an enhanced content of major Chl *a*-*b*-binding light-harvesting complexes (LHCII), associated with PSII, were obtained. Leong and Anderson (1984a,b) and Chow and Anderson (1987) also observed lesser number of reaction centres, reduced capacity for oxygen evolution, electron transport, CO_2 consumption, and lesser ratio of Chl *a*/*b* for plants grown under LL. Ambient light intensity also alters content of the thylakoid components as well as PSII/PSI ratios (Leong and Anderson 1986). LL conditions also downregulated photorespiratory mechanism in plants (Brestic *et al.* 1995). Bailey *et al.* (2001, 2004) showed in *Arabidopsis thaliana* an increase in the number of PSII units under HL and an

increase in the number of PSI units in LL. Sun plants have been reported to have higher activity of oxygen-evolving complex and electron transport rates, while all these characters were very low in shade plants (Zivcak *et al.* 2014).

Effect of light variations on Chl *a* fluorescence

Chl *a* fluorescence has proved to be a valuable technique to evaluate the photosynthetic efficiency of a plant (Kalaji *et al.* 2016). Chl fluorescence has been measured in sun and shade leaves and it can provide valuable information about primary photochemistry of PSII. The Chl fluorescence curve is characterized by a few inflection points observed clearly when plotted on a logarithmic time scale, O–J–I–P, with O being the minimal fluorescence (F_0), and P is the peak, equivalent to F_m. The F_0 to F_m kinetics can be divided into three rise phases: O–J (0–2 ms), J–I (2–30 ms), and I–P (30–300 ms) (Strasser *et al.*1995, Stirbet and Govindjee 2011). The fluorescence rise from F_0 to F_m reflects the reduction of Q_A, the first PQ electron acceptor of PSII. A representative Chl *a* transient for maize plants is shown in Fig. 2. No significant change was observed in F_m, F_0 for sun and shade plants (unpublished data). Zivcak *et al.* (2014) investigated effect of sun and shade on barley leaves using Chl fluorescence and reported that in shade plants, compared to sun plants, fast Chl induction curve showed no significant differences in F_0 and F_m values and hence, the maximum quantum yield of PSII photochemistry, φ_{Po}, was almost unaffected by the leaf ambient light environment. A decreased pool size of PSII and PSI electron carriers (from Q_A to ferredoxin), as well as a decrease in the number of Q_A turnover was reported. They reported that the probability of electron transport from the PSII to the PSI acceptor side estimated as $1 - V_i$ was higher in the sun than in the shade barley leaves and thus a major limitation of electron transport between Q_B and the PSI electron acceptors in the shade leaves was observed. In addition, Zivcak *et al*. (2014) also suggested the photoinhibition was slightly higher in the shade plants. Increase of relative variable fluorescence at 2 ms (V_J) indicates stronger limitation of electron transport from Q_A to Q_B, absorption per reaction centre represents apparent antenna size of active PSII RC. ABS/RC increased in shade plants which is in corroboration with our results on maize plants (unpublished data). Zivcak *et al.* (2014) also calculated PSII connectivity and found that PSII in shade plants were less connected as compared to sun plants.

Other fluorescence studies done by Shao *et al.* (2014) reported a decline in relative quantity of electrons passing through PSII during steady-state photosynthesis (ETR) (Tezara *et al.* 2003) in *Anoectochilus roxburghii*. q_P is an indicator of the proportion of open PSII RC (Maxwell and

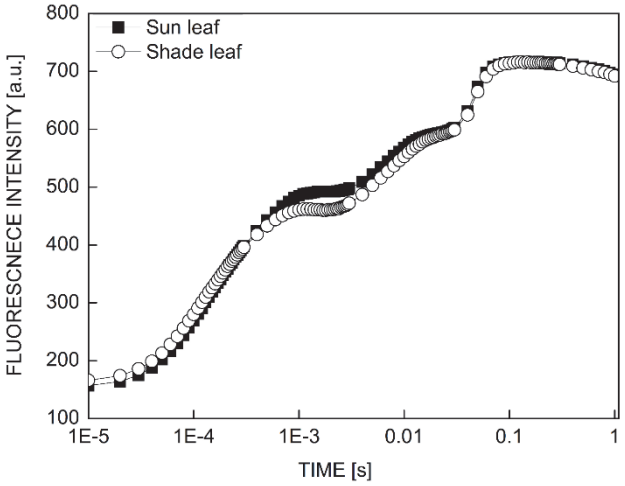

Fig. 2. The representative O-J-I-P chlorophyll *a* fluorescence curve in maize plants in response to sun and shade.

