PHOTOSYNTHETICA
International Journal for Photosynthesis Research

DOI 10.32615/ps.2025.024 PHOTOSYNTHETICA 63 (3): 267-281, 2025

HISTORY & BIOGRAPHY

In honor of Reto Jörg Strasser: A pioneer of chlorophyll *a* fluorescence research

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Abstract

Chlorophyll (Chl) *a* fluorescence measurements are widely used in the study of photosynthesis, and Reto Strasser is a well-known pioneer in this domain. In 2019, the current authors, together with Vineet Soni, and Neera Bhalla Sarin, celebrated his 75th birthday. Here, we pay tribute to him on his 82nd birthday through a brief description of the key results we had obtained with him, over the years, on the understanding and exploitation of the OJIP Chl *a* fluorescence transient. The topics of these studies have been quite diverse, from the oxygen clock, the bicarbonate effect in Photosystem II, the adaptability of plants to various stress factors, to mathematical modeling of the OJIP phase, but all based on the application of Chl *a* fluorescence for the understanding of oxygenic photosynthesis. Additionally, we have included here a list of the authors who have honored Reto Strasser in *Photosynthetica* in 2020, along with references of their papers.

Keywords: adaptability of plants to stress; bicarbonate effect in Photosystem II; Chl *a* fluorescence induction; the JIP-test; modeling the Chl *a* fluorescence rise OJIP; oxygenic photosynthesis.

Prelude

Five years ago, Kalaji and Goltsev (2020) grandly honored Reto Jörg Strasser in a special issue of *Photosynthetica*, featuring ~ 50 papers by ~ 200 authors from ~ 30 countries (*see* Appendices 1 and 2). This was just after 2019, when Reto was honored in Indore (India) at his 75th birthday; *see* Govindjee *et al*. (2019), where the authors discussed Reto's research and presented many of his photographs with those who had gathered at that conference. Here, we are honoring Reto Strasser, at his upcoming 82nd birthday, with a brief overview of what we have published with him, in three different sections, first with Govindjee, then with Sandra Stirbet, and lastly with Alaka Srivastava, and each chronologically, all dealing with the basics and the applications of chlorophyll *a* fluorescence in understanding different aspects of oxygenic photosynthesis. In addition, Reto Strasser has published with a large number of collaborators – not included here (*see e.g.*, https://www.researchgate.net/profile/Reto-Strasser; https://scispace.com/authors/reto-j-strasser-30pnc43kg1). We have also included a few photographs – all provided by Ronald Maldonado Rodriguez, who has also been associated with Reto for a long time.

Chlorophyll *a* fluorescence transient: the OJIP curve and what it means

When dark-adapted cells of cyanobacteria and algae or leaves of plants are exposed to high-intensity light, chlorophyll (Chl) *a* fluorescence begins at the "O" level at time "zero", and increases rapidly (within 1 s) to a "peak" (P), *via* two intermediate levels J and I (*see e.g.*, Govindjee 1995); then, this fluorescence declines to a terminal level T with two intermediate levels S and M; further, all these events are related to the activities of PSII and PSI

Highlights

- This paper honors Reto Strasser's work on Chl *a* fluorescence at his 82nd birthday
- Govindjee, A. Stirbet, and A. Srivastava present their research with Reto Strasser
- Included are lists of papers and names of scientists who honored Reto Strasser in 2020

Received 21 July 2025
Accepted 28 July 2025
Published online 7 August 2025

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Conflict of interest: The authors declare that they have no conflict of interest.

Fig. 1. *Left to right*: A 1998 photograph of Paulette Kummer, Reto Strasser, Alexandrina (Sandra) Stirbet, Marie-France Blanche, and Alaka Srivastava. Source: Ronald M. Rodriguez.

(*see e.g.*, Papageorgiou *et al*. 2007, Stirbet and Govindjee 2011, Bernát *et al.* 2018), and ultimately to photosynthesis performance – an area of research in which Reto Strasser is the World authority. Here, we honor him, personally, by summarizing below the work that we did with him during the early 1990s up to 2015 – mainly on the relation of the OJIP Chl *a* fluorescence transient curve to oxygenic photosynthesis.

Fig. 1 shows a photograph of Reto Strasser with a few others in his research group, including two of us (Stirbet and Srivastava) outside the Bioenergetics laboratory of the University of Geneva, in Jussy-Lullier, Switzerland.

A. Reto Strasser's research – with Govindjee

During 1991–1992

Govindjee's research interest had been in understanding where the "bicarbonate" ion functions in the "light reactions" of photosynthesis. His data had suggested that it functions on the electron acceptor side of PSII (*see e.g.*, a recent perspective: Vinyard and Govindjee 2024), most likely by binding to the D1 protein. Reto Strasser has been an authority for measuring Chl *a* fluorescence transient (the OJIP phase), and Jean David Rochaix (in Geneva) was (and is) an authority on the D1 mutants. Thus, Reto and Govindjee collaborated with Jean David Rochaix using many different D1 mutants available in Rochaix's laboratory. Based on their first observations (Govindjee *et al.* 1991), herbicide-resistant mutants of the eukaryotic green alga *Chlamydomonas reinhardtii* (altered in specific amino acids in the D1 protein) showed a differential bicarbonate-reversible formate effect (with formate displacing bicarbonate), and thus, showing a clear involvement of the D1 protein in the "bicarbonate" effect. Further, data on the BR-202 (L275F) mutant suggested that a significant change in bicarbonate binding must have occurred in helix V of the D1 protein near histidine, which is involved in Fe binding – thus, providing a clear idea that one of the major sites of bicarbonate binding is on D1 in PSII. Lastly, the absence of the formate effect on a PSII-lacking mutant (FuD-7) confirmed the sole involvement of PSII in the "bicarbonate effect". Then, Govindjee *et al*. (1992) analyzed the Chl *a* fluorescence decay to study the electron transfer between the two plastoquinones of PSII, Q_A and Q_B, using several herbicide-resistant mutants of *Chlamydomonas reinhardtii.* The electron transfer from Q_A^- to Q_B in some of the D1 mutants was very little affected compared to the control, but in other mutants, the forward electron transfer was altered, showing that the Q_B-pocket was significantly modified by the mutation. The conclusion was that the amino acid S264 has an important role in the binding and the function of both plastoquinone and bicarbonate in PSII. Additionally, after formate treatment, the lifetime of the forward electron transfer in the Q_AQ_B region increased in the wild type and five of the mutants used, but the apparent equilibrium of the reaction $Q_A^-Q_B \leftrightharpoons Q_AQ_B^-$ decreased, while the addition of bicarbonate reversed all these effects.

Govindjee's next two publications with Reto Strasser were presented at two different international conferences. Strasser and Govindjee (1991) showed their new data on the Chl *a* fluorescence transient, the OJIPT curves, from both algae and higher plants at a NATO workshop, held 28 July–3 August 1991, in Crete, Greece. Here, Chl *a* fluorescence transients, under different excitation light intensities, were presented with the "O" level at 20 microseconds, the "J" level at 2 milliseconds, the "I" level at 30 milliseconds, and the "P" level at 200 to 500 milliseconds under saturating red light from 500 to 600 W m^{-2}; we note that the ratio of the "P" to the "O" levels was ~ 5, reflecting a very high quantum yield of photosynthesis. Then, Strasser and Govindjee (1992) obtained new data on the OJIPT curves from the D1 mutants of the green alga *Chlamydomonas reinhardtii* and compared them with those from the thylakoids from the leaves of *Pisum sativum*, and these results were presented at the IXth International Congress on Photosynthesis, in Nagoya, Japan, held during 30 August–4 September 1992. Here, intact cells of several herbicide-resistant mutants of *Chlamydomonas reinhardtii*, altered in single amino acids in the D1 protein, were used. The D1 mutants Ar-207 (F255Y), Br-202 (L275F), and Dr-18 (V2191) had normal, unchanged OJIP transient, and they all

had an unchanged (0.8–0.9) ratio of the fast to the slow PSII centers, compared to that from the wild type. Thus, the Q_A/Q_B binding pocket(s) were minimally modified. However, analysis of Chl *a* fluorescence data on the Ar-204 (G256D) and DCMU-4 (S264A) mutants led Strasser and Govindjee to conclude that these mutants had altered forward electron transfer rates, as well as an abnormally high ratio (0.6–0.8) of the slow to the fast PSII centers. Furthermore, removal of bicarbonate, by the addition of formate, led to an increase in the lifetime of the forward (Q_A^- to Q_B) electron transfer in the wild type, as well as in the five mutants (used in their study), with the largest change in the S264A, and the smallest in the L275F mutant. Importantly, all these effects were reversed by 20 mM bicarbonate. Further, Strasser and Govindjee (1992) suggested that the amino acid S264, but not L275, F255, and V219, plays an important role in the binding and the function of plastoquinone and bicarbonate in PSII. These results have had a clear impact on our understanding of the function of bicarbonate in PSII (*see e.g.*, Shevela *et al*. 2012).

In 1995

Since Govindjee had a great time working with Reto Strasser, he returned to his Laboratory in late 1994. During this time, he was fortunate to collaborate with Alaka Srivastava (also *see* section C), who had come from India to work in Strasser's Lab. They had a very productive time deciphering and understanding the polyphasic Chl *a* fluorescence transient, the so-called OJIPSMT curve. Strasser *et al*. (1995) measured and presented, for the first time, on a logarithmic time scale, the complete polyphasic Chl *a* fluorescence rise from the leaves of a variety of oxygenic plants (including *Pisum sativum* and *Camellia japonica*) and cell suspensions of cyanobacteria (*e.g.*, *Anabaena* P9, *Planktothrix rubescens*, and *Limnothrix redekei*) at different light intensities. In this research, Strasser *et al*. (1995) established that the O–J phase, of Chl *a* fluorescence transient, is the photochemical phase, involving the reduction of Q_A to Q_A^-, whereas the intermediate level I is related to a heterogeneity in the filling up of the plastoquinone (PQ) pool, while the P level is reached when all the PQ molecules are reduced to PQH_2. Further, it was established here that the addition of the herbicide 3-(3,4-dichlorophenyl)-1,l-dimethylurea (DCMU) leads to a transformation of the O–J–I–P rise into O–J rise, J being the P level. Almost in parallel, Srivastava *et al*. (1995a) focused on similar research on the green alga *Chlamydomonas reinhardtii*, and Srivastava *et al*. (1995b) on the thylakoids from spinach (*Spinacea oleracea*).

Fig. 2 shows a photograph of Alaka Srivastava in Reto Strasser's Bioenergetics laboratory in Switzerland. (For further research by Alaka in Strasser's Lab., *see* section C.)

In the paper by Srivastava *et al*. (1995a), the complete Chl *a* fluorescence transient curves are presented from *Chlamydomonas* and its many herbicide-resistant D1 mutants (V219I, A251V, F255Y, S264A, G256D, and L275F), as well as from a cell-wall-less mutant, CW-15.

Fig. 2. A 2000 photo of Alaka Srivastava (sitting) in Reto Strasser's laboratory in Switzerland; the person standing is Sophie Susplugas, who was then a student of Reto Strasser. Source: Ronald M. Rodriguez.

Clear differences were observed among the mutants in the kinetics of the filling up of the electron acceptor pool of PSII, but not in the ratio of the "P" level to the "O" level, which was about 4.4. However, at 600 W m^{-2} of 650 nm excitation light, there was a distinct hierarchy in the fraction of variable Chl *a* fluorescence at the J level in the different mutants: S264A > A251V ~ G256D > L275F ~ V219I > F255Y ~ CW-15 ~ WT. Further, at 60 and 300 W m^{-2} of 650 nm excitation, a somewhat similar hierarchy among the mutants was observed for both the J and the I levels. From Govindjee's interest, the addition of bicarbonate-reversible inhibitor formate did not change the O–J phase, but slowed the I–P rise, and in many cases, slowed the fluorescence decay from the P level to the T level. These observations were interpreted to imply that bicarbonate certainly works on the electron acceptor side of PSII; however, this effect was different in different mutants, with L275F being the most insensitive mutant!

