Light-harvesting chlorophyll a–b complex requirement for regulation of Photosystem II photochemistry by non-photochemical quenching.

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Abstract

Recently, it has been suggested (Horton et al. 1992) that aggregation of the light-harvesting a–b complex (LHC II) in vitro reflects the processes which occur in vivo during fluorescence induction and related to the major non-photochemical quenching (qE). Therefore the requirement of this chlorophyll a–b containing protein complex to produce qN was investigated by comparison of two barley mutants either lacking (chlorina f2) or depressed (chlorina 1°4) in LHC II to the wild-type and pea leaves submitted to intermittent light (IL) and during their greening in continuous light.

It was observed that qN was photoinduced in the absence of LHC II, i.e. in IL grown pea leaves and the barley mutants. Nevertheless, in these leaves qN had no (IL, peas) or little (barley mutants) inhibitory effect on the photochemical efficiency of QA reduction measured by flash dosage response curves of the chlorophyll fluorescence yield increase induced by a single turn-over flash.

During greening in continuous light of IL pea leaves, an inhibitory effect on QA photoreduction associated to qN developed as Photosystem II antenna size increased with LHC II synthesis. Utilizing data from the literature on connectivity between PS II units versus antenna size, the following hypothesis is put forward to explain the results summarized above, qN can occur in the core antenna or Reaction Center of a fraction of PS II units and these units will not exhibit variable fluorescence. Other PS II units are quenched indirectly through PS II–PS II exciton transfer which develops as the proportion of connected PS II units increases through LHC II synthesis.

Abbreviations: F – chlorophyll fluorescence levels, subscripts o and m are minimal and maximal levels of dark-adapted leaves; o', m' and s-minimal, maximal and steady state levels in the presence of actinic light; Fv and Fv' = (Fm'–Fo) and (Fm'–Fo') respectively; ∆F = (Fm'–Fv); δF – single turn- over flash-induced fluorescence yield increase; ΔFmax – single turn-over saturating flash-induced fluorescence yield increase; IL – intermittent light; LHC II – light-harvesting chl a–b complex associated with PS II; PFD – photon flux density; PS II – Photosystem II; QA – primary quinonic electron acceptor of PS II; qP – photochemical quenching; qN – non-photochemical quenching; σ – relative efficiency of PS II photoreduction of QA; σd – σ of dark-adapted leaves

Introduction

It has been shown by Horton and Hague (1988), in isolated protoplasts, and by Quick and Stitt (1989) and Hodges et al. (1989), in leaves, that non-photochemical quenching (qN) is heterogenous (composed of at least 3 components). Meanwhile, all types of qN seem to control the quantum yield of Photosystem II (PS II) and linear electron flow as Genty et al. (1985) observed in leaves a linear relationship between quantum yield of PS II (∆F/Fm') and quantum yield of CO₂ assimilation, in the absence of photorespiration, at all irradiances investigated.
Location(s) of qN(s) and the mechanistic basis of its control on PS II is only clearly understood for the state 1–state 2 transition component. Concerning the two other components and especially the major one, qE, associated to energization of the thylakoid membrane, a controversy still exists. Two main interpretations have been proposed: 1) induction of inactive PS II centers, 2) increase of heat deactivation of excitons in the antenna pigment bed.

Weis and Berry (1987) suggested that a fraction of PS II centers are converted, upon thylakoid membrane energization, to a state where dissipation of excitation occurs mostly by a non-radiative pathway. In these centers the chlorophyll fluorescence yield will be low and photochemical efficiency nil. This could result from an inhibition of electron donation to PS II induced by ΔpH acidification of the thylakoid lumen. Accumulation of P+680, or a fast charge recombination (Schreiber and Neubauer 1987) or a rapid PS II cyclic electron flow (Horton and Ruban 1992) would occur in these centers. According to this interpretation a quenching of Fm will occur but not of Fo. This hypothesis has been supported by recent results obtained by Krieger and Weis (1990) who showed that chemical acidification of PS II particles induced a quenching of Fm but not of Fo.

Among the effects of qN which support an increase of heat deactivation within the pigment bed, is firstly, an in vivo quenching of Fo in the presence of qN (Genty et al. 1990a; Rees et al. 1990) of which the amplitude is consistent with the decrease in the rate of the photochemical rise from Fo to F1 according to the nomenclature of Schreiber and Neubauer (1987) and secondly the reduction of the apparent antenna cross section as measured by single turn-over flash-induced chlorophyll fluorescence yield increase observed in leaves by Genty et al. (1991b). Another recent result which supports the second interpretation is the kinetics of qN relaxation upon addition of reductants to chloroplasts which develop upon illumination a quenching of Fo and Fm similar to those observed in leaves (Genty et al. 1992). Relaxation of qN induced by addition of reductants was as slow as the relaxation of fluorescence quenching in the dark without any additions. These data do not favor a quenching due to P+680 accumulation in vivo. Moreover, maximal qN in these chloroplasts was observed in the presence of ascorbate, a reducing mediator which reverses qN induced by chemical acidification of thylakoids (Crofts and Horton 1991; Rees et al. 1992).

If, in vivo, qN occurs in the antenna, does it take place in a particular compartment like the PS II core, LHC II or even a special complex of LHC II? Mostly based on results using isolated LHC II, Horton et al. (1992) and Ruban and Horton (1992) have recently proposed that qE could be due to LHC II aggregation induced by a ΔpH and that the resulting fluorescence quenching is amplified by zeaxanthin. Meanwhile in the chlorina f2 barley mutant which, according to Peter and Thornber (1991) lacks oligomeric LHC II complexes (especially LHC II b) Genty et al. (1990) and Lokstein et al. (1993) in another barley mutant have observed a non-photochemical quenching. Although in the f2 mutant the qN amplitude and its control on linear electron flow are smaller than in the wild-type. Therefore does antenna size influence the amplitude of qN and its effect on PS II photochemistry? Indeed, if as suggested by Schatz et al. (1987) there is an equilibrium for excitons between PS II reaction centers and their associated antenna, and if the quencher responsible for qN is localized in the antenna, then an increase in antenna size should enhance qN.

Therefore, I have studied the ability to develop qN and its effect on PS II during the stepwise assembly of PS II antenna complexes during the greening of etiolated pea leaves according to Argyrondi-Akoyunoglou and Akoyunoglou (1970) and Armond et al. (1976). Indeed, firstly exposed to intermittent light these leaves synthesize only the PS II core antenna but when they are subsequently exposed to continuous light, a biphasic synthesis of LHC II and grana formation occurs (Arntzen et al. 1976). Plastids isolated from intermittent light leaves were fully competent in all photochemical energy coupling processes (Arntzen et al. 1976) and therefore they are able to build up a photoinduced ΔpH which is a prerequisite for high energy quenching qE (Briantais et al. 1979). As intermediate situations of PS II complexity, may be obtained through the greening procedure of intermittent and continuous light, I expected to obtain quantitative relationships between antenna size or increasing proportion of PS II units with a LHC II antenna and qN amplitude and also effect of qN on PS II photochemistry.

Material and methods

Material

As described in Armond et al. (1976), peas (Pisum sativum Petit Provençal) were grown in the dark for