American Journal of Plant Physiology

ISSN 1557-4539

Academic Journals Inc.

www.academicjournals.com

OPEN ACCESS American Journal of Plant Physiology

ISSN 1557-4539
DOI: 10.3923/ajpp.2017.1.9

Review Article
Cyclic Electron Transport Around Photosystem II: Mechanisms and Methods of Study

[1]Vladimir Lysenko, [2]Ya Guo and [1]Olga Chugueva

[1]Academy of Biology and Biotechnology, Southern Federal University, Rostov-on-Don, Russia
[2]School of IOT Engineering, Jiangnan University, Wuxi, China

Abstract
In contrast to the thylakoid cyclic electron transport around photosystem I, cyclic electron transport around photosystem II (CET-PSII) is a little studied process. The functional mechanisms of CET-PSII and methods of their study are discussed in the review. The position occupied by this process in the ensemble of the pathways of electron sink from photosystem II is discussed as well as the role of CET-PSII in regulating the ATP/NADPH ratio and participation of cytochrome b-559 in CET-PSII. In green leaves of higher plants, CET-PSII may be underestimated because of the limited possibilities of the standard methods most frequently used in photosynthesis study. In stomata guard cells of chlorophyll-deficient leaves, where the rate of non-cyclic electron transport is insufficient under blue light excitation, CET-PSII is of separate interest. A special attention should be paid to the photoacoustic methods of CET-PSII studies.

Key words: Photosystem II, cyclic electron transport, stomata guard cells, photoacoustics

Received: October 31, 2016 Accepted: November 30, 2016 Published: December 15, 2016

Citation: Vladimir Lysenko, Ya Guo and Olga Chugueva, 2017. Cyclic electron transport around photosystem II: Mechanisms and methods of study. Am. J. Plant Physiol., 12: 1-9.

Corresponding Author: Vladimir Lysenko, Academy of Biology and Biotechnology, Southern Federal University, Rostov-on-Don, Russia

Copyright: © 2017 Vladimir Lysenko *et al.* This is an open access article distributed under the terms of the creative commons attribution License, which permits unrestricted use, distribution and reproduction in any medium, provided the original author and source are credited.

Competing Interest: The authors have declared that no competing interest exists.

Data Availability: All relevant data are within the paper and its supporting information files.

INTRODUCTION

Concurrent electron sink pathways in thylakoids: Under standard conditions the light phase of photosynthesis of higher plants is facilitated by the linear (non-cyclic) electron transport (LET) in the thylakoid membrane. The LET enables electron flow from H_2O to $NADP^+$ yielding the oxygen, NADPH and building a difference of electrochemical potentials of protons ($\Delta\mu H^+$) across the thylakoid membrane, which is necessary for ATP synthesis. At a LET level, a set of the photosynthetic light reactions is formed by the components of PSII, cytochrome b6/f-complex and PSI, which operate in series, thus providing electron flow through the single Electron Transport Chain (ETC). In contrast, in the Cyclic Electron Transport (CET), the ETC is a closed-loop[1-5]. The LET is referred to the oxygenic photosynthesis considering that water is the electron donor for the ETC[6]. The ATP and NADPH are produced in a constant ratio in the results of LET[7]. The anoxygenic photosynthesis occurs in bacteria so that in the narrow sense this term is traditionally used mainly in the context of the bacterial photosynthesis. Evidently, in the broad sense, once the CET in higher plants is established, it may be referred as the anoxygenic photosynthesis because the photolysis of water does not occur but it still stores light energy in the phosphoanhydride bonds of ATP.

In a wide range of physiological conditions, plants require a fairly high lability of ATP/NADPH ratio. For example, the absolute and relative demands of cells of euhalophyte plants in ATP are strongly increased under conditions of soil salinization, when considerable ATP resources are necessary to support high osmotic pressure and activity of cationic and anionic antiporters[8,9]. At the same time, the plant growth under salinity is limited, the C O_2-assimilation is decreased and correspondingly plant cells have decreased requirements for NADPH, which is the main acceptor of the electron sink of the linear ETC. In regard to the utilization of the photoinduced thylakoid electron flow overall, the basic idea here is the hierarchical arrangement of a set of acceptors, cyclic and pseudocyclic electron transport processes competing with each other. All of them have different affinities to electrons[10]. These processes are: CO_2-assimilation (LET), nitrate reduction, malate (C4) cycle, photoreduction of O_2, H_2O_2, water-water cycle (WWC) in whole, activity of plastid terminal oxidase (PTOX) and CET. The first three processes involve utilization of NADPH and therefore, their activity causes a decrease in ATP/NADPH ratio.

There are two processes among them, which allow to avoid the excess of the photoinduced electron flow via pseudocycling of electron transport: WWC and PTOX. The WWC (also known as a pseudocyclic electron transport) supports electron flow from ferredoxin to oxygen, producing water[11]. However, the contribution of WWC in the total electron transport does not exceed 5% for C3-plants[12]. The PTOX-dependent reduction of O_2 is realized by the electron transfer from plastoquinone[13] but the activity of this process in C3-plants is even less significant[14]. Thus, WWC and PTOX cannot substantially influence the ATP/NADPH balance by competing with LET.

There are enzymatic and non-enzymatic components related to WWC, both of them parcipitate in scavenging of reduced oxygen. Particularly, O_2 can be reduced in non-enzymatic reactions via the electron transfer from ferredoxin that provides H_2O_2 in photosynthesis, especially under conditions of oxidative stress[15].

