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Letter to the editor/hypothesis

The physiological significance of photosystem II heterogeneity in chloroplasts

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Abstract

Photosystem II in green plant chloroplasts displays heterogeneity both in the composition of its light-harvesting antenna and in the ability to reduce the plastoquinone pool. These two features are discussed in terms of chloroplast development and in view of a proposed photosystem II repair cycle.

Introduction

The concept of photosystem II (PS II) heterogeneity in chloroplasts was introduced to explain the biphasic nature of the kinetics of primary PS II activity. It was observed that illumination of green plant chloroplasts in the presence of PS II herbicides produced distinct biphasic chlorophyll (Chl) fluorescence induction kinetics and biphasic kinetics in the reduction of the primary quinone, Q_A, of PS II. Analysis of the biphasic data suggested the presence of two distinct populations of PS II centers in the chloroplast, termed PS II_α and PS II_β (Melis and Homann 1976, Melis and Duysens 1979, Black et al. 1986). The rate difference between the two kinetic components (α and β) was attributed to different light-harvesting antenna size for PS II_α and PS II_β (Melis and Duysens 1979, Thielen and Van Gorkom 1981a). In mature chloroplasts of wild type plants, PS II_α centers account for 75–80% for all PS II centers and are localized in the membrane of the grana partition regions (Anderson and Melis 1983). In addition to the Chl *a*-binding proteins of the PS II core, PS II_α contains both components of the Chl *ab* light-harvesting (LHC II-inner and LHC II-peripheral) (Larsson et al. 1987, Ghirardi and Melis 1988, Greene et al. 1988). In total, the light-harvesting antenna of PS II_α contains 210–255 Chl molecules.

The PS II_β centers account for the remaining 20–25% and contain only one component of the auxiliary Chl *ab* light-harvesting antenna (LHC II-inner) (Ghirardi and Melis 1988, Greene et al. 1988) with 130 Chl molecules. They are localized in the stroma exposed regions of the chloroplast lamellae.

In addition to antenna heterogeneity (α,β heterogeneity), PS II centers display heterogeneity with respect to electron flow from the reaction center to plastoquinone. There is evidence in the literature that some PS II centers, though photochemically competent, are unable to transfer electrons efficiently from Q_A to the secondary electron acceptor, Q_B (Thielen and Van Gorkom 1981b, Lavergne 1982, Melis 1985, Graan and Ort 1986, Ghirardi and Melis 1988, Greene et al. 1988, Guenther et al. 1988). Using Lavergne's nomenclature (Lavergne 1982), these centers are termed PS II–Q_B-nonreducing in order to distinguish them from the plastoquinone reducing centers (Q_B-reducing). The PS II–Q_B-nonreducing centers account for 20–25% of the total PS II pool in the thyladoid membrane (Melis 1985, Greene et al. 1988).

There is overlap between PS II_β and PS II–Q_B-nonreducing centers (Fig. 1). The extent of this overlap depends strongly on the developmental stage of the chloroplast and/or PS II antenna. Work with spinach (Melis 1985), barley (Ghirardi

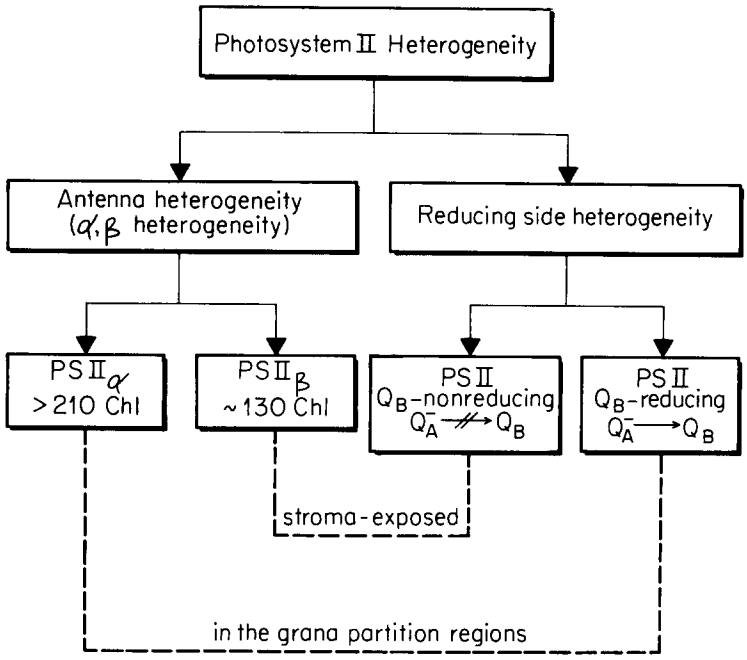

Fig. 1. Schematic delineating the two aspects of photosystem II heterogeneity discussed in the text.

and Melis 1988) and maize (Greene et al. 1988) suggested that in mature, wild-type chloroplasts PS II_β and PS II-Q_B-nonreducing are one and the same pool of PS II centers (20–25% of the total PS II).

