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Review

Cyclic electron flow in C3 plants

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Abstract

This paper summarized our present view on the mechanism of cyclic electron flow in C3 plants. We propose that cyclic and linear pathways are in competition for the reoxidation of the soluble primary PSI acceptor, Ferredoxin (Fd), that freely diffuses in the stromal compartment. In the linear mode, Fd binds ferredoxin-NADP-reductase and electrons are transferred to $NADP^+$ and then to the Benson and Calvin cycle. In the cyclic mode, Fd binds a site localized on the stromal side of the cytochrome b_6f complex and electrons are transferred to P_{700} via a mechanism derived from the Q-cycle. In dark-adapted leaves, the cyclic flow operates at maximum rate, owing to the partial inactivation of the Benson and Calvin cycle. For increasing time of illumination, the activation of the Benson and Calvin cycle, and thus, that of the linear flow, is associated with a subsequent decrease in the rate of the cyclic flow. Under steady-state conditions of illumination, the contribution of cyclic flow to PSI turnover increases as a function of the light intensity (from 0 to ~50% for weak to saturating light, respectively). Lack of CO_2 is associated with an increase in the efficiency of the cyclic flow. ATP concentration could be one of the parameters that control the transition between linear and cyclic modes.

Keywords: Cyclic and Linear electron flows; Photosystem I; cytochrome b_6f

The photosynthetic process in algae and in plants can operate through linear and cyclic electron flows. In the linear mode, electrons are transferred from water to NADP and then to the Benson and Calvin cycle, a process that involves the three major complexes of the electron transfer chain: PSII, PSI and cytochrome (cyt) b_6f complex. The occurrence of a cyclic process has been first demonstrated by Arnon and coworkers [1], who observed that illumination of broken chloroplasts under anaerobic conditions induces ATP synthesis in the presence of different cofactors as vitamin K or phenazine methosulfate. It was later demonstrated by Tagawa et al. [2] that cyclic phosphorylation can also be catalyzed by Ferredoxin (Fd), the soluble primary PSI acceptor. It thus suggests that a similar process involving PSI, cyt b_6f complex and two soluble carriers, Fd and plastocyanin (PC) can occur in vivo. Although cyclic electron flow operates efficiently in unicellular algae in anaerobic conditions [3], the occurrence of cyclic flow in plants in the presence of oxygen is a subject of controversy, especially in the steady state reached after a long illumination.

We have recently developed new approaches to quantify the efficiency of cyclic and linear flows in leaves of upper plants: First, the rate of cyclic and linear flows has been determined under saturating light excitation by measuring the rate of decay of the membrane potential at the time the light is switched off [4,5]. During the first seconds of illumination of a dark-adapted leaf, cyclic flow operates at a rate of ~130 s^{-1}. Linear flow operates at a lower rate (~15 s^{-1}), owing to the inactivation of the Benson and Calvin cycle in a dark-adapted leaf. In the presence of 3-(3,4-dichloro-phenyl)-1,1-dimethylurea, cyclic flow operates transiently at similar rate [4,5]. Such a rapid turnover of the cyclic process excludes the involvement of the NADPH quinone reductase (NDH) that is present at a concentration of a few percents of PSI in thylakoid membranes [6]. We have proposed a mechanism, derived from the Q-cycle process [5], in which Fd formed on the acceptor side of PSI binds the stromal side of cyt b_6f complex. It then transfers electrons to the Q_i-site via cyt c_i, recently identified in the structure of cyt b_6f [7,8]. It has been shown that FNR co-purifies with cyt b_6f complex [9]. FNR-cyt b_6f could represent the Fd-binding site. The same mechanism is likely involved in the cyclic process characterized in vitro that

Abbreviations: cyt, cytochrome; Fd, ferredoxin; FNR, Ferredoxin-NADP reductase; NPQ, non-photochemical quenching; P_{700}, PSI primary donor; PC, plastocyanin; PQ, plastoquinone; PQH_2, plastoquinol; PS, Photosystem

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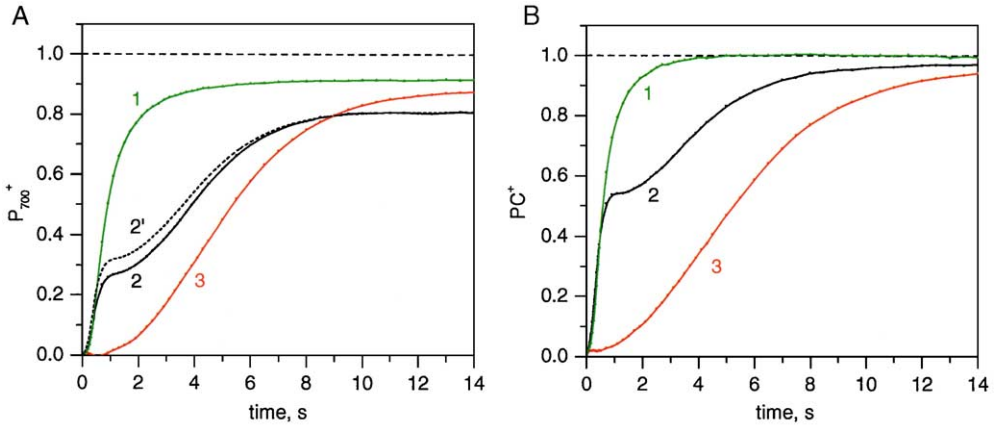

