Biochemistry and Biophysics Reports 24 (2020) 100813

Contents lists available at ScienceDirect

Biochemistry and Biophysics Reports

journal homepage: www.elsevier.com/locate/bbrep

Chlorophyll *a* fluorescence kinetics of mung bean (*Vigna radiata L.*) grown under artificial continuous light

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ARTICLE INFO

Keywords:
Chlorophyll fluorescence
Continuous light
OJIP test
Performance index
Specific energy fluxes
Vigna radiata

ABSTRACT

Continuous light can be used as a tool to understand the diurnal rhythm of plants and it can also be used to increase the plant production. In the present research, we aimed to investigate the photosynthetic performance of *V. radiata* under continuous light as compared with the plants grown under normal light duration. Chlorophyll a fluorescence transient (OJIP test) technique was used to understand the effect on various stages of photosynthesis and their consequences under continuous light condition. Various Chl a Fluorescence kinetic parameters such as Specific energy fluxes (per Q_A-reducing PSII reaction center (RC)) (ABS /RC; TR_0/RC; ET_0/RC; DI_0/RC), phenomenological fluxes, leaf model, (ABS/CSm; TR/CSm; ETo/CSm), Quantum yields and efficiencies (φPo; φEo; Ψo) and Performance index (PI_{abs}) was extracted and analysed in our investigation. Conclusively, our study has revealed that continuous light alters the photosynthetic performance of *V. radiata* at a different point but also improve plant productivity.

1. Introduction

The plant interacts with various abiotic factors in their life cycle, among them light is also an important factor. The energy embedded in photon perceived by chlorophyll and converted into energy molecules ATP and NADPH. This energy consumed in fixation of CO_2 and synthesize photosynthetic assimilate. Apart from, the light also up-regulates various processes such as seed germination, seedling development, plant growth, biomass production, flowering, reproduction, and circadian rhythms [1]. Nowadays, use of artificial light is enhanced in the greenhouse, plant factories and glasshouse to improve the crop production at the commercial scale to meet the demands of the growing population [2]. To achieve high production plant growers are using the different type of light based on their quality, quantity and duration. Extension of light period to 24 h light periods (continuous light) is also in trend for crop improvement [3]. In northern countries, supplementary artificial light is used in the greenhouse to gain higher production [4]. Velez-Ramirez et al. (2011) reported that cultivation of tomato under continuous light is more beneficial for production [5].

The circadian rhythm regulates the plant physiological processes by sensing the length of day/night periods. Nowadays, an extension of light period by using supplement lighting is a common method for the plant breeder to improve crop yield. However, plants respond in different ways to this increased photoperiod. Demers et al. (2002) reported that the continuous light can hasten the flowering in tomato initially but later on no change during 14 h and 24 h photoperiod [6]. In *Ficus benjamina* the dry weight progressively due to the lack of diurnal rhythm in photosynthesis under continuous light with increasing lighting periods at 16, 20 and 24 h/day [7]. It has been reported that in *Brassica rapa* L continuous light increases chlorophyll content [8], while in some plants such as soybean, wheat, barley, millet, pea, alfalfa, sunflower, kale etc have no chlorosis effect [9]. The negative effect of continuous light reported in the form of leaf injury in onion [10], cucumber [11]. In tomato species (*Solanum lycopersicum*) grown under continuous light with constant temperature decrease in the rate of photosynthesis and the maximum quantum efficiency of photosystem II (PSII) were found [5, 12]. Dorais 1992 found that continuous light causes a reduction in the size and increased activity of PSII in pepper plants [13].

Chlorophyll fluorescence parameters are important tools to study the effects of different environmental stresses on photosynthesis [14]. It is one of the important methods to analyses the role of PSII and its response towards changes in the environment and growth conditions [15,16]. The PIabs and Fv/Fo are sensitive parameters related to PSII related damage and efficiency. As the above-mentioned fluorescence parameters, the effects of continuous light conditions on primary photochemistry of PSII of *Vigna radiata* and fate of dark reactions are also clearly reflected by

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https://doi.org/10.1016/j.bbrep.2020.100813
Received 7 July 2020; Received in revised form 31 July 2020; Accepted 31 August 2020

chlorophyll fluorescence parameters. However, relevant research has not been reported yet. In the present study, the aim is to analyse the chlorophyll fluorescence characteristics of *Vigna radiata* grown under continuous light conditions, an effort is proposed to known about the effects of continuous light on photosystem efficiency.

