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REVIEW ARTICLE

Chlorophyll fluorometry in evaluating photosynthetic performance: key limitations, possibilities, perspectives and alternatives

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Abstract Non-destructive methods for the assessment of photosynthetic parameters of plants are widely applied to evaluate rapidly the photosynthetic performance, plant health, and shifts in plant productivity induced by environmental and cultivation conditions. Most of these methods are based on measurements of chlorophyll fluorescence kinetics, particularly on pulse modulation (PAM) fluorometry. In this paper, fluorescence methods are critically discussed in regard to some their possibilities and limitations inherent to vascular plants and microalgae. Attention is paid to the potential errors related to the underestimation of thylakoidal cyclic electron transport and anoxygenic photosynthesis. PAM-methods are also observed considering the color-addressed measurements. Photoacoustic methods are discussed as an alternative and supplement to fluorometry. Novel Fourier modifications of PAM-fluorometry and photoacoustics are noted as tools allowing simultaneous application of a dual or multi frequency measuring light for one sample.

Keywords Fourier PAM · Multicolor PAM · Fourier photoacoustics · Anoxygenic photosynthesis · Quantum yield · Photosystem II

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Introduction

Photosynthesis is generally accepted to be a primary determinant of crop yield (Long et al. 2006; Simkin et al. 2019). Efforts to improve the photosynthetic performance of agricultural plants are being made through transgenic manipulations and breeding that require convenient and rapid methods allowing to assess the rate and effectiveness of photosynthesis (Baker and Rosenqvist 2004; Baker 2008). Evaluations of photosynthetic parameters are needed to predict current productivity and evaluate the consequences of the impact of environmental stress on agricultural plants (Narina et al. 2014). It is also necessary to control the photosynthetic effectiveness of microalgae cultivated in the bioreactors for biotechnological purposes (Havlik et al. 2022) and to evaluate the productivity of marine and freshwater bodies (Hughes et al. 2018). Photosynthetic parameters are also widely studied in microalgae cells as test objects for water quality monitoring (Czaplicka-Kotas and Lodowska 2014; Chen et al. 2021). Most of the rapid methods developed for assessing the photosynthetic performance of plants are based on the measurements of fluorescence kinetics (Zavafer et al. 2020). In this work, we are discussing their advantages, limitations, and perspectives and, in addition, discussing the photoacoustic methods as their alternative or supplement.

Evaluating photosynthetic performance and productivity of plants using fluorescence kinetic methods—a bit of basics

Primary light reactions are often considered as a main pattern of photosynthesis, determining the biomass accumulation rate, and, therefore, plant productivity. A number of efforts (reviewed by Walter and Kromdijk 2022) have been

undertaken to improve the light steps of photosynthesis and hence productivity of plants (including agricultural crops) by use of genetic engineering aimed at achieving the overexpression or knockout of the genes controlling processes in the thylakoid electron transport chain. Consequently, methods for evaluating the effectiveness of light reactions in photosynthesis are required to the assess results of such genetic manipulations. Most of these methods use the measurements of the chlorophyll fluorescence kinetics excited by turning the saturation or actinic light on.

The history of the application of chlorophyll fluorescence-based methods for the quantitative assessment of photosynthesis began with the pioneering work of Kautsky and Hirsch (1931). It was demonstrated, that the chlorophyll fluorescence emitted from the leaf rapidly increased in the first few seconds after turning the light on, and then gradually decreased within minutes. This effect (Kautsky effect) was later explained in terms of electron transport processes in the thylakoid membranes (Govindjee 2004). Being excited by the energy of visible light quanta, electrons of the P_{680} molecules have three ways to leave the excited orbital states: (i) return to the ground state of P_{680} and emit fluorescence, (ii) transfer to the pheophytin, Q_A, and the subsequent electron carriers providing energy for the photochemical processes (Govindjee 2004; Krause and Jahns 2004), and (iii) transfer to the O_2 molecules, providing the superoxide-ion, O_2^{*-} (Kozuleva et al. 2020)**.** Kautsky effect is determined by the first two possibilities. Thylakoid electron transfer, especially the non-cyclic (linear, LET) electron transport cannot start immediately after turning the actinic light on because it requires an electron sink from the electron transport chain. It means that the first few seconds of reaction centers of PSII are closed and the fluorescence attains its peak value (F_p). In the first few minutes, it declines to achieve a steady-state level (F_{st}) mainly as a result of the photochemical quenching (Govindjee 2004; Krause and Jahns 2004).

The simplest way to evaluate photosynthesis by fluorescence kinetics (excited by continuous actinic light) is to calculate the ratio of the fluorescence decrease:

$$R_{fd} = \left(F_p - F_{st}\right)/F_{st} \quad (1)$$

where F_p is a peak (maximal) fluorescence value achieved during the first 1–3 s and F_{st} is a steady-state fluorescence usually achieved 5–6 min after turning the continuous actinic light on.

The value of R_{fd} (also called as "vitability index") is considered an appropriate index for assessing the photosynthetic performance and correlates with CO_2 assimilation rates (Lichtenthaler et al. 2007; Lichtenthaler et al. 2021). However, F_p reflects the dark-adapted state of plants because it is measured after dark adaptation, whereas F_{st} relates to the light adapted state. This evidently may lead to uncertainty in the physiological interpretations of the R_{fd} parameter because it's impossible to define what state it refers to.

Measurement of the chlorophyll fluorescence parameters based on a pulse amplitude modulation (PAM) method is another method that has become much more widespread than the measurements of fluorescence kinetics excited by continuous light. It implies the possibility of separation of the chlorophyll fluorescence signal excited by alternating, extremely low (about 0.1 µmol photons m^{-2} c^{-1}) measuring light from the continuous background fluorescence excited either under actinic or saturating light (Schreiber 2004). In other words, PAM-fluorometer detects only the alternating component of the fluorescence signal. It allows measuring how much the fluorescence excited by the measuring light is quenched in the absence of other light sources or in the presence of actinic or saturating light. The saturating light is assumed to be an instrument for "turning off" photosynthesis excited by the measuring light, when photons of measuring light excite P_{680} and P_{700}, but excitation energy cannot be utilized for the photochemistry as far as the ETC is overloaded in consequence of application of the saturating light (Kalaji et al. 2017). Thus, the fluorescence excited by measuring light in the absence of other light sources is minimal (F_0), and in the presence of saturating light it is maximal (F_m). The value F_m–F_0 is the so called "variable fluorescence", and the value F_v/F_m is the "maximal quantum yield of photosystem II for the dark-adapted states" (Schreiber 2004). This parameter is widely used for evaluating the plant stress response (Ibaraki and Murakami 2007) or even the maximal photosynthetic productivity of plants (Kramer and Evans 2011; Nemeskéri et al. 2019). At that time, the "maximal fluorescence", F_m, as well as the F_v/F_m, cannot be determined strictly as far as they may depend on the adaptation (light or dark) state of PSII and, besides, F_v/F_m value has a very poor correlation with the oxygen evolution rate (Sipka et al. 2021). It may be partially explained to be due to the existence of a dark adapted charge-separated closed state and light-adapted charge-separated state of PSII ($PSII_C$ and $PSII_L$, respectively) (Sipka et al. 2021). The F'_v/F'_m parameter, in contrast to F_v/F_m, is measured in plants adapted to the actinic light (Krause and Jahns 2004; Govindjee 2004). F'_v/F'_m and ETR (electron transport rate) values, being both related to the light adapted states, show a better correlation with the O_2 evolution, than F_v/F_m, but they still often remain non-linear (Kalaji et al. 2017).