Fig. 1. Kinetics of P_{700} and PC oxidation under far-red illumination (ki_{PSI} ~8 s^{-1}). (A) P_{700} oxidation. Curve 1: >10-min green-light preillumination (ki_{PSII} ~30 s^{-1}) plus 2-min dark. Curve 2: dark-adapted leaf. Curve 2': absorption changes at 810 nm (normalized to the same maximum amplitude as curve 2). Curve 3: dark-adapted leaf preilluminated by 200-ms saturating light plus 5-s dark before far-red illumination. P_{700}^+ concentration has been normalized to the total P_{700} concentration computed as in [10]. (B) PC oxidation. Curves 1–3, same conditions as in A, curves 1–3.

requires the addition of Fd but not of NADP [2], excluding any involvement of NDH.

In a second approach, we have analyzed kinetics of P_{700} and PC oxidation under weak far-red excitation (ki_{PSI} ~8 s^{-1}), i.e., at a rate constant much lower than the rate-limiting step of both cyclic and linear flows. The illumination of a leaf under far-red excitation provides a simple way to determine whether the photosynthetic apparatus is operating through linear or cyclic mode [10]. In the linear mode, electrons formed on the stromal side of PSI are transferred to $NADP^+$ via Fd and Fd-NADP reductase (FNR). One thus expects that a far-red illumination induces a fast oxidation, first of PSI secondary donors and then of P_{700}. In the cyclic mode, Fd is reoxidized on the stromal side of the cyt b_6f complex and electrons are back-transferred to P_{700} that is maintained reduced.

1. Materials and methods

Experiments are performed with market spinach leaves. Absorption changes are measured in an apparatus similar to that used in [10]. The absorption changes are sampled by 12-μs detecting flashes provided by light-emitting diodes with peak emission at 810 and 870 nm, respectively. The light-detecting diodes are protected from actinic illumination by 2 RG780 filters and 2 RG850 filters at 810 and 870 nm, respectively. These filters cut off the short-wavelength emission of the light-emitting diodes. The leaf is placed in a cuvette in which air bubbled in water is continuously blown. When indicated, CO_2 is removed by flowing air on a sodium hydroxide column. The input and output faces of the cuvette are covered with light-scattering powder. Light-scattering that occurs on the two faces of the cuvette and within the leaf increases the optical path of the far-red detecting beams, which leads to an increase in the amplitude of the photoinduced absorption changes (up to 1% at 810 nm). The absorption changes associated with P_{700} and PC redox states are computed as $\Delta I/I$ $P_{700}=\Delta I/I$ 810 nm $-0.8\times\Delta I/I$ 870 nm and $\Delta I/I$ PC $=\Delta I/I$ 870 nm $-0.25\times\Delta I/I$ P_{700}, respectively. In this optical device, the optical path at 870 nm is longer than at 810 nm. The photochemical rate constants ki_{PSI} and ki_{PSII} are determined on the basis of membrane potential measurements [10] and fluorescence kinetics [4].

2. Results

Fig. 1 displays the kinetics of P_{700} and PC oxidation induced by a far-red excitation of dark-adapted or preilluminated leaf. P_{700} and PC redox changes have been determined by measuring the absorption changes at 810 and 870 nm, respectively. In curves 1, the leaf has been preilluminated for more than 10 min under green light (ki_{PSI} and ki_{PSII} ~40 s^{-1}) in the presence of CO_2 in order to activate the Benson and Calvin cycle. After 2-min dark, the far-red excitation induces a fast oxidation of P_{700} and PC; the kinetics is close to that measured in the presence of an efficient PSI acceptor such as methylviologen, suggesting that the photosynthetic process operates linearly ([10] and Fig. 3 below). In a dark-adapted leaf (curves 2, kinetics of P_{700} and PC oxidation display two phases. Surprisingly enough, depending of the leaf, the relative amplitude of the two phases varies in large proportion. In curves 3, the dark-adapted leaf has been first illuminated by a 200-ms pulse of saturating light that induces the reduction of most of the PQ pool. After 5-s dark, the leaf is submitted to far-red excitation. Kinetics of P_{700} and PC oxidation displays a lag phase followed by a slow monophasic increase. Thus, after a pulse of saturating light, all PSI centers contribute to the cyclic electron flow, at variance of what is observed in the absence of the pulse of saturating light (curves 2). When decreasing the far-red light by a factor 2, kinetics of P_{700} oxidation is ~2 times slower, showing that, in this range of intensities, this process is light-limited (not shown). It thus excludes that a dark process limits the rate of P_{700} oxidation.