2. Material and method

2.1. Collection of plant material and growth condition

The seeds of the *Vigna radiata* were collected from the MPUAT Udaipur. Before the experiment seeds were disinfected by immersing in 1% (v/v) NaClO for 3–5 min, then washed thrice with double distilled water. The seeds were grown in pots (12 × 36cm) and labelled 12 h and 24 h artificial light treatment (Figs. 1 and 2a). Both plants were grown under artificial light (maximum photosynthetically active radiation (PAR) 1800 μmol photons m^{-2} s^{-1}) for 12 h and 24 h of light period respectively and maintain the relative humidity 50–60% and temperature at 28 ± 2 °C.

2.2. Chlorophyll fluorescence measurement

Chlorophyll a fluorescence was measured using plant efficiency analyser (Handy PEA fluorimeter, Hansatech instruments Ltd. England) after 10 days of seedling emergence on the middle region of mature leaves. Before measurement mung seedling was dark-adapted for 50–60 min at 26 °C. Thereafter, Chl a fluorescence signals were analysed with the Biolyzer v.3.0.6 software (developed by Laboratory of Bioenergetics, University of Geneva, Switzerland). Appropriate numbers of replicates were taken and the experiment was repeated three times to ensure the results. Abbreviations, formulas, and definitions of the JIP-test parameters used in the current study are presented in Table 1, [17,18].

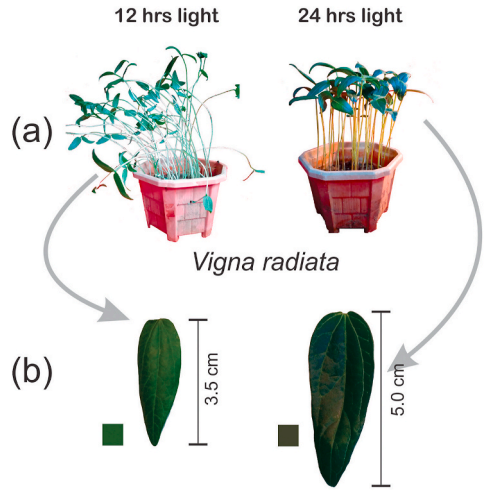

Fig. 2. (a) Effect of continuous light and morphological differences on *V. radiata.* and (b) effect on leaf size of *V.* radiata.

3. Results and discussion

After emerging from seeds seedling has to start photosynthesis. In the natural environment, many abiotic and biotic factors affect the process of photosynthesis. The photosystem photochemistry is mostly affected by these factors. Plants have different mechanisms to manage with different environmental conditions by changes in photosystem II apparatus (Fig. 3). In our study effect of continuous light on *V. radiata* plant is