Moreover, PAM fluorescence measurements may be represented by two methods which lead to different F_v/F_m and F'_v/F'_m values: (i) based on the multiple turnover (MT) excitation and (ii) on the single turnover (ST) excitation. MT-method uses relatively long (0.1–0.5 s) saturating flashes that result in the reduction of the primary (Q_A), secondary (Q_B) electron acceptors and, probably, of a part of the subsequent electron carriers. ST-method measures the

fluorescence transients induced by a series of brief subsaturating excitation pulses, or "flashlets", composing a single turnover flash short enough and just sufficient to cause a single reduction of all the primary acceptor molecules, Q_A (Kromkamp and Forster 2003). See also Sect. 3.

A general problem of the fluorescence-based methods applied for the indirect quantitative evaluations (predictions) of photosynthetic productivity is that fluorescence corresponds only to about 1/10—1/9 of the energy utilized in photosynthesis (Buonasera et al. 2011).

Difficulties and limitations of PAM-fluorometry: microalgae

Necessity of the extensive monitoring of the microalgae photosynthetic productivity is determined both by the development of local and global ecological models of water bodies for environmental purposes (Vasechkina 2020; Mattei et al. 2021) and for the evaluations of the food supply for fishery resources (Fu et al. 2020). In addition, parameters of microalgae productivity are important in biotechnology, where the cultivation of the green unicellular alga *Chlorella* has become widespread (Chauhan et al. 2020; Raji et al. 2020; Ru et al. 2020). The use of *Chlorella* as an object of fundamental science has led to a number of major discoveries in the field of photosynthesis (Nickelsen 2010), the necessary link of which was often associated with the assessment of the CO_2 assimilation rate.

The advantage of using microalgae in fundamental photosynthesis studies over terrestrial plants is the ability to easily measure CO_2 assimilation by the radiocarbon method. Accurate dosing of ^{14}C label can be carried out by adding $NaH^{14}CO_3$ to the liquid medium for microalgae cultivation (Camargo et al. 2022; Kromkamp et al. 2017), while radiocarbon treatment of the terrestrial plants is possible only from a gaseous medium that creates additional experimental difficulties and brings an uncertainty related to the degree of stomata opening. Easy detection of the ^{14}C label assimilated by microalgae (sedimentation on the filter) provides the conditions for processing a large number of samples. In this regard, the comparative estimates of the photosynthetic productivity by direct (radiocarbon) and indirect (fluorescent) methods using microalgae are of particular interest (Camargo et al. 2022).

For the purpose of fluorescent measurements of the PSII quantum yield in microalgae, researchers apply multiple turnovers (MT, traditional PAM), and a single turnover (ST) method (see Sect. 2). Camargo et al. (2022) compared PAM fluorometry (MT method) with radiocarbon technique for the determination of inorganic carbon fixation in *Chlorella vulgaris*. Authors calculated chlorophyll-specific carbon fixation rate (P^B, μmol C [mg chl *a*]$^{-1}$ h^{-1}) using radiocarbon method, and calculated ETR (μmol e$^-$ [mg chl *a*]$^{-1}$ h^{-1}) in accordance with Eq. 2, further obtaining the electron yield for carbon fixation from these two values as $\Phi_e = P^B/ETR$. In this work, for the undersaturating PPFD, Φ_e was shown to be about 0.37 whereas theoretically it cannot exceed 0.25 considering four charge separations occurring in PSII for each realized O_2 molecule (Gilbert et al. 2000) and, therefore, for each assimilated CO_2 molecule as far, as the photosynthetic O_2/CO_2 ratio is very close to 1 (Kaplan and Björkman 1980). If we take into account that the fraction of absorbed light which is transferred to PSII is 0.5, as it is generally assumed considering a 1:1 ratio between PSII and PSI (Perkins et al. 2002), then the theoretical Φ_e value cannot exceed 0.125 (Gilbert et al. 2000). However, there are significantly lower Φ_e values varied below this maximum in the microalgae studied within a number of works: from 0.02–0.04 (Schofield et al. 1996), from 0.003 to 0.009 (Moisan and Mitchell 1999), from 0.02 to 0.87 (other works were reviewed by Lawrenz et al. 2013). It follows that microalgae productivity, if expressed as $P^B = ETR \times \Phi_e$, cannot be calculated using the theoretical value $\Phi_e = 0.125$, and, therefore, the necessary calibration should be performed by the radiocarbon method before the application of the fluorescence methods each time when they are applied to the particular algae species and environmental conditions.

In addition, ETR determination in the microalgae is also a weak point in the calculations of P^B. Thus, the following equation is generally applied (Kromkamp and Forster 2003) if calculating on the basis of MT-method:

$$ETR = F'_v/F'_m \cdot E\ 0.5a* \quad (2)$$

where E is the incident irradiance (μmol photons m^{-1}), and a* is the chlorophyll-specific absorption cross-section (m^2 mg chl a^{-1}), which may be calculated as: = 2.303 × OD/l with 2.303 being the transformation factor of decimal to natural logarithm, l—the path length in m through the suspension, and OD—the average (400–700 nm) optical density measured with an UV/VIS spectrophotometer (Cosgrove and Borowitzka 2010; Figueroa et al. 2013; Camargo et al. 2022). Note that Eq. (2) is applicable only for the diluted suspensions of microalgae, but not for the plant leaves. The cause of this is that leaves have a very strong scattering, whose contribution is difficult to evaluate even using chlorophylless leaf sectors (from variegated leaves, for example) as a blank. Thus, those quanta that are scattered in the chlorophylless leaf may be not scattered in the green leaf as they may be absorbed before. In addition, mean path-length of light is increased in the chlorophylless tissues compared to that of green leaf tissues. It means that strong scattering and absorption are not additive values and absorption cannot be corrected by scattering using a simple subtraction (Macnicol et al. 1976). Consequently, microalgae may often be a more

suitable object for the fundamental studies of energy dissipation processes in photosynthesis, than leaves.