2.1. Structural organization of the membrane

The biphasic oxidation of P_{700} observed in dark-adapted leaves (Fig. 1, curves 2) has been first interpreted assuming that chloroplasts include two compartments [10]. In a first compartment, PSI contributes exclusively to the linear pathway (fast phase) while, in a second compartment, PSI is mainly involved in the cyclic pathway (slow phase). In contradiction with this interpretation, the experiment shown in Fig. 1, curves 3 demonstrates that, following a short green-light pulse given to a dark-adapted leaf, all PSI centers contribute to the cyclic process. It leads us to propose a model of structural organization of the membrane (Fig. 2) in which, at variance of what was proposed in [10], Fd freely

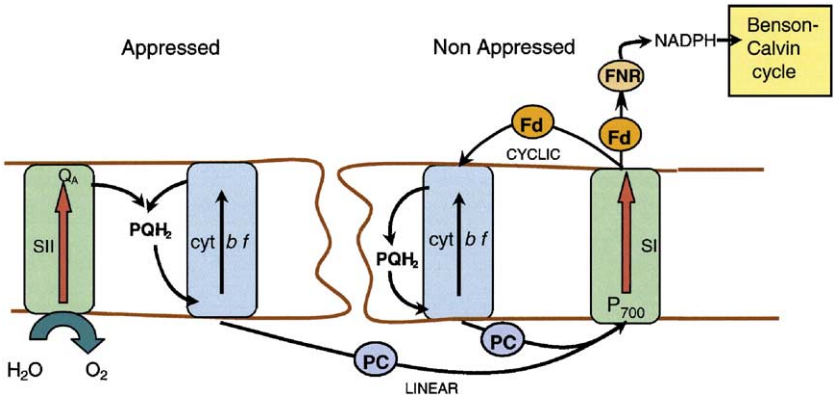

Fig. 2. A model of the structural organization of the photosynthetic membrane.

diffuses in the stromal compartment and FNR does not bind PSI. In this model, FNR and the cyt b_6f-stromal site are in competition for Fd reoxidation [5]. To explain that electrons are first transferred from Fd to the downhill-oxidized acceptors, including $NADP^+$ (fast phase of P_{700} oxidation), we must assume that the probability for Fd to bind FNR is much larger than that to bind the cyt b_6f-stromal site. Fd becomes able to bind the cyt b_6f-stromal site, thus initiating the cyclic flow only when FNR is fully reduced. Following a pulse of saturating light that induces the reduction of $NADP^+$ and of a fraction of PQ pool, reduced Fd formed at the level of PSI is immediately available to transfer electron to the cyt b_6f complex, which initiates cyclic electron flow with no delay (Fig. 1, curves 3). An alternate structural model to Fig. 2 takes into account experimental evidences that suggest the formation of a complex that associates PSI and FNR [11–14]. Owing to the proximity of PSI and FNR, electrons formed on the stromal side of PSI are first transferred to $NADP^+$. Since after reduction of the pool of $NADP^+$ electrons are transferred to the cyt-b_6f stromal site, we must assume that the association between FNR and PSI does not prevent the interaction of soluble Fd with its PSI binding site. This model also predicts a sequential process of electron transfer, first to $NADP^+$ and then to the cyt b_6f complex.

New experiments presented here bring additional support to the models discussed above. In Fig. 3, a leaf has been infiltrated under low pressure with 2 mM methyl-viologen (MV). In the presence of an efficient PSI acceptor at such a large concentration, one expects that all electrons formed on the donor side of PSI are transferred to MV, thus preventing any electron transfer via the cyclic pathway. We thus assume that the photosynthetic process operates exclusively through the linear mode (black curves). The same leaf, but non-infiltrated, has been preilluminated for more than 10 min under green light (ki_{PSII} ~40 s^{-1}) and then dark-adapted for 2 min before illumination by a weak far-red light (red curves). After adjustment of intensity of the far-red light (see legend), similar kinetics of P_{700} and PC oxidation are observed in the presence or absence of MV. This experiment confirms on a quantitative basis that, in preilluminated leaves, the photosynthetic process operates exclusively in the linear mode.

