Electron Transport in Chloroplast Membranes of Shade-Tolerant and Light Loving Tradescantia Species

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Abstract—The processes of electronic transport in chloroplasts of two contrasting species of *Tradescantia*, the shade-tolerant species *Tradescantia fluminensis* and the light loving species *T. sillamontana*, grown in moderate or strong light conditions were investigated. The parameters of fast (OJIP test) and slow induction of fluorescence (SIF) of chlorophyll *a* in chloroplasts in vivo and in situ were used as indicators reflecting the photochemical activity of photosystem 2 (PS2). The coefficient of nonphotochemical quenching of chlorophyll *a* fluorescence, which provides protection of the photosynthetic apparatus from light stress, was determined from the SIF kinetics. The functioning of photosystem 1 (PS1) was monitored by the kinetics of photoinduced changes in the redox state of P_{700}, the reaction center of PS1, recorded by electron paramagnetic resonance. A significant difference in the dynamics of changes in photosynthetic parameters of shade-tolerant and light loving tradescantia species under conditions of prolonged acclimation of plants (up to 5 months) to moderate (50–125 μmol photons m^{-2} s^{-1}) or strong (850–1000 μmol photons m^{-2} s^{-1}) illumination with photosynthetically active white light was observed. In the light loving species *T. sillamontana*, photosynthetic parameters of chloroplasts changed slightly during acclimation of plants to moderate and strong light. Photosynthetic characteristics of leaves of shade-tolerant species *T. fluminenesis* were sensitive to the conditions of illumination, which indicated a weakening of photochemical activity with an increase in light intensity during acclimation of plants. The effect of attenuation of photosynthetic parameters of the leaves was reversible, that is, the fluorescence parameters returned to the initial level after attenuation of light.

Keywords: Tradescantia, shade-tolerant and light loving species, acclimation, chlorophyll fluorescence induction, EPR

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INTRODUCTION

Photosynthetic organisms of the oxygenic type (plants, algae, and cyanobacteria) contain pigment–protein complexes of two types, photosystem 1 (PS1) and photosystem 2 (PS2), which absorb light and provide electron transfer from water oxidized in PS2 to $NADP^+$, the terminal electron acceptor in PS1. Electron transfer along the electron transport chain (ETC) occurs with the participation of the cytochrome b_6f complex and mobile electron carriers, plastoquinone and plastocyanin [1–6]. In plants, ETC carriers are embedded into the thylakoid membranes of chloroplasts. The functioning of the ETC leads to the generation of a trans-thylakoid difference in the electrochemical potentials of hydrogen ions $(\Delta\mu_{H^+})$, which is an energy source for the operation of ATP synthase [7–9]. ATP and NADPH are macroergic products of the "light" stages of photosynthesis, used in Calvin–Benson cycle reactions for CO_2 fixation and carbohydrate synthesis [10].

The structural organization of the photosynthetic apparatus (PSA) of plants is well studied. Currently, one of the main tasks of biophysics and biochemistry of photosynthesis is to elucidate the mechanisms of regulation of electron transport in chloroplasts. In natural conditions, the intensity and spectral composition of light change during the day and depend on weather conditions. Shortage of light reduces the productivity of photosynthesis. An excess of light can lead to destructive processes, for example, it may cause oxidative stress and impairment of plant PSA [11, 12]. In the course of biological evolution, photosynthetic organisms have developed mechanisms to optimize

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Abbreviations: FIF, fast induction of fluorescence; SIF, slow induction of fluorescence; NPQ, non-photochemical quenching; P_{700}, primary electron donor in photosystem 1; SL and ML, strong light and moderate light; PSA, photosynthetic apparatus; PS1 and PS2, photosystem 1 and photosystem 2; CBC, Calvin–Benson cycle; ETC, cyclic electron transport; Chl, chlorophyll; EPR, electron paramagnetic resonance; ETC, electron-transport chain; PQ, plastoquinone. q_E, q_Z, and q_I, three components of NPQ; FRL, far-red light; WL, white light.

bioenergetic processes under varying external conditions (lighting [13] and temperature [14−17]). These mechanisms provide "fast" (seconds−minutes) and "long-term" (hours−days) regulation of photosynthesis. Fast regulation processes are carried out due to feedbacks that affect: (1) activation/deactivation of CBC reactions [18, 19], (2) pH-dependent regulation of ETC operation [20−23], (3) redistribution of absorbed light energy between PS1 and PS2 [24], and (4) structural and functional rearrangements of PSA in membranes [25−29]. The long-term regulatory mechanisms are associated with the synthesis or degradation of those components of PSA (including pigment−protein complexes) that affect the architecture and functional properties of chloroplasts. The ability of plants to adapt to changing environmental conditions is determined by the type of plants [30].

In the context of the problem of the mechanisms of acclimation of plants to living conditions, a comparative study of closely related plant species belonging to "contrasting" species (for example, plant species of the same genus adapted to grow in shady conditions or under intense lighting) is of interest. Previously, we studied photosynthetic parameters of two species of *Tradescantia*, the shade-tolerant species *T. fluminensis* (an endemic species growing in the humid tropical forests of southeastern Brazil) and the light loving species *T. sillamontana* [31−37], whose historical homeland is the semi-desert regions of Mexico and Peru [38]. Another example of this kind of research is a comparative study of the properties of PSA of two species of *Cucumis* plants growing in areas with hot and temperate climates, namely, *C. melo* (melon) and *C. sativus* (cucumber). The properties of chloroplast membranes isolated from melon and cucumber seedlings grown under the same experimental conditions were previously studied with the help of lipid-soluble spin probes [39]. At the same time, however, it turned out that thermally induced structural transitions in the thylakoid membranes of melon chloroplasts occurred at higher temperatures (≥35°C) than in cucumber chloroplasts (~20−25°C). Obviously, this observation demonstrated that the melon (*C. melo*) has adapted to the growth at relatively high temperatures characteristic of the hot climate in the areas of origin of this species.

This paper presents the results of a comparative study of the dynamics of acclimation of leaves of two "contrasting" species of Tradescantia (*T. fluminensis* and *T. sillamontana*) that occurred during long-term (months) cultivation of plants at high or low light intensity. PS2 is the most vulnerable pigment−protein complex of PSA of plants, damaged by light stress or temperature increase [40−44]. To determine the functional parameters reflecting the activity of PS2 in chloroplasts in situ (plant leaves), we studied the induction of chlorophyll *a* (Chl *a*) fluorescence emitted mainly by the pigments of the PS2 light harvesting antenna [45−48]. The contribution of non-photochemical quenching (NPQ) of the fluorescence of Chl *a*,

reflecting the effectiveness of protective mechanisms caused by increased dissipation of excess energy in the light harvesting antenna of PS2, was also evaluated [42, 49−53]. Using the fluorescence analysis, we studied the changes in the efficiency of PS2 and NPQ generation during a long (several months) acclimation of *T. fluminensis* and *T. sillamontana* to light of high or low intensity. In addition, we investigated the functioning of PS1 by recording the redox transformations of the P_{700} photoreaction centers (the primary electron donor in PS1) by electron paramagnetic resonance. Our studies have shown that with an increase in the duration of acclimation of shade-tolerant *T. fluminensis* plants they obtained an enhanced protective reaction, manifested in the generation of NPQ already at moderate light fluxes (~200 µmol photons m^{-2} s^{-1}). As a result of prolonged acclimation (more than 2 months) to high-intensity light (≥ 500 µmol photons m^{-2} s^{-1}) chloroplasts of *T. fluminensis* lost photochemical activity faster, which was not observed for the light loving species *T. sillamontana*. Attenuation of photochemical activity of PSA in *T. fluminensis* was reversible, that is, after returning to the light of moderate intensity, their photochemical activity was restored to the level characteristic of plants acclimated to moderate light.