In Chl *b*-deficient mutants and developing chloroplasts, the proportion of PS II_β is much greater than in mature wild-type chloroplasts, often accounting for as much as 80–90% of the total PS II (Thielen and Van Gorkom 1981a, Ghirardi and Melis 1988, Greene et al. 1988). In such chloroplasts, the rate of Chl *b* biosynthesis lags behind that of Chl *a*, resulting in higher Chl *a*/Chl *b* ratios in the thylakoid membrane. Quantitation measurements with Chl *b*-deficient and developing chloroplasts revealed a positive correlation between acquisition of Chl *b* and content in LHC II-peripheral, and a negative correlation between acquisition of Chl *b* and PS II_β concentration in the thylakoid membrane. These results suggested a developmental relationship between PS II_β and PS II_α in which PS II_β serves as a precursor form to PS II_α (Fig. 2). In the absence of sufficient LHC II-peripheral antenna, the formation of PS II_α units is inhibited and PS II_β units, with a substantially smaller antenna size (130 Chl molecules), accumulate in the thylakoid membrane (Fig. 2). Under these conditions, however, the fraction of PS II-Q_B-nonreducing remains relatively small (approximately 20% of total PS II), suggesting that in Chl *b*-deficient mutants and developing chloroplasts, PS II-Q_B-nonreducing is only a subpopulation of PS II_β. The greater fraction of PS II_β than PS II-Q_B-nonreducing in developing thylakoids does indicate the presence of PS II lacking LHC II-peripheral but fully active in the process of plastoquinone reduction (Ghirardi and Melis 1988, Greene et al. 1988, Guenther et al. 1988).

The foregoing suggest that the two aspects of photosystem II heterogeneity, i.e., PS II antenna heterogeneity (α,β heterogeneity) and PS II reducing side heterogeneity (Q_B and non-Q_B) may underline different, although interrelated phenomena. It is clearly understood that a PS II antenna heterogeneity may arise as a consequence of the development of the PS II unit (Fig. 2). However, this consideration is not sufficient to explain the consistent presence of PS II_β in mature higher plant chloroplasts and green algae in which chlorophyll biosynthesis is not limiting. Moreover, it does not explain the existence and physiological significance of the PS II-Q_B-nonreducing centers or the inter-

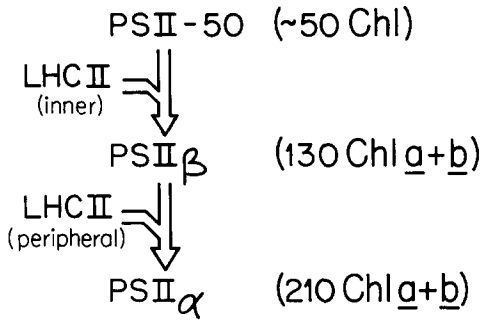

Fig. 2. Schematic defining a step-wise process in the development of the light-harvesting antenna of PS II. The PS II-50 configuration contains 50 Chl *a* molecules and lacks LHC II. PS II_β is obtained upon the addition of the LHC II-inner antenna and PS II_α is obtained by the further addition of the LHC II-peripheral antenna.

relationship between PS II_β and PS II-Q_B-nonreducing. The following model provides a working hypothesis for the physiological significance of the 'PS II reducing side heterogeneity' and explains the relationship with the 'PS II antenna size heterogeneity'

Proposal of a model

It is proposed that PS II-Q_B-nonreducing units constitute a repair state of the photochemicl reaction center in which the damaged 32 kDa reaction center (Q_B-binding) protein has been replaced. According to the model, which we term 'the PS II repair cycle' (Fig. 3), the following sequence of events is postulated to occur after damage to the PS II reaction center: (a) uncoupling of the LHC II-peripheral antenna from the damaged PS II_α unit in the grana partition region, (b) movement of the damaged PS II_β-like center from the grana partition region to the stroma-exposed region of the membrane, (c) replacement of the damaged 32 kDa reaction center protein resulting in the formation of