Johnson 2000). A high q_P is advantageous for the separation of electric charge in the RC, and is also beneficial to electron transport and PSII yield. Differences in q_P values revealed that *A. roxburghii* had significant differences in PSII electron transport activities when plants were grown under varied shade treatments. Electric charge separation in the RC, electron transport ability, and quantum yield of PSII were enhanced under 30% shade and weakened under 50% shade. NPQ is a reflection of the amount of unused energy from photosynthetic electron transport that is dissipated harmlessly as heat energy from PSII antennae (Muller *et al.* 2001, Shao *et al.* 2014). The low NPQ measured for 30% irradiance-treated plants indicates that these plants were able to effectively reduce heat dissipation and efficiently utilize the energy absorbed by PSII antenna pigments (Guo *et al.* 2006, Shao *et al.* 2014). Li et *al.* (2014) studied light response curve for HL and LL in *Aeschynanthus longicaulis* plants. The light-response curves revealed that the maximum photosynthetic rate of the plants under low irradiance was greater than that of the plants under high irradiance. Leaves under LL had higher net photosynthetic rates and light-saturation point (LSP) and lower light-compensation point (LCP), while the plants under HL had significantly lower net photosynthetic rates and LSP and higher LCP. However, they observed a higher quantum yield in plants under HL than that of the LL.

Effect of light fluctuations on dark reactions

The photosynthetic apparatus adjusts and acclimates to light fluctuations by undergoing alterations in carbon reduction cycle enzymes, electron transport components, and proteins and pigments. Rubisco activity is light-dependent in two senses: first, substrate ribulose-1,5-biphosphate (RuBP) production is solely dependent on ATP and NADPH production in light reaction and second, the mechanism for regulation of Rubisco enzyme activity is associated with photon flux density (PFD). Efficacy of Rubisco is affected by carbamylation–decarbamylation, Rubisco activase, and CA1P metabolism. At low PFDs (shade), where the capacity for RuBP regeneration typically limits photosynthesis, the efficiency of Rubisco use is potentially low, as evidenced by the fact that the activity of the enzyme is generally reduced by these regulatory mechanisms to match the reduced capacity for RuBP regeneration (Kobza and Seemann 1988).

Sun leaves with their sun-type chloroplasts as compared to shade leaves have high photosynthetic net CO_2 assimilation rates (P_N) on a leaf area basis. It is established that sun plants generally have higher Chl content. It is assumed that higher Chl content of sun plants could be one of the probable reasons for their higher P_N. This is only a partial reason for higher Chl content in sun plants, while the actual reason for a higher Chl content is that the sun-type chloroplast consists of various structural and functional organization of their relative Chl and carotenoid contents. The higher photosynthetic rates of sun leaves are supported by considerably higher values for the stomatal conductance (g_s). Sun-type plants have higher g_s than that of shade plants suggesting that stomata opening is apparently greater in sun leaves as compared to shade ones (Schulze *et al.* 1975, Farquhar and Sharkey 1982, Martins *et al.* 2014). This is evidence for increased intercellular CO_2 concentrations and higher CO_2 assimilation ratios and higher stomatal density of sun leaves (Lichtenthaler *et al.* 1981, Pearcy and Sims 1994). Increased g_s of sun plants is mainly due to a large stomatal aperture rather than stomatal density. P_N is also affected by diffusion of CO_2, which is influenced by mesophyll structure of leaves. Light penetration is also a major cause for changes in high P_N (Terashima 1992, Vogelmann and Martin 1993). Sun leaves contain thicker and more cells per unit area and section as compared to shade leaves (Lichtenthaler *et al.* 1981, Pearcy and Sims 1994). Plants grown under LL have shown low photorespiration (Brestic *et al.*1995, Muraoka *et al.* 2000, Zivcak *et al.* 2014).