MATERIALS AND METHODS

Plants. The objects of the study were the leaves of the Tradescantia species *T. fluminensis* and *T. sillamontana*, obtained from the Main Botanical Garden of the Russian Academy of Sciences. The plants were grown in soil culture at room temperature (24−26°C) and relative humidity of 40−60%. Pots with plants were placed in a dark chamber, inside which there were two illuminated compartments, differing in light intensity. The light source was the lamp USS 90 highway Sh (TH FOCUS LLC, Russia), equipped with white LEDs with a color temperature of 5000 K (Nichia, Japan). The spectral composition of light produced by this lamp included the components of blue, red and far-red light necessary for the normal growth and development of plants. The intensity of illumination was measured using a Li250A quantum meter (LiCOR Biosciences, USA). The duration of the light period in the daytime was 14 h, the light fluxes were equal to 800−1000 µmol photons m^{-2} s^{-1} ("strong" light, SL) or 50−125 µmol photons m^{-2} s^{-1} ("moderate" light, ML). To measure the photosynthetic parameters of the leaves, a second or third mature leaf located in the upper part of the shoot was used. When the characteristics of the leaf were measured by biophysical methods (fluorescence analysis and EPR), the sample was illuminated from the abaxial (dorsal) side of the leaf facing the upper epidermis. Several series of long-term acclimation experiments were conducted for various plantings in the spring−summer−autumn seasons of 2015−2022. The general
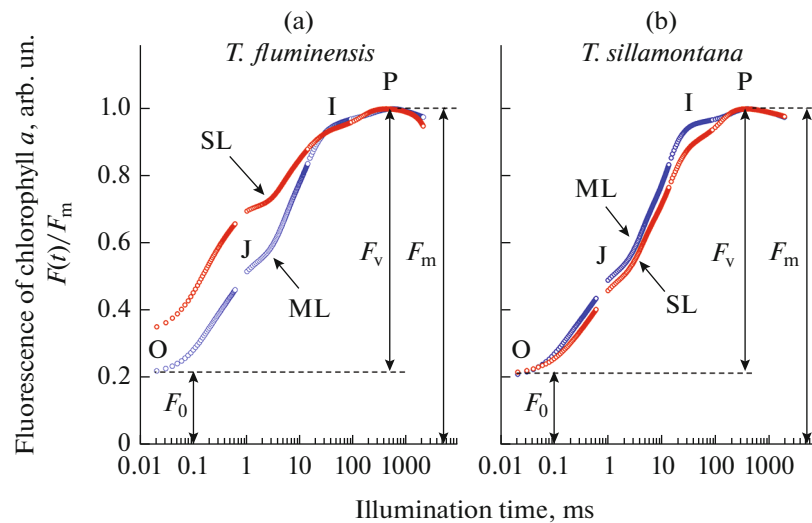
Fig. 1. Kinetics of fast induction of fluorescence (FIF) of chlorophyll *a* in the leaves of *T. fluminensis* (a) and *T. sillamontana* (b) grown for 2 months under strong (SL) and moderate (ML) illumination. The measurements were carried out in accordance with the protocol described in the Materials and Methods section. The beginning of the measurements was preceded by the adaptation of the samples to darkness for 10 min. All FIF curves were normalized to the maximum intensity of fluorescence F_m.

patterns of the dynamics of changes in the biophysical parameters of the leaves of two species of Tradescantia, *T. fluminenesis* and *T. sillamontana*, studied in different seasons, were the same. In this paper, to illustrate these patterns, we present the results of studies conducted in 2019−2021.

Fluorescence measurements and NPQ determination. The fluorescence of Chl *a* was measured in vivo using a PAM FluorPen FP100 fluorimeter (Photon Systems Instruments, Czech Republic), as described earlier [32−37, 54]. The spectra of continuous light ("actinic" light) and weak pulses of measuring light exciting the fluorescence of Chl *a* had a maximum at 475 nm and a half-width of the spectral band $\Delta\lambda_{1/2} = 25$ nm. Before starting the measurements, the leaf was pre-illuminated with actinic light for 1 min (to standardize the experimental conditions), and then kept in the darkness for 10 min. The parameters of the fluorescence induction curves of Chl *a* and non-photochemical fluorescence quenching were determined according to traditional protocols [46−48].

The characteristic kinetic curves of fast induction of fluorescence (FIF) of Chl *a* in leaves in two plant species (*T. fluminensis* and *T. sillamontana*) that grew for 2 months under strong (SL) or moderate (ML) light are shown in Fig. 1. The kinetic curves of FIF show how the level of fluorescence changed during the action of the saturating pulse of light with a 2-s duration (light flux of 3000 µmol photons m^{-2} s^{-1}). All these curves have characteristic features (kinks or local extremes), indicated by the symbols O, J, I and P. Parameter F_0 is the initial fluorescence level of Chl *a* in leaves adapted to darkness. F_m is the maximum level of fluorescence measured in response to the action of

a saturating pulse of light. The variable fluorescence parameter (ratio $F_v/F_m = (F_m - F_0)/F_m$) is a measure of the maximum photochemical activity of PS2 (relative quantum yield) in leaves adapted to darkness [46−48].

Figure 2 shows the typical kinetics of slow induction of fluorescence (SIF) of Chl *a* caused by the action of continuous light (often called "actinic" light in the literature) and short (1 s) flashes of light ($\lambda_{max} = 475$ nm) of high intensity (3000 µmol photons m^{-2} s^{-1}). The values of F_m and F_m' are the fluorescence levels measured during the action of intense flashes on a sample of a leaf adapted to darkness (F_m) or during its illumination with actinic light $\left(F_m'\right)$. $F(t)$ is the fluorescence intensity measured immediately before the intense flash was applied. The parameters $\Phi_{PSII} = 1 - F(t)/F_m'$ and $q_{NPQ} = F_m^0/F_m' - 1$ characterize the so-called operational efficiency of the photochemical centers of PS2 (Φ_{PSII}) and the NPQ coefficient (q_{NPQ}), respectively [46−48].

Electron paramagnetic resonance (EPR). The characteristic EPR signal from oxidized P_{700}^+ centers allows monitoring electron transport in chloroplasts in situ [54, 55]. A sample (a freshly cut piece of leaf of 4×25 mm) was fixed in a well-ventilated holder and placed in a rectangular resonator of a E-4 EPR spectrometer (Varian, USA). The power of the microwave radiation was 10 mW, the amplitude of the high frequency modulation of magnetic field was equal to 0.4 mT. The samples were illuminated with white light (WL, 320 W m^{-2}), effectively exciting both photosystems, or with far-red light (FRL, $\lambda_{max} = 707$ nm, 8 W m^{-2}), exciting predominantly PS1. The kinetics

of redox transformations of P_{700} was monitored by changes in the magnitude of the low-field extremum of the first derivative of the EPR signal from P_{700}^+. Illumination conditions and EPR signal recording in plant leaves were described in [54].