Further, in spinach thylakoids, Srivastava *et al*. (1995b) made the following new observations concerning changes in the ratio of active to inactive PSII reaction centers. By systematically re-investigating this phenomenon – using different concentrations of dimethyl-quinone (DMQ) and dichloro-benzoquinone (DCBQ) – in spinach thylakoids under different light intensities, it was shown that the DCBQ causes a larger decrease in the variable Chl *a* fluorescence than the DMQ, confirming the results of Lavergne and Leci (1993), and thus sustaining the conclusion that the effects of DMQ and DCBQ on Chl *a* fluorescence cannot be used to distinguish between the active and the inactive PSII centers. Further, the data obtained by Srivastava *et al*. (1995b) confirmed that the rate of O_2 evolution is higher in the DCBQ-supported Hill reaction than in the DMQ-supported one. These results were explained by a more efficient ability of DCBQ to oxidize the plastoquinone pool, rather than activating

the inactive PSII centers. However, all of the above did not imply that "inactive PSIIs" do not exist.

During 1998–1999

Alaka Srivastava continued working with Reto and Govindjee during 1998–1999. Govindjee *et al.* (1998) presented their findings on the "oxygen clock" as it "forms" or "evolves" during the greening of pea leaves – starting from the "etiolated" condition. This was followed by a detailed paper by Srivastava *et al.* (1999a), also on greening peas, where parallel measurements were made on 77K emission spectra, OJIP fluorescence transients (*see* Fig. 3), and period 4 oscillations of the "O" level, of delayed light emission (DLE), and of changes in PSI (through P700* measurements).

Quantitative analysis of Chl *a* fluorescence data led Srivastava *et al.* (1999a) to the following conclusions: (*1*) the intermittent irradiation (IMI) grown plants, but not those grown in flashing light (FL), have almost fully developed reaction centers, as well as fully functional oxygen clock; (*2*) greening of IMI plants, under continuous illumination (CI), involves two phases: (a) during 3–4 h of CI, both the number of PSII units and the connectivity between them increase, and only then (b) the amount of light-harvesting antenna increase; (*3*) under FL, 10 min CI activates fully the "oxygen clock" functioning on the electron donor side of PSII.

During the late 1990s, Alexandrina (Sandra) Stirbet joined Reto and Govindjee and began asking questions about the molecular models involved in the photosynthetic processes and their regulation (Stirbet *et al.* 1998a). [This research by Stirbet continued even in 2024 (*see e.g.*, Stirbet *et al.* 2024)]. In Stirbet *et al.* (1998a), the experimental Chl *a* fluorescence transients, measured on dark-adapted plants illuminated with saturating light, were simulated through numerical integration using a theoretical model; here, the authors considered, for the first time, the redox reactions at both the electron acceptor and the electron donor sides of PSII, as well as the nonphotochemical quenching (NPQ) of Chl *a* fluorescence by the oxidized plastoquinone molecules – present in the lipid matrix of the thylakoid membrane. During this research, it was indeed possible to simulate the entire OJIP phase, including the "dip" (D) between "I" and "P", that had been discovered long ago by Munday and Govindjee (1969).

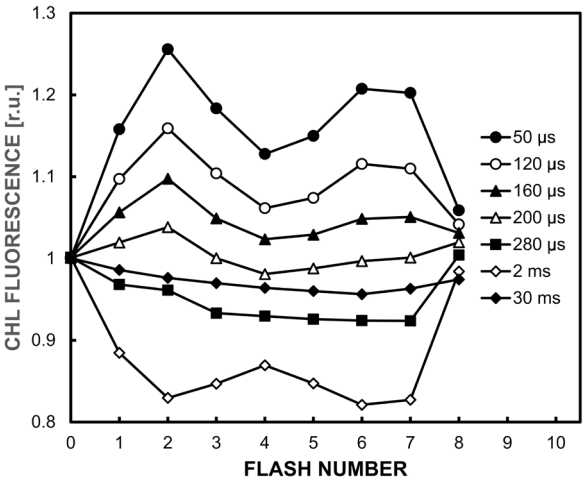

Fig. 3. Chlorophyll *a* fluorescence intensity of green pea leaves at specific time intervals of the OJIP-rise, as a function of the number of saturating pre-flashes. The leaves were dark-adapted for 10 min before the onset of the actinic irradiation. Modified from the original figure in Srivastava *et al.* (1999a).

During 2001–2003

It was in Strasser *et al.* (2001) that the major goal of simultaneously measuring PSI (*via* P700) and of PSII (*via* Chl *a* fluorescence) in sub-ms to second time range was attempted and presented. This was fully quantified and analyzed soon thereafter by Schansker *et al.* (2003) (*see* Fig. 4), and it was shown that 820 nm absorption changes, in *Pisum sativum* and *Camelia* sp., measure both P700 and plastocyanin, in about 1:1 ratio. Thus, additional measurements and analysis are needed to separate the two (*see e.g.*, Schreiber and Klughammer 2016).

During 2010–2012

During this period, collaborative research of Strasser and Govindjee was extended to include work not only in India

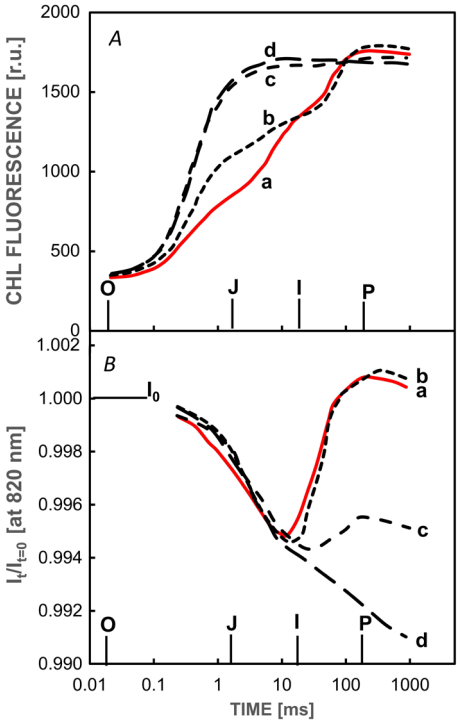

Fig. 4. Effect of DCMU [3-(3,4-dichlorophenyl)-1,1'-dimethyl urea] on the induction curves of chlorophyll *a* fluorescence (*A*) and the transmission at 820 nm (*B*) measured simultaneously. The leaves were dark-adapted for 60 min before the measurements. Pea leaves were treated by submerging them for 0 (a), 15 (b), 30 (c), or 60 (d) min in a solution of 100 µM DCMU. The level I_0 is the transmission level just before the measurement. Modified from the original figure in Schansker *et al.* (2003).

(Yusuf *et al*. 2010), but in China (Chen *et al*. 2012, 2013), as well as in Eastern Europe (Kalaji *et al*. 2012).

Yusuf *et al*. (2010), working in the laboratory of Neera Bhalla Sarin at Jawaharlal Nehru University (JNU) in New Delhi, India, discovered that the overexpression of gamma-tocopherol methyl transferase gene in transgenic *Brassica juncea* plants causes alleviation of various types of abiotic stress, a remarkable achievement. (We note that tocopherols, *e.g*., vitamin E, are indeed lipid-soluble antioxidants synthesized by plants and some cyanobacteria.) Further, Yusuf *et al*. (2010) found that in *Brassica juncea*, not only salt, but heavy metals and osmotic stress induce an increase in the total tocopherol contents. Measurements of seed germination, shoot growth, and leaf disc senescence showed that transgenic *Brassica juncea* plants overexpressing a specific gene have enhanced tolerance to the induced stresses. Further, in the same research, it was clearly and dramatically shown that α-tocopherol really plays an important role in the alleviation of stress induced not only by salt, but by heavy metals in *Brassica juncea*.

During a visit of Reto Strasser to China, together with one of us (Govindjee), it was shown (*cf*. Chen *et al*. 2012) that reactive oxygen from chloroplasts contributes to 3-acetyl-5-isopropyltetramic acid (*see* Fig. 5) induced leaf necrosis in *Arabidopsis thaliana.* All the researchers had great fun doing the experiments that led to the above conclusion. Further, Chen *et al*. (2013) showed that tenuazonic acid inhibits electron flow by binding to the Q_B site of PSII – just as diuron (DCMU) does!

In addition to all of the above, and collaboration with Hazem Kalaji (of Poland), Vasilij Goltsev (of Bulgaria), and Suleyman Allakhverdiev (of Russia), Reto Strasser, and Govindjee (*see* Kalaji *et al*. 2012) contributed to a major review on all the experimental *in vivo* light emission measurements that provided key information on their usefulness in understanding the function and the regulation of the overall photosynthetic process. We note that this review was dedicated to David Alan Walker (1928–2014), one of the top scientists of the century (for Walker, *see* Edwards and Heber 2012).

During 2014–2015

It was for quite a few years that Reto Strasser and Govindjee did not publish any joint research paper, although they had continued to be in contact with each other, first through e-mail and then by telephone. However, they were coauthors in Kalaji *et al*. (2014a), which essentially dealt with the same topic as Kalaji *et al*. (2012), mentioned above. Govindjee's last research paper with Reto Strasser, done in Paradha-Saradhi's research group at the University of Delhi in New Delhi, India, is by Shabnam *et al*. (2015); for Govindjee, this paper was and is great fun, since it dealt with an area that was new to him – mitochondrial electron transport! Here, investigations were carried out to unravel the mechanism(s) for the higher tolerance of floating over submerged leaves of long-leaf pondweed (*Potamogeton nodosus* Poir) against photoinhibition. Chloroplasts from the floating leaves showed 5- and 6.4-fold higher PSI and

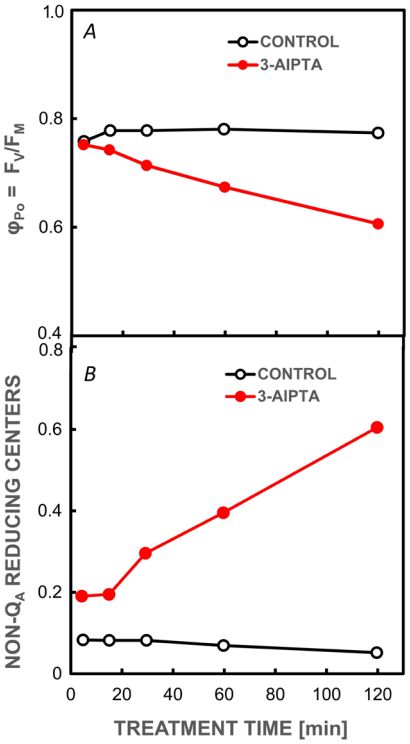

Fig. 5. Changes, with time, of two parameters of the photosynthetic machinery in epidermis-less leaf segments of *Arabidopsis thaliana* during treatment with water (CONTROL) or with 500 mM 3-acetyl-5-isopropyltetramic acid (3-AIPTA). (*A*) The maximum yield of primary photochemistry in PSII (φ_{Po}); (*B*) relative concentration of the non-Q_A reducing centers. Modified from the original figure in Chen *et al*. (2012).