In turn, photoreduction of H_2O_2 is carried out in two ways:

- Via the thylakoid ascorbate peroxidase in the presence of excess of ascorbate, which is oxidized to MDA radical followed by reduction with thylakoid monodehydroascorbate reductase (MDA reductase)[16]. Ferredoxine is used as the electron donor for this process[17]
- Via the water-soluble enzymes of chloroplast stroma. In particular, dehydroascorbate reductase reduce H_2O_2 in the presence of excess of ascorbate, which is regenerated by accepting electron from glutathione[18]. In turn, the oxidized glutathione is reduced by NADPH-dependent glutathion reductase[19]

Both these enzymatic and non-enzymatic pathways participate in the stabilization of ATP/NADPH ratio, providing an "internal" sink for excess electrons but they cannot compete with the assimilation processes[10]. In addition, it should be noted that the H_2O_2 concentration in non-stressed plants may be low[20].

Considering the question as a whole, it is evident that the capability of LET-dependent metabolic processes to support the effective electron sink under conditions of the limited CO_2-assimilation (and correspondingly, under limited requirements for NADPH) is low. In other words, ETC electron output (sink) is limited by an external acceptor. However, the increased requirements for the additional electron sink from ETC most frequently occur under conditions which facilitate anoxygenic photosynthesis (i.e., CET)[16,18] for instance at CO_2 deficiency.

The CET can occur in two ways: Cyclic electron transport around photosystem I (CET-PSI) and around photosystem II (CET-PSII).

The sequence of CET-PSI events includes the excitation of the valence electron of P700 which is then trapped by the primary PSI acceptor, transferred to the ferredoxin and returned to P700 through the plastoquinone shuttle, providing $\Delta\mu H^+$, ATP and leads to the increase in ATP/NADPH ratio[3,21]. The CET-PSI can be selectively excited and regulated by far-red light owing to that it can be detected by the photoacoustic method[22-24] independently of PSII activity. The alternative way to reveal CET-PSI is the combining of PAM-fluorometry with measurements of the redox state of P700 using the IR kinetic absorption data in the range of 830/875 nm[25,26]. In this case, a pronounced level of CET-PSI is detected only in C4-plants under selective excitation by far-red light or/and in the presence of DCMU (3-(3,4-dichlorophenyl)-1,1-dimethylurea), an inhibitor of PSII[27,28]. Thus, CET-PSI activity, as well as WWC and PTOX could not be a significant factor, providing the sink of excess photoinduced electron flow and the regulation of ATP/NADPH ratio under natural conditions.

MECHANISMS OF CYCLIC ELECTRON TRANSPORT AROUND PHOTOSYSTEM II

In their studies, based on the pulse electrochemical detection and computer mathematical modeling of the amplitude and phase parameters of oxygen evolution in *Chlorella vulgaris* culture, Sinclair *et al.*[29] have shown the existence of the reversed electron flux in PSII from the acceptor to the donor side. The obtained data suggested the existence of such a process only under low light and anaerobic conditions. Heber *et al.*[30] have shown the occurrence CET-PSII by analyzing the oxidation kinetics of cytochrome b-559 and demonstrated that it is an electron carrier in a cyclic but not in a linear chain.

The direct and forcible argument for the existence of CET-PSII has been obtained by Falkowski *et al.*[31]. Using electrochemical methods, they detected pulse oxygen evolution (YO_2) and amplitude of fluorescence pulses ($\Delta\phi$) (That is analogous to the variable fluorescence measured by PAM-fluorometry) in parallel in response to the saturating flashes. Amplitude of fluorescence pulses ($\Delta\phi$) was calculated as:

$$\Delta\phi = \frac{Fp}{Fs - 1}$$

where, Fp is a fluorescence yield under the saturating flash and Fs is a fluorescence measured before the saturating flash. The samples were simultaneously exposed under continuous light of different intensities. In the range of moderate illumination, the increase of the intensity of continuous light led to the proportional increase of YO_2 and $\Delta\phi$. However, in the range of high light illumination, the $\Delta\phi$ increased faster than YO_2. In these experiments the researchers have proved the occurrence of CET-PSII, considering that the variable fluorescence is determined only by PSII[32]. It should be noted here, that a high level of CET-PSII was detected in this study despite the usage of the conditions which strongly promote the LET activity. In particular, the *Chlorella pyrenoidosa* cells were studied in a logarithmic phase of growth under elevated CO_2 (1%). The researchers have also proposed the following way of the electron transfer: $P680 \rightarrow Q_A \rightarrow Q_B \rightarrow PQ \rightarrow$ (Cyt b-559) $\rightarrow Z$ to account the cycle, where, Z is a primary electron acceptor of the chain.

In the studies of the effects of the uncouplers of electron transport on light-induced redox state of cytochrome b-559 in the presence of ferredoxin-$NADP^+$, Arnon and Tang[33] have demonstrated the ability of CET-PSII to provide $\Delta\mu H^+$ and ATP. In addition, the researchers have shown that the electron transfer in this case follows in a pathway close to that proposed by Falkowski *et al.*[31] but describing the participation of low-(LP) and high-potential (HP) forms of cytochrome b-559. Calculations of the relative electron transfer rates, water splitting and CO_2-assimilation rates have enabled to establish[34] that CET-PSII can participate in the regulation of the ratio of the photosynthetically generated ATP and NADPH. On the other hand, some models have been proposed to demonstrate the possibility of a CET-PSII functioning that is unrelated to the $\Delta\mu H^+$ and ATP generation, in these models the electron transfer is realized as: $P680 \rightarrow Pheophytin \rightarrow Q_A \rightarrow Q_B \rightarrow ChlZ \rightarrow P680$[35,36] or $P680 \rightarrow Pheophytin \rightarrow Q_A \rightarrow Q_B \rightarrow ChlZ \rightarrow LP\ b\text{-}559 \rightarrow P680$[37], where, ChlZ is an accessory pigment.

