

Non-photochemical quenching of chlorophyll fluorescence and its components – recent advances

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To protect themselves from fluctuating light environments, plants have evolved non-photochemical quenching (NPQ) as a protective mechanism. NPQ comprises the thermal dissipation of excess light energy via the de-excitation of singlet excited chlorophyll (Chl) in photosystem II of photosynthetic organisms. In this review, all available data on the NPQ and its components have been summarized. NPQ components were primarily distinguished based on the NPQ relaxation and its sensitivity to chemical inhibitors. However, numerous diverse processes contribute to NPQ therefore, it has been suggested to separate NPQ components based on the molecular players involved as well as on Chl fluorescence relaxation kinetics. These types of NPQ include energy-dependent quenching (qE), state transition quenching (qT), photoinhibitory quenching (qI), sustained quenching (qH), zeaxanthin-dependent quenching (qZ), and chloroplast movement-dependent quenching (qM). Although molecular players and regulatory elements that modulate these quenching types are not discussed in this review, they may differ and afford to adapt to the environmental stresses that plants are experiencing. Finally, the role of the investigation of NPQ components, their molecular players, and regulatory mechanisms involved in NPQ as promising targets for strategies to breed highly productive and tolerant crop plants was suggested.

Keywords: *Chlorophyll fluorescence, chloroplast movement-dependent quenching, energy-dependent quenching, non-photochemical quenching, plant, state transition quenching, photoinhibitory quenching, sustained quenching, zeaxanthin-dependent quenching*

INTRODUCTION

A biological process that converts the energy from sunlight into chemical energy is called photosynthesis. In plants, this process assimilates CO₂ and produces biological compounds through the Calvin–Benson–Bassham cycle. Although light is mandatory for photosynthesis, excess light becomes a damaging factor to the photosynthetic apparatus. Usually, the quantity of light changes in natural environments therefore, photosynthetic organisms are often exposed to light stress. When sunlight is in excess, over-excitation of the photosystems occurs and it results in damage to the photosynthetic apparatus. Finally, it may lead to cell death in photosynthesizing organisms. The reaction center of photosystem II

(PSII) consumes the energy captured by the antenna and causes a decrease in the density of excited states. This leads to the decrease in the fluorescence intensity/lifetime of the antenna chlorophylls (Chl) and is called photochemical quenching (qP) (Krause and Weis, 1991). Another type of quenching exists when the reaction center of the RCII is closed. This type of quenching mechanism is called non-photochemical quenching (NPQ) of Chl fluorescence (Demmig-Adams et al., 2014). Plants have evolved this NPQ as a protective mechanism that dissipates excess light energy as heat (Müller et al., 2001; Ruban, 2016). NPQ involves the thermal dissipation of excess absorbed energy through the de-excitation of singlet excited Chl in photosystem II (PSII).

Chl fluorescence is actually an “instrument” that detects the total density of excited states in the photosynthetic antenna (Clayton, 1980; Blankenship, 2002; Ruban, 2012). Thus, NPQ is not a straight measure of dissipated excess energy absorbed by the antenna. Application of photosynthetically active radiance to the photosynthetic organisms drives electron transport following light harvesting by the antenna. Electron transport is associated with the proton gradient across the photosynthetic membrane, ΔpH , which activates NPQ (Briantais et al., 1979; Wraight and Crofts, 1970). Indeed, the acidification of the thylakoid membranes was found to induce the protonation in PSII and trigger the NPQ response (Rees et al., 1992; Liguori et al., 2019; Krishnan-Schmieden et al., 2021; Li et al., 2004). Although the minimum obligation for the NPQ activation is the presence of the LHCII and ΔpH , these factors alone are not enough to induce a significant and fast NPQ response under physiological ΔpH values (Saccon et al., 2020). The xanthophyll cycle and the photosystem II subunit S (PsbS) protein have a decisive role in the NPQ activation, especially under smaller ΔpH values (Johnson and Ruban, 2011). Because plants can alter the gathering of these factors based on metabolic and environmental signals, providing a complex control of the NPQ response. It is important to note that this has a great physiological meaning. It has been shown that NPQ can arise in the absence of PsbS or zeaxanthin, as in wild-type plants, in spite of losing the kinetics of fast activation and deactivation (Johnson and Ruban, 2010; Johnson et al., 2012).