PSII activities over those from the submerged leaves. We note that the floating leaves, as compared to the submerged leaves, showed higher F_v/F_m (variable to maximum chlorophyll fluorescence, a reflection of PSII efficiency), as well as a higher potential to withstand photoinhibitory damage by high light. Cells of floating leaves had not only a higher mitochondria to chloroplast ratio but also showed many mitochondria in close vicinity of chloroplasts. These data revealed the presence of alternative oxidase in mitochondria of floating, but not of submerged, leaves. Lastly, these experimental results established that floating leaves possess better photosynthetic efficiency and capacity to withstand photoinhibition compared to the submerged leaves; and that mitochondria play a pivotal role in protecting photosynthetic machinery of floating leaves against photoinhibition.

B. Reto Strasser's research – with Alexandrina (Sandra) Stirbet

During 1995–1996

In 1994, one of us (Sandra Stirbet) joined Reto Strasser's Lab in Switzerland from Romania and met him for the first time on a so-called "open day" of the University of Geneva. Dr. Strasser was very friendly, and since Sandra had her PhD in Biophysics, related to photosynthesis,

he invited her to work in his laboratory as a visiting scientist. Strasser proposed that she collaborate with him on "the mathematical modeling of the OJIP fluorescence transient", which Sandra Stirbet gladly accepted. Reto Strasser already had a publication on this topic with Ellen Baake, which was already presented at the 8th International Congress on Photosynthesis in Stockholm, Sweden (*see* Baake and Strasser 1990), and was very interested in continuing this line of work. Stirbet and Strasser (1995a) published their first modeling results in *Archives de Science Genève*. An improved version of this work was soon presented at the First International Symposium on Mathematical Modelling and Simulation in Agriculture and Bio-Industries (*see* Stirbet and Strasser 1995b), which was published, soon thereafter, in a refereed journal (Stirbet and Strasser 1996). In these studies, they considered the PSII charge stabilization and the steps involved in the two-electron-gate process on the (electron) acceptor side of PSII, at the "core" of two different models – presented in parallel. In the first model (called the "individual model"), the two plastoquinones of PSII, Q_A and Q_B, were considered as individual entities, while in the second model (called the "complex model"), Stirbet and Strasser took into consideration that Q_A and Q_B are in a 1:1 stoichiometry in most of the PSII reaction center complexes. The theoretical value of the variable Chl *a* fluorescence intensity at any time was considered to be dependent on the concentration of Q_A^-, since the oxidized Q_A was shown to be a quencher of the PSII fluorescence (*see* Duysens and Sweers 1963; and a review by Stirbet and Govindjee 2012). The dynamic data for both models were obtained with the simulation software *Gepasi* (Mendes 1993). As input parameters, Stirbet and Strasser (1996) used the initial concentrations of reactants and the rate constants of the redox reactions, as reported in the literature. However, to delay the reduction of the PQ pool, they introduced an additional reaction, in which PSII centers with Q_B^- are also reoxidized by another possible mechanism. The OJIP transients of Chl *a* fluorescence were simulated assuming different numbers of plastoquinone (PQ) molecules in the PQ pool, as well as by considering several experimental conditions: (*1*) variation of light intensity; (*2*) DCMU treatment; and (*3*) re-exposure of samples illuminated for 1 s after defined short periods of darkness. The theoretical curves obtained with these two models showed remarkable similarities with the experimental data. The variable Chl *a* fluorescence was shown to be mostly due to the gradual accumulation of Q_A^-. In later work (*see* below), Stirbet and Strasser used only models in which Q_A and Q_B interacted stoichiometrically (*i.e.*, the "complex model") for the simulation of the OJIP transient, but without the hypothetical Q_B^- reoxidation reaction. However, we note that later, Zhu *et al*. (2005) and Guo and Tan (2011) have used the "individual model" for the simulation of the OJIP fluorescence curve. Moreover, the Q_B^- reoxidation has also been suggested to be involved by others (*see e.g.*, Ananyev *et al*. 2016, and Zournas *et al*. 2023), who have suggested partitioning between the linear and the cyclic electron flow around PSII, as a way to control the quantum yield of oxygen evolution.

Further, in 1995, Stirbet with Strasser presented a still newer model of the fast Chl *a* fluorescence induction at the Xth International Photosynthesis Congress in Montpellier, France, 20–25 August 1995 (Stirbet *et al*. 1995). Compared to Stirbet and Strasser (1995a,b), here, they had additionally assumed that: (i) the rate of Q_A reduction is higher in the S_0 and S_1 than in S_2 and S_3 states of the oxygen-evolving complex of PSII; (ii) the connectivity between the PSII units influences the OJIP Chl *a* fluorescence rise; and (iii) the oxidized PQ molecules in the PQ pool are quenchers of Chl *a* fluorescence. These simulations showed, *e.g.*, that the dip D after the I step in the fluorescence transient (*see* Munday and Govindjee 1969) becomes deeper as the rate constant of PQ pool oxidation increases (*i.e.*, the PSI activity is enhanced). Since this model was updated by Stirbet *et al*. (1998a), we present further results of these simulations below.

During 1997–2001

The next modeling study, by Stirbet and Strasser, was first presented at the 2nd International Symposium on "Mathematical Modelling and Simulation in Agriculture and Bio-Industries" (M2SABI'97) in Budapest, Hungary, in 1997, and subsequently published in refereed journals (*see* Strasser and Stirbet 1997, 1998). Here, these authors compared the simulated OJIP curves calculated assuming homogeneous and heterogeneous PSII populations. Since the PSII population *in vivo* is heterogeneous concerning antenna size, the connectivity parameter, electron transport activity, and component localization (*see e.g.*, Govindjee 1990), the comparison is relevant. For the heterogeneous PSII population, Stirbet and Strasser considered a mixed population of 60% PSIIα and 40% PSIIβ, and the presence of 5–20% of non-Q_B active centers. For the non-Q_B active centers, these authors envisaged that the centers are either unconnected PSIIβ type or connected PSIIα type. In this work, they used for the integration not only *Gepasi 3* (*see* Mendes 1997), but also *SIMetrix 1.1* (*see* https://www.simetrix.co.uk/), which is a mixed-mode circuit simulator. The results of these simulations showed that systems with heterogeneous antenna size and connectivity can be acceptably simulated by assuming a homogeneous population of PSII centers with average values for antenna size and the connectivity constant C. However, it was also shown that this is not possible if non-Q_B active centers are also present in the system.

As mentioned earlier in section A (above), Stirbet *et al*. (1998a) have presented results obtained with a model in which they had considered, for the first time, the redox reactions on both the acceptor and the donor sides of PSII, and the nonphotochemical quenching (NPQ) of the excited state of Chl *a* by the oxidized plastoquinone molecules from the PQ pool in the lipid matrix of the thylakoid membrane. It was shown that different patterns of Chl *a* fluorescence rise kinetics can be simulated by varying the initial Q_B:Q_B^- ratio, the ratio between the initial states of the oxygen-evolving complex (*i.e.*, S_1:S_0) (*see* Fig. 6), the number of plastoquinone molecules in the PQ pool, the NPQ of

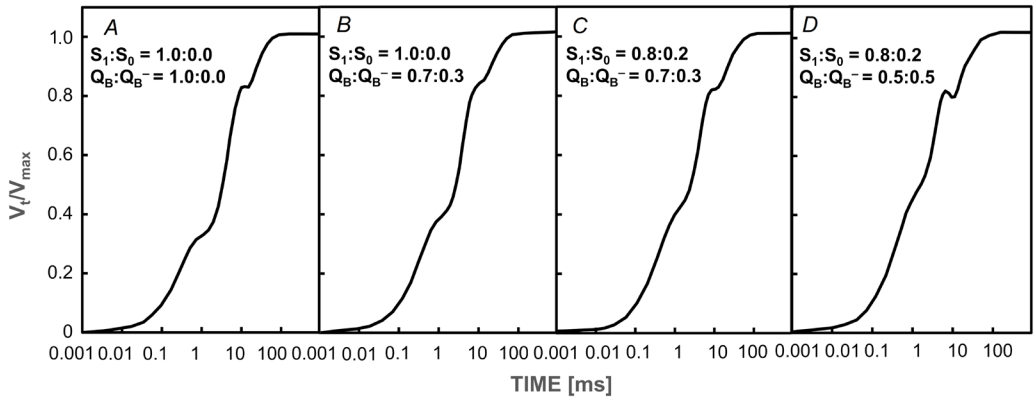

Fig. 6. Simulated relative Chl *a* fluorescence induction curves ($V_{(t)}/V_{max}$) – for photosynthetic systems in dark-adapted conditions. Curves *A–D* are for different values of initial S_1:S_0 and Q_B:Q_B^- ratios, where: S_0 and S_1 are the first two redox states of the oxygen-evolving complex of PSII; and Q_B is the second bound plastoquinone of PSII. Modified from the original figure in Stirbet *et al*. (1998a).

Chl fluorescence by the oxidized PQ pool molecules, and the connectivity constant between the PSII units. These results showed, *e.g.*, that: (i) different number(s) of PQ molecules in the PQ pool modify especially the I–P phase of the Chl fluorescence transient; (ii) the NPQ of Chl fluorescence by the PQ pool affects, in particular, the I step of the normalized OJIP transient, decreasing its value; (iii) PSII connectivity influences photosynthesis both quantitatively (by enhancing the electron transport) and qualitatively (by increasing its stability). Regarding the dip (D) after the I step in the fluorescence transient, which was mentioned earlier, these new simulations showed that it is more pronounced not only when the relative activity of PSI is increased, but also, when the connectivity parameter C is higher, the initial Q_B/Q_B^- ratio is close to 0.5:0.5 (*see* Fig. 6*D*), the number of PQ molecules in the PQ pool is higher, or when the initial number of oxidized PQ molecules in the PQ pool is on the high side.

Then, Stirbet and Strasser (1998) wrote a review on all their earlier modeling results. This was followed by three new studies in collaboration with two mathematicians from the Interdisciplinary Center for Scientific Computing in Heidelberg, Germany (Rosenau *et al*. 1998, Stirbet *et al*. 1999, 2001). In these publications, the software package *PARFIT* (*see* Bock 1981) was used to fit the experimental OJIP fluorescence curves with the model presented in Stirbet *et al*. (1998a), and to compare the fitted parameters with those cited in the literature. The results showed that the fittings of the OJIP curves were very good, but the estimated parameters matched only partially the values found in the literature. Moreover, there is also a similar issue in the paper by Strasser and Stirbet (2001), where the data were simulated and fitted with *PARFIT* – an experimental OJIP rise curve with a simple TEG-based model, but considering three different PSII redox states that contribute to the Chl *a* fluorescence signal. We note that the experimental OJIP curve was fitted quite well by all the models, but the kinetics parameters of the PSII redox states were different in each case. Further, Strasser and Stirbet (2001) concluded that overparametrized models cannot be validated by fitting one experimental curve, and other approaches must be used to reach firm conclusions. It should also be noted that later, the simulation of the OJIP transient was much improved by considering not only the PSII reactions in the model, but the entire linear electron transport (*see e.g.*, Lazár 2009). However, many of the results obtained with models based on PSII reactions remain qualitatively valuable.