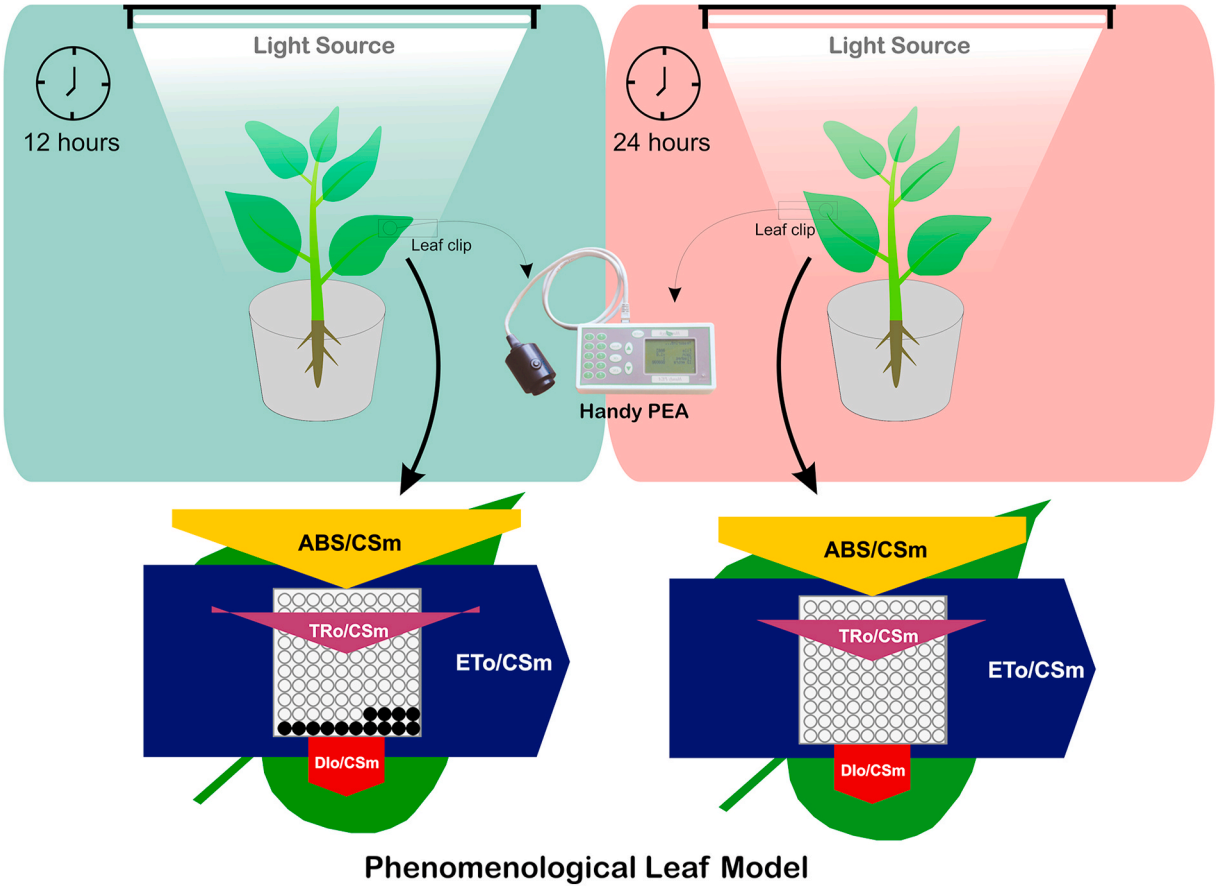

Fig. 1. (a) Schematic presentation of experiment design and effect of on *V. radiata.*

Table 1
Abbreviations, formulas, and definitions of the JIP-test parameters used in the current study (Strasser et al., 2000, 2004).

Technical fluorescence parameter	Formulas	Definitions
Data extracted from the recorded fluorescence transient O-J-I-P		
t_{FM}		Time (in ms) to reach the maximal fluorescence intensity FM
Area		total complementary area between the fluorescence induction curve and F = FM
F_0	≅ $F_{50\mu s}$ or ≅ $F_{20\mu s}$	minimal fluorescence (all PSII RCs are assumed to be open)
F_V	≡ F_M - F_0	maximal variable fluorescence
F_M (= F_P)		maximal fluorescence, when all PSII RCs are closed
Specific energy flux		
ABS /RC	= M_0 $(1/V_J)(1/\phi_{Po})$	absorption flux (of antenna Chls) per RC
TR_0/RC	= M_0 $(1/V_J)$	trapped energy flux (leading to Q_A reduction) per RC
ET_0/RC	= M_0 $(1/V_J)\psi_{Eo}$	electron transport flux (further than Q_A^-) per RC
Quantum yields and efficiencies		
ϕ_{Po}	≡ TR_0/ABS = [1-(F_0/F_M)]	maximum quantum yield for primary photochemistry
ψ_{Eo}	≡ ET_0/TR_0 = (1-V_J)	efficiency/probability for electron transport (ET), i.e. efficiency/probability that an electron moves further than Q_A^-
ϕ_{Eo}	≡ ET_0/ABS = [1-(F_0/F_M)]ψ_{Eo}	quantum yield for electron transport (ET)
PI_{ABS}	$\equiv \frac{\gamma_{RC}}{1-\gamma_{RC}} \cdot \frac{\varphi_{Po}}{1-\varphi_{Po}} \cdot \frac{\psi_o}{1-\psi_o}$	performance index (potential) for energy conservation from exciton to the reduction of intersystem electron acceptors
RC/ABS	= $\gamma_{RC}/(1-\gamma_{RC})$ = ϕ_{Po} (V_J/M_0)	Q_A-reducing RCs per PSII antenna Chl (reciprocal of ABS/RC)
S_m	= Area/(F_M - F_0)	normalized total area above the OJIP curve
N	= (*SM*/*SS*) = *SMM*0 (1/VJ)	the number of turnovers
DI_o/RC	= (ABS/RC) – (TR0/RC)	total energy dissipated per reaction center (RC)
F_V/F_O		ratio of rate constants for photochemical and nonphotochemical use of RC excitation energy
$(dV/dt)_0$	4. (F_{300} – F_0) /(F_M – F_0)	maximal rate of the accumulation of the fraction of closed reaction centers
k_N	= (ABS/CS). *k*F. (1 /*FM*)	Non-photochemical rate constant
k_P	= (ABS/CS). *k*F. {(1 /*F*0) – (1 /*FM*)}	photochemical rate constant
ABS /CS_m	F_m	absorption flux (of antenna Chls) per RC
Phenomological energy flux		
TR_0 /CS_m	(Fv/Fm) ·(ABS/CS_m)	trapped energy flux (leading to Q_A reduction) per RC
ET_0 /CS_m	(Fv/Fm) · (1 − Vj) ·(ABS/CS_m)	electron transport flux (further than Q_A^-) per RC
DI_0 /CS_m	(ABS /CS0) – (TR0 /CS_m)	total energy dissipated per reaction center (RC)
RC /CS_m	φPo. (V_J /M_0). F_m	Reaction centre per cross section

