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Review

Algal photosynthetic responses to toxic metals and herbicides assessed by chlorophyll *a* fluorescence

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ABSTRACT

Chlorophyll *a* fluorescence is established as a rapid, non-intrusive technique to monitor photosynthetic performance of plants and algae, as well as to analyze their protective responses. Apart from its utility in determining the physiological status of photosynthesizers in the natural environment, chlorophyll *a* fluorescence-based methods are applied in ecophysiological and toxicological studies to examine the effect of environmental changes and pollutants on plants and algae (microalgae and seaweeds). Pollutants or environmental changes cause alteration of the photosynthetic capacity which could be evaluated by fluorescence kinetics. Hence, evaluating key fluorescence parameters and assessing photosynthetic performances would provide an insight regarding the probable causes of changes in photosynthetic performances. This technique quintessentially provides non-invasive determination of changes in the photosynthetic apparatus prior to the appearance of visible damage. It is reliable, economically feasible, time-saving, highly sensitive, versatile, accurate, non-invasive and portable; thereby comprising an excellent alternative for detecting pollution. The present review demonstrates the applicability of chlorophyll *a* fluorescence in determining photochemical responses of algae exposed to environmental toxicants (such as toxic metals and herbicides).

Contents

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1. Introduction

Light constitutes the most abundant and constant type of energy available on earth, that directly or indirectly provides majority of energy used by biological systems for the past few billions of years. The mechanism of conversion of light energy to chemical energy, which is then used for metabolic processes, is called photosynthesis. The photosynthetic complexes are exquisitely tuned to capture solar light efficiently; they then transmit the excitation energy to reaction centers (RC), where long-term energy storage is initiated. The energy transfer mechanism is often described by semi-classical models that invoke 'hopping' of excited-state populations along discrete energy levels (Blankenship, 2002). Light-driven reactions of photosynthesis then convert the physical energy of light into a stable electrochemical potential, which is eventually stored as chemical energy through a series of dark reactions (Sundström et al., 1999). These light reactions occur in two closely coupled pigment systems: light energy is absorbed by a network of so-called antenna pigments bound to proteins and the excitation energy is very efficiently transported via chlorophyll *a* to the photochemical reaction center (RC) of photosystem II (PSII) and I (PSI), where the energy is converted into a stable trans-membrane charge separation through a sequence of electron-transfer reactions (Amerongen et al., 2000). The part of absorbed light energy not used in PSII photochemistry, is dissipated via non-radiative energy or chl *a* fluorescence emission associated with the PSII complex (Pullerits and Sundström, 1996; Popovic et al., 2003).

Concisely, light energy absorbed by chlorophyll molecules can undergo one of three fates: it can be used to drive photosynthesis (photochemistry), excess energy can be dissipated as heat or it can be re-emitted as light-chlorophyll *a* fluorescence. These three processes occur in competition, such that any increase in the efficiency of one will result in a decrease in the yield of the other two. Hence, by measuring the yield of chlorophyll (chl) *a* fluorescence, information about changes in the efficiency of photosynthesis and heat dissipation can be acquired (Maxwell and Johnson, 2000). Even though the amount of chl *a* fluorescence is very small (approximately 1–2 percent of the total light absorbed), its measurement is straightforward and reliable. Chl fluorescence is a physical signal defined as the radiative energy evolved from de-exciting chl *a* molecules ($\lambda = 690$ nm for PSII, $\lambda = 740$ nm for PSI) (Roháček et al., 2008). Govindjee (2004) explains how chl *a* fluorescence provides new and important information on the composition of pigment systems, excitation energy transfer, physical changes in pigment-protein complexes, primary photochemistry, kinetics and rates of electron transfer reactions in PSII, the sites of various inhibitors, and activators, as well as, lesions in newly constructed mutants. Any modification in the photosynthesis or related biochemical or physiological processes would lead to significant changes in the yield and kinetics of dissipated fluorescence. Therefore, alteration of the photosynthetic capacity evaluated by fluorescence kinetics could be used to indicate damage induced by pollutants or environmental changes. Chl *a* fluorescence measurement of PSII is a unique, rapid, non-intrusive and universal technique that reveals information on plant performance and protective responses. This intriguing tool, evaluating the ecophysiological status, could be applied in most studies that address photosynthetic responses of plants and algae in the environment (Maxwell and Johnson, 2000; Adams and Demmig-Adams, 2004; Murchie and Lawson, 2013). Several factors can lead to a decrease (quenching) of chl *a* fluorescence (for e.g., excessive irradiance, low or high temperature, drought, toxic chemicals, toxic metals, and herbicides). However, the interpretation of fluorescence signals and discrimination of the contributions of each factor depends on an individual (Roháček et al., 2008). Its rapid data generation, advanced software (Lazár and Nauš, 1998), and accurate statistical analysis provide a highly resolved relationship of the light and dark reactions of photosynthesis (Joshi and Mohanty, 2004). Several reports demonstrate the advantages of this technique (Juneau et al., 2007; Roháček et al., 2008); this makes chl *a* fluorescence a method of choice as compared to routine biotests based on growth inhibition..

There has been a growing interest in the practical application of chl *a* fluorescence as a rapid and sensitive bioindicator of plant stress in response to different chemicals in recent years (Kumar and Han, 2010). Chl *a* fluorescence analysis equates to a bioanalytical tool which can be used for evalualting exposure to mixtures of pollutants acting by a common mode of action (Muller et al., 2008). Apart from being helpful in determing temporal damage, it also provides an effect-based real-time assessment of the impact of toxicants in complex environmental conditions including mixtures. Endo and Omasa (2004) suggested chl *a* fluorescence measurements as an effective tool for determing toxicity of herbicides to aquatic plants and algae. Chl *a* fluorescence is also used as a powerful tool to investigate the ecophysiology of phytoplankton and to monitor its biomass (Muller et al., 2008). Reports also suggest parameters of chl *a* fluorescence to be widely used to assess the abundance and activity of phytoplankton in the natural habitat of algae, without affecting their physiological state (Antal et al., 2001).

Among the various fluorescence techniques, pulse amplitude modulated fluorometry (PAM) introduced by Schreiber et al. (1986), and supplemented with the saturation pulse method can be employed to obtain information on the functioning of the photosynthetic apparatus and photosynthetic activities of plants (Roháček et al., 2008). These "modulation fluorometers" in combination with the application of "saturating light pulses", generally provide essential information beyond that obtained by conventional chlorophyll fluorometers. This method (i.e. PAM) operates with three kinds of light (modulated, actinic, and saturating), which facilitate the analyses of fluorescence-induction kinetics in photosynthesizers and the evaluation of their primary productivity (Figueredo et al., 2009). These fluorometers provide information regarding several acclimatization and adaptive mechanisms adapted to cope with environmental stress, such as high light intensity, heat, chilling, dehydration, salinity and malnutrition (Roháček et al., 2008). The pulse amplitude modulation (PAM) fluorescence permits in vivo non-destructive determination of changes in the photosynthetic apparatus much earlier than the appearance of visible injury (Kumar and Han, 2010) Pulse amplitude modulated (PAM) fluorometry and the saturation pulse technique can be useful in measuring toxicant-induced changes in the effective PSII quantum efficiency (Muller et al. 2008; Schreiber, 2004). Several types of PAM including the Maxi Imaging-PAM, Diving PAM as well as the