RESULTS AND DISCUSSION

### Induction of Chlorophyll a Fluorescence

Fast induction of fluorescence. The kinetic curves shown in Fig. 1 were obtained on die-cuts from the leaves of plants acclimated to the conditions of strong or moderate illumination. Before starting the measurements, each sample was adapted to the darkness for 10 min. All FIF curves were normalized to the maximum value F_m of the signal. These curves had common patterns: in response to a short flash of intense light with $\lambda_{max} = 475$ nm, the fluorescence of Chl a quickly reached the level F_0 and then grew to the maximum level P, characterized by the parameter F_m, passing through inflection points or local extremes marked with the symbols J and I. After reaching the maximum P level, fluorescence slightly decreased. According to the generally accepted view, the O–J growth stage reflects the recovery of the primary plastoquinone PQ_A, which is tightly bound to PS2 [45–48]. The next phase of the signal growth (section J–I–P), called the "thermal phase" of fluorescence [56, 57], reflects the reduction of the secondary plastoquinone PQ_B (electron transfer $PQ_A \rightarrow PQ_B$) and further electron transfer to the ETC between PS2 and PS1, as well as the redistribution of absorbed energy between PS2 and PS1 [58]. Comparing the kinetics of FIF in the leaves of the shade-tolerant species *T. fluminensis* in plants acclimated to strong or moderate light for 2 months, we can note that in the first case, the initial level of fluorescence F_0 was higher than that of the leaves of the same species acclimated to a moderate light intensity. Considering that the parameter F_0 reflects the efficiency of energy transfer from the light harvesting antenna to the reaction center P_{680} [48], it can be assumed that the observed difference was a consequence of damage to the PS2 antenna during exposure of *T. fluminensis* leaves to strong light (light stress). This did not happen in the case of the leaves of the light loving species *T. sillamontana*, which may indicate a relatively weak susceptibility of plants of this species to increased light intensity during acclimation. The parameters of the FIF curve depended on the duration of acclimation of plants under different illumination conditions (Fig. 3). We conducted the observations of the fluorescent indicators of leaves in vivo (without separation of leaves from the stem) during the long-term cultivation of plants (more than 4 months), starting from the two-week age of the leaves, when the plants have already formed leaf blades. Figure 3a shows the results of measurements in
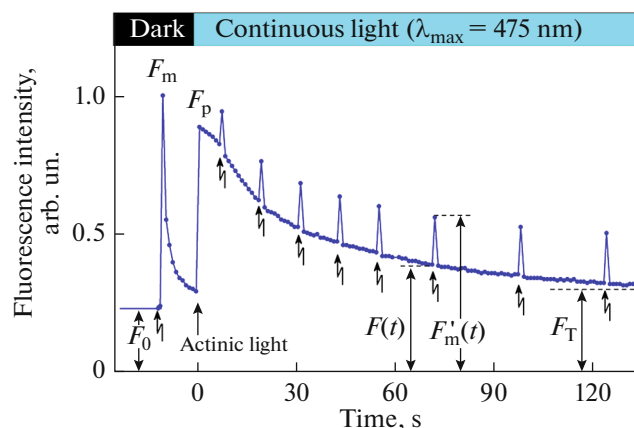
Fig. 2. Kinetics of chlorophyll a fluorescence induction in *T. fluminensis* leaves grown under "strong" illumination of plants. The measurements were carried out in accordance with the protocol described in the section "Materials and methods". *Zigzag arrows* show the moments of applying short saturating flashes of light. *Vertical arrow* shows the moment of switching on the continuous (actinic) light. The kinetic curve was normalized by the F_m value determined by the fluorescence level for the first saturating flash, applied after the leaf adapted to darkness for 10 min. F_T is a stationary fluorescence level, which is established after a long (~10 min) illumination of leaves with actinic light intensity of 800 μmol photons m^{-2} s^{-1}.

the experiment when, at first, plants grew under moderate illumination (50–125 μmol photons m^{-2} s^{-1}) for 80 days, and then they were illuminated with strong light (850–1000 μmol photons m^{-2} s^{-1}) of the same spectral composition. It can be seen that in both species the parameter F_0 remained almost unchanged when plants grew under light of moderate intensity. After a significant (by an order of magnitude) increase in the light flux, the dependences of F_0 on the acclimation time of the leaves of *T. fluminensis* and *T. sillamontana* changed. In the leaves of *T. fluminensis*, parameter F_0 began to increase as the duration of acclimation increased. Unlike *T. fluminensis*, in the leaves of *T. sillamontana* no statistically significant F_0 increase was observed (Fig. 3a).

Figure 3b shows the results of another series of measurements, in which the sequence of illumination conditions was the opposite: the plants first grew under strong light, and then the light intensity was weakened. In shade-tolerant plants (*T. fluminensis*), during the first 50 days of growth under strong light, parameter F_0 slightly changed. Then the F_0 value began to increase noticeably. The increase of F_0, observed when plants were illuminated with strong light, was reversible. After the weakening of the light on the 80th day, F_0 started to decrease, returning to the initial level. In the case of the light loving species *T. sillamontana* grown under strong light, initially there was a slight decrease in F_0. It can be suggested that this was because with an excess of light during acclimation to
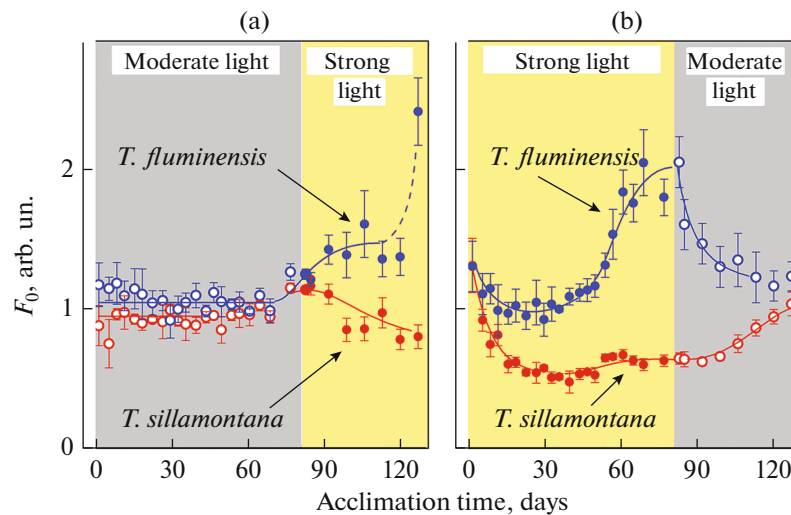
Fig. 3. Dynamics of changes in parameter F_0 of the fast fluorescence induction curve measured in the leaves of *T. fluminensis* and *T. sillamontana* grown under "strong" and "moderate" illumination. Vertical lines are the standard deviation from the average values obtained for $n = 4-8$ measurements.

strong light, plants had enough light quanta for optimal functioning, so it was "beneficial" for them to reduce the number of pigment−protein complexes in order to avoid negative consequences from light stress. After the light faded, as the plants acclimated, the value of F_0 increased, returning to the initial level. The described changes in the parameter F_0 reflected the processes of structural and functional reorganization of the PSA occurring during the acclimation of plants. At the same time, in both series of experiments (Figs. 3a and 3b), in the leaves of the shade-tolerant plant *T. fluminensis*, the fluorescent parameter F_0 was more sensitive to variations in light intensity during acclimation than in the leaves of the light loving species *T. sillamontana*.