In contrast to the MT-method, which uses values of the optical absorption cross section, a*, the ST method uses the functional absorption cross section, σ_{PSII}. The latter, as well as fluorescence kinetic parameters (F_v/F_m, F'_v/F'_m) can be calculated from the fluorescence transients excited in microalgae with the ST-flashes applying numerical iterative methods (Kolber et al. 1998).

Optical and functional absorption sections are connected by a simple equation:

$$\sigma_{PSII} = a * \times \Phi_T \quad (3)$$

where Φ_T is the trapping efficiency.

Note, that a* is the probability that photons will be absorbed by antenna complexes, whereas σ_{PSII} reflects the probability that photons will be involved in the charge separation in ETC. Moreover, ST and MT methods give different results in evaluating F_v/F_m, F'_v/F'_m and ETR because the maximum level of fluorescence, F_m, is about 50% higher during a prolonged, multiple turnover flash ($F_{m(MT)}$) than during a single turnover flash ($F_{m(ST)}$) (Kromkamp and Forster 2003). Difference between $F_{m(MT)}$ and $F_{m(ST)}$ is caused by the reduction of the secondary electron acceptors Q_B and plastoquinone pool (PQ) during MT-flash (saturating pulse) (Kromkamp and Forster 2003). It assumes, however, that electron sink from PQ is low or absent during the MT-flash (0.1–0.5 s) which may not be the case because of the simultaneous excitation of P700 and the beginning of the PSI activity. In addition, there is a PSI-independent electron sink from PQ, related to the plastid terminal oxidase (PTOX) activity and cyclic electron transport around PSII (CET-PSII, See Sect. 6). Quantitative participation of the last two processes at the early stage of ETC functioning after turning the actinic light on is an unknown and little bit known even during the steady-state photosynthesis. In this connection it should be noted that observations of F_v/F_m using ST-method (as it depends on σPSII) are more difficult to interpret than observations of F_v/F_m obtained using the MT-method (as it depends on a*), because σPSII is sensitive to the light history, nutrient status and displays species-specific variability of microalgae cells (Falkowski et al. 1992; Kolber et al. 1998; Moore et al. 2003).

Efforts to improve $ETR_{(ST)}$ parameter for the microalgae studies have led to the introduction of parameter of the amplitude-based electron transport rate, ETR_a, which is an ETR normalized by F_v/F_m (Schuback et al. 2021; Sezginer et al. 2021, Eq. (4)):

$$ETR_a = PAR \times \sigma_{PSII} \times \left(F'_v/F'_m\right)/\left(F_v/F_m\right) \times 6.022 \times 10^{-3}\left(\text{in } e^{-}s^{-1}RCII^{-1}\right) \quad (4)$$

The constant 6.022×10^{-3} converts σPSII units from $Å^2$ $PSII^{-1}$ to m^2 PS^{-1} and PPFD from μmol quanta to quanta.

The issue of such an approach is, however, that F_v/F_m and F'_v/F'_m relate to different adapted states: light-adapted and dark-adapted, respectively. In addition, F_v/F_m correlates very poorly with CO_2 assimilation rate (Sipka et al. 2021). Some part of the photosynthetic activity revealed using F_v/F_m and F'_v/F'_m values may reflect anoxygenic photosynthesis thus being weakly related to the plant productivity (see Sect. 6 below).

An additional problem in the interpretation of PAM fluorescence data in terms of the microalgae productivity is that they are calibrated by the radiocarbon method, which itself may lead to ambiguous results. Thus, it's still unclear whether this incubation method is a measure of gross primary production, net primary production or some value in between (Quay et al. 2010). Besides, it was criticized regarding the effects of incubation, respiration, activities of heterotrophs, and regarding that the biochemistry of the ^{14}C is not completely understood (Marra et al. 2021).

Difficulties and limitations of PAM-fluorometry: leaves of vascular plants

Compared to algae, measurements of photosynthetic productivity in vascular plants face difficulties and uncertainties caused by strong and uneven light absorption throughout the leaf thickness and also caused by shifts in stomata opening that hamper interpretations of the results obtained. Thus, while the diluted suspensions of microalgae are exposed under PPFD comparable within the thickness of the measuring cuvette (chamber), the leaves absorb blue and red light mostly by their upper cell layers. For example, under blue light, $^{14}CO_2$ fixation and light absorption in spinach leaves (thickness of 700 μm) by the upper cells is three times more intense than that of the medium cell layers (depth of 300 μm) and 15–20 times more intense than that of the lower layers (depth of 500 μm) (Evans and Vogelman 2003). Absorption profiles obtained for the red light only slightly differ from those obtained for the blue light (Smith et al. 2017). In this connection, it might seem an enigma, why plants have thick leaves and dense crowns, if ignore the green light, profiles of which are much more even across the leaf. Having lower molar extinction coefficients, green light penetrates deeper into the leaf thus providing light conditions enough to maintain physiologically sufficient levels of photosynthesis in the lower cell layers (Liu and van Iersel 2021). However, the most of the standard PAM-fluorometers use red and, more rarely, blue measuring light (Figueroa et al. 2013). It obviously results in ignoring photosynthetic processes in the lower cell layers of leaves (spongy mesophyll)

when evaluating photosynthetic productivity of leaves using methods based on the fluorescence kinetics measurements.

Studies on the quantum yields of PSII are often carried out on trees and shrubs to evaluate their photosynthetic performance, productivity (Murchie and Lawson 2013; Uhrin et al. 2018; González-Rodríguez et al. 2019) health, response to the soil pollution (Bęś et al. 2019), climatic stress conditions (Špulák and Martincová 2015) and to the other stress factors (Murchie and Lawson 2013). At the same time, it is unclear how much the photosynthetic parameters of leaves (needles) of different age, located in the different parts of crowns may be indicative in assessing photosynthetic performance of the whole plant. Only a small number of works have been devoted to the fluorescence kinetics parameters of sun and shade leaves in relation to their physiology (Kitao et al. 2006; Lichtenthaler et al. 2007; Slot et al. 2019).

Evaluation of photosynthetic performance of the leaves using the chlorophyll fluorescence measurements may be an informative method only if to compare the leaves having similar physiological characteristics, for example, for the intraspecific comparison of leaves of different ages or the interspecific comparison of leaves under the same light environments. (Miyazawa and Yahata 2006).

It is interesting, that light-green plants of the sunflower plastome mutant lines *Chlorina*, having only about 30% of normal chlorophyll content in leaves, may outperform the normal sunflower plants in productivity (by total and seed mass) under conditions of drought and salt stress (Mashkina et al. 2006).