In this review, we summarize all available pieces of information on NPQ and its components because, the rate of induction and relaxation of NPQ components become a leading factor for the growth of plants in the field (Murchie and Niyogi, 2011; Kromdijk et al., 2016). The knowledge about NPQ and its components might be helpful to breed crop plants with high productivity and tolerance to environmental stresses. NPQ components were initially defined based on NPQ relaxation kinetics and its sensitivity to chemical inhibitors (Ruban, 2016; Walters and Horton, 1991). Numerous diverse processes contribute to NPQ. Therefore, Malnoë (Malnoë, 2018) suggests separating them based on the molecular

players involved as well as on Chl fluorescence relaxation kinetics. Because of the complexity of the integral components of NPQ and its components, I will not discuss all the players and controllers in this review. These types of NPQ include energy-dependent quenching (qE), state transition quenching (qT), photoinhibitory quenching (qI), sustained quenching (qH), zeaxanthin-dependent quenching (qZ), and chloroplast movement-dependent quenching also called as blue light-dependent quenching (qM) (see Fig. 1).

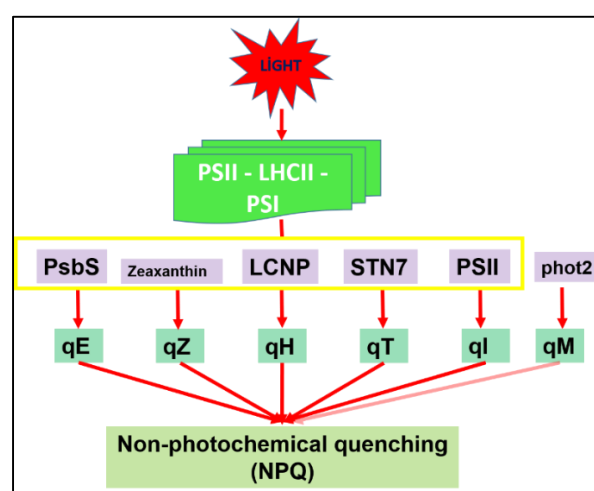


Fig. 1. A schematic diagram illustrating the process of non-photochemical quenching (NPQ) in plants.

Energy-dependent quenching – qE

The fastest and major component of NPQ is the energy-dependent quenching (qE), which is initiated under light and reversed in the dark (Li et al., 2002; Zulfugarov et al., 2007; Ruban et al., 2012; Niyogi and Truong, 2013; Goss and Lepetit, 2015). qE is determined by the acidification of the thylakoid lumen that occurs mainly under high light conditions (Wraight and Crofts, 1970; Briantais et al., 1979). This acidification alters the pigment composition of LHCII primarily through the xanthophyll cycle and triggers qE protein effectors, such as PsbS protein of PSII in plants (Pashayeva et al., 2021). Evidence collected during the last two decades suggests that the leading quenching site of qE in vivo is the LHCII (Ruban et al., 2012). qE is a ubiquitous energy dissipation mechanism among photosynthetic eukaryotes (Niyogi and Truong, 2013).

Goss and Lepetit, 2015). qE deficient plants become highly sensitive to photoinhibition (Ruban et al., 2012; Niyogi and Truong, 2013; Zulfugarov et al., 2014) and it protects PSII reaction centers against photodamage (Pashayeva et al., 2021; Zulfugarov et al., 2007; Zulfugarov et al., 2014; Zulfugarov et al., 2019). PsbS protein, xanthophyll cycle, and Δ pH co-operate together to induce conformational changes in the thylakoid membrane (Jeong et al., 2010; Zulfugarov et al., 2010). The conformational changes which occur in the thylakoid membranes of plants are proposed to initiate quenching (Ruban et al., 2012). Most importantly, it has been shown that genetic alteration of qE capacity improves crop productivity in the field (Kromdijk et al., 2016).

State transition quenching – qT

The redistribution of excitation energy between photosystems in response to light causes a disproportion in excitation between these photosystems, called state transition (qT) (Bellaflöre et al., 2015). State transition limits the over-reduction or over-oxidation of the photosynthetic electron transport chain and also the possibility of photo-oxidative damage (Derks, 2015). Usually, qT occurs under low-light conditions and involves the movement of phosphorylated antenna proteins away from PSII (Krause and Weis, 1991; Ruban and Johnson, 2009). In plants, state transitions occur through LHCII movement in a way different from that used in qE (Pashayeva et al., 2021). qE occurs due to the reversible phosphorylation of the antenna proteins and it regulates the relocation of some populations of LHCII from PSII to PSI.