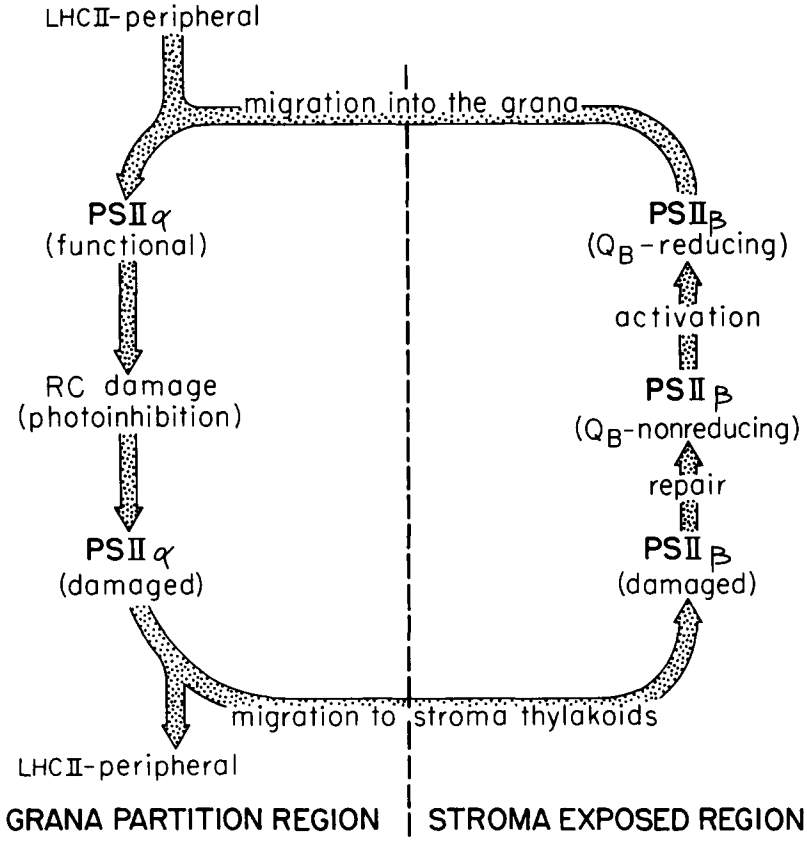

Fig. 3. Schematic of the PS II repair cycle model discussed in this work.

a photochemically competent center in which the Q_A to Q_B electron transfer interaction has not yet been established (PS II_β–Q_B-nonreducing stage), (d) activation of the Q_A–Q_B interaction converting the center to a PS II_β, Q_B-reducing form, (e) association of this center with the LHC II-peripheral antenna and incorporation into the grana partition region in the form of a newly functional PS II_α unit. The above sequence of events is hypothetical, nevertheless, it provides the basis for further experimentation to test the various steps of the proposed model.

A number of observations provide preliminary support for the proposed hypothesis. It is known that PS II centers are labile and a repair process operates in chloroplasts. Under physiological conditions, damage to PS II reaction centers occurs continuously, at a rate greater than that of other thylakoid membrane components. In addition, damage to PS II may arise from environmental stress such as, exposure to strong light (photoinhibition), to high temperature, and from inhibition of reaction center function by physiolgically produced or artificially added chemicals. The hypothesis of a 'PS II repair cycle' in chloroplasts is consistent with the rapid turnover of the reaction center 32 kDa protein (Mattoo et al. 1981), and with evidence that newly synthesized 32 kDa polypeptides first 'assemble' in the stroma-exposed regions of the chloroplast membrane and subsequently move to the grana partition regions (Mattoo and Edelman 1987). The hypothesis of a 'repair cycle' in chloroplasts explains the persistence of PS II_β and PS II–Q_B-nonreducing centers in the stroma exposed membranes of all mature higher plant chloroplasts and green algae examined to date. Moreover, the 'PS II repair cycle', schematically outlined in Fig. 3, provides a mechanism for the repair of damaged PS II reaction centers.

The proposed 'repair cycle' does not address several mechanistic details that remain open questions. For example, is the Q_B-nonreducing form of PS II_β intermediate in the biosynthesis/assembly of PS II as well as in the repair of damaged centers? Under physiological light conditions the 32 kDa protein is reported to be the only rapidly turning over PS II protein (Gounaris et al. 1987). However, the PS II reaction center complex is made of a 32/34 kDa heterodimer (Namba and Satoh 1987) in which the two polypeptides are tightly bound. What is the mechanism allowing for the separation of the two proteins during repair/turnover of the 32 kDa protein? During photoinhibition of photosynthesis under anaerobic conditions, the PS II reaction center is inactivated without loss of Q_B-binding function (Arntz and Trebst 1986). Yet, under aerobic conditions, the Q_B-binding function of the 32 kDa protein is rapidly lost (Kyle et al. 1984) and the protein is rapidly turned over (Schuster et al. 1988). Is the loss of the 32 kDa protein a secondary event in photoinhibition or is it an absolute requirement for the repair of PS II reaction center?

A novelty in the proposed 'PS II repair cycle' is the reversible binding of the LHC II-peripheral to a PS II_β complex (PS $II_\alpha \leftrightarrow$ PS II_β + LHC II-peripheral). This is not an unlikely idea since there are specific examples documenting the dissociation of the LHC II-peripheral from the PS II complex. Phosphorylation/dephosphorylation of the LHC II-peripheral leads to reversible dissociation of this antenna component from PS II (Sunby et al. 1986). Moderate heat treatment of chloroplasts (Larrson et al. 1987) leads to dissociation of the LHC II-peripheral from PS II and to the ensuing conversion of PS II_α into PS II_β. Also novel is the proposal of an 'activation' step required to initiate the Q_A–Q_B electron transfer interaction. This activation must represent a rate-limiting step in the overall repair cycle, resulting in the steady-state accumulation of PS II_β, Q_B-nonreducing centers in the thylakoid membrane. Preliminary evidence from this lab suggests that light mediates this activation step. The molecular events leading to this 'activation' in the electron transport process between Q_A and Q_B are not known and more research is needed to elucidate the precise mechanism involved.

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