From the above, it follows that the application of photosynthetic parameters of leaves for assessment of productivity (or even photosynthetic performance) of the whole plants or plant communities may be reliable only with the complex consideration of the physiological patterns of plants and the presence of environmental stress factors if any.

Of course, the evaluation of the photosynthetica parameters of leaves may be of interest from the point of view of the leaf physiology in itself. In this connection, the photosynthetic heterogeneity of leaves across their area seems to be poorly studied although some research showed a significant nonuniformity of distribution of the chlorophyll fluorescence kinetic parameters imaged in the leaves of both variegated (having chlorophyll-deficient leaf sectors) (Lysenko 2012, Fig. 1) and normal plants (Lichtenthaller et al. 2007; Lichtenthaller 2021). See Fig. 1. The latter method (Lysenko 2012) also allows obtaining photoinduction curves from regions of interest (from leaf), ROI, selected at any frame of video.

Imaging of R_{fd} in the dark-adapted leaves may be performed using a 5-min video recording of leaf fluorescence at 680–740 nm excited in response to turning the actinic light on. To calculate pixel values of

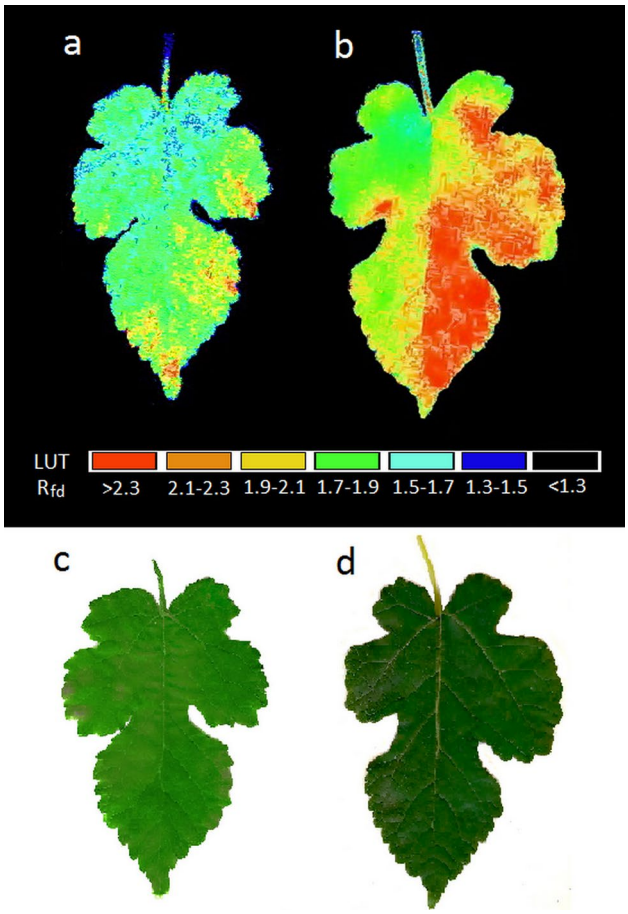


Fig. 1 Imaging of the ratio of fluorescence decrease rate values (R_{fd}) distributed over the areas of a light-green young leaf (**a**) and dark-green old leaf (**b**) of *Morus alba* L. The reference colors are given using a lookup table (LUT). Fluorescence was monitored at 740 nm through an interference filter and excited by blue light, $\lambda = 465$ nm. The corresponding images of the same original leaves under white light are shown below (**c**, **d**). The imaging was performed using the method of Lysenko (2012). Unpublished data

$R_{fd} = (F_p - F_{st})/F_{st} = F_p/F_{st} - 1$, the image obtained at the peak fluorescence, F_p, i.e. obtained shortly after turning the actinic light on, is divided, pixel-to-pixel, by the image obtained at the end of the video, at the steady-state fluorescence, F_{st}, with the subsequent subtraction of the unit. Such imaging may be carried out using specialized fluorescence-imaging systems and software (Lichtenthaller et al. 2007; Lichtenthaller 2021) or using standard far-red sensitive cameras with free software (VirtualDub, ImageJ) (Lysenko 2012). Imaging of the area distribution of F_v/F_m value (or related parameters) is also possible and more frequently applied than R_{fd} (see review: Rühle et al. 2018).

Color-addressed evaluations of photosynthetic performance and perspectives of Fourier PAM-fluorometry

Evaluations of the photosynthetic performance of plants based on the CO_2 assimilation measurements of more than 30 agricultural plant species showed that the highest CO_2 assimilation (per PPFD and leaf square) level was observed under red light, medium level—under green light and the lowest level—under blue light (Inada 1976).

The effectiveness of PSII in leaves is dependent on the wavelength of exciting light in the range from 450 to 690 nm (Pfündel 2009). The wavelength of light influences the growth, ultrastructure, and fluorescence kinetics parameters of agricultural and wild plants depending on plant species (Gao et al. 2020; Santabarbara et al. 2020). It requires the application of specialized devices capable to measure photosynthetic performance at the different wavelengths of exciting light.

Color-addressed measurements of fluorescence kinetics (F_v/F_m, F_v/F_m, ETR and other related parameters) may be performed using the multicolor fluorometers MULTI-COLOR-PAM and PHYTO-PAM (Waltz, Effeltrich, Germany) which, however, cannot simultaneously work with two or more sources of measuring light of different wavelengths (Shreiber et al. 2012; Szabó et al. 2014). In contrast, Fast-Fourier transform (FFT) PAM-fluorometry allows simultaneous measurement of these parameters in one sample, being a low-cost method at that. It requires only sources of measuring, actinic and saturating light of different wavelengths, photodiode, PC sound card and standard software (SpectraPlus or SpectraPro). Measuring lights of different colors are applied at different (specified) frequencies (see Fig. 2:f1 and f2).