An exclusive role of cytochrome b-559 in CET-PSII activity was proved in a number of studies[38]. Being an essential part of PSII, cytochrome b-559 does not exhibit photodependent redox reactions at that and weakly interact with linear electron transport chain under optimal physiological conditions, when LET is dominant[38,39]. Most probably the function of b-559 as electron donor in PSII occurs by an electron transfer from b-559 to P680 through ChlZ[40,41] with possible participation of β-carotene[42,43].

Along this, it was proposed[44] that, at least a part of cytochrome b-559-dependent PSII activity does not involve the electron transport through Q_A and Q_B. Particularly, a noticeable residual Energy Storage (ES) was detected in photoacoustics experiments, even when the electron transfer from Q_A to Q_B was fully blocked by DCMU and the variable fluorescence was absent.

Lapointe *et al.*[44] have supposed CET-PSII occurs in the PSII-β-centers, i.e., PSII centers with a smaller antenna[45] due to which they might be resistant to photoinhibition.

The possibility of the direct electron transfer from pheophytin to cytochrome b-559 and further to $P680^+$ was shown by Lazar *et al.*[46] using mathematical modeling. The proposed model demonstrated influence of the CET-PSII on Fm и F_0, fluorescence levels and correspondingly on maximal PSII quantum yield, which is determined by the Fv/Fm ratio.

Contrary to Lazar *et al.*[46] an older model proposed by Eichelmann *et al.*[47] assumes a somewhat different way for the electron transfer: from pheophytin to Q, b-559 and further to the primary electron donor (P680) to close the cycle. In addition, Lazar *et al.*[45] conclusions are not entirely consistent with our data[48], according to which there is a DCMU-dependent CET-PSII in stomata guard cells. However, these contradictions may be explained by the simultaneous functioning of two types of CET-PSII, with and without Q_A and Q_B participation.

The fluorescence kinetics of DCMU-dependent CET-PSII was obtained and studied[48] in the "pure" form, in the absence of LET that was being possible under excitation of stomata guard cells by blue light. In the case of CET-PSII the Fm level is reached faster than in the case of LET, probably because the cyclic path is shorter than linear. Under the simultaneous excitation by blue and red light, when both LET and CET-PSII were revealed, the fluorescence induction curves had two maxima[48]. Another characteristic feature of the fluorescence induction curve of stomata guard cells is the absence of the slow M-peake, the origin of which is referred to the kinetics of CO_2 exchange[49].

METHODS FOR THE DETECTION OF CYCLIC ELECTRON TRANSPORT

Direct methods for the quantitative evaluation of non-cyclic (linear) electron transport in the thylakoid membrane are based on the measurements of oxygen evolution and carbon dioxide consumption rates. The difficulties in revealing the cyclic electron transport (CET-PSI and CET-PSII) are determined by its anoxygenic character which does not participate in exchange of these gases. Photophosphorylation is the only result of CET-PSI and CET-PSII but even the qualitative evaluations based on measurements of ATP synthesis rate are collided with the evident difficulties of their interpretation. Thus, it couldn't be excluded that the time course of ATP release can be related to the photoinduced shifts in respiratory rates or (and) in photoinduced changes in ATP utilization.

Nevertheless, there is a direct, fairly simple and reliable way to quantify the CET-PSI which is based on the photoacoustic spectrometry. The CET-PSI can be selectively excited by far-red (FR) light (>710 nm), which drives PSI but not PSII. Passing through the photoacoustic cell, the pulsed FR-light induces the thermal oscillation of sample surface and the generated acoustic signal can be detected by the microphone. In the case, when there are no photochemical processes in the sample, almost 100% of the absorbed light is dissipated to heat. Otherwise, if oxygenic or anoxygenic photosynthesis occurs in the sample, some part of light energy is converted into photochemical products thus decreasing the photoacoustic signal. Switching on the background saturated light (which actually "Turn off" the photosynthesis) leads to the increased PA-signal (at 200-400 Hz) by the value of Energy Storage (ES), reflecting a portion of absorbed light energy which is consumed in the photosynthesis[50-53].

The optimal light pulse frequency of the photothermal signal in such studies (measuring ES) is in the range of about 200-400 Hz. At a lower frequency (<100 Hz) the photobaric component (pulse O_2 evolution) begin to contribute noticeably in the total PA-signal and at <40 Hz the photobaric signal is strongly dominant[50,54]. However, the detection of CET-PSII is hampered by the fact that the PSII, in contrast to PSI cannot be excited selectively, using a specific spectral range. Indirect methods of quantitative evaluation of CET-PSII activity are based mainly on matching of PSII activity and oxygen evolution rate.

Thus, for example, in extreme case when the PSII is active but the photosynthetic O_2 evolution is absent, PSII functioning should be attributed mainly to the cyclic mode[48]. In this connection, the PAM-fluorometry is the most frequently applied method that allows to evaluate the maximal quantum yield of photosystem II in the dark-adapted state as Fv/Fm, where, Fm is a maximum fluorescence yield under the saturation pulse and Fv is variable fluorescence[32,55]. It should be noted that PSII gives the major contribution in Fv (only slightly affected by PSI)[56] independently from whether the PSII works in linear or cyclic mode[56,57].