The interspecies difference in the dynamics of changes in the F_0 value during acclimation was also characteristic of the variable fluorescence of Chl *a*, defined as the ratio $F_v/F_m = (F_m - F_0)/F_m$. Figure 4 shows that in the leaves of *T. sillamontana* this ratio remained at the same level ($F_v/F_m \approx 0.78$) regardless of the growing conditions of plants (strong or moderate light). This indicated that the maximum quantum yield of Chl *a* fluorescence in *T. sillamontana* chloroplasts remained high at both moderate and high light intensity. Another pattern was observed in the case of *T. fluminensis,* namely, growth of these plants under strong light led to a certain drop in variable fluorescence F_v/F_m, which reflected a decrease in the photochemical activity of PS2. The decrease in the F_v/F_m ratio was reversible, that is, after the attenuation of the light intensity during acclimation of *T. fluminensis*, this ratio returns to the initial value of $F_v/F_m \approx 0.78$, characteristic of plants grown at moderate light intensities (Fig. 4b). Reversibility of the F_v/F_m attenuation

effect that occurred when *T. fluminensis* were grown under strong light illumination might indicate the functional "flexibility" of the PSA of these plants, that is, the photochemical activity of chloroplasts was restored relatively quickly (within a few days) after a decrease in illumination.

Non-photochemical quenching of fluorescence. The reversibility of the FIF parameters in *T. fluminensis* leaves occurring during acclimation of plants to light of various intensity (Figs. 3 and 4) indicated the functional flexibility of the PSA of these plants, which allowed protecting the PSA from light stress. The protection of the PSA from damage under excessive illumination (strong light) was manifested in an increase in the non-photochemical quenching of the excitation of Chl *a* molecules in the light harvesting antenna of PS2. The coefficient of non-photochemical quenching (the NPQ value) can be determined from the parameters of the slow fluorescence induction curve (SIF) shown in Fig. 2.

Figure 5 shows how the NPQ value changed during the illumination of *T. fluminensis* leaves with continuous actinic light, in plants acclimated for different times at high (SL, Fig. 5a) or moderate (ML, Fig. 5b) light intensity. The intensity of actinic light used in the recording of SIF was quite high, 800 µmol photons $m^{-2} s^{-1}$, which corresponded in order of magnitude to the intensity of strong light used in the acclimation of plants. In the kinetics of NPQ growth shown in Fig. 5, several components can be distinguished that reflect different mechanisms of regulation of the light stages of photosynthesis. The reversible component of NPQ, denoted as q_E (the so-called energy component), was characterized by a relatively rapid growth (~0.5−2 min). This component was related to the creation of a trans-thylakoid pH differ-
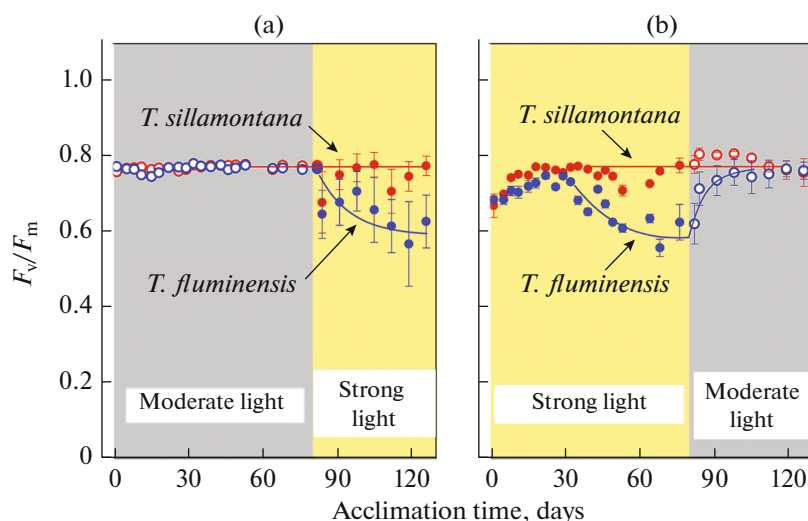
Fig. 4. Dynamics of changes in the variable fluorescence parameter F_v/F_m of the fast fluorescence induction curve measured in the leaves of *T. fluminensis* and *T. sillamontana* plants grown under "strong" and "moderate" illumination. Vertical lines are the standard deviation from the average values obtained for $n = 4-8$ measurements.

ence (ΔpH) when, as a result of acidification of the intrathylakoid space (lumen), when the regulatory protein PsbS was activated, thereby enhancing NPQ [59]. It is believed that the PsbS protein acts as a sensor that provides sensitivity to a light-induced decrease in intra-thylakoid pH (pH$_{in}$). Following the rapid growth of the NPQ (q_E component), a relatively slow component of NPQ (denoted as the q_Z component [50–52]) was often observed. This stage of the NPQ growth could be explained by two main reasons: (1) the reactions of the xanthophyll cycle (de-epoxidation of violaxanthin and the appearance of zeaxanthin) and (2) the redistribution of energy between PS2 and PS1 (state 1 $\leftrightarrow$ state 2 transitions) [24, 29]. Zeaxanthin enhances the binding of the regulatory protein PsbS to the light harvesting antenna of PS2 (LHCII). This causes aggregation of light harvesting complexes of PS2 (LHCII), which leads to an increase in NPQ; the energy dissipation of excited pigments of the PS2 antenna enhances and the efficiency of photochemical processes in PS2 decreases (for more detail, see the review [29]). Based on our previous studies [34], it can be concluded that in the leaves of Tradescantia, the growth of NPQ was associated with an increase in the expression of the PsbS protein.

After the actinic light was turned off, a decrease in NPQ was observed. The fall of the NPQ in the darkness was reversible, although not complete, namely, the residual level of NPQ remained comparatively long (tens of minutes), characterized by the parameter q_I (Fig. 5). The value of q_I is known to reflect, at least partially, the degree of inactivation of some of the photochemical centers of PS2 as a result of the action of sufficiently intense actinic light [30, 48–53]. The inhibition of PS2 occurred mainly due to damage to the

D1 protein as a result of its photo-oxidation under the action of strong light. PS2 was repaired by the removing damaged protein D1 from PS2, and a newly synthesized active protein D1 was inserted in its place [60].

The ability of plants to enhance NPQ depended on the illumination conditions upon plant cultivation, as well as on the duration of acclimation. It is seen from Fig. 5a that with an increase in the duration of acclimation of *T. fluminensis* plants grown under strong light, a relatively small increase in the reversible ("energy") component of q_E was observed. It should be noted that as the plants aged, the contribution of the second (slow) component of NPQ (q_Z) becomes more and more pronounced. This suggests that as the *T. fluminensis* leaves matured, their PSA acquired an additional ability to protect itself from light stress. Note that plants grown under moderate light also had two phases of NPQ growth (Fig. 5b), but the values of the q_E and q_Z parameters, reflecting the two mechanisms of NPQ generation, were slightly lower than those in plants grown under strong light (Fig. 5a). It is obvious that in plants grown under moderate light, the strengthening of the protective reaction caused by an increase in NPQ was less pronounced than in plants of the same species grown under strong light. Naturally, in strong light, plants have enough energy for photosynthesis, but at the same time they must protect themselves from light stress.