Fig. 4A illustrates the large variability of the kinetics of P_{700} and PC oxidation when measured with different leaves of the same species. The photo-induced absorption changes measured at 810 nm mainly reflect P_{700} oxidation with a small contribution due to PC oxidation (see Fig. 1, curves 2 and 2'). In the leaf analyzed in Fig. 4A, curve 1, kinetics of P700 oxidation displays a fast phase of larger amplitude. Thus, it suggests a pool of $NADP^+$ much larger than that of PSI donors. In the case of the leaf analyzed in Fig. 4A, curve 3, most of PSI contributes to the cyclic electron flow, suggesting that the size of the $NADP^+$ pool is much smaller than in the leaf analyzed in curve 1. The analysis of the fluorescence induction curves (Fig. 4B) performed with the same dark-adapted leaves than those used in Fig. 4A provides support to this interpretation (note that wavelengths and intensities differ for Fig. 4A and B). Curves 1–3 display a plateau of different duration. Such a well-defined plateau is only observed when all the chloroplasts within the leaf are illuminated homogeneously. This condition is fulfilled when illuminating the upper face of the leaf under a green light that is weakly absorbed (F. Rappaport, D. Béal, A. Joliot and P. Joliot, unpublished results). We ascribe this plateau, which is not seen in broken chloroplasts or in mutants lacking cyt b_6f or

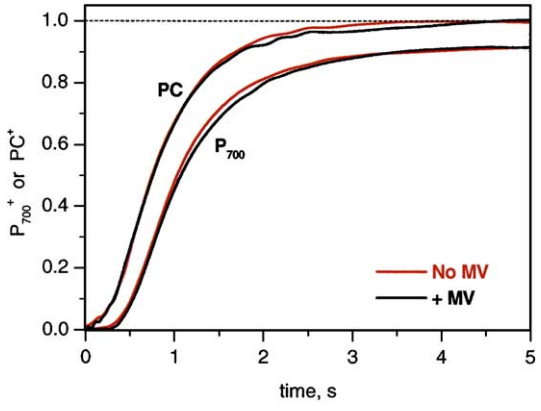

Fig. 3. Kinetics of P_{700} and PC oxidation under far-red illumination in the presence or absence of MV. Black curves: 150 mM sorbitol +2 mM MV. Sorbitol is added to avoid osmotic shock. Red curves: non-infiltrated leaf >10-min green light preillumination (ki_{PSII} ~13 s^{-1}) plus 2-min dark. Infiltration induces a decrease of far-red light scattering leading to a decrease in the optical path within the leaf. Thus, in order to obtain equal ki_{PSI} values, the intensity of far-red light is 1.3 times larger in the case of the infiltrated leaf.

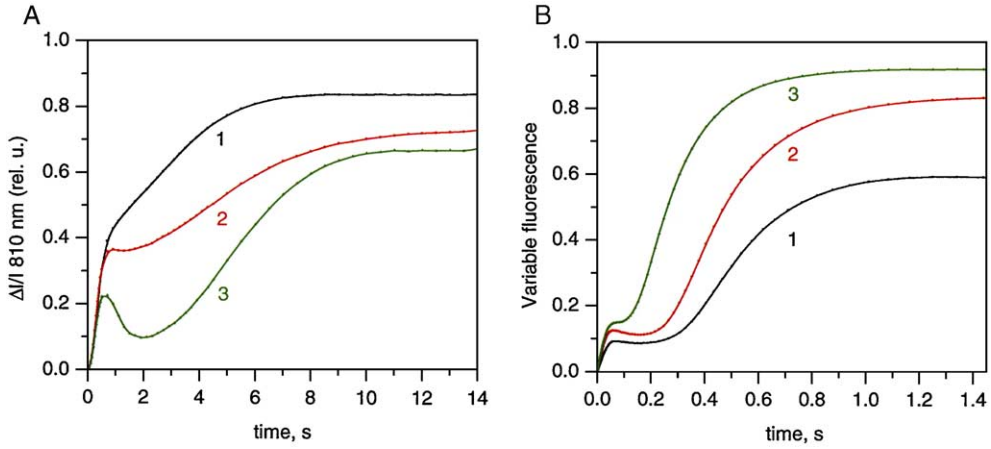

Fig. 4. (A) Absorption changes measured at 810 nm induced by far-red illumination of dark-adapted leaves. The experiments were performed with 3 leaves (curves 1–3). (B) Fluorescence induction curves measured with the same dark-adapted leaves as in Fig. 4A. Green-light excitation (ki_{PSII} ~40 s^{-1}). Curves 1–3 have been normalized to the same variable fluorescence F_v. Values of F_v/F_o are about equal for curves 1–3 (~4.5).