When the level of CET-PSII is evaluated, the oxygen evolution rate is most frequently measured by electrochemical methods[31,37,58-60] that is coupled with en error raised from the impossibility of differentiating the contribution of respiration and photorespiration in the total O_2 exchange. This error is not attributable to the photoacoustic method where the only photosynthetic oxygen is detected under pulse light excitation. At the frequencies of 10-30 Hz the photobaric component of the PA-signal is dominant[50,52,54,60-63] whereas the photothermal component only weakly contribute in total PA-signal. Both these components are in antiphase.

A remarkable feature of this approach is in that the determination of photosynthetic O_2 evolution via the photobaric signal is independent of respiration, photorespiration and pseudocyclic electron transport. The oxygen uptake during all these three processes is continuous under modulated light and thus cannot be detected by photoacoustics; relatively long chains of these biochemical reactions dump the pulsations.

The phase sensitivity of the traditional PA-method is its disadvantage arising from the application of lock-in amplifiers. There is an obvious risk of error in measurements of oxygen evolution rate under conditions when the phase responses of the photobaric signals could be different at different illumination[29]. At that time the phase insensitive detection is possible when applying real time Fast Fourier Transforms (FFT) of PA-signal, the capability of that was recently demonstrated[48,64]. In this case the microphone signal passes into the usual low noise operational amplifier and then to the PC sound card with the subsequent FFT-processing by standard software. The intriguing perspective of FFT application for PA-spectrometry is in that this method allows the selection of two or more frequencies. It means, for example, that it is possible to detect simultaneously the photobaric (PA_{O2}) and photothermal (PA_{ES}) signals. Obviously, the PA_{O2}/PA_{ES} decreased ratio can evidence for domination of the anoxygenic photosynthesis. Matching of PA_{O2}/PA_{ES} value with maximal quantum efficiency of photosystem II (Fv/Fm) may be a next step to detect CET-PSII quantitatively.

An attempt to detect the photobaric and photothermal signals simultaneously was performed by Han[65] in experiments with two lock-in operational amplifiers connected in parallel. However, the problem of phase sensitivity still remains in the given case. Besides, the application of this method for CET-PSII studies was not reported until now.

A reliable (at least semi-quantitative) detection of CET-PSII is possible using indirect methods. Thus, for example, detection of CET-PSI and CET-PSII in simultaneous photoacoustic (ES determination) and electrochemical (O_2 determination) was performed by varying the time intervals between saturating flashes along with the parallel application of specific inhibitors of ETC. It was assumed in these experiments that the CET, although it does not produce oxygen itself, influence on the phase characteristics of the signal which is generated by the oxygen electrode[66].

A major contribution in our understanding of qualitative and quantitative characteristics of CET-PSII can be made in studies on redox states of specific CET-PSII electron carriers, b-559, ChlZ. In tissues which intensively produce oxygen, where there are no significant CET-PSII activity, LP and IP forms of cytochrome b-559 are in a reduced state[44,67,68], i.e., the electron transfer through the corresponding ETC segment is blocked. Photoreduction of these carriers, however, is induced by photooxidation of chlorophyll, when (as assumed) CET-PSII is active[41].

PHYSIOLOGICAL FUNCTIONS OF CYCLIC ELECTRON TRANSPORT AROUND PHOTOSYSTEM II

The most studied function of CET-PSII is the protection from photoinhibition. As is known, photoinhibition relates to the utilization of excess quanta in photodestructive reactions, when the electron sink from ETC is restricted, for example, by low requirements of NADPH[69]. Under such conditions, the pool of primary acceptors of electrons is almost fully reduced that provide conditions for generation of reactive oxygen species related to the functioning of reactive centers[18]. Supporting electron transfer from acceptor to donor side of PSII, cyclic electron transport provides a sink-independent reoxidation of Q_A and Q_B. Fast electron turnover inside PSII, which is no longer limited by the electron sink (only by the throughput capacity of ETC), results in the thermal dissipation of energy of excess quanta. Its role in the wide spectrum of thermodissipative processes[70] an interesting subject for the future studies.

A number of studies argue in favor of photoprotection function of CET-PSII. Thus, it was shown in studies involving exogenic electron acceptors (silicomolybdate, DBMIB) that CET-PSII protects carotenoids of isolated pea chloroplasts from irreversible photobleaching under photoinhibitory conditions[71]. Photoprotection function of CET-PSII has been shown[72] with the use of artificial electron acceptor K15 (4-[methoxybis(trifluoromethyl) methyl]-2, 6-dinitrophenylhydrazine methyl ketone), which is able to accepts electrons from $Pheo^-$ thereby reducing the donor side of PSII and therefore, stimulating CET[73]. The K15-induced CET-PSII activity can protect PSII submembrane fractions from photoinhibitory impairment under anaerobic and aerobic conditions[37]. It was demonstrated that the cytochrome b-559 content increases simultaneously with the reduction of LHC antenna size that can evidence the adaptational role of CET-PSII in protection from photoinhibition[74]. These photoprotection functions also have been demonstrated in other studies[35,43,75].

In the framework of the theoretical model by Lazar *et al.*[46], where CET-PSII was assumed as the electron transport from the pheophytin through cytochrome b-559 to P680, the researchers suggested that increased amount of initially induced cytochrome b-559 might protect PSII against photoinhibition.