We have shown that the dynamics of NPQ changes during the illumination of Tradescantia leaves adapted to darkness depended on the duration of acclimation of plants to light of high or moderate intensity. This is especially evident in experiments with the shade-loving species *T. fluminensis*. In plants grown under strong light, the value of q_E increased markedly with
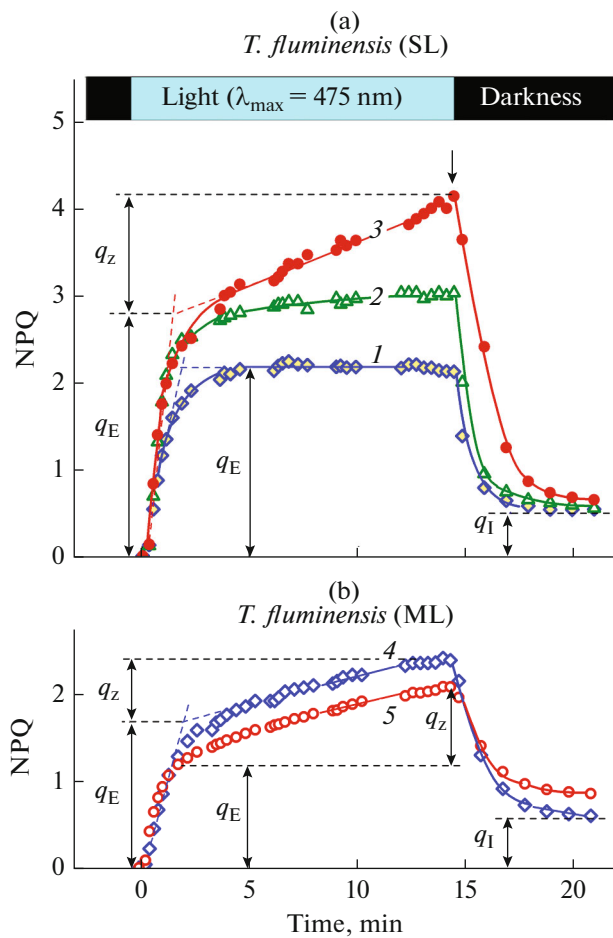
Fig. 5. The effect of the acclimation duration of *T. fluminensis* plants grown under strong (SL) and moderate (ML) light intensity on the kinetics of light-induced changes in the coefficient of non-photochemical fluorescence quenching (NPQ). Curves *1, 2,* and *3* were obtained for plants acclimated to strong light for 8, 20 and 40 days. Curves *4* and *5* were obtained for leaves of plants acclimated to moderate light for 8 and 45 days. The intensity of continuous (actinic) light acting on the measured samples was 800 μmol photons $m^{-2} s^{-1}$.

acclimation (Fig. 5a). At the same time, the slow q_Z component became more pronounced. Obviously, the plants of the shade-loving type *T. fluminensis*, grown under strong light, acquired an additional ability to protect themselves from light stress during acclimation. As the acclimation time increased, this reaction of the PSA of plants became more pronounced. At the same time, when plants were exposed to light of moderate intensity for a long time, this did not happen, even a slight decrease in q_E was observed as plants acclimated. It can be assumed that the decline in q_E was caused by changes in chloroplasts as plants aged, which might be due, for example, to a decrease in biosynthesis and/or increased degradation of some PSA proteins.

Electronic Paramagnetic Resonance

Differences in the leaves of plants grown under strong and moderate illumination manifested in fluorescent characteristics were also expressed in the kinetics of redox transformations of P_{700}, the primary electron donor in the reaction center of PS1. Figure 6 shows the typical curves of photoinduced changes in the intensity of the EPR signal from P_{700}^+ in the leaves of plants adapted to darkness for 10 min. The protocol of P_{700}^+ measurement was the same as in our previous studies [54, 55]: after preliminary illumination with white light (WL) for 1 min (to standardize experimental conditions), the samples were adapted to the darkness for 10 min. It can be seen that in response to the WL exciting both photosystems, the EPR signal from P_{700}^+ increased, reaching a stationary level. In leaves adapted to the darkness, a multiphase kinetics of signal growth was observed. Immediately after switching on the WL, a small jump in the signal occurred, then its relatively slow growth to the stationary A_{WL} level was observed. The delay in the signal growth, characterized by the $t_{1/2}$ parameter, was because, when the leaf adapted to darkness, the CBC reactions were inactivated, therefore, due to an overabundance of NADPH, the outflow of electrons from PS1 to $NADP^+$ was hindered [10, 61]. As the chloroplasts were illuminated, CBC reactions were activated and the outflow of electrons from PS1 accelerated. In addition, the rate of electron influx from PS2 to P_{700}^+ decreased as a result of lumen acidification, and the activity of PS2 decreased due to the generation of NPQ. Along with this, the energy of the absorbed light was redistributed in favor of PS1 (transition state 1 → state 2), and there was a redistribution of electron flows (non-cyclic /cyclic electron transport) in favor of a non-cyclic flow [61]. All this should contribute to the growth of the EPR signal from P_{700}^+.

Figure 6 also shows that the rate of oxidation of P_{700} under WL depended on the conditions of plant growth. In both species of Tradescantia acclimated to strong light, photooxidation of P_{700} occurred noticeably faster than in plants grown under moderate light.

After switching from the WL to a weaker far-red light (FRL, $λ_{max}$ = 707 nm), which excited mainly PS1, the concentration of P_{700}^+ dropped but then monotonically increased. The rapid drop in the signal after switching from the WL to FRL is explained by the influx of electrons to P_{700}^+ from the pool of reduced carriers (these are mainly plastoquinol molecules) accumulated in the ETC between PS2 and PS1 during the action of the WL. The characteristic decay time of the signal from P_{700}^+ after switching off the WL was $t_{1/2}$ ~ 5−30 ms (depending on the duration of the WL action, data are not presented), which corre-

sponded to the electron transfer time from plastoquinol to P_{700}^+ [1, 4–6, 62–64]. After the reoxidation of the ETC carriers between PS2 and PS1 due to the work of PS1 excited by the FRL, the signal from P_{700}^+ increased again. After switching off the FRL, the oxidized P_{700}^+ centers were reduced by endogenous electron donors [48, 49]. Reduction of P_{700}^+ after switching off the FRL occurred several orders of magnitude slower ($t_{1/2} \sim 2$–5 s) than after switching off the WL (see the results of our research described in [64] for more details).

In the pattern described above, the acceleration of photooxidation of P_{700} in the leaves of plants grown at high light intensity, usually manifested in the kinetics of the SIF in the leaves of *T. fluminensis* and *T. sillamontana*. Earlier, in the studies of the effect of growth conditions (light intensity) on the kinetics of the SIF, we found that in the leaves of these plants grown under strong light, the SIF declined faster than in the leaves of plants grown at moderate light intensity [65]. The acceleration of the fluorescence decay of Chl *a* during the induction period might be due to the same regulatory mechanisms as the acceleration of photooxidation of P_{700} under the WL, namely, due to light-induced activation of CBC reactions, increased NPQ, ionic regulation of electron transport between PS2 and PS1, transitions like state 1 $\leftrightarrow$ state 2, etc. (for review, see [66–68]). It is obvious that the patterns characteristic for the kinetics of redox transformations of P_{700} and for the SIF in the leaves of plants acclimated to strong and moderate light reflected the fact that, as a result of acclimation of plants to strong light, their PSA reacted faster to illumination fluctuations, and therefore these plants could successfully withstand light stress.

It should be noted that the ratio of the amplitudes of the EPR signals from the oxidized P_{700}^+ centers induced by WL and FRL (parameters A_{WL} and A_{707}) depended on the species of plants and their growth conditions. The A_{WL}/A_{707} ratio was slightly higher for *T. fluminensis* leaves grown under high light compared to plants grown under low light (Fig. 6a). As we suggested earlier [65], this might indicate that in the leaves of *T. fluminensis*, acclimated to strong light, the contribution of cyclic electron transport around PS1 increased, which was manifested under FRL, which excited predominantly PS1. No such difference was observed in the case of *T. sillamontana* leaves. The exact reasons for this are still unknown.