A mixed frequency fluorescence signal (Fig. 2a) is processed step-by-step in real time. During each step (about 0.2–0.7 s) FFT-software collects data massive of a specified number of readings (FFT-size) and calculates a FFT-spectrum from which the amplitudes of the applied frequencies may also be calculated. At each such a step, every 0.2–0.7 s, the FFT-processing software save the signal amplitude values of the specified frequencies into a log (*.xlsx) file, wherefrom the photoinduction curves, F_v/F_m, F'_v/F'_m and ETR values may easily be obtained for each applied frequency, i.e. for each color of the measuring light (Lysenko et al. 2018, 2020). It has been demonstrated that FFT-PAM fluorometry can be efficiently and easily performed in the experiments where the measuring lights of different colors are cross-combined with actinic lights and saturation pulses of different colors. Thus, the blue saturation pulse was applied shortly after the red saturation pulse, and in reverse order. Coefficients of chromatic divergence of quantum yield of PSII were calculated as a ratio of the quantum yields

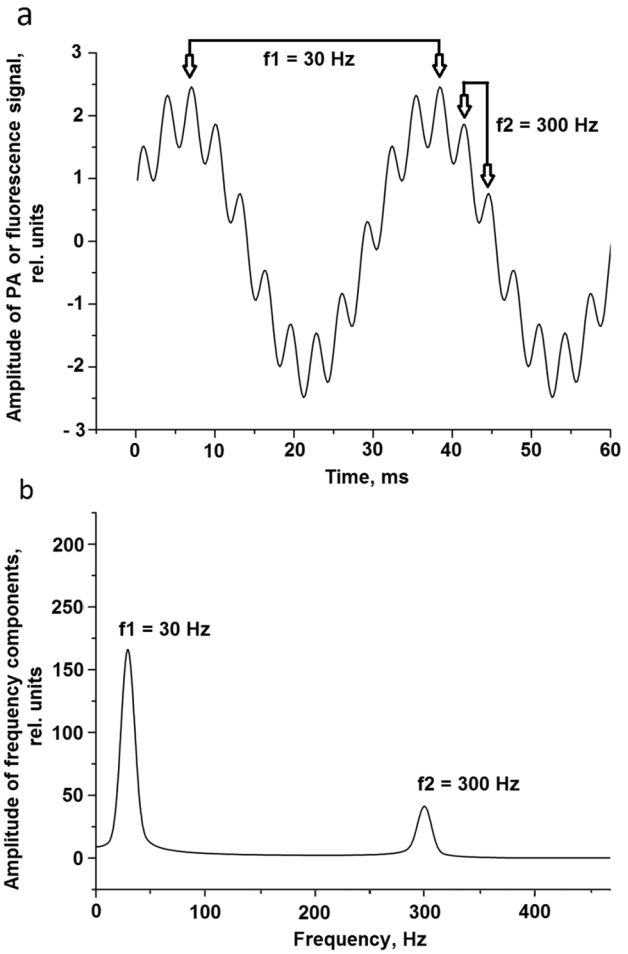


Fig. 2 Principle of the application of fast Fourier transform (FFT) to the PAM fluorometry and photoacoustics. **a** mixed fluorescence or PA-signal in the time domain simultaneously excited in one sample by two sources of measuring light with frequencies f1 and f2; **b** single FFT-spectrum (in the frequency domain) calculated every 0.7 s from a number of amplitude readings (data massive; for example, 131,072 readings in 0.7 s). Respectively, the program saves the peak values of the amplitudes at f1 and f2 frequencies (see panel b) every 0.7 s in a log file (*.xlsx), from which the photoinduction curves may easily be obtained. When the bicolor Fourier modification of PAM-fluorometry is applied, f1 and f2 may be, for example, 340 (blue light) and 360 Hz (red light). When the Fourier photoacoustics is applied, f1 and f2 may be 20–30 and 250–300 Hz, where 20–30 Hz corresponds mainly to the photobaric signal, and 250–350 Hz—to the photothermal signal (see the text)

of PSII in leaves obtained by red measuring light to that obtained by blue measuring light (Lysenko et al. 2018). They were found to be non-unit in the *Ficus benjamina* leaves and were increased after the adaptation of plants under blue (but not under red) light (Lysenko et al. 2018).

It cannot be excluded, that the observed chromatic adaptation of PSII to the blue light may be related to the following causes: (i) photoinhibition of PSII induced by blue light is higher than that by red light (Schreiber and Klughammer

2013); (ii) effects of phytochrome system which is sensitive to the red/far-red light and cryptochrome system which is sensitive to the blue light (Yu et al. 2010; Guo et al. 2016); (iii) effects of blue light-induced chloroplast movement (Baránková et al. 2016) as far as it known to be a factor influencing chlorophyll fluorescence kinetics (Pfündel et al. 2018).

Thus, the measuring wavelength, actinic and saturating light sources should be considered when evaluating the photosynthetic performance and productivity of plants. Unfortunately, as we mentioned above (Sect. 4), most of the manufactured PAM-fluorometers are not capable to operate with two or more colors of measuring, actinic and saturating light.

A special interest in the application of FFT PAM-fluorometry lies in the possibility of its unification with FFT photoacoustics (see below) which undoubtedly is an intriguing perspective in plant physiology.

A main problem of PAM-fluorometry: anoxygenic photosynthesis

Uncertainty in evaluations of the proportion between oxygenic and anoxygenic photosynthesis in vascular plants and green algae is the main challenge in questioning the applicability of the fluorescence kinetic methods for the assessment of plant photosynthetic performance and productivity.

The existing approach to the interpretation of the fluorescence-based photosynthetic parameters in terms of plant productivity commonly assumes that photosynthesis in vascular plants and green algae is mainly an oxygenic process originating from the non-cyclic (linear) thylakoidal electron transport (LET) (Baker 2008). It implies that fluorescence kinetics appears mainly due to the PSII activity, also considering that PSII is functioning within the linear ETC being coupled with PSI, thus providing reductant NADPH necessary for the activity of Calvin-Benson cycle, CO_2 assimilation, and therefore, keeping the productivity of plants at the levels required for their life (Govindjee 2004; Krause and Jahns 2004).

However, thylakoidal electron transport cannot be 100% linear. For example, one of the causes of this is that transfer of 4 electrons throughout LET produces 2 NADPH molecules and is coupled to the pumping of 12 protons into the thylakoid, whereas Calvin–Benson cycle needs 14 protons pumped to utilize these 2 NADPH molecules considering requirements in ATP. Therefore, two additional protons should be pumped through a photosynthetic process to meet the requirements of CO_2 (see review: Rochaix 2011). It is photosynthesis, based on the cyclic electron transport, for instance, around PSII (CET-PSII) or PSI (CET-PSI). There are also many other physiological functions of CET in plants (Rochaix 2011; Shinopoulos and Brudvig 2012; Lysenko et al. 2017). PSI, in contrast to the PSII, cannot drive chlorophyll fluorescence kinetics, and, therefore, its activity cannot be assessed by the F_v/F_m value, using conventional PAM-fluorometers (Govindjee 2004; Blankenship 2021). Thus, the uncertainty in the assessment of the CET-PSII and CET-PSI contribution may lead to uncertainty in the fluorescence-based evaluation of the total photosynthetic performance related to CO_2 assimilation. In addition, CET-PSII is much less investigated compared to CET-PSI (Lysenko et al. 2017). On one hand, it may be strongly underestimated and on the other hand it weakly (indirectly) promotes plant growth and CO_2 assimilation, supporting primarily the energetic status-quo of living plants (Shinopoulos and Brudvig 2012; Lysenko et al. 2017; Lysenko and Varduny 2022). Thus, evaluations of the CET-PSII may be the most significant source of errors in the assessment of total photosynthesis and productivity.