Protective mechanisms by plants for light fluctuations

Photoinhibition mechanisms under sun and shade conditions

Plants develop mechanisms to counteract photoinhibition and oxidative stress caused by excessive HL (Powles 1984, Osmond 1994, Foyer and Noctor 2000). Photoinhibitory conditions occur when the capacity for dark reactions to utilize electrons produced by the light reactions is insufficient. Such a situation creates excessive excitation leading to reduction of the plastoquinone (PQ) pool and modification of the functioning of PSII electron acceptors (Kyle *et al.* 1984, Setlik *et al.* 1990, Vass 2012). HL stimulates photoprotection and repair of PSI and PSII after photoinhibition (Melis 1999, Demmig-Adams *et al.* 1998, Adir *et al.* 2003). This protective or defence mechanism in plants is stimulated at various levels of light capture and electron transport (Zivcak *et al.* 2014). Sun and shade plants have different mechanism for photoinhibiton. In sun plants, an active repair cycle of PSII operates in order to replace photoinhibited RCs with photochemically active RCs conferring some protection against photoinhibition. However, in shade plants, this repair cycle is less important for protection against photoinhibition; instead, photoinhibited PSII reaction centres may confer, as they accumulate, increased protection of the remaining connected, functional PSII centres by controlled, nonphotochemical dissipation of excess energy (Oquist *et al.* 1992). Conventionally, photodamage has been related to D1 protein damage of PSII. This is supported by finding in unicellular algae, where photoinhibiton takes place if degradation of D1 is faster than its (D1) synthesis. D1 protein turnover is maximal under growth irradiance and changes or alters under very high or low light conditions in higher plants. If D1 protein is damaged in higher plants, it leads to photochemical inactivation of PSII RC. Non-functional PSII centres may accumulate in the grana and somehow increase thermal dissipation of excess light energy (Anderson and Aro 1994). Shade plants have larger granal stacks with a greater capacity to accumulate non-functional PSII centres, whereas sun plants rely on a higher rate of D1 turnover and larger xanthophyll pool sizes for their internal photoprotection. In either circumstances, photoprotection involves a prodigious turnover of PSII reaction centres.

Interconversions of xanthophylls in plants as protective strategy

NADPH and ATP produced in light reactions are used in dark reaction of photosynthesis. Some of them are also used in photorespiration and nitrate reduction. However, if photochemical capacity is exceeded by incoming energy, a plant engage photoprotective mechanisms which increase the amount of energy dissipated as heat. This nonphotochemical conversion of light energy is thought to occur in the PSII antennae and involves a group of

pigments known as xanthophylls, including violaxanthin, antheraxanthin, and zeaxanthin. When leaves are exposed to high light, the rate of CO_2 fixation is high, and excessive excitation energy is harmlessly dissipated through NPQ. The level of NPQ is positively correlated with the abundance of PsbS and further stimulated by de-epoxidation of violaxanthin to zeaxanthin by the enzyme violaxnthin de-epooxidase (VDE). Upon transition to LL, CO_2 fixation becomes limited by NADPH and ATP derived from photosynthetic electron transport, which in turn is limited by high NPQ. The rate of CO_2 fixation therefore remains depressed until relaxation of NPQ is complete. This can take minutes to hours and is correlated with the rate of zeaxanthin epoxidation, catalyzed by zeaxanthin de-epoxidase (ZEP) (Fig. 3) (Kromdijk *et al.* 2016). It was reported that leaves developed under sun conditions developed a larger xanthophyll cycle pool as compared to shade leaves (Demmig-Adams and Adams 1992, Thayer and Björkman 1990). Under LL conditions, violaxanthin predominates and is converted into zeaxanthin *via* antheraxanthin under HL conditions. Low thylakoid lumenal pH, ascorbate, and NADPH are required for the conversion. Such conditions are present in chloroplast lumen under HL. When light is no longer excessive, zeaxanthin slowly converts back to violaxanthin *via* antheraxanthin. Total pool sizes of the xanthophyll pigments increase with increasing exposure to excessive light. Sun plants can have three to four-fold larger pools of violaxanthin, antheraxanthin, and zeaxanthin than that of shade plants; and the presence of other stresses can also result in the increase of the pool size. Light received by mesophyll tissues also help to depict difference between sun and shade plants in terms of energy dissipation. *Cotyledon orbiculata*, a CAM plant, depicts this thoroughly. In this plant, xanthophylls are mainly present in the outermost layer where light reaches its maximum. If wax coating is present, cells do not require any internal photoprotection at growth irradiance and there is no formation of zeaxanthin. Instead, if wax coating is removed, cells require internal photoprotection and zeaxanthin is formed in outermost cell layer.