Photoinhibitory quenching – qI

Photoinhibitory quenching (qI) mainly includes a loss in the number of active PSII reaction centers from photodamage (Derks et al., 2015). Previously the mechanisms that resulted in the light-induced reduction in the quantum yield of PSII because of D1 photoinactivation were termed photoinhibitory quenching (qI) (Krause, 1988; Malnoë, 2018). However, qI is also connected with zeaxanthin maintenance. qI contains all mechanisms with slow relaxation kinetics,

such as photoinhibition and other un-considered modes of continuous thermal dissipation (Demmig-Adams and Adams, 1992). qI revenues several hours or longer to relax depending on both photoinhibition and other long-term photoprotective quenching mechanisms (Malnoë et al., 2017; Ruban and Horton, 1995). Thus, qI is the slowest component of NPQ (Zulfugarov et al., 2014).

Sustained quenching – qH

qH is the most newly recognized antenna-quenching component of NPQ, which protects the photosynthetic apparatus under stress conditions in Arabidopsis (Brooks et al., 2013; Malnoë et al., 2017). qH is a different NPQ component independent of PsbS protein of PSII, Δ pH, zeaxanthin, the STN7 kinase, and photoinhibition processes. Because qH is also a slow component of NPQ it is named a sustained quenching that occurs within a photosynthetic antenna (Brooks et al., 2013; Malnoë et al., 2018). This quenching mechanism involves the plastid lipocalin LCNP (Malnoë et al., 2017) and is prevented by the suppressor of quenching1 (SOQ1) under non-stress conditions. The molecular players of qH, LCNP, and the relaxation of qH1 (ROQH1) were suggested to play an antagonistic role in a dosage-dependent manner to protect the photosynthetic apparatus and in sustaining the light-harvesting efficiency in plants (Amstutz et al., 2020).

Zeaxanthin-dependent quenching – qZ

Using different NPQ mutants from Arabidopsis showed that the new type of quenching occurs in plants unrelated to qE, qT, or qI (Nilkens et al., 2010). The analysis of the NPQ induction and relaxation kinetics shows a lifetime in the range of 10–15 min. Because this lifetime correlates with zeaxanthin formation, authors identified this type of quenching as a zeaxanthin-dependent quenching – qZ (Nilkens et al., 2010). qZ is dependent upon the accumulation of zeaxanthin, but its induction is independent of both Δ pH and PsbS (Dall’Osto et al., 2005; Nilkens et al., 2010). qZ is supposed to arise within the minor antennae that persist attached to PSII, which includes minor LHC proteins (Jahns and Holzwarth, 2012). qZ relaxes more slowly than

fastest qE (Dall'Osto et al., 2005; Nilkens et al., 2010; Jahns and Holzwarth, 2012). It has been shown that qZ is the most variable NPQ component in different plants and its variation influenced the strength and the kinetic properties of the response to the given experimental conditions (Sello et al., 2019). Some plants can modulate qZ depending on growth conditions, but probably, this response may also be inclined by species-specific features.

Chloroplast movement-dependent quenching – qM

A blue light-dependent quenching (qM) is tempted by chloroplast movement (Cazzaniga et al., 2013; Dall'Osto et al., 2014). qM is also called chloroplast movement-dependent quenching and it was detected in *phot2* mutant of Arabidopsis with impaired chloroplast movement (Kasahara et al., 2002) as a module lacking in the Chl fluorescence decay (Cazzaniga et al., 2013). More recently it has been shown that qM has little influence on the photoprotection efficiency under high-light conditions in “shade”-grown Arabidopsis plants. Consequently, the existence of NPQ component qM and its influence on photoinhibition should be carefully reevaluated (Wilson and Ruban, 2020).

CONCLUSIONS

As drawn in this review, up-to-date research has shifted toward a dynamic role for NPQ and its components. From an alliance of this literature review, it is clear that NPQ response changes dynamically via its different components under light to balance between protection and light utilization. From our existing state of information, we suppose that the regulatory mechanisms of the different NPQ components play a dynamic role in the acclimation and adaptation of plants to fluctuating light environments as well as to other biotic stresses. It is well likely that the fundamental mechanisms of the NPQ components are the same for most of them. However, molecular players and regulatory elements that modulate these quenching types differ and might afford to adapt to the range of environmental conditions that

photosynthetic organisms are experiencing. To end, I suggest that investigating the regulatory mechanisms of NPQ components and molecular players involved in these processes are promising targets for strategies to breed highly productive and tolerant crop plants.