PSI centers, to the reduction of the soluble PSI acceptors Fd^+ and $NADP^+$ [4]. Thus, we assume that the changes in the duration of the plateau reflect the changes in the concentration of the soluble acceptor of higher mid-point potential, i.e., $NADP^+$. As proposed above, the comparison of Figs. 4A and B shows that the amplitude of the fast phase of P_{700} oxidation increases with the duration of the plateau and thus with $NADP^+$ concentration.

In Fig. 4B, the difference between the fluorescence yield reached after 1.5-s illumination and F_{max} (Q_A fully reduced) is proportional to the residual rate of the linear pathway. On the other hand, P_{700} still reduced after 10- to 14-s illumination is an increasing function of the efficiency of the cyclic pathway. Thus, comparison of Figs. 4A and B shows that lower the residual rate of the linear pathway (Fig. 4B), larger the rate of the cyclic pathway (Fig. 4A). This correlation fits our proposal that cyclic and linear pathways compete for the reoxidation of Fd.

In Fig. 5, we have determined the contribution of cyclic electron flow in condition that the Benson and Calvin cycle is fully activated, i.e., after a long period of illumination. The leaf has been submitted to 20-min green illumination of various intensities. After switching off the green light, kinetics of P_{700} oxidation induced by a weak far-red illumination is analyzed after 200-ms (curves 1, 3, 4 and 5) or 2-min dark-adaptation (curve 2). Kinetics of P_{700} oxidation displays lag phases of various duration (0.2–0.4 s), which reflect small differences in the concentration of PQH_2 at the time the far-red light is switched on. In Fig. 5, we defined time zero at the end of the lag phase and we assume that, at this time, PQH_2 is already oxidized by the far-red illumination. In curves 1–2, the leaf has been illuminated under weak light (ki_{PSII} ~20 s^{-1}). In condition of curve 2, we have shown (see Fig. 3) that the photosynthetic process operates exclusively in the linear mode. Curves 1 and 2 display similar time-course, which implies that, under an illumination largely below saturation, the contribution of the cyclic electron flow is negligible. In curve 3, the leaf has been preilluminated for more than 20-min at higher intensity (ki_{PSII} ~44 s^{-1}). The rate of P_{700} oxidation is slower than in curves 1–2, thus showing a significant contribution of cyclic flow. The rate of P_{700} oxidation induced by far-red light has been analyzed as a function of the time of dark adaptation following the green-light preillumination (not shown). The rate of P_{700} oxidation increases with the time of dark adaptation and reaches, after 2 min, a maximum value similar to that obtained after a preillumination of weaker intensity (Fig. 5, curves 1 and 2). This transition occurs with a half time of ~20 s. For longer time of dark-adaptation, the kinetics of P_{700} oxidation progressively slows down, showing a reverse transition from the linear to the cyclic mode [10]. The contribution of the cyclic flow has been estimated by measuring the half time of P_{700} oxidation, which is roughly proportional to the number of PSI turnovers that occur during the far-red illumination. In curve 2 (linear mode), the number of PSI turnovers is equal to the number of charges stored in PSI donors at time zero. In curve 3, involvement of the cyclic flow induces a slowdown of P_{700} oxidation. If t_2 and t_3 are the half

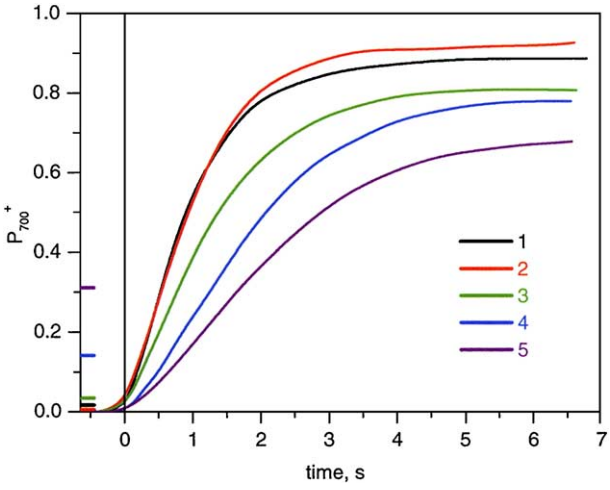

Fig. 5. Kinetics of P^+_{700} under far-red excitation measured with a leaf preilluminated for 20 min in green light. Intensity of preillumination: Curves 1–2, ki_{PSII} ~20 s^{-1}. Curve 3, ki_{PSII} ~44 s^{-1}. Curves 4–5, ki_{PSII} ~195 s^{-1}. Curves 1, 3–5, 200-ms dark before far-red excitation. Curve 2, 2-min dark before far-red excitation. Curves 1–4, air blown on the surface of the leaf. Curve 5, air with no CO_2 blown on the surface of the leaf.