Lastly, during the period of collaboration of one of us (Sandra Stirbet) with Reto Strasser, he was also working with his research group on how to use the OJIP fluorescence data to obtain an original set of fluorescence parameters that can be used to characterize the PSII activity, which he called the "JIP-test" (Strasser and Strasser 1995). Stirbet *et al*. (1998b) presented a new method to estimate the energetic connectivity of PSII centers in plants, by establishing an original formula, based on fluorescence data from the OJIP curve (*see* Fig. 7), which was then added to the JIP-test (*see* also Strasser and Stirbet 1999, 2000, 2001). As an example, they calculated the connectivity constant (p) among the PSII units for normal as well as for DCMU-treated pea leaves, and obtained for both cases very close values: $p_{control} = 0.25$ and $p_{DCMU} = 0.26$. For earlier work of Reto Strasser on PSII connectivity, *see e.g.*, Strasser (1978, 1981), and for a review on this topic discussing his contributions, *see* Stirbet (2013). Later, this method was revisited by Strasser *et al*. (2000, 2004) (*see* section C below – for Strasser's work with Alaka Srivastava). Furthermore, the JIP-test has been extended to include also properties of PSI electron transport (Tsimilli-Michael and Strasser 2008), and today it is a very popular tool for the exploitation and understanding of Chl *a* fluorescence measurements (*see e.g.*, Tsimilli-Michael 2020).

C. Reto Strasser's research – with Alaka Srivastava

One of us (Alaka Srivastava) came to Switzerland in 1992 and met, for the first time, Reto Strasser at the University of Geneva. He showed a lot of interest in Alaka's earlier work done at the University of California in Los Angeles

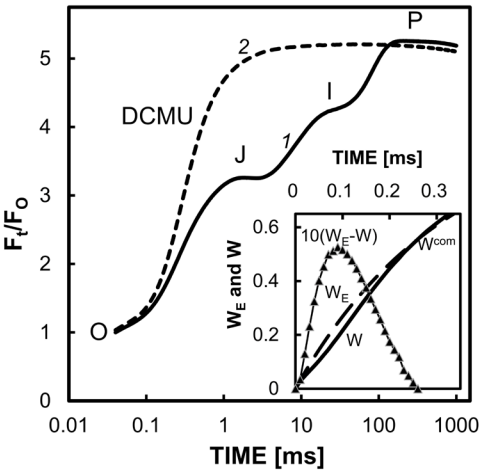

Fig. 7. Chlorophyll *a* fluorescence rise normalized to the initial fluorescence (F_t/F_O), of a pea leaf (*solid curve*, #1), and a DCMU-treated pea leaf (*dashed curve*, *#2*). *Inset*: curve $W = (F_t - F_O)/(F_J - F_O)$: the normalized O–J part of the F_t curve in the control pea leaf, presented until 0.4 ms only, on a linear time scale; curve W_E*:* theoretical exponential curve, corresponding to an unconnected system; W^{com}: the intersection point of the curves W and W_E (common point); curve #10(W_E – W): the difference (W_E – W) multiplied 10 times, which shows that the O–J part of curve *1* is sigmoidal, and thus, the PSII units in the pea leaf are energetically connected. Modified from the original figure in Stirbet *et al*. (1998b).

(UCLA), where she had been investigating the influence of chlorophyll on the stomatal movement, and offered her a position in his laboratory. During the eight years of work with Reto Strasser, Alaka's research had been related to the adaptability of plants to light, heat, and water stress, and all was by using Chl *a* fluorescence as a major investigating tool. She, indeed, had a very productive career in Strasser's laboratory, as she published ~ 20 refereed journal papers, 6 book chapters, and more than a dozen papers in the proceedings of several national and international conferences.

During 1995–1996

In Reto's laboratory, Alaka Srivastava (Alaka S) also had the pleasure to meet and work with Govindjee (one of the coauthors of this tribute to Reto Strasser), also a well-recognized senior leader on Chl fluorescence research, according to her. In Strasser *et al*. (1995), in which Govindjee was a coauthor, Alaka S used a new shutter-less system (*Plant Efficiency Analyzer*, *Hansatech*, UK), which allows fluorescence data accumulation over several orders of magnitude of time (40 μs to 120 s). In this work, the authors studied the complete polyphasic fluorescence rise for a variety of oxygenic plants and cyanobacteria at different light intensities. They concluded that "*watching these fluorescence signals of photosynthetic organisms in physiological conditions is like listening to the stethoscope by medical doctors*". For further discussion of this paper, and two others (Srivastava *et al*. 1995a,b), *see* above (section A).

In the paper by Guissé *et al*. (1995), the effect of high temperature (above 44°C) on the OJIP fluorescence transient was examined in the leaves of both potatoes and peas; it was observed that the variable Chl *a* fluorescence was not only dramatically quenched under this treatment, but a new rapid step, that was called the "K-step", had appeared between ~ 200 to 300 μs of illumination. After prolonged heat treatment, this K-step became a dominant peak in the Chl *a* fluorescence transient, followed by a big dip, and then by an increase in the Chl *a* fluorescence intensity. After studying the effects of DCMU (an inhibitor of electron flow) and NH_2OH (a PSII electron donor), the authors concluded that the K-step is due to a severe inhibition of the water-splitting system (*i.e*., the electron donor side of PSII).

In addition to the above, in Reto Strasser's Lab, Alaka S made investigations on the response of photosynthetic organisms to environmental abiotic stress, by using Chl *a* fluorescence induction measurements. For example, Srivastava *et al*. (1995c) measured both direct and modulated Chl *a* fluorescence in leaves of higher plants adapted to different light intensities, as well as, in parallel, changes in P700 (PSI reaction center). It was found that all the leaf samples exhibited an optimum curve for the steady-state Chl *a* fluorescence yield (F_s) *vs.* the light intensity, and the optimum level of F_s was always at a moderate light intensity, which, however, differed from species to species, or even from one sample to another. Further, the fraction of open RCs decreased with increasing light intensity, while the fraction of closed RCs increased. Moreover, both the maximum quantum efficiency (Φ_{Po}) and the actual quantum efficiency (Φ_P) of photosynthesis decreased with increasing light intensity. Since the optimum level of F_s was observed when the fraction of the closed RCs of each sample was about 0.2, the authors (Strasser, Alaka S, and others) concluded that there is a common quenching mechanism which determines the Chl *a* fluorescence properties under steady-state condition; this also explains why the Chl *a* fluorescence yield, under steady-state conditions, can increase or decrease upon increase of the actinic light.

Furthermore, Srivastava and Strasser (1995, 1996) studied pea plants subjected not only to light, but to heat and water stress. It was found that high temperatures (> 40°C) exacerbate the damage in PSII under high-light conditions. However, it was observed that low light acts as an efficient "protector" against PSII inactivation by heat. Indeed, leaves kept at a moderately elevated temperature (30°C) and illuminated with low light (30 W m^{-2}) before exposure to higher temperatures, had their thermotolerance increased by more than 5 to 10°C. Moreover, the stability of PSII against high heat was found to increase strongly in water-stressed leaf discs. A comparable behavior has not yet been found in unicellular organisms. These results, obtained under the leadership of Reto Strasser, demonstrate an antagonism between different abiotic stresses (heat, light, water deficit) and show that there is an adaptive mechanism of land plants to protect themselves against strong light and high temperature during usual changes in the diurnal cycle. We note that, in a recent study

on the effects of high light stress on lettuce plants exposed to a moderately low temperature (13°C) or the growth temperature (23°C), the same type of behavior has been observed (*see* Lempiäinen *et al*. 2025).

In addition to the above, one of us (Alaka Srivastava) has also coauthored a review on light stress in plants (Strasser *et al*. 1996) and five other presentations in the Proceedings of the Xth International Photosynthesis Congress in Montpellier, France, held in 1995.

During 1997–1998

Srivastava and Strasser (1997) reviewed different constructive and destructive aspects of light stress in land and aquatic plants, while Srivastava *et al*. (1997) updated an earlier study on heat stress of plants (*see* Guissé *et al*. 1995; and Fig. 8). From these new data, these authors proposed that the appearance of the K-step is due to two reasons: (i) inhibition of the water-splitting system, which leads to a much slower turnover of Q_A reduction; and, (ii) changes in the architecture of the PSII antenna that affect the energy migration properties within the photosynthetic unit. Thus, the K-step can be seen as an indicator of the heterogeneity of PSII units.

In 1998, Alaka Srivastava coauthored with Reto Strasser five presentations published in the Proceedings of the XIth International Congress on Photosynthesis in Budapest, Hungary, as well as a paper (Srivastava *et al*. 1998) on the action of the allelochemical, fischerellin A (FS) on PSII, where they used the fast Chl *a* fluorescence transient to study the effects of FS on diverse photosynthetic samples (*i.e.*, cyanobacterium *Anabaena* P9, cells of green alga *Chlamydomonas reinhardtii*, pea leaves, and spinach thylakoid membranes). It was found that FS acts on several sites of PSII, with increasing half-time of interaction, in the sequence (i) the rate constant of Q_A^- reoxidation; (ii) the primary PSII photochemistry; (iii) inactivation of PSII reaction center; and (iv) segregation of individual units from grouped units.

During 1999–2000

During this period, Srivastava *et al*. (1999a) studied the process of greening in pea plants, as mentioned in section A (*see* above). In addition, two more papers were published – in collaboration with Alberto Darszon from Mexico (Srivastava *et al*. 1999b,c). Srivastava *et al*. (1999b) analyzed the influence of water on the stability and the activity of photosynthetic complexes, membranes, and cells in apolar systems. Further, Srivastava *et al*. (1999c) described the role of water on the photochemical activities of membrane protein complexes obtained from the purple bacterium *Rhodospirillum rubrum*, as measured by using bacteriochlorophyll (BChl) fluorescence changes. These results clearly demonstrate that the amount and the physical state of water determine the primary photosynthetic activity in these photosynthetic systems.

Besides the papers cited above, Strasser *et al*. (1999) published a review on screening the vitality and photosynthetic activity of plants by Chl *a* fluorescence

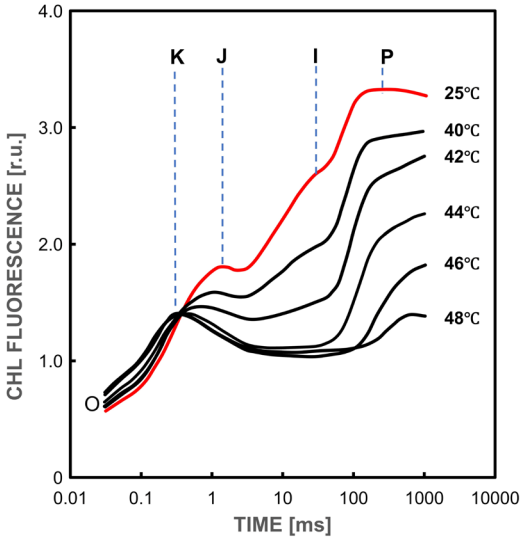

Fig. 8. Temperature dependence of the appearance of the K-step in chlorophyll *a* fluorescence induction curves of pea leaf discs. The samples were heated at the indicated temperatures for 5 min and readapted for room temperature for 10 s before the measurements. Modified from the original figure in Srivastava *et al*. (1997).

transient, and Srivastava and Strasser (1999) reviewed the survival strategies that plants adopt to cope with the stress of daily atmospheric changes. Further, Strasser *et al*. (1999) presented in detail the JIP-test, with additional theoretical explanations, and with several supplementary parameters, such as the performance index PI_{ABS}, which is a combination of three independent JIP parameters: (i) RC/ABS, the number of active PSII reaction centers per light absorption; (ii) φ_{Po}, the maximum quantum yield of PSII photochemistry; and (iii) ψ_{Eo}, the probability that an exciton trapped by PSII can move an electron beyond Q_A. We note that Strasser *et al*. (2000) also published a comprehensive review on the so-called JIP-test.