CET-PSII is known since the former work of Sinclair et al. (1979) where it was shown as a process embracing the reversed electron flux in PSII from the acceptor to donor side by a pathway $P_{680} \rightarrow QA \rightarrow QB \rightarrow PQ \rightarrow$ (Cyt b_{559}) $\rightarrow Z \rightarrow P_{680}$. In this sequence, cytochrome b_{559} is a specific electron carrier that is not involved in the linear electron flow (Pospíšil 2011). CET-PSII in green algae and vascular plants may be referred to as anoxygenic photosynthesis in a broad sense (Lysenko and Varduny 2022), in contrast to the specific electron transport process in the photosynthesizing bacteria which is known as anoxygenic photosynthesis in a narrow sense (Pal et al. 2020; Blankenship 2021). Both these processes may be considered a true anoxygenic photosynthesis as they do not support water photolysis and oxygen evolution. In contrast, quasi-anoxygenic photosynthesis may be classified as a part of the thylakoid electron transport, that supports water photolysis, but that is compensated by various processes of oxygen uptake: photorespiration, respiration, Mehler cycle, PTOX activity, and rerouting of reducing power to the mitochondria (Lysenko and Varduny 2022).

In addition, some models have been proposed to demonstrate the possibility of the CET-PSII functioning without providing ΔpH^+ and ATP. These models are based on the following electron transport pathways: $P_{680} \rightarrow$ Pheophytin $\rightarrow Q_A \rightarrow Q_B \rightarrow ChI_Z \rightarrow P_{680}$ (Buser et al. 1992; Pospíšil 2011) or $P_{680} \rightarrow$ Pheophytin $\rightarrow Q_A \rightarrow Q_B \rightarrow Chl_Z \rightarrow$ (LP Cyt b_{559}) $\rightarrow P_{680}$ (Prasil 1996) where ChlZ is an accessory pigment and LP $Cytb_{559}$ is a low potential form of Cyt b_{559}.

However, CET-PSII pathways, independent of whether they can be related to the ΔpH^+ and ATP generation, may have an indirect influence on plant productivity as far as they play their role in protection against photoinhibition (Hamilton et al. 2014; Gu et al. 2015).

The problem is that standard PAM-fluorometers cannot distinguish whether the PSII quantum yield originates from the PSII functioning in the linear mode or the cyclic mode,

and, respectively, between oxygenic and anoxygenic photosynthesis. Moreover, quantifying the CET-PSII is a difficult task and its portion in the total photosynthesis mostly remains unknown, often being a subject of controversy. Thus, an unexpected conclusion on the CET-PSII activity may be drawn from the efforts to measure CET-PSI rates in higher plants using Antimycin A. Initially, it has been shown as an inhibitor of CET-PSI (Moss and Bendall 1984; Ivanov et al. 1998). Using Antimycin A, Kou et al. (2013) assumed that CET-PSI in the spinach leaves is almost equal to LET under full-sun irradiance. Similarly, it was also proposed that CET-PSI was about 50% of LET in *Arabidopsis* leaves under low light (Kou et al. 2015). Later, Takagi et al. (2019) demonstrated that Antimycin A inhibits the CET-PSII via cytochrome b_{559}, but not the CET-PSI. Based on this, it can be concluded that CET-PSII is quite matched with LET at least in some plant species.

A general approach to evaluate CET-PSII may be to compare PSII quantum yields obtained using PAM-fluorometry and measurements of CO_2 assimilation/O_2 evolution rates. In several studies, CET-PSII activity was revealed by combining chlorophyll fluorescence methods with the analysis of O_2 evolution using Clark electrodes (Falkowski et al. 1986; Prasil et al. 1996; Lavaud et al. 2002; Feikema et al. 2006). However, the evaluation of CET-PSII in such experiments may be overestimated due to the quasi-anoxygenic photosynthesis.

Although the increase of CET-PSII in and of itself, or in addition to O_2/CO_2 measurements, is out of sense from the point of view of the productivity assessment, because the quantitative determination of O_2 evolution (or CO_2 assimilation) is a good single-applied, self-sufficient and general characteristic of productivity.

If we consider plant productivity as some difference between CO_2 assimilation and CO_2 evolution, as well as between O_2 evolution and O_2 uptake, it is important to know, besides this difference, how intensive these processes are if we evaluate them by their absolute values, i.e., how high the level of the dynamic equilibrium is. At the high equilibrium level, plants will convert most parts of the energy of quanta into heat despite these quanta being primarily utilized in the photochemical processes. Thus, for example, it is evident, that under high PPFD, a certain level of productivity may theoretically be achieved at high levels of O_2 evolution and O_2 uptake, but with low effectiveness of the final quanta utilization. Therefore, high equilibrium states of productivity require elevated levels of PPFD compared to the levels necessary for the low equilibrium states at the same productivity. From this point of view, rates of anoxygenic photosynthesis seem to be important to evaluate the "light cost" of productivity. Obviously, it is desirable to have a parameter of "anoxygenity" of photosynthesis reflecting a "pure" oxygen evolution originating from the water photolysis, which rate, in turn, may be compared to the net O_2 evolution to measure the difference between them—quasi-anoxygenic photosynthesis.

However, only one method is known to be suitable for the determination of "pure" photolytic oxygen evolution, and it is photoacoustics (see below).

Photoacoustics—an alternative and supplement to fluorescence kinetic methods

Photoacoustic methods are based on the detection mainly of three different types of photoacoustic signals: (i) photothermal signals; (ii) photobaric signals and (iii) signals originating from pohotoinduced molecular volume changes. The third type of signal is excited by only picosecond and femtosecond lasers and detected by piezoceramic sensors. They are studied in the research of separate chemical (biochemical) reactions, their enthalpy, and entropy, and changes in molecular conformations, including that occurred in photosynthesis (Hou and Mauzerall 2011). We do not discuss this third kind of photoacoustics in our review as it does not apply to evaluations of the overall photosynthetic performance or(and) oxygen evolution.

Photothermal signal is a result of absorption of light pulse quanta that causes generating alternate heating and cooling of outer layers of the sample followed by alternate heating and cooling, expansion, and compression of the surrounding gaseous medium. Photobaric signal is generated in the photodependent chemical (biochemical) reactions accompanied by the evolution of gaseous reaction products. It may be a photosynthetic oxygen evolution.