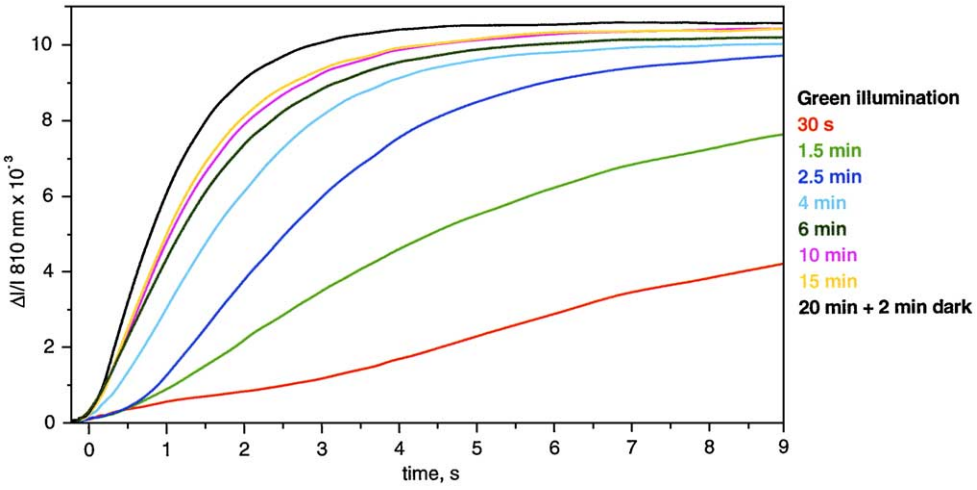

Fig. 6. Absorption changes at 810 nm induced by far-red illumination measured for different times of green-light illumination (ki_{PSII} ~44 s^{-1}). Steady-state is reached for ~15-min green-light illumination.

times for curves 2 and 3, respectively, the probability for Fd formed on the stromal side of PSI to be oxidized via the linear pathway is t_2/t_3 while its probability to be oxidized via the cyclic pathway is t_3-t_2/t_3. On this basis, we estimate that ~25% of the electrons formed on the stromal side of PSI are transferred to the cyt b_6f complex (cyclic process) and ~75% to FNR (linear process). In curve 4, the leaf has been illuminated by green light close to saturation (ki_{PSII} ~195 s^{-1}). In this condition, we estimate that ~50% of Fd is oxidized via the cyt b_6f complex (cyclic process). In curve 5, air with no CO_2 is blown at the surface of the leaf. Lack of CO_2 induces an increase in the contribution of cyclic flow in PSI turnover (~63%), in agreement with previous conclusions of Heber et al. [15]. As expected, the minimum concentration of reduced (active) P_{700} reached after a few seconds of illumination is an increasing function of the efficiency of the cyclic flow. We thus conclude that, in steady-state conditions of illumination, the contribution of cyclic flow to PSI turnover is an increasing function of the light intensity.

In Fig. 6, a dark-adapted leaf has been submitted to 20-min green-light illumination (ki_{PSII} ~44 s^{-1}). During the course of illumination, the green light is switched off for 8 periods of 10 s, during which kinetics of P_{700} oxidation induced by a far-red excitation are analyzed as a function of the time of green light. The curve in black displays the kinetics of P_{700} oxidation after 2-min dark following 20-min green illumination, i.e., in condition that the photosynthetic process operates exclusively through the linear mode. In Fig. 7 (curve in green), the efficiency of the cyclic flow, estimated from Fig. 6, has been plotted as a function of the time of the green illumination. The linear flow has been estimated from the measure of the time course of the fluorescence yield F induced during the green illumination of the same dark-adapted leaf as in Fig. 6. After various periods of illumination, the leaf is submitted to pulses of saturating light (150-ms duration) in order to determine the maximum fluorescence yield (F'_{max}) (not shown). The rate of PSII reaction (R_{PSII}), which is equal to the rate of the linear flow, is computed

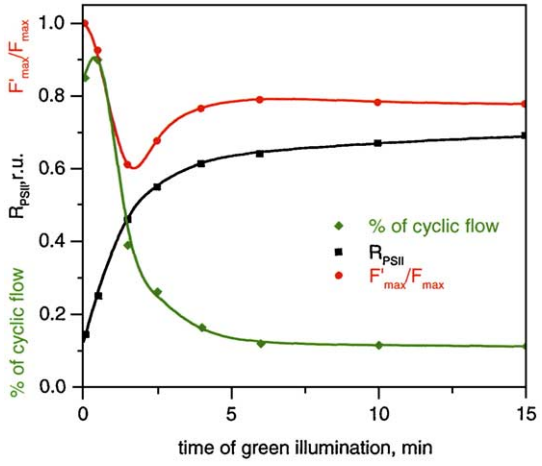

Fig. 7. Efficiency of the cyclic flow, R_{PSII} and F'_{max}/F_{max} as a function of the time of green-light illumination (ki_{PSII} ~44 s^{-1}). Same illumination and same leaf fragment as in Fig. 6.