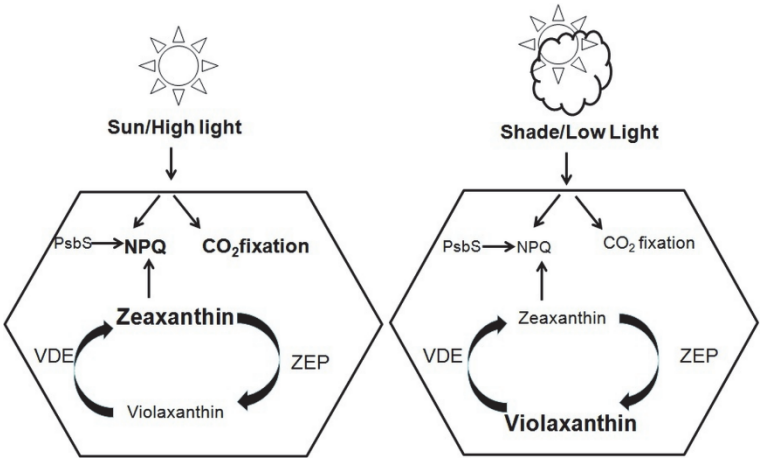

Fig. 3. Protective role of violaxanthin under sun and shade plants.

PGR5 as a major component of acclimation to fluctuating light in plant chloroplasts

Proton gradient regulation (*pgr5)* mutant was identified in *A. thaliana*; it did not have the capacity to perform NPQ upon exposure to high light (Munekage *et al.* 2002). Wild type has the capacity to oxidize P700 under high actinic light, while the *pgr5* mutant cannot. This may be due to limitation at the acceptor side of PSI rather than a non-functional PSI. Importantly, PSI in *pgr5* was shown to be prone to photodamage upon exposure to HL. The corresponding mutation was subsequently identified as an amino acid substitution in a previously unknown chloroplast protein of low molecular mass, named PGR5, which was suggested to have a role as a mediator of antimycin-A sensitive cyclic electron flow (CET) around PSI (Munekage *et al.* 2002, Sugimoto *et al.* 2013). Although the *pgr5* mutant shows a wild-type-like phenotype under constant light conditions, the *pgr5 crr2* double mutant, which also lacks another CET route mediated by the NAD(P)H dehydrogenase (NDH)-like complex, revealed a stunted phenotype and impaired photosynthetic parameters. Thus, the PSI CET is important not only for C_4 plants but also for C_3 plants (Munekage *et al.* 2004). Yet another protein, PGR5-LIKE PHOTO-SYNTHETIC PHENOTYPE1 (PGRL1), has been characterized and shown to interact with PGR5 and with PSI (Dal Corso *et al.* 2008). PGRL1 has demonstrated a capacity to accept electrons from ferredoxin and reducing quinones, thus strongly suggesting that PGRL1 is actually the long-sought ferredoxin-plastoquinone reductase, FQR (Hertle *et al.* 2013). Some reports provide evidence that, to some extent, the *pgr5* and *pgrl1* mutants are also capable of performing CET only under specific conditions; for example, under HL or CO_2 limitation, the CET was found

to be impaired in these mutants (Nandha *et al.* 2007, Dal Corso *et al.* 2008, Joliot and Johnson 2011, Kono *et al.* 2014). Thus, it is likely that rather than being absolute requirements, the PGR5 and PGRL1 proteins are needed to regulate and facilitate CET. The safeguarding of PSI against photodamage is particularly important under fluctuating light. Such protection involves redox poising of stromal components downstream of PSI *via* PGR5-dependent control of linear electron flow through the Cyt b_6f complex (Suorsa *et al.* 2012). In contrast to the wild type, *pgr5* was unable to oxidize P700 under high intensities of actinic light.

