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Chlorophyll fluorescence in the leaves of *Tradescantia* species of different ecological groups: Induction events at different intensities of actinic light

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ABSTRACT

Chlorophyll fluorescence analysis is one of the most convenient and widespread techniques used to monitor photosynthesis performance in plants. In this work, after a brief overview of the mechanisms of regulation of photosynthetic electron transport and protection of photosynthetic apparatus against photodamage, we describe results of our study of the effects of actinic light intensity on photosynthetic performance in *Tradescantia* species of different ecological groups. Using the chlorophyll fluorescence as a probe of photosynthetic activity, we have found that the shade-tolerant species *Tradescantia fluminensis* shows a higher sensitivity to short-term illumination (≤20 min) with low and moderate light (≤200 μE m^{-2} s^{-1}) as compared with the light-resistant species *Tradescantia sillamontana*. In *T. fluminensis*, non-photochemical quenching of chlorophyll fluorescence (NPQ) and photosystem II operational efficiency (parameter Φ_{PSII}) saturate as soon as actinic light reaches ≈200 μE m^{-2} s^{-1}. Otherwise, *T. sillamontana* revealed a higher capacity for NPQ at strong light (≥800 μE m^{-2} s^{-1}). The post-illumination adaptation of shade-tolerant plants occurs slower than in the light-resistant species. The data obtained are discussed in terms of reactivity of photosynthetic apparatus to short-term variations of the environment light.

1. Introduction

1.1. Overview of photosynthetic electron transport and its regulation

Photosynthesis is one of the most important processes in nature, which converts light energy into energy of organic compounds, produces the molecular oxygen (O_2) and provides the assimilation of carbon dioxide (CO_2). In photosynthetic systems of oxygenic type (cyanobacteria, algae, chloroplasts of higher plants), two photosystems, photosystem I (PSI) and photosystem II (PSII), operating in tandem provide transfer of two electrons from the water molecule oxidized by PSII to $NADP^+$, the terminal electron acceptor of PSI ($H_2O \rightarrow PSII \rightarrow PSI \rightarrow NADP^+$). There has been great progress toward elucidating the structure and functioning of electron transport chain (ETC) at the atomic level based on X-ray crystallography studies of multiprotein complexes (see for review Fromme et al., 2001; Cramer et al., 2006; Nelson and Yocum, 2006; Barber, 2008; Semenov et al., 2011; Cardona et al., 2012; Müh et al., 2012; Hasan et al., 2013).

A simplified scheme of ETC and light-induced events in chloroplasts is shown in Fig. 1. Pigment-protein complexes PSI and PSII are embedded into the thylakoid membrane. These complexes are interconnected via the membrane-bound cytochrome b_6f complex and mobile electron carriers, plastoquinone (PQ) and plastocyanin (Pc). PSII provides the actuation of the water-splitting complex and reduction of PQ; two protons are translocated from stroma (H^+_{out}) to the intrathylakoid lumen (H^+_{in}) per one PQ molecule reduced ($H_2O + PQ + 2H^+_{out} \rightarrow 1/2O_2 + PQH_2 + 2H^+_{in}$). The cytochrome b_6f complex mediates electron transfer between PSII and PSI by oxidizing plastoquinol (PQH_2) and reducing Pc. Oxidation of PQH_2 by the cytochrome b_6f complex is accompanied by dissociation of

Abbreviations: AL, actinic light; BBC cycle, Bassham–Benson–Calvin cycle; ETC, electron transport chain; HL, high light; LL, low light; ML, moderate light; NPQ, non-photochemical quenching; PAM, pulse-amplitude modulation; PSI and PSII, photosystem I and photosystem II, respectively; PQ and PQH_2, plastoquinone and plastoquinol, respectively; Vx, violaxanthin; Zx, zeaxanthin.

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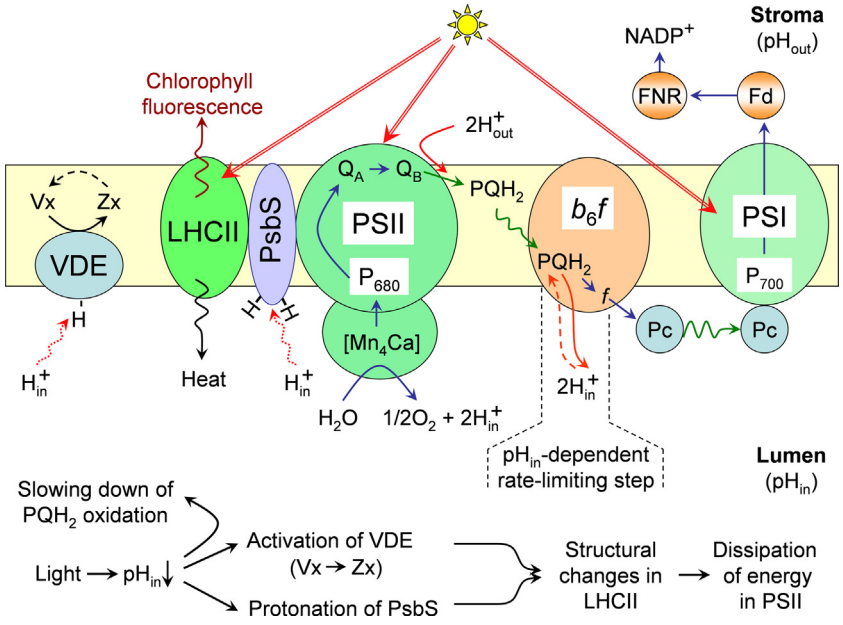