Thus, the leaves of both studied species of Tradescantia, cultivated under different light intensities, showed differences in the kinetics of photoinduced changes in P_{700}. The main difference concerns the oxidation rate of P_{700} upon the WL illumination. For example, as the leaves of the shade-tolerant species *T. fluminenesis*, grown under moderate light, aged, the
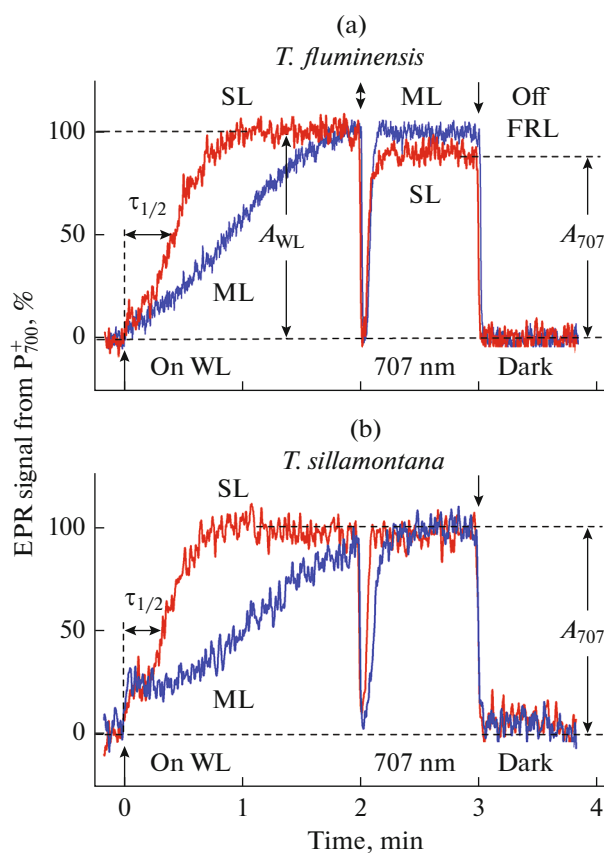

Fig. 6. Kinetics of photoinduced changes in the amplitude of the EPR signal from P_{700}^+ in the leaves of *T. fluminensis* and *T. sillamontana* grown under illumination with strong (SL) or moderate (ML) light. Before switching on the white light (WL), the samples were adapted to the darkness for 10 min.

oxidation of P_{700}, induced by the WL, slowed down (Fig. 7). At the same time, the leaves of the same plant species grown under strong light showed a faster rate of photooxidation of P_{700} compared to plants acclimated to moderate light. This means that the PS1 of plants grown under strong light reacted faster to the turning on of the WL, which was consistent with the data of fluorescent studies.

The question on how the quantitative composition of electron transport complexes and pigments of light harvesting antennas of PS1 and PS2 changed during prolonged acclimation of tradescantia to light of different intensity requires special analysis. According to our preliminary data, in both types of Tradescantia acclimated to strong light, the total content of Chl *a* and Chl *b*, relative to the unit mass of the green leaf, decreased (the data will be presented in our next paper). This observation is in good agreement with the literature data that in the leaves of other plant species, the relative sizes of the light harvesting antenna of PS2
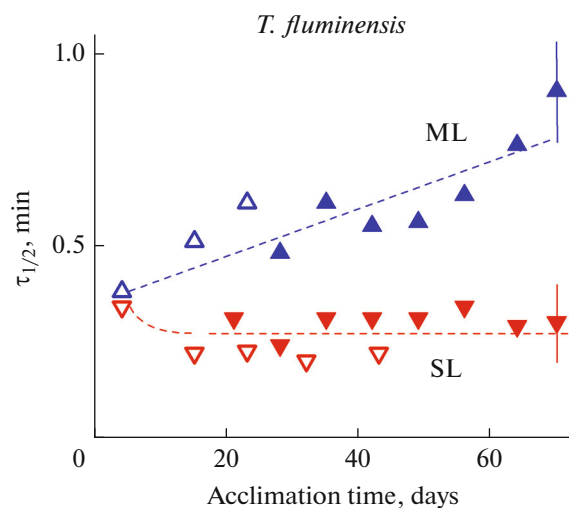
Fig. 7. Dependence of the kinetic parameter $t_{1/2}$ characterizing the rate of photooxidation of P_{700} under the white light (see the determination of $t_{1/2}$ in Fig. 6) in the leaves of *T. fluminensis*, depending on the duration of acclimation of plants to light of strong and moderate intensity. *Closed* and *open symbols* correspond to the data obtained for different series of experiments.

decreased when plants were acclimated to strong light [25−27, 33, 40, 66].

CONCLUSIONS

A comparative study of two contrasting species of Tradescantia showed a noticeable difference in the dynamics of changes in photosynthetic parameters of shade-tolerant (*T. fluminenesis*) and light loving (*T. sillamontana*) species during prolonged acclimation of these plants to light of strong and moderate intensity. A noticeable difference in the functioning of the PSA of these species was revealed, manifested during prolonged acclimation of plants (up to 5 months). In the light-tolerant species *T. sillamontana*, photosynthetic parameters of PSA changed relatively little when plants acclimated to light of varying intensity. Photosynthetic parameters of chloroplasts of the shade-tolerant species *T. fluminenesis* showed higher lability. The damage of their PSA with increasing light intensity was accompanied by an increase in NPQ, which was manifested as the duration of leaf exposure increased (Fig. 6). One of the most effective mechanisms for enhancing the protection of the PSA of Tradescantia leaves from light stress was an increase in the expression of the regulatory protein PsbS, leading to an additional increase in NPQ [33].

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COMPLIANCE WITH ETHICAL STANDARDS

The authors declare that there is no conflict of interest.

This article does not contain a description of research involving humans or using animals as objects.

AUTHOR CONTRIBUTIONS

I.S. Suslichenko conducted fluorescence and EPR measurements; M.A. Benkov, D.A. Kovalishina, and M.O. Petrova participated in long-term experiments on measuring the fluorescent characteristics of leaves; B.V. Trubitsin provided instrumentation and EPR measurements; A.N. Tikhonov developed general work plan, performed the analysis of the literary data, prepared graphs and wrote the paper.

REFERENCES

1. Haehnel W. 1984. Photosynthetic electron transport in higher plants. *Annu. Rev. Plant Physiol. Plant Mol. Biol.* **35**, 659−693.

2. Nelson N., Yocum C.F. 2006. Structure and function of photosystems I and II. *Annu. Rev. Plant. Biol.* **57**, 521−565.

3. Mamedov M., Govindjee, Nadtochenko V., Semenov A. 2015. Primary electron transfer processes in photosynthetic reaction centers from oxygenic organisms. *Photosynth. Res.* **125**, 51−63.

4. Tikhonov A.N. 2014. The cytochrome b_6f complex at the crossroad of photosynthetic electron transport pathways. *Plant Physiol. Biochem.* **81**, 163−183.

5. Malone L.A., Proctor M.S., Hitchcock A., Hunter C.N., Johnson M.P. 2021.Cytochrome b_6f − Orchestrator of photosynthetic electron transfer. *Biochim. Biophis. Acta.* 1862, **148380**. https://doi.org/10.1016/j.bbabio.2021.148380

6. Höhner R., Pribil M., Herbstová M., Lopez L.S., Kunz H.-H., Li M., Wood M., Svoboda V., Puthiyaveetil S., Leister D., Kirchhoff H. 2020. Plastocyanin is the long-range electron carrier between photosystem II and photosystem I in plants. *Proc. Natl. Acad. Sci. USA.* **117**, 15354−15362.