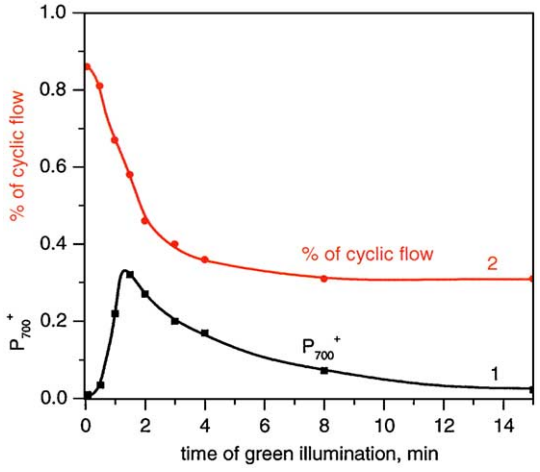

Fig. 8. Concentration of P^+_{700} and efficiency of the cyclic electron flow as a function of the time of green-light illumination (ki_{PSII} ~100 s^{-1}). P^+_{700} concentration has been normalized to the total P_{700} concentration.

according to Genty formula [16]: $R_{PSII}=(F-F'_{max})/F_{max}$, (black curve), in which F_{max} is the maximum fluorescence yield in the absence of the non-photochemical quenching (NPQ). F'_{max}/F_{max} gives a qualitative estimate of the efficiency of NPQ (red curve). The cyclic flow operates at high rate during the first minute of illumination, owing to the reduction of the pool of PSI acceptors induced by the partial inactivation of the Benson and Calvin cycle. A decrease in the rate of the cyclic flow occurs in the same time range than the increase in the rate of the linear flow.

In Fig. 8, a dark-adapted leaf has been submitted to 20-min green-light illumination (ki_{PSII} ~100 s^{-1}) and the concentration of P^+_{700} is plotted as a function of the time of illumination (curve 1). A partial oxidation of P_{700} (P^+_{700} ~0.35) observed during the firsts min of illumination is followed by a decrease in P^+_{700} concentration completed in ~15 min. Such an increase in P^+_{700} concentration observed during the firsts min of illumination has been previously reported by Harbinson and Hedley [17]. In the same way, the concentration of P^+_{700} is larger in the absence than in the presence of CO_2 (Fig. 5, curves 4–5). Thus, the inactivation of the Benson and Calvin cycle induced by a lack of CO_2 is associated with an increase rather than a decrease in P^+_{700} concentration, as previously shown in [18]. If the photosynthetic chain were operating through the linear mode, the inactivation of the Benson and Calvin cycle during the first minutes of illumination or in the absence of CO_2 would induce a partial reduction of all carriers uphill from NADP, including P_{700}, contrary to the observed results.

3. Conclusion

In this paper, we suggest that the relative efficiency of linear and cyclic flows depends upon the rate of electron transfer, from Fd to $NADP^+$ via FNR. ATP concentration is one of the parameters that control the rate of electron flow through the Benson and Calvin cycle. We assume that in dark-adapted leaves, the Benson and Calvin cycle is partially inactivated, owing to low ATP concentrations. The efficient cyclic process that occurs during the firsts min of illumination leads to an increase in ATP concentration and thus, to an activation of the linear flow and a slowdown of the cyclic flow. One thus expects that cyclic electron flow induces the formation of large proton gradient in equilibrium with a large ATP/ADP ratio while, owing to the partial inactivation of the Benson and Calvin cycle, ATP consumption remains low. Increase of the pH in the lumenal compartment will induce a slowdown of the pH-dependent process of PQH_2 oxidation at the Q_o-site that leads to a partial P_{700} oxidation (Fig. 8). Golding and Johnson [18] previously suggested that, in condition that carbon fixation is inhibited (drought or CO_2 limitation), the formation of a large pH gradient by cyclic electron flow leads to a down-regulation of the linear flow via the development of NPQ and a partial oxidation of P_{700}. During the course of illumination, the activation of the Benson and Calvin, correlated with a decrease in the efficiency of the cyclic flow and thus with a decrease in the proton gradient, induces the reduction of P^+_{700}. As shown in Fig. 8, P^+_{700} reduction occurs in a longer time-range than the inactivation of the cyclic flow. This difference in time course can be related to the delay required to consume ATP that accumulates during the firsts min of illumination in the stromal compartment. Removal of CO_2 that inhibits linear flow and stimulates cyclic flow also induces the formation of a large proton gradient and P_{700} oxidation (Fig. 5, curve 5). Heber and Walker [19] proposed that the NPQ increase observed during the firsts min of illumination is associated with the formation of a proton gradient induced by cyclic electron flow. In agreement with this proposal, we assume that the initial NPQ increase (Fig. 7) is a consequence of the large pH gradient induced by the cyclic flow while the subsequent decrease is associated with the transition from cyclic to linear flow that partially collapses the pH gradient.