Components of thylakoid membranes that help to adjust plants under changing light conditions

Beside PGR 5, various proteins have been reported under fluctuating light (Tikkanen *et al.* 2010, Grieco *et al.* 2012). *stn7* and *tlp18.3* mutants exhibit remarkable phenotypes. The STN7 kinase (Bellafiore *et al.* 2005, Bonardi *et al.* 2005) is responsible for phosphorylation of LHCII proteins Lhcb1 and Lhcb2. LHCII is phosphorylated when plants are transferred from dark to light or HL to LL (Rintamäki *et al*. 2000). Plants have also acquired additional dynamic mechanisms, which respond to fast changes in the light environment, specifically, the PsbS-mediated NPQ mechanism (Allahverdiyeva *et al.* 2014). PSII antennas of shade plants are large in their size. The peripheral antenna protein gets modified according to the light conditions, while the core antenna proteins and minor peripheral proteins do not change (Zivcak *et al.* 2014). Biochemical analysis of *Arabidopsis thaliana* acclimated to various light intensities revealed a diverse regulation of both the composition and size of the antenna system of PSII and also the level of the PsbS protein. Immuno-blotting studies performed by Kouřil *et al.* (2013) for the same suggested an alteration in the component of CP24, CP29, and Lhcb3 (component of M trimer of LHCII). They reported that under HL intensities CP43 per Chl was higher as compared to LL conditions. This could be probably due to reduced LHCII proteins and an enhanced PSII/PSI ratio. They also reported a lower content of PsbS per PSII core in HL plants and a partial increase in plants (Kouřil *et al.* 2013). The work conducted by Kouřil *et al.* (2013) also indicated a decline in Lhcb 1–3 and CP24 proteins in HL plants, but an increase in Lhcb 1,2 in LL plants. A lower PSI/PSII ratio was observed in shade leaves by Hogewoning *et al.* (2012).

Antioxidant defence mechanism in plants

Reactive oxygen species (ROS) are thought to be responsible for photoinhibition if they hamper *de novo* synthesis of D1 protein which is needed for recovery from photoinhibition (Nishiyama *et al.* 2001). The chloroplast consists of 20 to 300 mM ascorbate in the stroma as a protective mechanism against ROS-generated photo-inhibition (Smirnoff 2000).