revealed, by using OJIP curve, specific energy flux, phenomenological energy flux.

After continuous light treatment no change in the primary quinone acceptor of electrons Q_A in PSII (O-J phase), whereas quenching of the fluorescence controlled by the donor site of PSII and the characteristic activity of water splitting system (J-I phase) were slightly altered showed weaker I and P peaks compared with normal 12 h light treated plants. After reaching F_o the fluorescence yields continuously rise more

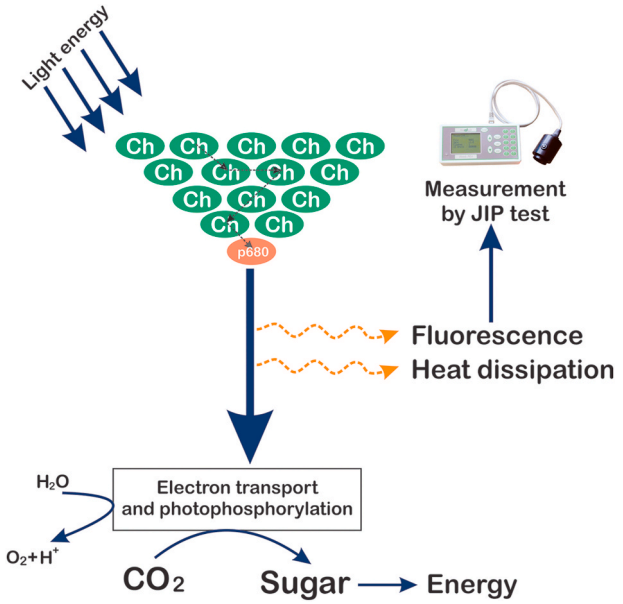

Fig. 3. Hypothetical mechanism of fluorescence emission and photosynthetic electron transport in V. radiata. under continuous light. (Ch - Chlorophyll molecule).

slowly reaching a peak after 1–2 s. This fluorescence is variable (F_v) as it is responsive to changes in electron flow through photosystem, being regulated by the redox state of photosystem II electron acceptors, inhibition of a reaction on the photo oxidizing site of photosystem II decreases the F_v. The decrease in fluorescence at J, I, P (Fig. 4) may be due to two reasons, first by inhibition of electron transport at the donor site of the PS II which results in the accumulation of $P680^+$ [19,20] and second due to a decrease in the pool size of Q_A^-. The area over the fluorescence induction curve between F_o and F_m is proportional to the pool size of the electron acceptor Q_A on the reducing side of PS II.

A decline in F_m is often associated with the protective interconversion of violaxanthin to zeaxanthin, in two independent reactions (the xanthophyll cycle), which leads to non-radiative (non-photochemical quenching, NPQ) energy dissipation [21].

3.1. Tf (max)

Time to reach maximal fluorescence Tf (max) of mung plant treated with continuous light (24 h) decreases as compared to the plant growing under natural light condition (12 h). A decrease in the time to reach Fm (Tfm) (Fig. 3) by continuous light led to an increase in the average redox state of Q_A in the period from 0 to Tfm [18].