Role of CET-PSII can be supposed easily but CET-PSII has been little studied as an electron acceptor process regulating ATP/NADPH ratio. In a changeable environment plants require different ATP/NADPH values for maintaining homeostasis and hydrocarbons synthesis[5]. The ATP/NADPH ratio increases under stress conditions that is partially provided in studies on the pseudocyclic electron transport and CET-PSI[5,76,77]. It is unclear, whether the CET-PSII fulfills an analogous regulatory role. This question is of interest in regard of the fact that the CET-PSI and WWC cannot provide an electron transport rate comparable with LET.

Cyclic electron transport simultaneously occurs in guard cell thylakoids around photosystems I and II under blue light, whereas linear electron transport is absent or insufficient[48]. This fact is in a good agrreement with the data obtained by Shimazaki and Zeiger[78] who have demonstrated that the exposure of Vicia faba chloroplasts by blue light, in contrast to red light, does not lead to the oxygen evolution. The CO_2 has been shown to be incorporated into malate in guard cells[79] but in a non-photosynthetic way from starch with participation of PEP carboxylase and NAD-malate dehydrogenase[80]. Moreover, stomata guard cell chloroplasts accumulates starch in the dark which disappears in the light[81]. Therefore, malate-dependent CO_2-assimilation in guard cells wouldn't be a process that utilize electrons come from ETC. Thus the dominance of the cyclic electron transport in stomata guard cells is not surprising in the absence of a powerful external (beyond ETC) acceptor.

CONCLUSION

The known data on CET-PSII allow to conclude that the existence of this cycle is reliably proved but it remains relatively (in comparison to LET and CET-PSI) little studied and probably underestimated. To summarize the above, the following reasons for the difficulties in studying CET-PSII should be noted:

- Impossibility of a selective excitation of PSII and therefore, impossibility to observe "pure" CET-PSII activity, without background LET activity (except stomata guard cells)
- Absence of reliable fluorescence kinetic methods allowing to determining whether the fluorescence kinetics originated from the PSII functioning in linear or cyclic mode
- A small number of studies carried out on mathematical modeling in combination with the experimental measurements, which might be helpful in understanding of CET-PSII
- The only direct method for evaluating CET-PSII activity is a photoacoustic method which, however is not widely used because of absence of commercially available equipment suitable for the photosynthesis researches

The researchers hope that this study would be a stimulus for the further studies on CET-PSII and related processes including the use of novel photoacoustic methods which, undoubtedly would overcome the discussed here difficulties and problems.

ACKNOWLEDGEMENT

The authors are grateful to Southern Federal University (Russia, Rostov-on-Don) for the grant No. 213.01-07-2014/06 PChVG provided to achieve the aims of the present study.

REFERENCES

1. Bukhov, N. and R. Carpentier, 2004. Alternative photosystem I-driven electron transport routes: Mechanisms and functions. Photosynt. Res., 82: 17-33.
2. Johnson, G.N., 2011. Physiology of PSI cyclic electron transport in higher plants. Biochim. Biophys. Acta (BBA)-Bioenerg., 1807: 384-389.
3. Joliot, P., A. Joliot and G. Johnson, 2006. Cyclic Electron Transfer around Photosystem I. In: Photosystem I: The Light-Driven Plastocyanin: Ferredoxin Oxidoreductase, Golbeck, J.H. (Eds.). Springer, Dordrecht, The Netherlands, ISBN: 978-1-4020-4255-3, pp: 639-656.
4. Munekage, Y. and T. Shikanai, 2005. Cyclic electron transport through photosystem I. Plant Biotechnol., 22: 361-369.
5. Munekage, Y., M. Hashimoto, C. Miyake, K.I. Tomizawa, T. Endo, M. Tasaka and T. Shikanai, 2004. Cyclic electron flow around photosystem I is essential for photosynthesis. Nature, 429: 579-582.
6. Nelson, N., 2011. Photosystems and global effects of oxygenic photosynthesis. Biochim. Biophys. Acta (BBA)-Bioenerg., 1807: 856-863.
7. Rubin, A.B. and T.E. Krendeleva, 2003. Regulation of primary photosynthetic processes. Uspekhi Biologicheskoy Khimii (Adv. Biol. Chem.), 43: 225-266.
8. Chinnusamy, V. and J.K. Zhu, 2004. Plant Salt Tolerance. In: Plant Responses to Abiotic Stress, Hirt, H. and K. Shinozaki (Eds.). Springer-Verlag, Berlin, Heidelberg, ISBN: 978-3-540-20037-6, pp: 241-270.
9. Shuvalov, A.V., J.V. Orlova, L.A. Khalilova, N.A. Myasoedov, I.M. Andreev, D.V. Belyaev and Y.V. Balnokin, 2015. Evidence for the functioning of a Cl^-/H^+ antiporter in the membranes isolated from root cells of the halophyte *Suaeda altissima* and enriched with Golgi membranes. Russian J. Plant Physiol., 62: 45-56.