Photoacoustics based on measurements of the photothermal and photobaric signals is a powerful tool for evaluating photosynthetic activity that has not yet exhausted its potential. It involves the use of a transparent PA-cell in which the samples of plant tissues are placed. The PA-cell is communicated with an electret microphone commonly connected with a selective lock-in amplifier and PC data processing system. Samples are illuminated with a low PPFD, amplitude-modulated (pulsed) measuring light exciting an acoustic signal in the sample. At 200–400 Hz, if there are no photochemical processes in the sample, the absorbed light energy is mainly converted to heat and to an acoustic signal (photothermal signal) generated due to the pulse heating of the surface, and a minor part—to the fluorescence (Malkin, Canaani 1994). If there are photochemical processes in the sample, some portion of the energy of absorbed quanta becomes inaccessible for conversion to heat (and, therefore, to the acoustic signal) because it is transformed into the energy of chemical bonds—absolute photochemical energy storage, ES' (Havaux 1998; Buschmann 1999; Delosme 2003; Hou and Sakmar 2010; Pinchasov-Grinblat and Dubinsky 2013). As

result, the PA-signal appears to be lowered reaching a $\boldsymbol{PA}_0$ value. When applying strong background (non-modulated) light, the photosynthesis becomes saturated and PA-signal increases up to its maximal value, $\boldsymbol{PA}_m$. The relative value characterizing energy storage is commonly accepted as: $ES = ES'/\boldsymbol{PA}_m = (\boldsymbol{PA}_m - \boldsymbol{PA}_0)/\boldsymbol{PA}_m$. ES represents a portion of the absorbed light energy that is utilized in photochemistry. It is very important that ES is a value comprising the total photosynthesis, oxygenic and anoxygenic, and PA-method, therefore, is the only direct method for assessing total photosynthesis, including PSII and PSI activity (Lysenko and Varduny 2022). When applying far-red light, it excites only PSI (Joët et al. 2002; Zhen and Bugbee 2020), excluding two cases of laser excitation (Pettai et al. 2005; Thapper et al. 2009), which however may be due to a two-photon excitation (Leupold et al. 2022), and, therefore, PA-method allows to selectively measure only CET-PSI activity (Joët et al. 2002). Generally, ES value may vary in the range with the upper limit of about 0.4.

At that time, if the frequency of measuring light falls in the range of 20–40 Hz, the PA-signal begins to be mainly photobaric, depending mostly on O_2 evolution, as far, as the latter begins to pulsate (Frandas et al. 1997; Veljović-Jovanović et al. 2016; Gordillo-Delgado and Botero-Zuluaga 2020). In contrast, at frequencies of about 200–400 Hz, O_2 evolution is detected as continuous, and photobaric signal no longer contributes to the total photoacoustic signal. Photobaric signal oscillates in the opposite phase to the photothermal signal and exceeds it in amplitude by approximately 8–10 times (Bults et al. 1982; Canaani et al. 1988; Buschmann 1999).

The most intriguing possibility of the PA-method is that the PA-signal at 20–40 Hz is insensitive to the O_2 exchange occurring from the processes of respiration, photorespiration and other processes associated with the quasi-anoxygenic photosynthesis. Buffer capacity of the molecular pools participating in these processes dumps the O_2 pulsations (Malkin 1996, 1998; Buschmann 1999) excluding Mehler cycle (Malkin and Canaani 1994). The latter, however, is less than 5% of total photosynthesis (Malkin and Canaani 1994; Clarke and Johnson 2001). It follows that PA-method gives researchers a promising tool to measure values of the O_2 evolution rates (rates of water photolysis) that are not influenced by O_2 uptake processes.

Unfortunately, PA-method was undeservedly forgotten in photosynthesis research last decade, when only a few works were published, although methods of the PA-imaging were successfully developed this time for biomedical applications (Hidayanto 2020). Perhaps it was due to the absence of the commercially available PA-devices designed for the photosynthesis studies.

Recent fast-Fourier transform (FFT) modification of the PA-method (Lysenko and Varduny 2022) is based on the use of an easy-to-make device and allows for simple but reliable simultaneous determination of the O_2 evolution and ES (at low and high frequencies) in one sample that, in turn, provides a possibility to calculate oxygen coefficients of photosynthesis as:

$$\boldsymbol{\Psi}_{02}\frac{\mathrm{PA_{bar}}}{\mathrm{PA_{therm}}} = (\mathrm{PA_{ac20}} - \mathrm{PA_{sat20}}) + \frac{\mathrm{PA_{sat20}}}{\mathrm{PA_{sat280}}} \quad (5)$$

where $\boldsymbol{PA}_{bar}$ and $\boldsymbol{PA}_{therm}$ are photobaric and photothermal signals respectively, $\boldsymbol{PA}_{ac}$ is a PA-signal measured under the measuring light alone at 20 Hz; $\boldsymbol{PA}_{sat20}$ is a PA-signal measured under the measuring light and saturating flash at 20 Hz; $\boldsymbol{PA}_{sat280}$ is a PA-signal measured under the measuring light and saturating flash at 280 Hz. The equation considers the contribution of the minor photothermal component of the PA-signal at 20 Hz.

$\boldsymbol{\Psi}_{02}$ is a relative parameter dependent on the value of the "pure" photolytic O_2 evolution normalized by the value of the photochemical energy storage, ES.

Thus, in contrast to PAM-fluorescence methods, the PA method is a direct way to evaluate the photosynthetic productivity of plant tissues and to evaluate the participation of the true anoxygenic photosynthesis, if used in a Fourier modification. At the same time, it has a perspective to be applied simultaneously (in one sample) with the Fourier-PAM fluorometry, as both these methods may use the same sources of measuring, actinic and saturating light as well as real-time data processing software.

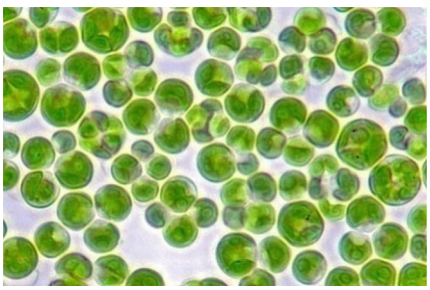
In addition, Fourier-photoacoustics has an advantage in that it is a phase-insensitive method, whereas traditional photoacoustics, which is based on the use of selective lock-in amplifiers, is a phase-sensitive method (Mesquita et al. 2006; Hou and Sakmar 2010). Theoretically, the latter may result in errors in measurements of the oxygen evolution because the photoinduced oxygen pulse is delayed (shifted) relative to the exciting light pulse (Buschmann 1999).