Fig. 1. Cartoon illustrating pH-dependent mechanism of down-regulation of PSII activity in chloroplasts (modified Fig. 13 from Tikhonov, 2013).

two protons into the bulk phase of the thylakoid lumen. As a result, the operation of PSII and b_6f complex generates a transmembrane difference in electrochemical potentials of protons ($\Delta\tilde{\mu}_{H^+}$), which serves as the driving force for ATP synthase ($ADP + P_i \rightarrow ATP$). The products of the light-induced stages of photosynthesis, NADPH and ATP, are used for synthesis of carbohydrates in the Bassham–Benson–Calvin (BBC) cycle.

Elucidation of the mechanisms providing the optimal functioning of photosynthetic apparatus and its adaptation to varying environmental conditions is a topical problem of biophysics and biochemistry of photosynthesis (see for review Edwards and Walker, 1983; Allen, 1992, 2003; Noctor and Foyer, 2000; Wollman, 2001; Pfannschmidt, 2003; Kramer et al., 2004; Cruz et al., 2007; Allakhverdiev et al., 2008; Minagawa, 2011; Rochaix, 2011; Tikhonov, 2012, 2013; Tikkanen and Aro, 2012; and references therein). The flexibility of photosynthetic apparatus in response to environmental changes is achieved by several mechanisms of regulation of photosynthetic electron transport:

(i) redistribution of electron flows through different pathways (noncyclic/cyclic/pseudocyclic electron transport) (Bendall and Manasse, 1995; Ivanov et al., 1998; Asada, 1999; Heber, 2002; Ort and Baker, 2002; Munekage et al., 2004; Johnson, 2005, 2011; Joliot and Joliot, 2005),
(ii) redistribution of light quanta between PSI and PSII ("state transitions") (Allen, 1992; Wollman, 2001; Minagawa, 2011; Tikkanen and Aro, 2012),
(iii) light-induced activation of the BBC cycle enzymes (Mott and Berry, 1986; Woodrow and Berry, 1988; Buchanan, 1991; Igamberdiev and Lea, 2006; Andersson, 2008; Igamberdiev and Kleczkowski, 2011),
(iv) down-regulation of the intersystem electron transport and PSII activity. These mechanisms are governed by the light-induced changes in the intrathylakoid (lumen) pH_{in}. Acidification of the lumen is known to decelerate the plastoquinol (PQH_2) oxidation by the cytochrome b_6f complex, thus impeding the electron flow to P_{700}^+ (Rumberg and Siggel, 1969; Tikhonov et al., 1981, 1984; Nishio and Whitmarsh, 1993; Kramer et al., 1999, 2004; Tikhonov, 2012, 2013). Acidification of the lumen also triggers thermal dissipation of excess energy in the light-harvesting antenna of PSII (collectively called LHCII) known as non-photochemical quenching (NPQ), providing protection of photosynthetic apparatus against a solar stress (Rees et al., 1989, 1992; Demmig-Adams, 1990; Noctor et al., 1991; Horton et al., 1996; Li et al., 2000, 2002, 2004; Demmig-Adams et al., 2006a,b, 2012; Jahns and Holzwarth, 2012; Ruban et al., 2012).

1.2. *Chlorophyll fluorescence as an indicator of photoprotective mechanisms in chloroplasts*

Chlorophyll *a* fluorescence analysis is one of the most convenient and widespread methods for in vivo monitoring photosynthesis performance and stress in plants and algae (see for review Barber, 1976; Lazar, 1999; Maxwell and Johnson, 2000; Adams and Demmig-Adams, 2004; Baker and Oxborough, 2004; Baker, 2008). Light-induced changes in the yield of chlorophyll fluorescence are correlated (at least qualitatively) with changes in the functional state of photosynthetic apparatus and CO_2 assimilation (Genty et al., 1989). Measurements of chlorophyll fluorescence bring valuable information about the efficiency of photochemical processes of energy conversion in photoreaction centers of PSII ("photochemical quenching") and heat dissipation of excess light energy absorbed by the light-harvesting antenna ("non-photochemical quenching"). Non-photochemical quenching (NPQ) reveals itself as a decrease in chlorophyll fluorescence caused by enhanced dissipation as heat of excess light energy absorbed by the light-harvesting antenna of PSII. Deconvolution of fluorescence quenching into photochemical and non-photochemical components can be performed using the PAM-fluorometry (Pulse Amplitude Modulation) technique (Schreiber et al., 1986).

Chlorophyll fluorescence analysis has been widely applied in physiological and ecophysiological studies, because it can give insights into plant responses to environmental stress (see for review Adams and Demmig-Adams, 2004; Baker and Oxborough, 2004; Lichtenthaler and Babani, 2004; Demmig-Adams et al., 2012). Under natural conditions, photosynthetic organisms are exposed to variable light of a wide range of intensities, including high light (HL), which are potentially destructive to photosynthetic apparatus. Plants developed several mechanisms for protection