10. Backhausen, J.E., C. Kitzmann, P. Horton and R. Scheibe, 2000. Electron acceptors in isolated intact spinach chloroplasts act hierarchically to prevent over-reduction and competition for electrons. Photosynth. Res., 64: 1-13.
11. Rochaix, J.D., 2011. Regulation of photosynthetic electron transport. Biochim. Biophys. Acta (BBA)-Bioenerg., 1807: 375-383.
12. Clarke, J.E. and G.N. Johnson, 2001. *In vivo* temperature dependence of cyclic and pseudocyclic electron transport in barley. Planta, 212: 808-816.
13. McDonald, A.E., A.G. Ivanov, R. Bode, D.P. Maxwell, S.R. Rodermel and N.P.A. Huner, 2011. Flexibility in photosynthetic electron transport: The physiological role of Plastoquinol Terminal Oxidase (PTOX). Biochim. Biophys. Acta (BBA)-Bioenerg., 1807: 954-967.
14. Josse, E.M., A.J. Simkin, J. Gaffe, A.M. Laboure, M. Kuntz and P. Carol, 2000. A plastid terminal oxidase associated with carotenoid desaturation during chromoplast differentiation. Plant Physiol., 123: 1427-1436.
15. Kramer, D.M. and J.R. Evans, 2011. The importance of energy balance in improving photosynthetic productivity. Plant Physiol., 155: 70-78.
16. Miyake, C. and K. Asada, 1992. Thylakoid-bound ascorbate peroxidase in spinach chloroplasts and photoreduction of its primary oxidation product monodehydroascorbate radicals in thylakoids. Plant Cell Physiol., 33: 541-553.
17. Groden, D. and E. Beck, 1979. H_2O_2 destruction by ascorbate-dependent systems from chloroplasts. Biochim. Biophys. Acta (BBA)-Bioenerg., 546: 426-435.
18. Asada, K. and M. Takahashi, 1987. Production and Scavenging of Active Oxygen in Chloroplasts. In: Photoinhibition: Topics in Photosynthesis, Kyle, D.J., C.B. Osmond and C.J. Arntzen (Eds.). Elsevier, Amsterdam, pp: 227-287.
19. Foyer, C.H. and B. Halliwell, 1976. The presence of glutathione and glutathione reductase in chloroplasts: A proposed role in ascorbic acid metabolism. Planta, 133: 21-25.
20. Slesak, I., M. Libik, B. Karpinska, S. Karpinski and Z. Miszalski, 2007. The role of hydrogen peroxide in regulation of plant metabolism and cellular signalling in response to environmental stresses. Acta Biochimica Polonica, 54: 39-50.
21. Nakamura, N., M. Iwano, M. Havaux, A. Yokota and Y.N. Munekage, 2013. Promotion of cyclic electron transport around photosystem I during the evolution of NADP-malic enzyme-type C_4 photosynthesis in the genus *Flaveria*. New Phytol., 199: 832-842.
22. Herbert, S.K., D.C. Fork and S. Malkin, 1990. Photoacoustic measurements *in vivo* of energy storage by cyclic electron flow in algae and higher plants. Plant Physiol., 94: 926-934.
23. Lysenko, V.S., T.V. Varduny, E.I. Simonovich, O.I. Chugueva and V.A. Chokheli *et al*., 2014. Far-red spectrum of second emerson effect: A study using dual-wavelength pulse amplitude modulation fluorometry. Am. J. Biochem. Biotechnol., 10: 234-240.
24. Lenbaum, V.V., A.A. Bulychev and D.N. Matorin, 2015. Effects of far red light on the induction changes of prompt and delayed fluorescence and the redox state of P700 in *Scenedesmus quadricauda*. Russian J. Plant Physiol., 62: 210-218.
25. Asada, K., U. Heber and U. Schreiber, 1993. Electron flow to the intersystem chain from stromal components and cyclic electron flow in maize chloroplasts, as detected in intact leaves by monitoring redox change of P700 and chlorophyll fluorescence. Plant Cell Physiol., 34: 39-50.
26. Tongra, T., S. Bharti and A. Jajoo, 2014. Cyclic electron flow around photosystem I is enhanced at low pH. Plant Physiol. Biochem., 83: 194-199.
27. Joet, T., L. Cournac, G. Peltier and M. Havaux, 2002. Cyclic electron flow around photosystem I in C_3 plants. *In vivo* control by the redox state of chloroplasts and involvement of the NADH-dehydrogenase complex. Plant Physiol., 128: 760-769.
28. Tongra, T. and A. Jajoo, 2015. Investigating changes in the redox state of Photosystem I at low pH. J. Photochem. Photobiol. B: Biol., 151: 25-30.
29. Sinclair, J., A. Sarai and S. Garland, 1979. A backflow of electrons around photosystem II in *Chlorella* cells. Biochim. Biophys. Acta (BBA)-Bioenerg., 546: 256-269.
30. Heber, U., M.R. Kirk and N.K. Boardman, 1979. Photoreactions of cytochrome b_{559} and cyclic electron flow in photosystem II of intact chloroplasts. Biochim. Biophys. Acta (BBA)-Bioenerg., 546: 292-306.
31. Falkowski, P.G., Y. Fujita, A. Ley and D. Mauzerall, 1986. Evidence for cyclic electron flow around photosystem II in *Chlorella pyrenoidosa*. Plant Physiol., 81: 310-312.
32. Lazar, D., 2015. Parameters of photosynthetic energy partitioning. J. Plant Physiol., 175: 131-147.
33. Arnon, D.I. and G.M.S. Tang, 1988. Cytochrome b_{559} and proton conductance in oxygenic photosynthesis. Proc. Natl. Acad. Sci. USA., 85: 9524-9528.
34. Laisk, A., H. Eichelmann, V. Oja, B. Rasulov and H. Ramma, 2006. Photosystem II cycle and alternative electron flow in leaves. Plant Cell Physiol., 47: 972-983.
35. Buser, C.A., B.A. Diner and C.W. Brudvig, 1992. Photooxidation of cytochrome b_{559} in oxygen-evolving photosystem II. Biochemistry, 31: 11449-11459.
36. Pospisil, P., 2011. Enzymatic function of cytochrome b_{559} in photosystem II. J. Photochem. Photobiol. B: Biol., 104: 341-347.
37. Prasil, O., Z. Kolber, J.A. Berry and P.G. Falkowski, 1996. Cyclic electron flow around photosystem II *in vivo*. Photosynth. Res., 48: 395-410.
38. Whitmarsh, J. and H.B. Pakrasi, 1996. Form and Function of Cytochrome *B*-559 in Oxygenic Photosynthesis. In: Oxygenic Photosynthesis: The Light Reactions, Ort, D.R. and C.F. Yocum (Eds.)., Springer, New York, USA., ISBN: 9780792336839, pp: 249-264.