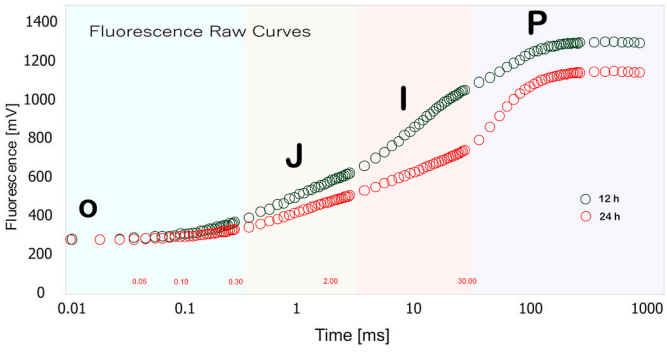

Fig. 4. OJIP fluorescence induction curve. Transient curves of each line represent the average of 10 measurements per treatment.

3.2. Area

Area parameter (the total complementary area between the fluorescence induction curve and Fm) was higher for 24 h light treated plant than 12 h light treated plant. The Area is relative to the pool size of the electron acceptors QA on the reducing side of PSII. Previously it was reported that a decrease in Area parameter will be due to electron transfer from the RCs to the quinone pool is blocked. Hence, improving the Area (Fig. 3) of mung bean by application of continuous light may be the result of increasing the electron transfer from the RC to the quinone pool [22].

3.3. F_O and Fm

Fluorescence at 50μs is denoted as F_o when the all primary quinone acceptor (Q_A) is in the oxidized state (open). Plants exposed to CL shows no significant effect on Fo while a decrease in Fm meanwhile variations are also reported in value of Fv/Fo (Fig. 5a). Parameter Fo can be used as an indicator for irreversible damage in PSII, associated with LHCII dissociation and blocking of electron transference on the reductant side of PSII [23]. Decreasing *Fm* by application of CL may be associated with the less efficiency of PSII activity due to conformational changes in the D1 protein, causing alterations in the properties of PSII electron acceptors [24].

3.4. Fv/Fo

Fv/Fo, a parameter that accounts for the simultaneous variations in Fm and Fo in determinations of the maximum quantum yield of PSII is higher in the plant under NL condition as compare than plants under CL. Fv/Fo is the most sensitive component in the photosynthetic electron transport chain [25]. The decrease in Fv/Fo is due to either by a decrease in Fv or increase in Fo. In the present study, there is no significant difference in Fo hance the decrement of Fv/Fo Is due to a decrease in variable fluorescence (Fv). The lower value of *Fv/Fo* (Fig. 5a) in treated leaves indicates the change in the rate of electron transport from PSII to the primary electron acceptors with the reduction in the number and the size of RC, which have also been reported in different plants exposed to the disease and the environmental stresses [26,27].

3.5. Variable fluorescence V_j

Relative variable fluorescence at the J-step (2 ms) was decreased in plants under CL condition. V_j was a measure of the fraction of the primary quinine electron acceptor of PSII that was in its reduced state [$Q_{A-}/Q_{A(total)}$] [28]. Fig. 5a shows that there is a decrease in value of Vj indicate that under continuous light the electron transfer at the donor side of PSII was affected.

3.6. S_m and N

Complementary Area (S_m) increased in continuous light condition than natural light. The parameters S_m, assessing of the electron transporter PQ pool between PS II and PSI. increase in S_m in continuous light displayed a reduced electron transport between these photosystems [29] (Fig. 5a). Turnover number (N) is higher in continuous light condition than natural light. N indicates how many times Q_A has been reduced in the period from 0 to Tf_m [17]. However, an increase in N also shown by PSI cyclic electron transport, as a photoprotection method.

3.7. Specific energy flux (membrane model)

Specific energy flux i. e. ABs /RC, TRo/RC, ETo/RC and DIo/RC were lower in plants treated with CL as compare to NL (Fig. 6a). ABs/RC is lower in CL treated plants; TRo/RC and DIo/RC is equal in both conditions. According to leaf pipeline model in continuous light, there is more active RC but the lower value of specific energy flux (ABs /RC, TRo/RC, ETo/RC and DIo/RC) shows the decreased ability of RC to the

