Regular paper

The importance of PS I chlorophyll red forms in light-harvesting by leaves

Andrea Rivadossi, Giuseppe Zucchelli, Flavio M. Garlaschi & Robert C. Jennings*
Centro C.N.R. Biologia Cellulare e Molecolare delle Piante, Dipartimento di Biologia dell’Università di Milano, 20133 Milano, Italy; *Author for correspondence (e-mail: Robert.Jennings@unimi.it; fax: +39-02-2660-4399)

Received 3 December 1998; accepted in revised form 17 March 1999

Key words: chloroplast, light absorption, light environment, optical cross-section, photosystem

Abstract

We have investigated the importance of the long wavelength absorbing spectral forms (red forms) of Photosystem I in photosynthetic light harvesting by leaves. To this end leaf spectra were simulated by using a linear combination of absorption (OD) spectra of purified Photosystem I, Photosystem II and LHC II, multiplied by an empirical multiple scattering chloroplast/leaf conversion function. In this way it is demonstrated that while the PS I red forms account for only about 4–5% of light absorption in a normal ‘daylight’ environment, in different ‘shadelight’ environments these long wavelength pigments may be responsible for up to 40% of total photon capture. In the context of maximising the photosynthetic quantum efficiency under the low light conditions of ‘shadelight’, this relative increase in the absorption cross section of PS I can be understood by considering the increased synthesis of the major PS II antenna complex, LHC II, known to occur in plants growing under these light conditions. It is demonstrated that for plants in a moderate to deep ‘shadelight’ regime the PS II cross section needs to increase by 50% to 100% via LHC II synthesis to balance the increased PS I absorption by the red forms. The possibility that under ‘shade light’ conditions the increased PS I cross section may serve in cyclic phosphorylation is also discussed.

Abbreviation: LHCII – light harvesting complex of PS II

Introduction

It is well known that plant and cyanobacterial Photosystem I is characterised by a small number of red absorbing Chl spectral forms which are energetically lower than the primary photochemical trap, P700, by as much as 2–3 k_BT at room temperature (for review see van Grondelle et al. 1994). As a consequence of this, excited states are rapidly transferred from the bulk antenna to the red forms with a time constant in the 10–20 ps range (e.g. Turconi et al. 1994; Jennings et al. 1998), giving rise to a steady state distribution of excited states in which 80–90% are associated with the red forms (Croce et al. 1996; Pålsson et al. 1998). For plant PS I at least two distinct spectral forms were distinguished in the earlier literature, with fluorescence maxima near 720 nm and 735 nm (Mullet et al. 1980; Wittmershaus 1987; Mukerji and Sauer 1993; Pålsson et al. 1995) though more recently three and possibly four have been identified, on the basis of steady state and time resolved fluorescence spectroscopy, emitting near 720 nm, 730 nm and 740 nm. (Croce et al. 1996; D. Dorra, personal communication). To date the absorption origin bands of these red forms have not however been clearly identified in plant PS I, mainly due to the structureless nature of the red absorption wing. Evidence exists however that their Q_y absorption bands may be unusually broad for protein bound antenna Chls, probably due to very strong electron-phonon coupling (Gobets et al. 1994; Croce et al. 1998; Jennings et al. 1998). Thus at RT the half band widths may be of the order of 25 nm for the red forms with respect to about 10 nm for ‘normal’ antenna Chls (Zucchelli et al. 1996; Croce et al. 1998; Jennings et al. 1998). This fact is also important in determining the rather large energy spread of the long wavelength ab-
sorption tail. The possibility that these red forms may be excitonic Chl dimers has been suggested (Gobets et al. 1994) but not yet demonstrated. Recent evidence furthermore suggests that in plant PS I about 80% of the red forms may be associated with the outer antenna complexes (LHC I) with no more than 1–2 molecule equivalents in the core antenna (Croce et al. 1998). This situation is in marked contrast to that for cyanobacteria where these low energy Chls are all in the core antenna (e.g. Shubin et al. 1992; Gobets et al. 1994).

Thus while a considerable amount of biophysical information has accumulated on the red forms, little is known on their exact biological function. Three possibilities are usually considered.

1) They serve to increase the overall trapping rate by focusing energy on P700 (Wittmershaus 1987; van Dorssen et al. 1988; van Grondelle et al. 1988; Bergström et al. 1989; Sundstrom and van Grondelle 1990; Mimuro 1992; Mukerji and Sauer 1993). This possibility was examined by Fischer and Hoff (1992) and Trissl (1993) who demonstrated by model calculations that this role is rather unlikely as the energy gap between P700 and the low energy red forms is so great that even if they were physically associated with P700 they would, if anything, slow trapping down. Furthermore, as mentioned above, it has recently been demonstrated that in plant PS I most red forms are not closely associated with P700 but are present in the outer antenna complexes where they impose a diffusional limitation to excitation trapping (Jennings et al. 1998). Thus the red forms do in fact seem to slow trapping down.

2) They have a photoprotective function. As we have previously discussed for PS II (Jennings et al. 1996), a slowing down of the overall trapping rate leads to a greater efficiency of photoprotective, non-photochemical, quenching mechanisms. However, as discussed above, while the red forms do in fact slow down the overall trapping rate, to date there is no demonstration that non-photochemical quenching mechanisms exist in PS I.

3) They have a role in light harvesting. Owing to their low absorption intensity this effect will not be significant under normal ‘daylight’ environments in which the photon fluence is approximately constant between 400–750 nm, even though multiple internal scattering within a leaf does in fact increase their ‘absorption efficiency’ several times (Garlaschi et al. 1989). On the other hand, the light environment is strongly modified within or underneath a vegetation system leading to the so called ‘shadelight’ environment which, apart from being of low intensity, displays a markedly different spectral distribution due to light filtration and light reflection from the uppermost leaf layers (for a review see Holmes 1996). Thus the ‘shadelight’ spectral distribution is strongly enriched in wavelengths above 690 nm which are selectively absorbed by the PS I red forms. The suggestion that the red forms may have an important light harvesting role in this kind of light environment was initially made by Anderson (1986) and subsequently investigated in a semiquantitative way by Garlaschi et al. (1989).

In the present paper we analyse this aspect in more detail by simulating leaf photon absorption spectra using linear combinations of the absorption (OD) spectra of PS II, PS I and LHC II, converted into leaf spectra by means of an empirical multiple scattering function and taking into consideration the light environment spectral distribution.

**Methods**

Thylakoids were extracted from freshly harvested leaves as previously described (Garlaschi et al. 1989). Photosystem II membranes (BBY grana) were prepared as described by Berthold et al. (1981). Photosystem I (PS I 200) was prepared by an octyl glucopyranoside based fractionation procedure as described by Croce et al. (1996). LHC II was prepared as described by Ryrie et al. (1980). Absorption spectra of PS I 200, PS II membranes and LHC II were measured in a Jasco Uvivdec 510 spectrophotometer using the opal glass technique to minimise light scattering. Leaf and isolated chloroplast transmittance and reflectance spectra were measured in a Jasco Uvivdec 510 spectrophotometer equipped with the integration sphere attachment (TIS 314), as previously described (Garlaschi et al. 1989). From these measurements the OD and (1-T) spectra, corrected for reflectance, were determined. This correction, which is strongly wavelength dependent, was significant only for the leaf spectrum.