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Xlorofil flüoressensiyasının qeyri-fotokimyəsi sönməsi və onun komponentləri: son irəliləyişlər

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Dəyişən işıq mühitinin təsirindən qorunmaq üçün bitkilər qoruyucu mexanizm kimi qeyri-fotokimyəvi sönmə (QFS) inkişaf etdirmişlər. QFS, fotosintetik orqanizmlərin fotosistem II-də singlet həyəcanlanmış xlorofilin (Xl) sönməsi yolu ilə artıq işıq enerjisinin istilik enerjisi kimi yayılmasından ibarətdir. Bu icmalda QFS və onun komponentləri haqqında bilinənləri ümumiləşdirdik. QFS komponentləri ilk növbədə həm QFS relaksasiyasına, həm də onun kimyəvi inhibitorlara qarşı həssaslığına görə fərqləndirilirdi. Bununla belə, çoxsaylı müxtəlif proseslər QFS-da iştirak edirlər, buna görə də QFS komponentlərinin formalaşmasında iştirak edən molekulyar iştirakçılara, eləcə də Xl flüoressensiyasının relaksasiya kinetikasına əsaslanaraq ayrılması təklif edilmişdir. Bu QFS növlərinə - enerjidən asılı sönmə (qE), vəziyyətə keçid sönmə (qT), fotoinhibirləşdirici sönmə (qI), davamlı sönmə (qH), zeaksantindən asılı sönmə (qZ) və xloroplastın hərəkətindən asılı sönmə (qM) daxildir. Bu sönmə növlərini modullaşdıran molekulyar iştirakçılar və tənzimləyici elementlər bu icmalda müzakirə edilməsə də, onlar fərqli ola və bitkilərin məruz qaldığı ətraf mühit streslərə uyğunlaşmasına kömək edə bilərlər. Nəhayət, yüksək məhsuldar və dözümlü bitkilərinin yetişdirilməsi strategiyaları üçün perspektiv hədəflər kimi QFS komponentlərinin, onların molekulyar iştirakçılarının və QFS-i tənzim edən mexanizmlərin tədqiqinin rolu təklif edilmişdir.

Açar sözlər: *Xlorofil flüoressensiyası, xloroplastın hərəkətindən asılı sönmə, enerjidən asılı sönmə, qeyri-fotokimyəvi sönmə, bitki, vəziyyətə keçid sönmə, fotoinhibirləşdirici sönmə, davamlı sönmə, zeaksantindən asılı sönmə*

Нефотохимическое тушение флуоресценции хлорофилла и его компоненты – последние достижения

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В качестве защитного механизма в ответ на воздействие изменяющейся световой энергии растения развили нефотохимическое тушение (НФТ). НФТ включает тушение синглетно-возбужденного хлорофилла (Xl) в фотосинтезирующих организмах в фотосистеме II в виде тепловой энергии. В этом обзоре мы обобщили все, что известно о НФТ и его компонентах. Компоненты НФТ отличались в первую очередь релаксацией и чувствительностью к химическим ингибиторам. Однако в НФТ вовлечено множество различных процессов, поэтому было предложено провести разделение на основе отличий молекулярных составляющих, участвующих в формировании компонентов НФТ, а также флуоресценции Xl, на основе кинетики релаксации. Эти типы НФТ включают энергозависимое тушение (qE), тушение «переходов состояний» (qT), фотоингибирующее тушение (qI), непрерывное тушение (qH), зеаксантин-зависимое тушение (qZ) и тушение, зависящее от движения хлоропластов

(qM). Хотя молекулярные участники и регуляторные элементы, которые модулируют эти виды, в данном обзоре не обсуждаются, они могут быть разными и помогают растениям адаптироваться к стрессам окружающей среды, которым они подвергаются. В заключение, было высказано мнение о роли изучения компонентов НФТ, их молекулярных участников и механизмов, регулирующих НФТ, как перспективных мишеней для стратегий выращивания высокоурожайных и толерантных растений.

Ключевые слова: *Флуоресценция хлорофилла, тушение, зависящее от движения хлоропластов, энергозависимое тушение, нефотохимическое тушение, растение, тушение состояний, тушение фотоингибирования, непрерывное тушение, зеаксантин-зависимое тушение*