39. Klughammer, C., J. Kolbowski and U. Schreiber, 1990. LED array spectrophotometer for measurement of time resolved difference spectra in the 530-600 nm wavelength region. Photosynth. Res., 25: 317-327.
40. Visser, J.W.M., C.P. Rijgersberg and P. Gast, 1977. Photooxidation of chlorophyll in Spinach chloroplasts between 10 and 180 K. Biochim. Biophys. Acta (BBA)-Bioenerg., 460: 36-46.
41. Thompson, L.K. and G.W. Brudvig, 1988. Cytochrome b_{559} may function to protect photosystem II from photoinhibition. Biochemistry, 27: 6653-6658.
42. Faller, P., C. Fufezan and W. Rutherford, 2005. Side-Path Electron Donors: Cytochrome b_{559}, Chlorophyll Z and β-Carotene. In: Advances in Photosynthesis and Respiration, Wydrzynski, T.J. and K. Satoh (Eds.). Springer, New York, USA., pp: 347-365.
43. Shinopoulos, K.E. and G.W. Brudvig, 2012. Cytochrome b_{559} and cyclic electron transfer within photosystem II. Biochim. Biophys. Acta (BBA)-Bioenerg., 1817: 66-75.
44. Lapointe, L., N.P.A. Huner, R.M. Leblanc and R. Carpentier, 1993. Possible photoacoustic detection of cyclic electron transport around photosystem II in photoinhibited thylakoid preparations. Biochim. Biophys. Acta (BBA)-Bioenerg., 1142: 43-48.
45. Lazar, D., P. Tomek, P. Ilik and J. Naus, 2001. Determination of the antenna heterogeneity of photosystem II by direct simultaneous fitting of several fluorescence rise curves measured with DCMU at different light intensities. Photosynth. Res., 68: 247-257.
46. Lazar, D., P. Ilik, J. Kruk, K. Strzalka and J. Naus, 2005. A theoretical study on effect of the initial redox state of cytochrome b_{559} on maximal chlorophyll fluorescence level (F_M): Implications for photoinhibition of photosystem II. J. Theor. Biol., 233: 287-300.
47. Eichelmann, H., E. Weis and A. Laisk, 1990. The Effect of Electron Cycling Around PSII on Fluorescence Induction: Mathematical Modeling. In: Current Research in Photosynthesis, Baltscheffsky, M. (Ed.). Vol. 1, Springer, New York, USA., pp: 663-666.
48. Lysenko, V., 2012. Fluorescence kinetic parameters and cyclic electron transport in guard cell chloroplasts of chlorophyll-deficient leaf tissues from variegated weeping fig (*Ficus benjamina* L.). Planta, 235: 1023-1033.
49. Lysenko, V.S., T.V. Varduny, P.O. Kosenko, Y.V. Kosenko and O.I. Chugueva *et al*., 2014. Video registration as a method for studying kinetic parameters of chlorophyll fluorescence in *Ficus benjamina* leaves. Russ. J. Plant Physiol., 61: 419-425.
50. Buschmann, C., 1999. Thermal dissipation related to chlorophyll fluorescence and photosynthesis. Bulg. J. Plant Physiol., 25: 77-88.
51. Delosme, R., 2003. On some aspects of photosynthesis revealed by photoacoustic studies: A critical evaluation. Photosynth. Res., 76: 289-301.
52. Hou, H.J.M. and T.P. Sakmar, 2010. Methodology of pulsed photoacoustics and its application to probe photosystems and receptors. Sensors, 10: 5642-5667.
53. Pinchasov-Grinblat, Y. and Z. Dubinsky, 2013. Photoacoustics-A Novel Tool for the Study of Aquatic Photosynthesis. In: Photosynthesis, Dubinsky, Z. (Ed.). InTech, Croatia, pp: 285-296.
54. Bults, G., B.A. Horwitz, S. Malkin and D. Cahen, 1982. Photoacoustic measurements of photosynthetic activities in whole leaves. Photochemistry and gas exchange. Biochim. Biophys. Acta (BBA)-Bioenerg., 679: 452-465.
55. Schreiber, U., 2004. PAM Pulse-amplitude Fluorometry and Saturation Pulse Method. In: Chlorophyll Fluorescence: A Signature of Photosynthesis, Advances in Photosynthesis and Respiration Series, Papageorgiou, G. and Govindjee (Eds.). Kluwer Academic Publishers, Dordrecht, The Netherlands, pp: 279-319.
56. Lazar, D., 2013. Simulations show that a small part of variable chlorophyll a fluorescence originates in photosystem I and contributes to overall fluorescence rise. J. Theor. Biol., 335: 249-264.
57. Itoh, S. and K. Sugiura, 2004. Fluorescence of Photosystem I. In: Chlorophyll a Fluorescence: A Signature of Photosynthesis, Papageorgiou, G. and C. Govindjee (Eds.). Springer, The Netherlands, pp: 231-250.
58. Lavaud, J., H.J. van Gorkom and A.L. Etienne, 2002. Photosystem II electron transfer cycle and chlororespiration in planktonic diatoms. Photosynth. Res., 74: 51-59.
59. Miyake, C. and A. Yokota, 2001. Cyclic flow of electrons within PSII in thylakoid membranes. Plant Cell Physiol., 42: 508-515.
60. Feikema, W.O., M.A. Marosvolgyi, J. Lavaud and H.J. van Gorkom, 2006. Cyclic electron transfer in photosystem II in the marine diatom *Phaeodactylum tricornutum*. Biochim. Biophys. Acta (BBA)-Bioenerg., 1757: 829-834.
61. Frandas, A., H. Jalink and R. van der Schoor, 1997. Low frequency photoacoustics for monitoring the photobaric component *in vivo* of green leaves. Photosynth. Res., 52: 65-67.
62. Havaux, M., 1998. Probing electron transport through and around photosystem II *in vivo* by the combined use of photoacoustic spectroscopy and chlorophyll fluorometry. Israel J. Chem., 38: 247-256.
63. Canaani, O., S. Malkin and D. Mauzerall, 1988. Pulsed photoacoustic detection of flash-induced oxygen evolution from intact leaves and its oscillations. Proc. Natl. Acad. Sci. USA., 85: 4725-4729.
64. Lysenko, V. and T. Varduny, 2013. Anthocyanin-dependent anoxygenic photosynthesis in coloured flower petals?. Sci. Rep. 10.1038/srep03373.
65. Han, T., 2002. Portable dual frequency photoacoustic spectrometer. US Pataent 20020093658 A1, July 18, 2002. https://www.google.com.au/patents/US20020093658