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References

[1] D.I. Arnon, F.R. Whatley, M.B. Allen, Vitamin K as a cofactor of photosynthetic phosphorylation, Biochim. Biophys. Acta 16 (1955) 607–608.
[2] K. Tagawa, H.Y. Tsujimoto, D.I. Arnon, Role of chloroplast ferredoxin in the energy conversion process of photosynthesis, Proc. Natl. Acad. Sci. U. S. A. 49 (1963) 567–572.
[3] G. Finazzi, A. Furia, R.P. Barbagallo, G. Forti, State transitions, cyclic and linear electron transport and photophosphorylation in *Chlamydomonas reinhardtii*, Biochim. Biophys. Acta 1413 (1999) 117–129.
[4] P. Joliot, A. Joliot, Cyclic electron transfer in plant leaf, Proc. Natl. Acad. Sci. U. S. A. 99 (2002) 10209–10214.
[5] P. Joliot, D. Beal, A. Joliot, Cyclic electron flow under saturating excitation of dark-adapted Arabidopsis leaves, Biochim. Biophys. Acta 1656 (2004) 166–176.
[6] L.A. Sazanov, P. Burrows, P.J. Nixon, Photosynthesis: from Light to Biosphere, in: P. Mathis (Ed.), Xth Int. Cong. on Photosynthesis, Vol. 2, Kluwer Academic Publishers, Montpellier, France, 1995, pp. 705–708.
[7] G. Kurisu, H.M. Zhang, J.L. Smith, W.A. Cramer, Structure of the cytochrome b_6f complex of oxygenic photosynthesis: tuning the cavity, Science 302 (2003) 1009–1014.
[8] D. Stroebel, Y. Choquet, J.-L. Popot, D. Picot, An atypical haem in the cytochrome b_6f complex, Nature 426 (2003) 413–418.
[9] H.M. Zhang, J.P. Whitelegge, W.A. Cramer, Ferredoxin:NADP(+) oxidoreductase is a subunit of the chloroplast cytochrome b(6)f complex, J. Biol. Chem. 276 (2001) 38159–38165.
[10] P. Joliot, A. Joliot, Quantification of cyclic and linear flows in plants, Proc. Natl. Acad. Sci. U. S. A. 102 (2005) 4913–4918.
[11] R. Wagner, N. Carillo, W. Junge, R.H. Vallejos, On the conformation of reconstituted Ferredoxin:NADP+ oxidoreductase in the thylakoid membrane. Studies via triplet lifetime and rotational diffusion with eosin isothiocyanate as label, Biochim. Biophys. Acta 680 (1982) 317–330.
[12] B. Andersen, H.V. Scheller, B.L. Moller, The PSI-E subunit of photosystem I binds ferredoxin:NADP+ oxidoreductase, FEBS Lett. 311 (1992) 169–173.
[13] J.J. van Thor, T.H. Geerlings, H.P. Matthijs, K.J. Hellingwerf, Kinetic evidence for the PsaE-dependent transient ternary complex photosystem I/Ferredoxin/Ferredoxin:NADP(+) reductase in a cyanobacterium, Biochemistry 38 (1999) 12735–12746.
[14] H. Naver, N. Scott, B. Andersen, B. Moller, H. Scheller, Reconstitution of barley photosystem-I reveals that the N-terminus of the PSI-D subunit is essential for tight-binding of PSI-C, Physiol. Plant. 95 (1995) 19–26.
[15] U. Heber, U. Gerst, A. Krieger, S. Neimanis, Y. Kobayashi, Coupled cyclic electron transport in intact chloroplasts and leaves of C3 plants: does it exist? If so, what is its function? Photosynth. Res. 46 (1995) 269–275.
[16] B. Genty, J.-M. Briantais, N.R. Baker, The relationship between the

quantum yield of photosynthetic electron transport and quenching of chlorophyll fluorescence, Biochim. Biophys. Acta 990 (1989) 87–92.
[17] J. Harbinson, C.L. Hedley, Changes in P-700 oxidation during the early stages of the induction of photosynthesis, Plant. Physiol. 103 (1993) 649–660.
[18] A.J. Golding, G.N. Johnson, Down-regulation of linear and activation of cyclic electron transport during drought, Planta 218 (2003) 107–114.
[19] U. Heber, D. Walker, Concerning a dual function of coupled cyclic electron-transport in leaves, Plant. Physiol. 100 (1992) 1621–1626.