In addition to the above, together with others in Strasser's Lab, one of us (Alaka S) studied changes in the photosynthetic activities during several stages of the vegetative growth of *Spirodela polyrhiza*, under chromate ($Cr_2O_7^{-2}$) stress (*see* Susplugas *et al*. 2000). We note that although the fresh green fronds have a normal Chl *a* fluorescence transient, *i.e.*, the OJIP phase, but the mother fronds, that carry turions, show an additional K step (*see* an earlier paper by Guissé *et al*. 1995), suggesting a limitation in the function of the water-splitting system. Furthermore, the photosynthetic performance index of turions was more than 46% lower under chromate treatment than that of fresh green plants, showing that the overall photosynthetic efficiency of PSII and PSI of green fronds decreases after this treatment.

During 2001–2004

Even after one of us (Alaka S) left Geneva in 2000, her collaboration with Reto Strasser continued for a few more years, on topics that were interesting to her. For

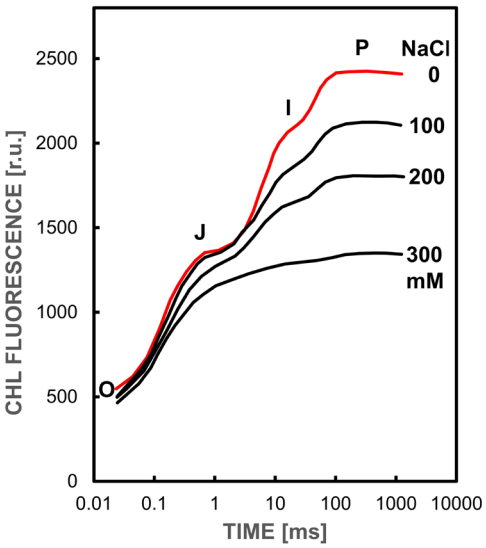

Fig. 9. NaCl effect on the chlorophyll *a* fluorescence induction kinetics of *Brassica* seedlings. Six-day-old seedlings were treated with NaCl solutions of different concentrations, and fluorescence measurements were made after three days. Modified from the original figure in Misra *et al*. (2001).

example, the two published a review on biomolecules in reverse micelles (Srivastava and Strasser 2001). Further, in Appenroth *et al*. (2001), they continued their study on the chromate stress effects on the growth of *Spirodela polyrhiza*. After the chromate treatment of the plants, they observed a partial loss of photosynthetic pigments and a decrease in O_2 evolution, in a dose-dependent manner. However, these authors also noticed that the chromate sensitivity varies within plant populations. Moreover, the analysis with the JIP-test of the fast Chl *a* fluorescence transients indicated that the chromate treatment damages the oxygen-evolving complex and decreases the number of active PSII reaction centers, which leads to a decrease in the quantum yield of PSII photochemistry and a lower performance index. Further, Misra *et al*. (2001) published on the salt/ion sensitivity of mung bean and brassica seedlings. For this, plant seedlings were treated with NaCl and KCl alone (*see* Fig. 9), or in combination with $CaCl_2$, Na_2SO_4, or K_2SO_4. Compared with the control, the salt/ion treatments showed large effects on the OJIP kinetics. An analysis with the JIP-test of these experimental curves suggests that the most prominent difference in the sensitivity of a system or genotype to different salts or ions is due to changes in the number of active PSII reaction centers per leaf cross-section (RC_0/CS_0). Then, in another paper, in collaboration with Prasanna Mohanty's group (in India), Strasser's research team studied the senescence-induced alterations of the PSII functions in *Cucumis sativus* (*see* Prakash *et al*. 2003). Here, too, the analysis of OJIP transients with Strasser's JIP-test has been a valuable tool in terms of measuring photosynthetic activities and different types of PSII heterogeneity.

In addition to all of the above, Alaka S was also a coauthor in Schansker *et al*. (2003), which is, in our opinion, an important paper on the characterization of the 820-nm transmission signal paralleling the OJIP fluorescence rise in pea leaves (discussed above in section A). And finally, Alaka's last publication with Reto Strasser was a detailed review on the JIP test (*see* Strasser *et al*. 2004); this continues to be extensively used as a sensitive tool to investigate the "health" of photosynthetic samples *in vivo*, especially under stress conditions (*see e.g.*, Stirbet and Govindjee 2011, Kalaji *et al*. 2014a,b; 2017; Goltsev *et al*. 2016, Stirbet *et al*. 2018, Tsimilli-Michael 2020).

Fig. 10. A 2024 photograph of Reto Strasser (*on the left*) and Ronald Rodriguez. Source: Ronald M. Rodriguez.

Concluding remarks

With the current paper, we honor respected Reto J. Strasser on his upcoming birthday. We wish him the best. We note that Reto Strasser was also honored, just a few years ago, by Da Silva Pontes *et al*. (2019), for 40 years of his theory on energy fluxes in photosynthesis (*see e.g.*, Strasser 1978, Tsimilli-Michael and Strasser 2013). Fig. 10 shows a 2024 photograph of Reto Strasser with Ronald Rodriguez, coauthor of Da Silva Pontes *et al*. (2019).

References

Ananyev G., Gates C., Dismukes G.C.: The oxygen quantum yield in diverse algae and cyanobacteria is controlled by partitioning of flux between linear and cyclic electron flow within photosystem II. – BBA-Bioenergetics **1857**: 1380-1391, 2016.

Appenroth K.-J., Stöckel J., Srivastava A., Strasser R.J.: Multiple effects of chromate on the photosynthetic apparatus of *Spirodela polyrhiza* as probed by OJIP chlorophyll *a* fluorescence measurements. – Environ. Pollut. **115**: 49-64, 2001.

Baake E., Strasser R.J.: A differential equation model for the description of the fast fluorescence rise (O-I-D-P transient) in leaves. – In: Baltscheffsky M. (ed.): Current Research in Photosynthesis. Pp. 567-570. Springer, Dordrecht 1990.

Bernát G., Steinbach G., Kaňa R. *et al.*: On the origin of the slow M–T chlorophyll *a* fluorescence decline in cyanobacteria: interplay of short-term light-responses. – Photosynth. Res. **136**: 183-198, 2018.

Bock H.G.: Numerical treatment of inverse problems in chemical reaction kinetics. – In: Ebert K.H., Deuflhard P., Jäger W. (ed.): Modelling of Chemical Reaction Systems. Springer Series in Chemical Physics. Vol. 18. Pp. 102-125. Springer, Berlin-Heidelberg 1981.

Chen S., Strasser R.J., Qiang S., Govindjee [G.]: Tenuazonic acid, a novel natural PSII inhibitor, impacts on photosynthetic activity by occupying the Q_B-binding site and inhibiting forward electron flow. – In: Photosynthesis Research for Food, Fuel and the Future. Advanced Topics in Science and Technology in China. Pp. 447-450. Springer, Berlin-Heidelberg 2013.

Chen S., Yin C., Strasser R.J. *et al.*: Reactive oxygen species from chloroplasts contribute to 3-acetyl-5-isopropyltetramic acid-induced leaf necrosis of *Arabidopsis thaliana*. – Plant Physiol. Biochem. **52**: 38-51, 2012.

Da Silva Pontes M., Rodriguez R.M., Santiago E.F.: The energy flux theory celebrates 40 years: Toward a systems biology concept? – Photosynthetica **57**: 521-522, 2019.

Duysens L.M.N., Sweers H.T.: Mechanism of the two photochemical reactions in algae as studied by means of fluorescence. – In: Japanese Society of Plant Physiologists (ed.): Studies on Microalgae and Photosynthetic Bacteria. Pp. 353-372. University of Tokyo Press, Tokyo 1963.

Edwards G.E., Heber U.: David Alan Walker (1928–2012). – Photosynth. Res. **112**: 91-102, 2012.

Goltsev V.N., Kalaji H.M., Paunov M. *et al.*: Variable chlorophyll fluorescence and its use for assessing physiological condition of plant photosynthetic apparatus. – Russ. J. Plant Physiol. **63**: 869-893, 2016.

Govindjee: Photosystem II heterogeneity: the acceptor side. – Photosynth. Res. 25: 151-160, 1990.

Govindjee: Sixty-three years since Kautsky: chlorophyll *a* fluorescence. – Aust. J. Plant Physiol. **22**: 131-160, 1995.

Govindjee, Eggenberg P., Pfister K., Strasser R.J.: Chlorophyll *a* fluorescence yield decay in herbicide-resistant D1 mutants of *Chlamydomonas reinhardtii* and the formate effect. – BBA-Bioenergetics **1101**: 353-358, 1992.

Govindjee, Schwarz B., Rochaix J.D., Strasser R.J.: The herbicide-resistant D1 mutant L275F of *Chlamydomonas reinhardtii* fails to show the bicarbonate-reversible formate effect on chlorophyll *a* fluorescence transients. – Photosynth. Res. **27**: 199-208, 1991.

Govindjee, Srivastava A., Stirbet A. *et al.*: Reto Jörg Strasser: An innovator, a wonderful friend and "Professor of the World". – J. Plant Sci. Res. **35**: 147-158, 2019.

Govindjee, Srivastava A., Strasser R.J.: The "oxygen clock" in greening pea leaves as probed by the period four oscillations in the fluorescence intensity at 50 μs and 2 ms after pre-flashing during the OJIP transient. – In: Garab G. (ed.): Photosynthesis: Mechanisms and Effects. Pp. 1467-1470. Springer, Dordrecht 1998.

Guissé B., Srivastava A., Strasser R.J.: The polyphasic rise of the chlorophyll a fluorescence (O-K-J-I-P) in heat-stressed leaves. – Arch. Sci. Genève **48**: 147-160, 1995.

Guo Y., Tan J.: Modeling and simulation of the initial phases of chlorophyll fluorescence from photosystem II. – BioSystems **103**: 152-157, 2011.

Kalaji H.M., Goltsev V.: Foreword: Special issue in honour of Prof. Reto J. Strasser. – Photosynthetica **58**: 1-5, 2020.

Kalaji H.M., Goltsev V., Bosa K. *et al.*: Experimental *in vivo* measurements of light emission in plants: a perspective dedicated to David Walker. – Photosynth. Res. **114**: 69-96, 2012.

Kalaji H.M., Goltsev V., Brestič M. *et al.*: *In vivo* measurements of light emission in plants. – In: Allakhverdiev S.I., Rubin A.B., Shuvalov V.A. (ed.): Contemporary Problems of Photosynthesis. Vol. 1. Pp. 1-39. Institute of Computer Science, Izhevsk-Moscow 2014a.

Kalaji H.M., Schansker G., Brestic M. *et al.*: Frequently asked questions about chlorophyll fluorescence, the sequel. – Photosynth. Res. **132**: 13-66, 2017.

Kalaji H.M., Schansker G., Ladle R.J. *et al.*: Frequently asked questions about chlorophyll fluorescence: practical issues. – Photosynth. Res. **122**: 121-158, 2014b.

Lavergne J., Leci E.: Properties of inactive photosystem II centers. – Photosynth. Res. **35**: 323-343, 1993.

Lazár D.: Modelling of light-induced chlorophyll *a* fluorescence rise (O-J-I-P transient) and changes in 820 nm-transmittance signal of photosynthesis. – Photosynthetica **47**: 483-498, 2009.

Lempiäinen T., Muth-Pawlak D., Vainonen J.P. *et al.*: Moderate temperature reduction changes the high-light acclimation strategy of lettuce plants. – Physiol. Plantarum **177**: e70298, 2025.

Mendes P.: GEPASI: a software package for modelling the dynamics, steady states and control of biochemical and other systems. – Bioinformatics **9**: 563-571, 1993.

Mendes P.: Biochemistry by numbers: simulation of biochemical pathways with Gepasi 3. – Trends Biochem. Sci. **22**: 361-363, 1997.

Misra A.N., Srivastava A., Strasser R.J.: Utilisation of fast chlorophyll *a* fluorescence technique in assessing the salt/ion sensitivity of mung bean and *Brassica seedlings*. – J. Plant Physiol. **158**: 1173-1181, 2001.