7. Boyer P.D. 1997. The ATP synthase − a splendid molecular machine. *Annu. Rev. Biochem.* **66**, 717−749.

8. Junge W., Nelson N. 2015. ATP synthase. *Annu. Rev. Biochem.* **83**, 631−657.

9. Romanovsky Yu.M., Tikhonov A.N. 2010. Molecular energy converters of a living cell. Proton ATP synthase is a rotating molecular motor. *Uspekhi fizicheskikh nauk* (Rus.). **180**, 931−956.

10. Edwards J., Walker D. 1986. *Fotosintez C3 i C4 v rasteniy: mehanizmi i reguliatsiya.* (Photosynthesis of C3 and C4 in plants: Mechanisms and regulation). M.: Mir.

11. Allakhverdiev S.I., Murata N. 2004. Environmental stress inhibits the synthesis *de novo* of proteins involved

in the photodamage-repair cycle of photosystem II in *Synechocystis* sp. PCC 6803. *Biochim. Biophis. Acta*. **1657**, 23−32.

12. Järvi S., Suorsa M., Aro E.-M. 2015. Photosystem II repair in plant chloroplasts — Regulation, assisting proteins and shared components with photosystem II biogenesis. *Biochim. Biophys. Acta*. **1847**, 900−909.

13. Kono M., Terashima I. 2014. Long-term and short-term responses of the photosynthetic electron transport to fluctuating light. *J. Photochem. Photobiol. B*. **137**, 89−99.

14. Berry J., Björkman O. 1980. Photosynthetic response and adaptation to temperature in higher plants. *Annu. Rev. Plant Physiol*. **31**, 491−543.

15. Allakhverdiev S.I., Kreslavski V.D., Klimov V.V., Los D.A., Carpentier R., Mohanty P. 2008. Heat stress: An overview of molecular responses in photosynthesis. *Photosynth. Res*. **98**, 541−550.

16. Allen D.J., Ort D.R. 2001. Impact of chilling temperatures on photosynthesis in warm climate plants. *Trends Plant Sci*. **6**, 36−42.

17. Tikhonov A.N., Vershubskii A.V. 2020. Temperature-dependent regulation of electron transport and ATP synthesis in chloroplasts *in vitro* and *in silico*. *Photosynth. Res*. **146**, 299−329.

18. Michelet L., Zaffagnini M., Morisse S., Sparla F., Pérez-Pérez M.E., Francia F., Danon A., Marchand C.H., Fermani S., Trost P., Lemaire S.D. 2013. Redox regulation of the Calvin-Benson cycle: Something old, something new. *Front. Plant Sci*. **4**, 470. https://doi.org/10.3389/fpls.2013.00470

19. Balsera M., Schumann P., Buchanan B.B. 2016. Redox regulation in chloroplasts. In: *Chloroplasts. Current research and future trends*. Ed. Kirchhoff H. Norfolk, UK: Caister Academic Press, p. 187−207.

20. Rumberg B., Siggel U. 1969. pH changes in the inner phase of the thylakoids during photosynthesis. *Naturwissenschaften*. **56**, 130−132.

21. Kramer D.M., Sacksteder C.A., Cruz J.A. 1999. How acidic is the lumen? *Photosynth. Res*. **60**, 151−163.

22. Tikhonov A.N. 2013. pH-Dependent regulation of electron transport and ATP synthesis in chloroplasts. *Photosynth. Res*. **116**, 511−534.

23. Schansker G. 2022. Determining photosynthetic control, a probe for the balance between electron transport and Calvin−Benson cycle activity, with the DUAL-KLAS-NIR. *Photosynth. Res*. **153**, 191−204.

24. Lemeille S., Rochaix J.-D. 2010. State transitions at the crossroad of thylakoid signalling pathways. *Photosynth. Res*. **106**, 33−46.

25. Lichtenthaler H.K., Babani F. 2004. Light adaptation and senescence of the photosynthetic apparatus. Changes in pigment composition, chlorophyll fluorescence parameters and photosynthetic activity. In: *Chlorophyll a Fluorescence*. Springer, p. 713−736.

26. Lichtenthaler H.K., Babani F., Navrátil M., Buschmann C. 2013. Chlorophyll fluorescence kinetics, photosynthetic activity, and pigment composition of blue-shade and half-shade leaves as compared to sun and shade leaves of different trees. *Photosynth. Res*. **117**, 355−366.

27. Kirchhoff H. 2013. Architectural switches in plant thylakoid membranes. *Photosynth. Res*. **116**, 481−487.

28. Tikkanen M., Jarvi S., Aro E.-M. 2015. Light acclimation involves dynamic re-organization of the pigment−protein megacomplexes in non-appressed thylakoid domains. *The Plant J*. **84**, 360−373.

29. Puthiyaveetil S., Kirchhoff H., Höhner R. 2016. Structural and functional dynamics of the thylakoid membrane system. In: *Chloroplasts. Current research and future trends*. Ed. Kirchhoff H. Norfolk, UK: Caister Academic Press, p. 59−87.

30. Demmig-Adams B. 1998. Survey of thermal energy dissipation and pigment composition in sun and shade leaves. *Plant Cell Physiol*. **39**, 474−482.

31. Samoilova O.P., Ptushenko V.V., Kuvykin I.V., Kiselev S.A., Ptushenko O.S., Tikhonov A.N. 2011. Effects of light environment on the induction of chlorophyll fluorescence in leaves: A comparative study of *Tradescantia* species of different ecotypes. *BioSystems*. **105**, 41−48.

32. Ptushenko V.V., Ptushenko E.A., Samoilova O.P., Tikhonov A.N. 2013. Chlorophyll fluorescence in the leaves of *Tradescantia* species of different ecological groups: Induction events at different intensities of actinic light. *Biosystems*. **114**, 85−97.

33. Mishanin V.I., Trubitsin B.V., Benkov M.A., Minin A.A., Tikhonov A.N. 2016. Light acclimation of shade-tolerant and light-resistant *Tradescantia* species: Induction of chlorophyll *a* fluorescence and P_{700} photooxidation, expression of PsbS and Lhcb1 proteins. *Photosynth. Res*. **130**, 275−291.

34. Mishanin V.I., Trubitsin B.V., Patsaeva S.V., Ptushenko V.V., Solovchenko A.E., Tikhonov A.N. 2017. Acclimation of shade-tolerant and light-resistant *Tradescantia* species to growth light: Chlorophyll *a* fluorescence, electron transport, and xanthophyll content. *Photosynth. Res*. **133**, 87−102.

35. Ptushenko V.V., Zhigalova T.V., Avercheva O.V., Tikhonov A.N. 2019. Three phases of energy-dependent induction of P_{700}^+ and Chl *a* fluorescence in *Tradescantia fluminensis* leaves. *Photosynth. Res*. **139**, 509−522.

36. Benkov M.A., Yatsenko A.M., Tikhonov A.N. 2019. Light acclimation of shade-tolerant and sun-resistant *Tradescantia* species: Photochemical activity of PSII and its sensitivity to heat treatment. *Photosynth. Res*. **139**, 203−214.

37. Suslichenko I.S., Tikhonov A.N. 2019. Photo-reducible plastoquinone pools in chloroplasts of *Tradescantia* plants acclimated to high and low light. *FEBS Lett*. **593**, 788−798.