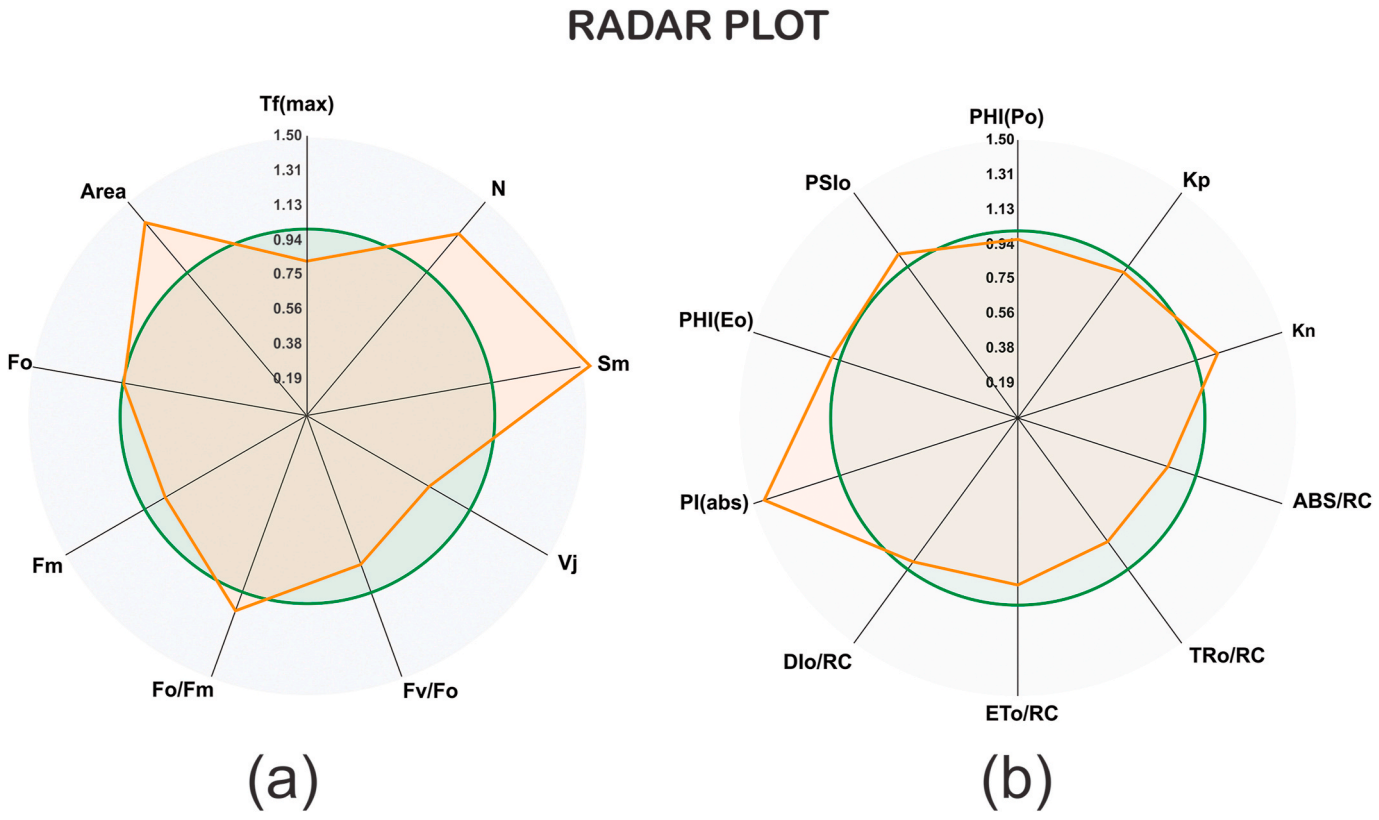

Fig. 5. Radar Plot showing various Technical fluorescence parameter. Each line represents the average of 10 measurements per treatment.

