



## Review article

## Parameters of photosynthetic energy partitioning



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## ABSTRACT

Almost every laboratory dealing with plant physiology, photosynthesis research, remote sensing, and plant phenotyping possesses a fluorometer to measure a kind of chlorophyll (Chl) fluorescence induction (FLI). When the slow Chl FLI is measured with addition of saturating pulses and far-red illumination, the so-called quenching analysis followed by the so-called relaxation analysis in darkness can be realized. These measurements then serve for evaluation of the so-called energy partitioning, that is, calculation of quantum yields of photochemical and of different types of non-photochemical processes. Several theories have been suggested for photosynthetic energy partitioning. The current work aims to summarize all the existing theories, namely their equations for the quantum yields, their meaning and their assumptions. In the framework of these theories it is also found here that the well-known NPQ parameter ( $= (F_M - F'_M)/F'_M$ ; Bilger and Björkman, 1990) equals the ratio of the quantum yield of regulatory light-induced non-photochemical quenching to the quantum yield of constitutive non-regulatory non-photochemical quenching ( $\Phi_{NPQ}/\Phi_{f,D}$ ). A similar relationship is also found here for the PQ parameter ( $\Phi_P/\Phi_{f,D}$ ).

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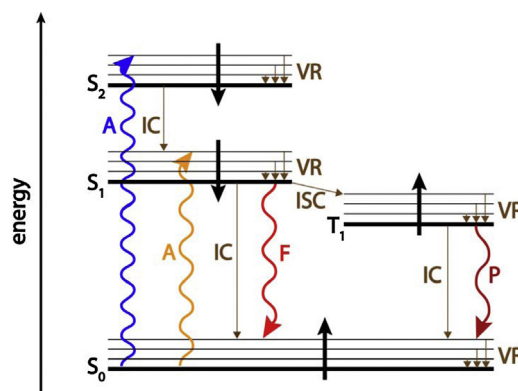
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## Introduction

Chlorophyll (Chl) fluorescence induction (FLI) is one of the most frequently used methods of all Chl fluorescence measurements. Therefore, it is widely and extensively used not only in plant physiology and photosynthesis research, but also in remote sensing and plant phenotyping. The Chl FLI was first observed by [Kautsky and Hirsch \(1931\)](#) by their own eyes; the curve constructed based on their observation started with a fast fluorescence rise (FLR) followed by a slow fluorescence decrease (FLD) to a steady state. The FLR and FLD are also known as the fast and the slow phases of FLI, respectively (e.g., [Govindjee, 1995](#)). Later, with improvements in fluorimeters, use of the Chl FLI was in fact split into two types of measurements: (i) measurement of the Chl FLR with a high time resolution and usually under high intensity of excitation light (the O-J-I-P curve) and (ii) measurements of whole Chl FLI for a long time and applying different sources of excitation light (the quenching analysis). These two types of measurements are also related to different excitation and detection of fluorescence signal (see below). The fast Chl FLR was reviewed, e.g., by [Lazár \(2006\)](#), [Stirbet and Govindjee \(2011, 2012\)](#), and [Schansker et al. \(2014\)](#), while the slow Chl FLD and Chl FLI were reviewed, e.g., by [Lazár \(1999\)](#), [Maxwell and Johnson \(2000\)](#), [Papageorgiou et al. \(2007\)](#), [Baker \(2008\)](#), and [Porcar-Castell et al. \(2014\)](#). The Chl FLI was also theoretically modeled and this effort was reviewed by [Lazár and Schansker \(2009\)](#), [Vredenberg and Prášil \(2009\)](#), [Rubin and Riznichenko \(2009\)](#), and [Stirbet et al. \(2014\)](#).

In the past two decades, a lot of effort has been made to define the so-called photosynthetic energy partitioning, i.e., to define parameters (quantum yields) which will reflect the fraction of absorbed light energy utilized by particular processes (photochemistry vs. non-photochemical dissipations). Irrespective of many publications on this topic, there exists no review article that summarizes all of the derived parameters. Therefore, a researcher can be confused by the existence of so many parameters, their interpretation and the assumptions under which the derivations are made. The reader thus should be introduced and correctly informed about differences among the parameters and their proper usage. Even experts are not familiar with all of the existing theories. It is, therefore, the main aim of this review to contribute a summary of all known approaches and parameters of photosynthetic energy partitioning. In the current review, the basics of the Chl fluorescence and quantum yields are described first, followed by a description of the measuring techniques together with explanation of basic fluorescence levels and quenching coefficients and parameters, followed by detailed description and discussion of the parameters (quantum yields) of the photosynthetic energy partitioning. A side product of reviewing the theories is that it is found here that the well-known NPQ and PQ parameters are equal to a ratio of two quantum yields (Eqs. (38) and (39); see below).

The topic of this review is very closely related to the mechanisms of the light-induced regulatory non-photochemical Chl



**Fig. 1.** A scheme of energetic levels (the so-called Jablonski diagram) of a single molecule showing routes of formation and deactivation of the energetic levels. The thin horizontal lines show vibrational energy levels which are superimposed on electronic energy levels of the ground state ( $S_0$ ), excited singlet states ( $S_1$  and  $S_2$ ) and excited triplet state ( $T_1$ ) shown by thick horizontal lines. Vertical thick arrows symbolically show orientation of spin; when the arrows in the ground and excited states are in the opposite/same directions, the singlet/triplet excited state is realized. Vertical wavy arrows indicate radiative transitions by means of absorption of light (A) of different wavelengths (shorter wavelength (blue) means higher energy whereas longer wavelength (orange) means lower energy) and by means of emission of light by fluorescence (F;  $S_1-S_0$  transition) and by phosphorescence (P;  $T_1-S_0$  transition). Thin vertical or skew arrows indicate non-radiative transitions by means of vibrational relaxation (VR), internal conversion (IC), and inter-system crossing (ISC) which all represent a loss of energy by heat dissipation. For the case of a photosynthetic pigment molecule, additional deactivations of the excited states not shown in the figure can occur: via energy transfer to another molecule and via photochemistry (the primary charge separation). Each of all the above mentioned processes is characterized by its rate constant (not shown in the figure). In the dark-adapted state of healthy non-stressed sample the non-radiative transitions are the origins of the basal constitutive non-regulatory heat dissipations characterized by its overall apparent rate constant  $k_D$  (see the text and [Fig. 2](#)). In a light-adapted state of the sample, light-induced changes (increase) in the values of the rate constants of the non-radiative transitions occur (with respect to their values in the dark-adapted state) which cause the light-induced regulatory heat dissipation characterized by its overall apparent rate constant  $k_{NPQ}$  (see the text and [Fig. 2](#)). When the sustained regulatory non-photochemical quenching is present, it also affects the non-radiative transitions of the dark-adapted state (increase of  $k_D$ ). The same is true when a photoinhibition occurs.

fluorescence quenching as such. Much discussion is still ongoing on these mechanisms. As this is beyond of the scope of this review, it does not deal with these mechanisms and the readers are referred to a recent review on the biodiversity of the non-photochemical Chl fluorescence quenching ([Goss and Lepetit, 2014](#)) and to a recent book on all aspects of the non-photochemical Chl fluorescence quenching edited by [Demmig-Adams et al. \(2014\)](#).

## Chl fluorescence and quantum yields

To access the photosynthetic energy partitioning, the Chl fluorescence signal is used. By definition, fluorescence is a radiative deactivation of an excited singlet state (usually the first singlet

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