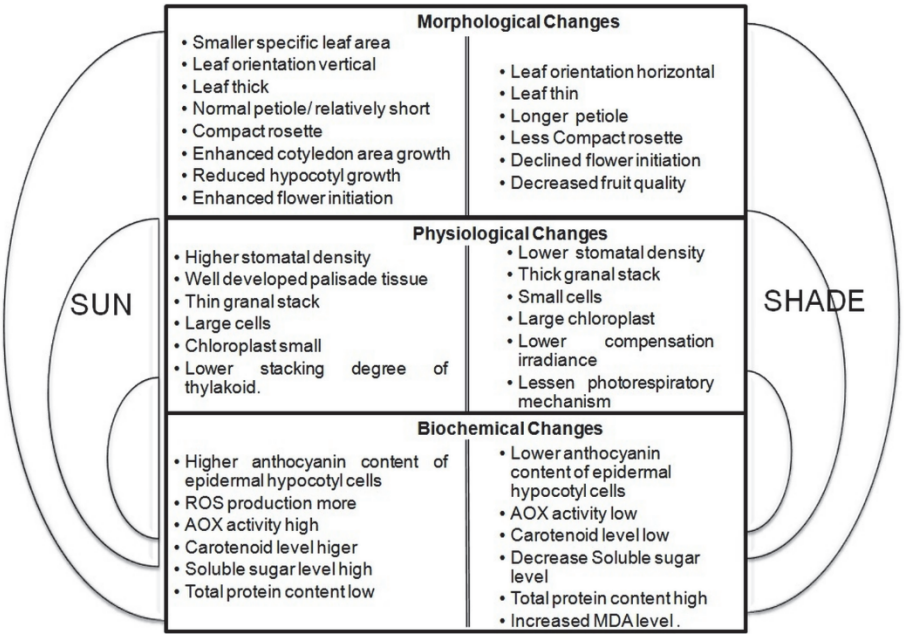

Fig. 4. Morphological, physiological, and biochemical effect of sun and shade plants.

Shao *et al.* (2014) also studied physiological and biochemical responses for *A. roxburghii* under different shade conditions. They reported that leaf protein content and antioxidant enzyme activity traits were under a strong genetic control, whereas soluble sugars (SS) and malondialdehyde (MDA) contents were largely determined by the degree of shading. Exposure to high (50%) shade conditions greatly increased the total protein

content. Activity profiles of the various antioxidant enzymes were not uniform. They suggested that peroxidase (POD), superoxide dismutase (SOD), and catalase (CAT) activities were not only markedly affected by the degree of imposed shading, but were also greatly influenced by the developmental status of the plants. SSs are an important carbon source and osmoregulator of plant growth. SS contents reflect plant nutritional status (Dong *et al.* 2011). They also explained that the plant SS content was the lowest one under HL treatments, and was responsive to shading sternness. Their results suggested that *A. roxburghii* responds differently to light with respect to carbohydrate metabolism. MDA content is considered to be an indicator of cellular membrane lipid peroxidation (Deng *et al.* 2011). The significantly high MDA content observed under high shade indicated the occurrence of damage due to excessive shade (Shao *et al.* 2014).

Future prospective

Light fluctuations intervene in many morphological, physiological, and biochemical changes in plants for their regulation (Fig.4). Plants have developed sophisticated strategies, with fascinating evolutionary differences, to cope with rapid variations in light fluctuations. Still there are few loop holes that should be filled for sun and shade study. The importance of the new technique for Chl fluorescence imaging for screening differences in the physiological function of the photosynthetic apparatus must be studied more. This will be beneficial for enhanced understanding of a difference between leaves and plants of different age and canopy light exposition, but also in the detection of early-stress symptoms long before damage becomes visually evident in sun and shade plants. It will also help improve adjustment and alterations of plants to sun and shade conditions. Although chloroplast photo-relocation movement has been extensively studied by many researchers, we still cannot accurately explain its molecular mechanism. Chloroplast movement under natural light conditions must also be examined because natural light is usually much more severe and always fluctuates compared to laboratory conditions. It would be of interest to carry out protein studies/analysis in plants grown in sun and shade. This would tell us about the role of various protein complexes in helping the plants to adapt to sun and shade conditions. Understanding the mechanisms that underlie efficient photosynthesis in fluctuating light can open doors to increased crop yields, and more broadly can reveal fundamental principles of robust energy conversion systems.

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Appendix. Calculated and measured fluorescence parameters derived from fast Chl kinetics

Description	Fluorescence parameter
Technical parameters	
Fluorescence intensity at 50 μs, minimal fluorescence F_0	O
Fluorescence intensity at 2 ms	J
Fluorescence intensity at 30 ms	I
F_m, maximal fluorescence intensity	P
Maximal variable fluorescence	$F_v = [F_m - F_{50\,\mu s}]$
Area between the fluorescence curve and F_m	Area
The phenomenological fluxes expressed per cross section of the leaf tissue [CS]	
Apparent antenna size of active PSII RC	ABS/RC
The yields [flux ratios]	
Maximum quantum yield of primary photochemistry	$\phi_{P0} = TR_0/ABS = [F_m - F_0]/F_m = F_v/F_m$
Probability with which a PSII trapped electron is transferred from reduced Q_A to Q_B	$\Psi_{ET20} = 1 - V_j$
Probability with which a PSII trapped electron is transferred from reduced Q_A beyond PSI	$\Psi_{RE10} = 1 - V_i$