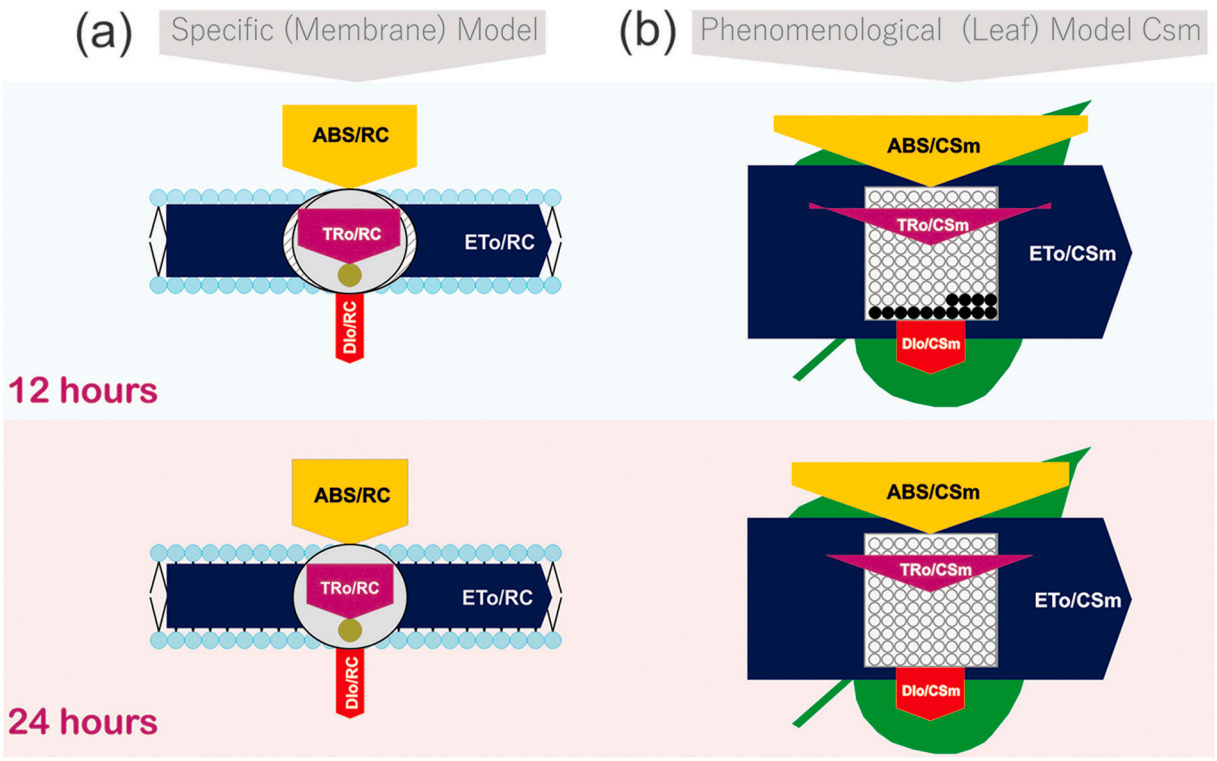

Fig. 6. Energy pipeline models (a) Specific energy flux (membrane model) of 12 h and 24 h light treatment and (b) Phenomenological energy flux (Leaf model) of 12 h and 24 h light treatment.

reduction of plastoquinone The flux ratios ABS/RC, TRo/RC, ETo/RC and DIo/RC decreased under continuous light treatment. The ABS/RC represents the total number of photons absorbed by Chl molecules of all RCs divide by the total number of active RCs. It is influenced by the ratio of active/inactive RCs and as the number of active centers increased, the ratio ABS/RC decreased. TRo/RC represents the maximal rate by which an exciton is trapped by the RC resulting in the reduction of Q_A. A decrease in this ratio indicates that all the Q_A has not been reduced. Reduced ETo/RC describes that the reoxidation of reduced Q_A via electron transport in an active RC is decreased because of a greater number of the active RC, hence it only reflects the activity of active RCs. Fig. 6a shows a decreased per active RC but overall increased electron transport, due to more active RCs. DIo/RC represents the ratio of the total dissipation of untrapped excitation energy from all RCs concerning the number of active RCs. Dissipation occurs as heat, fluorescence and energy transfer to other systems. It is also influenced by the ratios of active/inactive RCs. The ratio of total dissipation to the number of active RCs not so affected (DIo/RC) due to the efficient use of energy by the active RCs [30].

3.8. Phenomenological energy flux (leaf model)

Phenomenological energy fluxes i.e. ABS/CSm, TRo/CSm, ETo/CSm and DIo/CSm are shown in Fig. 6b. In phenomenological fluxes per cross-section and the leaf model, ABS/CSm,TR/CSm, ETo/CSm and DIo/CSm not significantly affected than control (Fig. 6b). Thus ABS/CSm reflects an increased density of active reaction centers in response to continuous light. Thus, TR0/CSm and ETo/CSm indicates that the efficiency of trapping and PSII activity are similar to control plants. An increase in the density of active RCs (indicated as open circles) and a decrease in the density of inactive RCs (indicated as filled circles) was observed in response to continuous light treatment [31,32]. CL light treated plants shows a broader leaf which can be proved by Boardman, (1977) [33] who reported that plants growing in full sunlight had increased leaf length, leaf size (Fig. 2b) and therefore increased leaf area. This can be assigned to the fact that leaves grown in full sunlight had higher stomatal conductance than shade leaves.