Munday Jr. J.C., Govindjee: Light-induced changes in the fluorescence yield of chlorophyll *a* in vivo. III. The dip and the peak in the fluorescence transient of *Chlorella pyrenoidosa*. – Biophys. J. **9**: 1-21, 1969.

Papageorgiou G.C., Tsimilli-Michael M., Stamatakis K.: The fast and slow kinetics of chlorophyll *a* fluorescence induction in plants, algae and cyanobacteria: a viewpoint. – Photosynth. Res. 94: 275-290, 2007.

Prakash J.S.S., Srivastava A., Strasser R.J., Mohanty P.: Senescence-induced alterations in the Photosystem II functions of *Cucumis sativus* cotyledons: Probing of senescence driven alterations of Photosystem II by chlorophyll *a* fluorescence induction O-J-I-P transients. – Indian J. Biochem. Biophys. **40**: 160-168, 2003.

Rosenau P., Ströder A.C., Stirbet A., Strasser R.J.: Recent advances in modelling the photosynthesis. Pp. 17. The Interdisciplinary Center for Scientific Computing (IWR), Heidelberg University, Heidelberg 1998.

Schansker G., Srivastava A., Govindjee, Strasser R.J.: Characterization of the 820-nm transmission signal paralleling the chlorophyll *a* fluorescence rise (OJIP) in pea leaves. – Funct. Plant Biol. **30**: 785-796, 2003.

Schreiber U., Klughammer C.: Analysis of photosystem I donor and acceptor sides with a new type of online-deconvoluting kinetic LED-array spectrophotometer. – Plant Cell Physiol. **57**: 1454-1467, 2016.

Shabnam N., Sharmila P., Sharma A. *et al.*: Mitochondrial electron transport protects floating leaves of long leaf pondweed (*Potamogeton nodosus* Poir) against photoinhibition: comparison with submerged leaves. – Photosynth. Res. **125**: 305-319, 2015.

Shevela D., Eaton-Rye J.J., Shen J.-R., Govindjee: Photosystem II and unique role of bicarbonate: a historical perspective. – BBA-Bioenergetics **1817**: 1134-1151, 2012.

Srivastava A., Darszon A., Strasser R.J.: The influence of water on the stability and activity of photosynthetic complexes, membranes and cells in apolar systems. – Arch. Sci. Genève

52: 73-99, 1999b.

Srivastava A., Greppin H., Strasser R.J.: The steady state chlorophyll *a* fluorescence exhibits *in vivo* an optimum as a function of light intensity which reflects the physiological state of the plant. – Plant Cell Physiol. **36**: 839-848, 1995c.

Srivastava A., Guissé B., Greppin H., Strasser R.J.: Regulation of antenna structure and electron transport in Photosystem II of *Pisum sativum* under elevated temperature probed by the fast polyphasic chlorophyll *a* fluorescence transient: OKJIP. – BBA-Bioenergetics **1320**: 95-106, 1997.

Srivastava A., Jüttner F., Strasser R.J.: Action of the allelochemical, fischerellin A on Photosystem II. – BBA-Bioenergetics **1364**: 326-336, 1998.

Srivastava A., Rivara-Minten E., Obregon C. *et al.*: The role of water on photochemical activities of membrane protein complexes of bacteria. – Arch. Sci. Genève **52**: 17-27, 1999c.

Srivastava A., Strasser R.J., Govindjee: Polyphasic rise of chlorophyll *a* fluorescence in herbicide-resistant D1 mutants of *Chlamydomonas reinhardtii*. – Photosynth. Res. **43**: 131-141, 1995a.

Srivastava A., Strasser R.J., Govindjee: Differential effects of dimethylbenzoquinone and dichlorobenzoquinone on chlorophyll fluorescence transient in spinach thylakoids. – J. Photoch. Photobio. B **31**: 163-169, 1995b.

Srivastava A., Strasser R.J., Govindjee: Greening of peas: parallel measurements of 77 K emission spectra, OJIP chlorophyll *a* fluorescence transient, period four oscillation of the initial fluorescence level, delayed light emission, and P700. – Photosynthetica **37**: 365-392, 1999a.

Srivastava A., Strasser R.J.: How do land plants respond to stress temperature and stress light? – Arch. Sci. Genève **48**: 135-146, 1995.

Srivastava A., Strasser R.J.: Stress and stress management of land plants during a regular day. – J. Plant Physiol. **148**: 445-455, 1996.

Srivastava A., Strasser R.J.: Constructive and destructive actions of light on the photosynthetic apparatus. – J. Sci. Industr. Res. **56**: 113-148, 1997.

Srivastava A., Strasser R.J.: Survival strategies of plants to cope with the stress of daily atmospheric changes. – In: Behl R.K., Punia M.S., Lather B.P.S. (ed.): Crop Improvement for Food Security. Pp. 60-71. SSARM, Hisar 1999.

Srivastava A., Strasser R.J.: Biomolecules in reverse micelles. – In: Saradhi P.P. (ed.): Biophysical Processes in Living Systems. Pp. 1-23. Science Publishers Inc., Enfield 2001.

Stirbet A.: Excitonic connectivity between photosystem II units: what is it, and how to measure it? – Photosynth. Res. **116**: 189-214, 2013.

Stirbet A., Govindjee: On the relation between the Kautsky effect (chlorophyll *a* fluorescence induction) and Photosystem II: basics and applications of the OJIP fluorescence transient. – J. Photoch. Photobio. B **104**: 236-257, 2011.

Stirbet A., Govindjee: Chlorophyll *a* fluorescence induction: a personal perspective of the thermal phase, the J-I-P rise. – Photosynth. Res. **113**: 15-61, 2012.

Stirbet A., Govindjee, Strasser B.J., Strasser R.J.: Numerical simulation of chlorophyll *a* fluorescence induction in plants. – In: Mathis P. (ed.): Photosynthesis: From Light to Biosphere. Vol. II. Pp. 919-922. Kluwer Academic Publishers, Dordrecht 1995.

Stirbet A., Govindjee, Strasser B.J., Strasser R.J.: Chlorophyll *a* fluorescence induction in higher plants: modelling and numerical simulation. – J. Theor. Biol. **193**: 131-151, 1998a.

Stirbet A., Guo Y., Lazár D., Govindjee G.: From leaf to multiscale models of photosynthesis: applications and challenges for crop improvement. – Photosynth. Res. 161: 21-49, 2024.

Stirbet A., Lazár D., Kromdijk J., Govindjee: Chlorophyll *a* fluorescence induction: Can just a one-second measurement be used to quantify abiotic stress responses? – Photosynthetica **56**: 86-104, 2018.

Stirbet A., Rosenau P., Ströder A.C., Strasser R.J.: Fast Chl *a* fluorescence induction models: parameter optimisation study. – In: Nybrant T. (ed.): Proceedings of the IMACS/IFAC Third International Symposium on Mathematical Modelling and Simulation in Agricultural and Bio-Industries, June 7–9, Uppsala, Sweden, 1999. Pp. 149-154. Swedish University of Agricultural Science, Uppsala 1999.

Stirbet A., Rosenau P., Ströder A.C., Strasser R.J.: Parameter optimisation of fast chlorophyll fluorescence induction model. – Math. Comput. Simulat. **56**: 443-450, 2001.

Stirbet A., Srivastava A., Strasser R.J.: The energetic connectivity of PSII centres in higher plants probed *in vivo* by the fast fluorescence rise O-J-I-P and numerical simulations. – In: Garab G. (ed.): Photosynthesis: Mechanisms and Effects. Proceedings of the XIth International Congress on Photosynthesis, Budapest, Hungary, 1998. Vol. V. Pp. 4317-4320. Kluwer Academic Publishers, Dordrecht 1998b.

Stirbet A., Strasser R.J.: Numerical simulation of the fluorescence induction in plants. – Arch. Sci. Genève **48**: 41-60, 1995a.

Stirbet A., Strasser R.J.: Numerical simulation of the *in vivo* fluorescence in plants. – In: Hanus R.J.L. (ed.): Proceedings of the 1st IMACS-IFAC Symposium on Mathematical Modelling and Simulation in Agriculture and Bio-Industries. Elsevier North-Holland, Inc., New York 1995b.

Stirbet A., Strasser R.J.: Numerical simulation of the *in vivo* fluorescence in plants. – Math. Comput. Simulat. **42**: 245-253, 1996.

Stirbet A., Strasser R.J.: Fast recordings of chlorophyll *a* fluorescence, modelling and numerical simulation as a tool to probe the interaction of living systems with our planet. – In: Greppin H., Degli Agosti R., Penel C. (ed.): The Co-Action Between Living Systems and the Planet. Pp. 101-115. University of Geneva, Geneva 1998.

Strasser B.J., Strasser R.J.: Measuring fast fluorescence transients to address environmental questions: the JIP-test. − In: Mathis P. (ed.): Photosynthesis: From Light to Biosphere. Vol. V. Pp. 977-980. Kluwer Academic Publishers, Dordrecht 1995.

Strasser R.J.: The grouping model of plant photosynthesis. – In: Argyroudi-Akoyunoglou J.H., Akoyunoglou G. (ed.): Chloroplast Development. Pp. 513-538. Elsevier/North Holland Biomedical Press, Amsterdam 1978.

Strasser R.J.: The grouping model of plant photosynthesis: heterogeneity of photosynthetic units in thylakoids. – In: Akoyunoglou G. (ed.): Photosynthesis: Structure and Molecular Organization of the Photosynthetic Apparatus. Vol. III. Pp. 727-737. Balaban International Science Services, Philadelphia 1981.

Strasser R.J., Govindjee: The Fo and the O-J-I-P fluorescence rise in higher plants and algae. – In: Argyroudi-Akoyunoglou J.H. (ed.): Regulation of Chloroplast Biogenesis. Pp. 423-426. Plenum Press, New York 1991.

Strasser R.J., Govindjee: On the O-J-I-P fluorescence transient in leaves and D1 mutants of *Chlamydomonas reinhardtii*. – In: Murata N. (ed.): Research in Photosynthesis. Vol. II. Pp. 29-32. Kluwer Academic Publishers, Dordrecht 1992.

Strasser R.J., Schansker G., Srivastava A., Govindjee: Simultaneous measurement of photosystem I and photosystem II probed by modulated transmission at 820 nm and by chlorophyll *a* fluorescence in the sub ms to second time range. – In: Proceedings, 12th International Congress on Photosynthesis, Brisbane. Pp. 6. CSIRO Publishing, Clayton 2001.

Strasser R.J., Srivastava A., Govindjee: Polyphasic chlorophyll *a* fluorescence transient in plants and cyanobacteria. – Photochem. Photobiol. **61**: 32-42, 1995.

Strasser R.J., Srivastava A., Haldimann P.: Licht. [Light.] – In: Brunold C., Brändle R., Rüegsegger A. (ed.): Stress bei Pflanzen: Ökologie, Physiologie, Biochemie, Molekularbiologie. [Stress in Plants: Ecology, Physiology, Biochemistry, Molecular Biology.] Pp. 89-102. Karl Haupt, Bern 1996. [In German]

Strasser R.J., Srivastava A., Tsimilli-Michael M.: Screening the vitality and photosynthetic activity of plants by the fluorescence transient. – In: Behl R.K., Punia M.S., Lather B.P.S. (ed.): Crop Improvement for Food Security. Pp. 72-115. SSARM, Hisar 1999.