In contrast to the PAM-fluorometry, which operates with intact leaves and plants, the photoacoustic method is capable of operating only with the leaves cut from the plant and placed into an airtight PA-cell that can cause errors in long-term experiments. Moreover, the PA cell should have a low ratio between its volume and the measured leaf surface. Otherwise, the signal may be lowered resulting in a decreased signal-to-noise ratio. However this problem may be solved using an open PA-cell (Mesquita et al. 2006) in which the leaf blade composes one of the walls of the PA-cell. In this case, a small PA-cell (0.5 ml, for example) may be placed into a larger vial (about 150–200 ml) to avoid increasing noise (Lysenko and Varduny 2022). It allows for maintaining the constancy of the gaseous environment during the long term experiment but still makes it difficult to perform studies on the whole intact plants.

Table 1 Comparative characteristics of the key fluorometric and photoacoustic parameters applied for evaluation of the photosynthetic performance

Parameters of photosynthesis	Fluorescence decrease ratio	Maximal quantum yield of PSII for the dark adapted plants	PSII operating efficiency or operating quantum yield of PSII	Photochemical energy storage or energy storage	Oxygen coefficient of photosynthesis
Notations	R_{fd}	F_v/F_m	F'_v/F'_m	ES	Ψ_{02}
Descriptions	Characterizes amplitude of the Kautsky's effect as a parameter of the PSII functioning	A maximal part of the absorbed light energy that can be utilized to drive electron transport through PSII measured for the dark-adapted plants	A part of the absorbed light energy that is utilized to drive electron transport through PSII under specific PPFD	A part of the absorbed light energy that is utilized in photochemistry	A "pure" photolytic O_2 evolution matching as per the total photochemical energy storage
Direct or indirect measurements	Indirect	Indirect	Indirect	Direct	Direct
States of photosynthetic system	Combined dark and light adapted (see Sect. 2)	Dark adapted	Light adapted	Light adapted	Dark or light adapted
Application of alternating measuring light	Applicable only in the case of PAM measurements	Necessary	Necessary	Necessary	Necessary
Application of saturating pulse	Applicable only in the case of PAM measurements	Necessary	Necessary	Necessary	Necessary
Application of Fourier modifications	Theoretically possible only in the case of PAM-measurements	Conventional PAM or Fourier PAM	Conventional PAM or Fourier PAM	Conventional PAM or Fourier PAM	Fourier PAM only
Measuring PSII and PSI activities	PSII only	PSII only	PSII only	PSII and PSI together or PSI separately	PSII and PSI together
Detection of anoxygenic photosynthesis	No	No	No	No	Yes
Applicability of imaging methods	Applicable	Applicable	Applicable	Theoretically applicable	Theoretically applicable
References	Govindjee 2004; Lichtenthaler et al. 2007	Schreiber 2004; Baker 2008; Blankenship 2021	Schreiber 2004; Blankenship 2021; Camargo et al. 2022	Malkin 1996; Buschmann 1999; Pinchasov-Grinblat and Dubinsky 2013	Lysenko and Varduny 2022

Table 2 Methods of assessment of the photosynthetic performance applied at different levels of biosystem organization

Levels of biosystem organization		Applicable methods					
		Direct biomass assessment	CO_2 assimilation, NDIR sensors[1]	CO_2 assimilation, radiocarbon methods[2]	Fluorescense kinetics[3]	Photoacoustics[4]	Remote hyperspectral methods[5]
Plant communities		−	−	−	−	−	+
Whole plants		+	−	−	−	−	−
Leaves		−	+	−	+	+	−
Microalgae, tissue cells		+	−	+	+	−	−

+ Frequently used or convenient methods − methods are not applied or rarely used

[1] Long and Hällgren 1993; Davis and Hidayati 2020; Liu and van Iersel 2021

[2] Kromkamp et al. 2017; Camargo et al. 2022

[3] Liu and van Iersel 2021

[4] Buschmann 1999; Delosme 2003; Malkin 1996; Hidayanto 2020

[5] Houborg et al. 2015; Dmitriev et al. 2022; Porcar-Castell et al. 2014

At the same time, in contrast to the PAM-fluorometry which operates with intact leaves and plants, the photoacoustic method is capable of operating only with the leaves cut from the plant that can obviously cause errors.

Necessity of the airtight PA-cell leads to that the photoacoustic method is capable of operating only with the leaves cut from the plant that can obviously cause errors. In contrast, PAM-fluorometry is devoid of this shortcoming as far as it operates with the intact leaves and plants.

Comparative characteristics of the key parameters of fluorometry and photoacoustics are given in the Table 1.

Conclusion

From the data discussed above, results obtained using the fluorescence kinetics methods should be considered with caution, in regard to the following issues:

1. Uncertainty in F_m, and, therefore, in the values of quantum yield of PSII
2. Uncertainty in the evaluation of the influence of the PSI fluorescence on the F_0, and therefore, uncertainty in the values of quantum yield of PSII.
3. Uncertainty in evaluating the full-spectrum quantum yield of PSII using a single-color measuring light, which is usually red in the majority of PAM-fluorometers.
4. Uncertainty in the contribution of the activity of PSII in the cyclic mode to the total PSII activity measured using PAM-fluorometry that is important considering a weak contribution of CET-PSII in the plant productivity.

In contrast to the PAM-fluorometry and other fluorometric methods, the photoacoustic spectrometry, being a direct method of assessing photosynthetic performance, is devoid of some of these shortcomings (although has its own) and may be a promising alternative or supplement to the PAM-fluorometry. Interpretations of data obtained using the fluorescence kinetics and photoacoustic methods may remain a subject of controversy despite all the improvements made in recent decades.

In addition, efforts to evaluate photosynthetic performance at different levels of biosystem organization require the application of different methods (Table 2) that makes the interlevel studies difficult to interpret. This is not just a problem for the set of optical methods (fluorometry, hyperspectral sensing), but even a problem for the direct measurement of CO_2 assimilation using infrared CO_2 sensors. Thus, it is applied for studying mostly the single leaves that is not the same as a whole pant, with roots contribute in the CO_2 balance by respiration. In other words, photosynthetic performance does not mean the productivity. Photosynthetic performance comprises both oxygenic and anoxygenic photosynthesis. The first is the main base of biomass growth and productivity, the second helps plants to withstand the environmental stress. Fluorescence kinetic methods may reveal a high performance of light reactions of anoxygenic photosynthesis (high rate of thylakoid cyclic electron transport) in plants that have low productivity, for example under stress (Rumeau et al. 2007). High photosynthetic performance is a necessary, but insufficient component of productivity. It follows from the above, that the direct method of evaluating plant productivity by biomass still seems to be the most reliable in the nearest future and should be chosen whenever possible. At the same time, fluorometry and other indirect methods for assessing the photosynthetic performance should be developed to increase our understanding of the physiological structure of plant productivity as well as to perform more detailed and complex studies in this field.

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Declarations

Conflict of interest The authors declare that there are no conflicts of interest.

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