38. Randall R.P. 2012. *A global compendium of weeds*. 2nd edn. Department of Agriculture and Food, Western Australia.

39. Lyutova M.I., Tikhonov A.N. 1988. Comparison of the temperature dependence of lipid-soluble spin label mobility in thylakoid membranes of melon and cucumber chloroplasts. Biofizika (Rus.). **33**, 460−464.

40. Anderson J.M., Chow W.S., Park Y., Franklin L.A., Robinson S.P.-A., van Hasselt P.R. 2001. Response of *Tradescantia alRFIora* to growth irradiance: Change versus changeability. *Photosynth. Res*. **67**, 103−112.

41. Gounaris K., Brain A.P.R., Quinn P.J., Williams W.P. 1984. Structural reorganization of chloroplast thylakoid membranes in response to heat-stress. *Biochim. Biophys. Acta*. **766**, 198−208.

42. Li Z., Wakao S., Fischer B.B., Niyogi K.K. 2009. Sensing and responding to excess light. *Annu. Rev. Plant Biol*. **60**, 239−260.

43. Murata N., Takahashi S., Nishiyama Y., Allakhverdiev S.I. 2007. Photoinhibition of photosystem II under environmental stress. *Biochim. Biophis. Acta*. **1767**, 414−421.

44. Tikhonov A.N. 2020. Structure-function relationships in chloroplasts: EPR study of temperature-dependent regulation of photosynthesis, an overview. In *Photosynthesis: Molecular approaches to solar energy conversion*. Eds. Shen J.R., Satoh K., Allakhverdiev S.I. p. 343−373, https://doi.org/10.1007/978-3-030-67407-6_13

45. Lazár D. 1999. Chlorophyll *a* fluorescence induction. *Biochim. Biophys. Acta*. **1412**, 1−28.

46. Baker N.R. 2008. Chlorophyll fluorescence: A probe of photosynthesis in vivo. *Annu. Rev. Plant Biol*. **59**, 89−113.

47. Adams W.W. III, Demmig-Adams B. 2004. Chlorophyll fluorescence as a tool to monitor plant response to the environment. In: *Chlorophyll a fuorescence: A signature of photosynthesis. Advances in photosynthesis and respiration*. Eds. Papageorgiou G.C., Govindjee G. Springer, Dordrecht, p. 583−604.

48. Kalaji H.M., Schansker G., Ladle R.J., Goltsev V., Bosa K., Allakhverdiev S.I., Brestic M., Bussotti F., Calatayud A., Dąbrowski P., Elsheery N.I., Ferroni L., Guidi L., Hogewoning S.W, Jajoo A., Misra A.N., Nebauer S.G., Pancaldi S., Penella C., Poli D., Pollastrini M., Romanowska-Duda Z.B., Rutkowska B., Serôdio J., Suresh K., Szulc W., Tambussi E., Yanniccari M., Zivcak M. 2014. Frequently asked questions about in vivo chlorophyll fluorescence: Practical issues. *Photosynth. Res*. **122**, 121−158.

49. Niyogi K.K., Truong T.B. 2013. Evolution of flexible non-photochemical quenching mechanisms that regulate light harvesting in oxygenic photosynthesis. *Curr. Opin. Plant Biol*. **16**, 307−314.

50. Nilkens M., Kress E., Lambrev P., Miloslavina Y., Müller M., Holzwarth A.R., Jahns P. 2010. Identification of a slowly inducible zeaxanthin-dependent component of non-photochemical quenching of chlorophyll fluorescence generated under steady-state conditions in Arabidopsis. *Biochim. Biophys. Acta*. **1797**, 466−475.

51. Jahns P., Holzwarth A.R. 2012. The role of the xanthophyll cycle and of lutein in photoprotection of photosystem II. *Biochim. Biophys. Acta*. **1817**, 182−193.

52. Ruban A.V. 2016. Nonphotochemical chlorophyll fluorescence quenching: mechanism and effectiveness in protecting plants from photodamage, *Plant Physiol*. **170**, 1903−1916.

53. Murchie E.H., Ruban A.V. 2020. Dynamic non-photochemical quenching in plants: From molecular mechanism to productivity. *Plant J*. **101**, 885-896.

54. Kuvykin I.V., Ptushenko V.V., Vershoubsky A.V., Tikhonov A.N. 2011. Regulation of electron transport in C3 plant chloroplasts *in situ* and *in silico*. Short-term effects of atmospheric CO_2 and O_2. *Biochim. Biophys. Acta*. **1807**, 336−347.

55. Trubitsin B.V., Vershubskii A.V., Priklonskii V.I., Tikhonov A.N. 2015. Short-term regulation and alternative pathways of photosynthetic electron transport in *Hibiscus rosa-sinensis* leaves. *J. Photochem. Photobiol. B*. **152**, 400−415.

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

57. Stirbet A., Govindjee G. 2011. On the relation between the Kautsky effect (chlorophyll *a* fluorescence induction) and photosystem II: Basics and applications of the *OJIP* fluorescence transient. *J. Photoch. Photobiol. B*. **104**, 236−257.

58. Schansker G., Tóth S.Z., Strasser R.J. 2006. Dark recovery of the Chl *a* fluorescence transient (*OJIP*) after light adaptation: The *qT*-component of non-photochemical quenching is related to an activated photosystem I acceptor side. *Biochim. Biophys. Acta*. **1757**, 787−797.

59. Jallet D., Cantrell M., Peers G. 2016. New players for photoprotection and light acclimation. In: *Chloroplasts. Current research and future trends*. Ed. Kirchhoff H. Norfolk, UK: Caister Academic Press, p. 133−159.

60. Tikkanen M., Mekala N.R., Aro E.-M. 2014. Photosystem II photoinhibition-repair cycle protects Photosystem I from irreversible damage. *Biochim. Biophis. Acta*. **1837**, 210−215.

61. Strand D.D., Fisher N., Kramer D.M. 2016. Distinct energetics and regulatory functions of the two major cyclic electron flow pathways in chloroplasts. In: *Chloroplasts: Current Research and Future Trends*. Ed. Kirchhoff H. Norfolk, UK: Caister Academic Press, p. 89−100.

62. Stiehl H.H., Witt H.T. 1969. Quantitative treatment of the function of plastoquinone in photosynthesis. *Z. Naturforsch*. **24b**, 1588−1598.

63. Ryzhikov S.B., Tikhonov A.N. 1988. Regulation of the electron transfer rate in photosynthetic membranes of higher plants. *Biofizika* (Rus.). **33**, 642−646.

64. Suslichenko I.S., Trubitsin B.V., Vershubskii A.V., Tikhonov A.N. 2022. The noninvasive monitoring of the redox status of photosynthetic electron transport chains in *Hibiscus rosa-sinensis* and *Tradescantia* leaves. *Plant Physiol. Biochem*. **185**, 233−243.

65. Kalmatskaya O.A., Trubitsin B.V., Suslichenko I.S., Karavaev V.A., Tikhonov A.N. 2020. Electron transport in *Tradescantia* leaves acclimated to high and low light: Thermoluminescence, PAM-fluorometry, and EPR studies. *Photosynth. Res*. **146**, 123−141.

66. Eberhard S., Finazzi G., Wollman F.-A. 2008. The dynamics of photosynthesis. *Annu. Rev. Genet*. **42**, 463−515.

67. Foyer C.H., Neukermans J., Queval G., Noctor G., Harbinson J. 2012. Photosynthetic control of electron transport and the regulation of gene expression. *J. Exp. Bot*. **63**, 1637−1661.

68. Tikhonov A.N. 2015. Induction events and short-term regulation of electron transport in chloroplasts: An overview. *Photosynth. Res*. **125**, 65−94.

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