66. Cha, Y. and D.C. Mauzerall, 1992. Energy storage of linear and cyclic electron flows in photosynthesis. Plant Physiol., 100: 1869-1877.
67. Thompson, L.K., A.F. Miller, C.A. Buser, J.C. De Paula and G.W. Brudvig, 1989. Characterization of the multiple forms of cytochrome b_{559} in photosystem II. Biochemistry, 28: 8048-8056.
68. Kaminskaya, O., J. Kurreck, K.D. Irrgang, G. Renger and V.A. Shuvalov, 1999. Redox and spectral properties of cytochrome b_{559} in different preparations of photosystem II. Biochemistry, 38: 16223-16235.
69. Tyystjarvi, E., 2013. Photoinhibition of photosystem II. Int. Rev. Cell Mol. Biol., 300: 243-303.
70. Sofronova, V.E., T.K. Antal, O.V. Dymova and T.K. Golovko, 2014. Photoprotective mechanisms in photosystem II of *Ephedra monosperma* during development of frost tolerance. Russian J. Plant Physiol., 61: 751-759.
71. Telfer, A., J. De Las Rivas and J. Barber, 1991. β-Carotene within the isolated photosystem II reaction centre: Photooxidation and irreversible bleaching of this chromophore by oxidised P680. Biochim. Biophys. Acta (BBA)-Bioenerg., 1060: 106-114.
72. Allakhverdiev, S.I., V.V. Klimov and R. Carpentier, 1997. Evidence for the involvement of cyclic electron transport in the protection of photosystem II against photoinhibition:? Influence of a new phenolic compound. Biochemistry, 36: 4149-4154.
73. Klimov, V.V., S.K. Zharmukhamedov, S.I. Allakhverdiev, L.P. Kolobanova and Y.A. Baskakov, 1993. New group of inhibitors of electron transfer in photo-system 2 of plants. Chemical structure and efficiency of inhibition. Biol. Membr., 10: 565-570.
74. Gu, W., L. Huan, R. Yu, G. Pan and G. Wang, 2015. Enhancement of cytochrome b_{559} indicates its possible involvement in long-term high light stress tolerance in intertidal macroalgae. Plant Mol. Biol. Rep., 33: 1918-1927.
75. Hamilton, M., E. Franco, Z. Deak, E. Schlodder, I. Vass and P.J. Nixon, 2014. Investigating the photoprotective role of cytochrome b_{559} in photosystem II in a mutant with altered ligation of the haem. Plant Cell Physiol., 55: 1276-1285.
76. Rumeau, D., G. Peltier and L. Cournac, 2007. Chlororespiration and cyclic electron flow around PSI during photosynthesis and plant stress response. Plant Cell Environ., 30: 1041-1051.
77. Plyusnina, T.Y., G.Y. Riznichenko and A.B. Rubin, 2013. Regulation of electron-transport pathways in cells of *Chlamydomonas reinhardtii* under stress conditions. Russian J. Plant Physiol., 60: 518-528.
78. Shimazaki, K.I. and E. Zeiger, 1987. Red light-dependent CO_2 uptake and oxygen evolution in guard cell protoplasts of *Vicia faba* L.: Evidence for photosynthetic CO_2 fixation. Plant Physiol., 84: 7-9.
79. Raschke, K. and P. Dittrich, 1977. [^{14}C]Carbon-dioxide fixation by isolated leaf epidermes with stomata closed or open. Planta, 134: 69-75.
80. Talbott, L.D. and E. Zeiger, 1998. The role of sucrose in guard cell osmoregulation. J. Exp. Bot., 49: 329-337.
81. Willmer, C. and M. Fricker, 1996. Stomata.1996 Springer Science and Business Media, Netherlands, ISBN: 9780412574306, Pages: 375.