Strasser R.J., Srivastava A., Tsimilli-Michael M.: The fluorescence transient as a tool to characterize and screen photosynthetic samples. – In: Yunus M., Pathre U., Mohanty P. (ed.): Probing Photosynthesis: Mechanism, Regulation and Adaptation. Pp. 443-480. Taylor and Francis, London 2000.

Strasser R.J., Stirbet A.: Influence of photosystem II heterogeneity on the simulated Chl *a* fluorescence induction transients. – IFAC Proc. Vol. **30**: 21-26, 1997.

Strasser R.J., Stirbet A.: Heterogeneity of photosystem II probed by the numerically simulated chlorophyll *a* fluorescence rise (O-J-I-P). – Math. Comput. Simulat. **48**: 3-9, 1998.

Strasser R.J., Stirbet A.: Numerical simulation of the fast fluorescence rise OJIP allows [us] to extend the JIP-test for probing energetic connectivity of PSII centres in higher plants. – In: Nybrant T. (ed.): Proceedings of the IMACS/IFAC Third International Symposium on Mathematical Modelling and Simulation in Agricultural and Bio-Industries, June 7–9, Uppsala, Sweden, 1999. Pp. 175-180. Swedish University of Agricultural Science, Uppsala 1999.

Strasser R.J., Stirbet A.: Energetic connectivity creates heterogeneity of PS II centres in plants probed by the fluorescence rise O-J-I-P: fitting of experimental data to three different PS II models. – In: Greppin H., Penel C., Broughton W.J., Strasser R.J. (ed.): Integrated Plant Systems. Pp. 81-93. University of Geneva, Geneva 2000.

Strasser R.J., Stirbet A.D.: Estimation of the energetic connectivity of PS II centres in plants using the fluorescence rise O-J-I-P: fitting of experimental data to three different PS II models. – Math. Comput. Simulat. **56**: 451-462, 2001.

Strasser R.J., Tsimilli-Michael M., Srivastava A.: Analysis of the chlorophyll *a* fluorescence transient. – In: Papageorgiou G.C., Govindjee (ed.): Chlorophyll *a* Fluorescence: A Signature of Photosynthesis. Advances in Photosynthesis and Respiration. Pp. 321-362. Springer, Dordrecht 2004.

Susplugas S., Srivastava A., Strasser R.J.: Changes in the photosynthetic activities during several stages of vegetative growth of *Spirodela polyrhiza*: effect of chromate. – J. Plant Physiol. **157**: 503-512, 2000.

Tsimilli-Michael M.: Revisiting JIP-test: an educative review on concepts, assumptions, approximations, definitions and terminology. – Photosynthetica **58**: 275-292, 2020.

Tsimilli-Michael M., Strasser R.J.: *In vivo* assessment of plants' vitality: applications in detecting and evaluating the impact of mycorrhization on host plants. – In: Varma A. (ed.): Mycorrhiza: State of the Art, Genetics and Molecular Biology, Eco-Function, Biotechnology, Eco-Physiology, Structure and Systematics. 3rd Edition. Pp. 679-703. Springer, Berlin-Heidelberg 2008.

Tsimilli-Michael M., Strasser R.J.: The energy fluxes theory 35 years later: formulations and applications. – Photosynth. Res. **117**: 289-320, 2013.

Vinyard D., Govindjee G.: Bicarbonate is a key regulator but not a substrate for O_2 evolution in Photosystem II. – Photosynth. Res. **162**: 93-99, 2024.

Yusuf M.A., Kumar D., Rajwanshi R. *et al.*: Overexpression of γ-tocopherol methyl transferase gene in transgenic Brassica juncea plants alleviates abiotic stress: physiological and chlorophyll *a* fluorescence measurements. – BBA-Bioenergetics **1797**: 1428-1438, 2010.

Zhu X.-G., Govindjee, Baker N.R. *et al.*: Chlorophyll *a* fluorescence induction kinetics in leaves predicted from model describing each discrete step of excitation energy and electron transfer associated with photosystem II. – Planta **223**: 114-133, 2005.

Zournas A., Mani K., Dismukes G.C.: Cyclic electron flow around photosystem II *in silico*: How it works and functions *in vivo*. – Photosynth. Res. **156**: 129-145, 2023.

Appendix 1. List of names of scientists who honored Reto Jörg Strasser in "Photosynthetica" in 2020 (prepared by G. Govindjee, and checked by Ivana Štětinová and Vasilij Goltsev). This list contains almost 230 scientists from 33 countries; the special issue (in honor of R.J. Strasser) was organized and edited by Hazem M. Kalaji (from Poland) and by Vasilij Goltsev (from Bulgaria); it included 43 papers (*see* Appendix 2).

Argentina: V. Blackhall; M.G. Colavita; and G.A. Orioli; **Australia:** A. Zavafer; **Austria:** A.J. Keutgen; and N. Keutgen; **Azerbaijan:** S. Ibrahimova; **Belarus:** M.A. Charnysh; and V.V. Demidchik; **Brazil:** M.A. Bacarin; J.F. De Carvalho Gonçalves; R. Kirmayr Jaquetti; E.G. Martinazzo; A.B. Moura; A.T. Perboni; N. Petrova; and K.C. Pires da Costa; **Bulgaria:** S. Anev; G. Chaneva; K. Dankov; S. Dimitrova; V. Goltsev; M. Kouzmanova; S. Krumova; B. Pavlova; M. Paunov; A. Raycheva; K. Sapunov; S. Stoichev; S. Taneva; D. Teofanova; S. Todinova; A. Traianova; T. Tsonev; N. Tzvetkova; V. Velikova; L. Zagorchev; and M. Zhiponova; **China:** L-S. Chen; S. Chen; F.Q. Dong; Y. Guo; Y. Han; X. He; Z. Hu; W. Huang; Z.R. Huang; S. Hussain; C.D. Jiang; J. Li; X. Li; J.G. Liu; L.A. Liu; T. Liu; W. Liu; Y. Lu; S. Qiang; J.W. Ren; J. Shi; L. Shi; G.Y. Sun; Z.Y. Teng; H. Wang; X. Wang; H.Y. Wu; W. Xiao; N. Xu; R. Xu; R.Y. Yang; Y.-J. Yang; S. Zhai; H. Zhang; L.T. Zhang; S.-B. Zhang; W.F. Zhang; and Y. Zhang; **Croatia:** V.M. Franić; V. Galić; D. Mazur; D. Šimić; V. Španić; M. Viljevac Vulvetić; and Z. Zdunić; **Cyprus:** M. Tsimilli-Michael; **The Czech Republic:** M. Barták; M. Bednaříková; J. Hájek; Z. Kučerová; D. Lazár; R. Longauer; M. Skalicky; and M. Špundová; **Egypt:** A. Badr; N.I. Elsheery; and J. Mojski; **France:** V. Lefebvre; and A. Palloix; **Germany:** F. Bantis; W. Brüggemann; S.F. Bucher; E. Früchtenicht; A. Gast; J. Graap; V. Holland; S. Koller; N. Reininger; C. Römermann; L. Schäfer; and S. Ströll; **Greece:** K. Radoglou; **Hungary:** A. Barócsi; S. Lenk; M. Szabó; and S.Z. Tóth; **India:** K. Chakraborty; K. Chattopadhyay; P. Faseela; S. Kataria; J.T. Puthur; A.S. Raghavendra; A. Ray; R.K. Sarkar; A.K. Sinisha; B. Sunil; and J. Vijayan; **Iran:** S. Hajihashemi; and F. Noedoost; **Italy:** F. Bussotti; M. Pollastrini; and R. Tognetti; **Mexico:** G.A. Aguado-Santacruz; H. Campos; F.V. Conde-Martínez; B. Jiménez-Francisco; D. Padilla-Chacón; and C. Trejo; **Morocco:** A. Oukarroum; **The Netherlands:** J.A. Dieleman; E. Heuvelink; and F.A. Van Eeuwijk; **Norway:** R. Bakke; E. Janka; M. Sposob; and I. Umetani; **Poland:** W. Bąba;

A.H. Baczewska-Dąbrowska; B. Borawska-Jarmułowicz; W. Borucki; M.D. Cetner; P. Dąbrowski; A. Daszkowska-Golec; Ż. Gieroń; D. Gozdowski; T. Horaczek; H.M. Kalaji; A. Kornas; K. Kowalczyk; P. Latocha; E. Malkowski; G. Mastalerczuk; J. Oliwa; S. Pietkiewicz; M. Pogrzeba; A. Rastogi; S. Rusinowski; G. Rut; I.A. Samborska-Skutnik; L. Sieczko; K. Sitkov; A. Skoczowski; W. Stępień; T. Swoczyna; M. Tomaszewska-Sowa; and K. Wytrążek; **Russia:** V.I. Apollonov; A.I. Belyaeva; N.S. Degtereva; V.V. Demidchik; I.V. Drozdova; S.S. Khruschev; I.V. Konyukhov; O.N. Kovaleva; L.G. Loskutov; V. Murtuzova; T.Yu. Plyusnina; C.K. Rabadanova; G.Yu. Riznichenko; A.B. Rubin; A.E. Solovchenko; E. Tyutereva; and O.V. Voitsekhovskaja; **Slovakia:** M. Brestič; Ľ. Ditmarová; D. Gömöry; H. Húdoková; G. Jamnická; M. Ježík; A. Konôpková; M. Kovar; D. Kurjak; E. Pšidová; and M. Živčák; **Spain:** Y. Folgar-Cameán; and J.J. Magán; **Sweden:** K. Pawlowski; **Switzerland:** G. Schansker; **Thailand:** S. Chadchawan; L. Comai; K. Hungsaprug; W. Kasettranun; T. Kojonna; B. Kositup; K. Plaimas; C. Punchkhon; M. Samleepan; J.L. Siangliw; T. Toojinda; and W. Ut-Khao; **Tunisia:** S. Mbarki; **Turkey:** Ö. Arslan; A.S. Balkan Nalçaiyi; N. Çiçek; Ş. Çulha Erdal; Y. Ekmekçi; Y. Kaya; and V. Pekcan; **United States of America (USA):** C.L. Bernacchi; G. Govindjee; and A. Stirbet.

Appendix 2. List of papers, published in Photosynthetica, edited by Hazem Kalaji and Vasilej Goltsev, in honor of Reto Strasser, in 2020, arranged alphabetically.

Arslan Ö., Balkan Nalçaiyi A.S., Çulha Erdal S., Pekcan V., Kaya Y., Çiçek N., Ekmekçi Y.: Analysis of drought response of sunflower inbred lines by chlorophyll *a* fluorescence induction kinetics. –Photosynthetica **58**: 348-357, 2020.

Badr A., Brüggemann W.: Comparative analysis of drought stress response of maize genotypes using chlorophyll fluorescence measurements and leaf relative water content. – Photosynthetica **58**: 638-645, 2020.

Bantis F., Früchtenicht E., Graap J., Ströll S., Reininger N., Schäfer L., Pollastrini M., Holland V., Bussotti F., Radoglou K., Bruggemann W.: The JIP-test as a tool for forestry in times of climate change. – Photosynthetica **58**: 409-421, 2020.

Bednaříková M., Folgar-Cameán Y., Kučerová Z., Lazár D., Špundová M., Hájek J., Barták M.: Analysis of K- and L-band appearance in OJIPs in Antarctic lichens in low and high temperature. – Photosynthetica **58**: 646-656, 2020.

Blackhall V., Orioli G.A., Colavita M.G.: JIP-test parameters to study apple peel photosystem II behavior under high solar radiation stress during fruit development. – Photosynthetica **58**: 314-322, 2020.

Borawska-Jarmułowicz B., Mastalerczuk G., Dąbrowski D.P., Kalaji H.M., Wytrążek K.: Improving tolerance in seedlings of some Polish varieties of *Dactylis glomerata* to water deficit by application of simulated drought during seed germination. – Photosynthetica **58**: 540-548, 2020.