Continuous light-grown plants have more leaf greenness due to enhanced chlorophyll content. Synthesis of chlorophyll can occur only when a plant is irradiated since the reduction of protochlorophyllide to chlorophyllide is light-dependent [34,35]. Furthermore, other steps of chlorophyll synthesis or degradation are regulated by light and controlled by phytochrome and the blue light receptor [34].

Besides chlorophyll, the role of carotenoids and tocopherols are found in process of photoprotection. Carotenoids play a major role in photoprotection by shading the reaction and xanthophyll cycle [36].

3.9. Kp and Kn

An increase in Kn (de-excitation rate constants for nonphotochemical reaction) whereas no significant effect on Kp (de-excitation rate constants for photochemical reaction). Under continuous light, the extra energy exceeds the capacity for utilization, then the extra Chl redials quenched by photoprotective processes and dissipation of extra energy as heat. These mechanisms are measured from the decrease of Chl fluorescence from PSII and are collectively referred to as non-photochemical quenching (NPQ) (Fig. 3). NPQ includes short-term responses to rapid fluctuations in light, as well as responses that occur over longer periods allowing for acclimation to high light exposure [37].

NPQ and antioxidant systems [38] have the protective roles, despite these the PSII centers chance to damage at all light intensities and hence, an efficient PSII repair cycle continues to resume the function of the PS II complexes. Besides the PSII repair cycle plant have another alternative cycle to cope with light stress, among them cyclic electron flow, the water cycle, photorespiration, mitochondrial respiration in excess light [39].

3.10. Maximum quantum yield

Besides, the quantum yield of primary photochemistry (φPo), the

quantum yield for electron transport (φEo) and the efficiency per trapped excitation (Ψo) were not affected (Fig. 5b). These parameters can provide relevant information on electron transport activity at the PSII acceptor sites [18]. These results suggested that continuous light enhance electron transport at the PSII acceptor site in *V. radiata*.

3.11. PIabs

Performance index (PI_{abs}) calculated on energy absorption basis and the value of PI_{abs} is higher in the plant under CL (Fig. 5b). PI_{abs} are increased due to increased activity of the RC so the overall activity of the RC is increased. The PI combines three independent functional steps of photosynthesis, the density of RCs in the chlorophyll bed((RC/ABS), excitation energy trapping (φPo) and conversion of excitation energy to electron transport (Ψo), into a single multi-parametric expression [18, 40].

The efficiency with which a trapped exciton can move an electron into the electron transport chain further than Q_A-is Ψo. The PI increased in continuous light, compared to the control, because of a higher number of active RCs and overall energy use efficiency which indicates that the leaves were growing well in continuous light.

4. Conclusion

In the present research paper, the effect of continuous light on chlorophyll fluorescence kinetics of *V. radiata* and their comparative study against control was presented. Based on our findings and analyses, we concluded that continuous light improves the PSII efficiency by suppressing the light-induced PSII damage and by promoting the repair system and photoprotective strategies. Continuous light has a positive impact on plant morphology, photochemical efficiency of the plant. The non-photochemical quenching and decapitation of excess light in form of heat are the main processes which makes plant acclimated to continuous light. It was also found that continuous light-grown plants had an increased number of active RC and lowered absorption per RC, to avail the excess light. Plants treated with artificial continuous light has increase in leaf size and pigment concentration which gives evidence that plant develops protection strategy towards excessive light. Rise in the Performance index (PI_{abs}) of the plant under continuous light shows that plants have high vitality and efficient use of excess light in electron transportation beyond PS II and carbon assimilation (Calvin cycle). An interruption in the oxygen-evolving complex (OEC) at the donor site of PS II can be managed by the various photoprotective strategy of the plant such as the use of alternative electron donor, antioxidant responses which were our future prospective.

Statistical analysis

The data analysis was done using Biolyzer v.3.0.6 software. All values presented in the paper are means of three independent replicates.

CRediT authorship contribution statement

Deepak Kumar: conceived the idea and designed the research plan, execute the experiment, Conceptualization, Writing - original draft, data analysis. **Hanwant Singh:** Conceptualization, Writing - original draft, data analysis, prepared all figures and graphical artworks. **Shani Raj:** execute the experiment. **Vineet Soni:** execute the experiment, supervised the complete work. All the authors contributed to discussing and reviewing the manuscript. Finally, all the authors read and approved the final version of the manuscript for publication.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgement

The authors thank the Mohanlal Sukhadia University, India for providing laboratory facilities. Authors are also grateful to Prof. Reto J. Strasser, University of Geneva, Switzerland for his help in the analysis of chlorophyll fluorescence data.

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