Cetner M.D., Kalaji H.M., Borucki W., Kowalczyk K.: Phosphorus deficiency affects the I-step of chlorophyll *a* fluorescence induction curve of radish. – Photosynthetica **58**: 671-681, 2020.

Chattopadhyay K., Vijayan J., Ray A., Chakraborty K., Sarkar R.K.: Additive main effect and digenic epistatic quantitative trait loci for chlorophyll fluorescence traits influencing salt tolerance at seedling stage in rice. – Photosynthetica **58**: 595-607, 2020.

Çicek N., Kalaji H.M., Ekmecki Y.: Probing the photosynthetic efficiency of some European and Anatolian Scots pine populations under UV-B radiation using polyphasic chlorophyll *a* fluorescence transient. – Photosynthetica **58**: 468-478, 2020.

Dimitrova S., Paunov M., Pavlova B., Dankov K., Kouzmanova M., Velikova V., Tsonev T., Kalaji H.M., Goltsev V.: Photosynthetic efficiency of two *Platanus orientalis* L. ecotypes exposed to moderately high temperature – JIP-test analysis. – Photosynthetica **58**: 657-670, 2020.

Faseela P., Sinisha A.K., Brestič M., Puthur J.T.: Chlorophyll *a* fluorescence parameters as indicators of a particular abiotic stress in rice. – Photosynthetica **58**: 293-300, 2020.

Galić V., Mazur M., Šimić D., Zdunić Z., Franić V.M.: Plant biomass in salt-stressed young maize plants can be modelled with photosynthetic performance. – Photosynthetica **58**: 194-204, 2020.

Gast A., Römermann C., Bucher S.F.: Seasonal variation and trade-off between frost resistance and photosynthetic performance in woody species. – Photosynthetica **58**: 331-340, 2020.

Guo Y., Zhang Y., Lu Y., Shi J., Chen S., Strasser R.J., Qiang S., Hu Z.: Effect of AtLFNR1 deficiency on chlorophyll *a* fluorescence rise kinetics OJIP of *Arabidopsis*. – Photosynthetica **58**: 391-398, 2020.

Hajihashemi S., Brestic M., Kalaji H.M., Skalicky M., Noedoost F.: Environmental pollution is reflected in the activity of the photosynthetic apparatus. – Photosynthetica **58**: 529-539, 2020.

Horaczek T., Dąbrowski P., Kalaji H.M., Baczewska-Dąbrowska A.H., Pietkiewicz S., Stępień W., Gozdowski D.: JIP-test as a tool for early detection of the macronutrients deficiency in *Miscanthus* plants. – Photosynthetica **58**: 507-517, 2020.

Hungsaprug K., Kojonna T., Samleepan M., Punchkhon C., Ut-Khao W., Kositsup B., Kasettranun W., Siangliw J.L., Toojinda T., Comai L., Plaimas K., Chadchawan S.: Chlorophyll fluorescence, leaf gas exchange, and genomic analysis of chromosome segment substitution rice lines exposed to drought stress. – Photosynthetica **58**: 214-227, 2020.

Iermak I., Szabó M, Zavafer A.: Analysis of OJIP transients during photoinactivation of photosystem II indicates the presence of multiple photosensitizers *in vivo* and *in vitro*. – Photosynthetica **58**: 497-506, 2020.

Janka E., Umetani I., Sposob M., Bakke R.: Photosynthesis response of microalgae (*Tetradesmus wisconsinensis*) to different inorganic carbon sources probed with chlorophyll fluorescence analysis. – Photosynthetica **58**: 236-244, 2020.

Jiménez-Francisco B., Stirbet A., Aguado-Santacruz G.A., Campos H., Conde-Martínez F.V., Padilla-Chacón D., Trejo C., Bernacchi C.J., Govindjee G.: A comparative chlorophyll *a* fluorescence study on isolated cells and intact leaves of *Bouteloua gracilis* (blue grama grass). – Photosynthetica **58**: 262-274, 2020.

Kalaji H.M., Goltsev V.: FOREWORD to the Special issue in honour of Prof. Reto J. Strasser. – Photosynthetica **58**: 1-5, 2020.

Keutgen N., Tomaszewska-Sowa M., Keutgen A.J.: Chlorophyll fluorescence of *Nicotiana tabacum* expressing the green fluorescent protein. – Photosynthetica **58**: 460-467, 2020.

Koller S., Holland V., Brüggemann W.: Seasonal monitoring of PSII functionality and relative chlorophyll content on a field site in two consecutive years: a case study of different oak species. – Photosynthetica **58**: 379-390, 2020.

Konôpková A., Húdoková H., Ježík M., Kurjak D., Jamnická G., Ditmarová Ľ., Gömöry D., Longauer R., Tognetti R., Pšidová E.: Origin rather than mild drought stress influenced chlorophyll *a* fluorescence in contrasting silver fir (*Abies alba* Mill.) provenances. – Photosynthetica **58**: 549-559, 2020.

Lenk S., Dieleman J.A., Lefebvre V., Heuvelink E., Magán J.J., Palloix A., Van Eeuwijk F.A., Barócsi A.: Phenotyping with fast fluorescence sensors approximates yield component measurements in pepper (*Capsicum annuum* L.) – Photosynthetica **58**: 622-637, 2020.

Perboni A.T., Martinazzo E.G., Moura A.B., Bacarin M.A.: Can be performance indexes used to select plant growth-promoting rhizobacteria? – Photosynthetica **58**: 253-261, 2020.

Petrova N., Paunov M., Stoichev S., Todinova S, Taneva S.G., Goltsev V., Krumova S.: Thylakoid membrane reorganization, induced by growth light intensity, affects the plants susceptibility to drought stress. – Photosynthetica **58**: 369-378, 2020.

Pires da Costa K.C., Kirmayr Jaquetti R., De Carvalho Gonçalves J.F.: Chlorophyll *a* fluorescence of *Bertholletia excelsa* Bonpl. plantations under thinning, liming, and phosphorus fertilization. – Photosynthetica **58**: 323-330, 2020.

Plyusnina T.Yu., Khruschev S.S., Degtereva N.S., Konyukhov I.V., Solovchenko A.E., Kouzmanova M., Goltsev V.N., Riznichenko G.Yu., Rubin A.B.: Gradual changes in the photosynthetic apparatus triggered by nitrogen depletion during microalgae cultivation in photobioreactor. – Photosynthetica **58**: 443-451, 2020.

Rastogi A., Kovar M., He X., Zivcak M., Kataria S., Kalaji H.M., Skalicky M., Ibrahimova U.F., Hussain S., Mbarki S., Brestic M.: JIP-test as a tool to identify salinity tolerance in sweet sorghum genotypes. – Photosynthetica **58**: 518-528, 2020.

Samborska-Skutnik I.A., Kalaji H.M., Sieczko L., Bąba W.: Structural and functional response of photosynthetic apparatus of radish plants to iron deficiency. – Photosynthetica **58**: 205-213, 2020.

Sitko K., Rusinowski S., Pogrzeba M., Daszkowska-Golec A., Gieroń Ż., Kalaji H.M., Malkowski E.: Development and aging of photosynthetic apparatus of *Vitis vinifera* L. during growing season. – Photosynthetica **58**: 186-193, 2020.

Skoczowski A., Rut G., Oliwa J., Kornas A.: Sporulation modifies the photosynthetic activity of sporotrophophyll leaves of *Platycerium bifurcatum*. – Photosynthetica **58**: 488-496, 2020.

Sunil B., Strasser R.J., Raghavendra A.S.: Targets of nitric oxide (NO) during modulation of photosystems in pea mesophyll protoplasts: studies using chlorophyll *a* fluorescence. – Photosynthetica **58**: 452-459, 2020.

Swoczyna T., Latocha P.: Monitoring seasonal damage of photosynthetic apparatus in mature street trees exposed to road-side salinity caused by heavy traffic. – Photosynthetica **58**: 573-584, 2020.

Swoczyna T., Mojski J., Baczewska-Dąbrowska A.H., Kalaji H.M., Elsheery N.I.: Can we predict winter survival in plants using chlorophyll *a* fluorescence? – Photosynthetica **58**: 433-442, 2020.

Tóth S.Z., Oukarroum A., Schansker G.: Probing the photosynthetic apparatus noninvasively in the laboratory of Reto Strasser in the countryside of Geneva between 2001 and 2009. – Photosynthetica **58**: 560-572, 2020.

Tsimilli-Michael M.: Revisiting JIP-test: an educative review on concepts, assumptions, approximations, definitions and terminology. – Photosynthetica **58**: 275-292, 2020.

Viljevac Vulvetić M., Španić V.: Characterization of photosynthetic performance during natural leaf senescence in winter wheat: multivariate analysis as a tool for phenotypic characterization. – Photosynthetica **58**: 301-313, 2020.

Voitsekhovskaja O.V., Apollonov V.I., Murtuzova A.V., Rabadanova C.K., Charnysh M.A., Drozdova I.V., Belyaeva A.I., Kovaleva O.N., Loskutov I.G., Pawlowski K., Demidchik V.V., Tyutereva E.V.: Photosynthetic activity as assessed *via* chlorophyll *a* fluorescence suggests a role of potassium channels in root to shoot signaling. – Photosynthetica **58**: 608-621, 2020.

Wu H.Y., Dong F.Q., Liu L.A., Shi L., Zhang W.F., Jiang C.D.: Dorsoventral variation in photosynthesis during leaf senescence probed by chlorophyll *a* fluorescence induction kinetics in cucumber and maize plants. – Photosynthetica **58**: 479-487, 2020.

Xiao W., Wang H., Liu W., Wang X., Guo Y., Strasser R.J., Qiang S., Chen S., Hu Z.: Action of alamethicin in photosystem II probed by the fast chlorophyll fluorescence rise kinetics and the JIP-test. – Photosynthetica **58**: 358-368, 2020.

Yang Y.-J., Liu T., Zhang S.-B., Huang W.: Photoinhibition of oxygen-evolving complex and photosystem II at chilling stress in the tropical tree species *Dalbergia odorifera*. – Photosynthetica **58**: 245-252, 2020.

Zagorchev L., Traianova A., Teofanova D., Li J., Kouzmanova M., Goltsev V.: Influence of *Cuscuta campestris* Yunck. on the photosynthetic activity of *Ipomoea tricolor* Cav. – *in vivo* chlorophyll *a* fluorescence assessment. – Photosynthetica **58**: 422-432, 2020.

Zhang H., Li X.Y., Chen L.-S., Huang Z.R.: The photosynthetic performance of two *Citrus* species under long-term aluminum treatment. – Photosynthetica **58**: 228-235, 2020.

Zhang H.H., Xu N., Li X., Han Y., Ren J.W., Li M.B., Zhai S., Yang R.Y., Teng Z.Y., Sun G.Y.: Effects of exogenous abscisic acid on the photosynthetic function and reactive oxygen species metabolism of tobacco leaves under drought stress. – Photosynthetica **58**: 585-594, 2020.

Zhang L.T., Xu R., Liu J.G.: Efficacy of botanical pesticide for rotifer extermination during the cultivation of *Nannochloropsis oculata* probed by chlorophyll *a* fluorescence transient. – Photosynthetica **58**: 341-347, 2020.

Zhipinova M., Paunov M., Anev S., Petrova N., Krumova S., Raycheva A., Goltsev V., Tzvetkova N., Taneva S., Sapunov K., Chaneva G.: JIP-test as a tool for early diagnostics of plant growth and flowering upon selected light recipe. – Photosynthetica **58**: 399-408, 2020.

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