Biochimica et Biophysica Acta 934 (1988) 14–21
Elsevier

BBA 42270

The changing contribution of LHC I to Photosystem I activity during chloroplast biogenesis in wheat

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(Received 6 January 1988)

Key words: Chlorophyll fluorescence; Chlorophyll-protein complex; Chloroplast development; Electron transport; Photosystem I; (Wheat)

During chloroplast biogenesis in 5-day-old wheat leaves, the apparent quantum yield of Photosystem I (PS I) electron transport activity of isolated thylakoids increases. From measurements of apparent PS I quantum yield using 440 and 470 nm radiation, it is demonstrated that this increase is attributable to an increase in the contribution of a chlorophyll-*b*-containing component of the PS I antenna. Immunoblot analyses of constituent polypeptides of the core complex of PS I (core complex I) and the light-harvesting chlorophyll *a*/*b*-protein complexes associated with PS I (LHC I) and PS II (LHC II) indicated that during chloroplast development the appearance and accumulation of LHC I in the thylakoids lag behind those of LHC II and core complex I. This finding was supported by changes observed in the 77 K fluorescence emission spectra of isolated thylakoids; the 740 nm emission peak, associated with LHC I, increased markedly relative to the 686 nm peak during development. The effects of Mg^{2+} depletion on the apparent PS I quantum yield indicated that light captured by LHC II did not make an increasing contribution to PS I photochemical activity during development. It is concluded that the increase in the light capture ability of PS I in wheat thylakoids during chloroplast biogenesis is attributable to the delay in accumulation of LHC I relative to core complex I.

Introduction

Preliminary studies of PS I photochemical activity in thylakoids isolated from wheat leaves grown under a diurnal light regime have shown that the light intensity required for saturation of PS I electron transport decreases markedly during chloroplast development [1]. Such a decrease in the light saturation point for PS I activity may be indicative of an increase in the average antenna size of PS I complexes or may alternatively be due to an increase in the concentration of PS I complexes relative to PS II complexes within the thylakoid membranes. Since the number of photochemically active PS I complexes per unit chlorophyll has been found to decrease in developing wheat chloroplasts, whilst the number of active PS II complexes per chlorophyll increases, an increase in the antenna size of PS I complexes is the more plausible explanation [1,2]. The antenna of PS I complexes could increase by a number of mecha-

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Abbreviations: DCMU, 3-(3,4-dichlorophenyl)-1,1-dimethylurea; LHC I, light-harvesting chlorophyll *a*/*b* protein complex associated with Photosystem I; LHC II, light-harvesting chlorophyll *a*/*b* protein complex associated with Photosystem II; PS, Photosystem; Hepes, 4-(2-hydroxyethyl)-1-piperazineethanesulphonic acid; TMPD, tetramethyl-*p*-phenylene diamine; Tricine, *N*-[2-hydroxy-1,1-bis(hydroxymethyl)-ethyl]glycine.

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nisms: (i) the size of the primary chlorophyll *a* antenna of the core complex of PS I (core complex I) may increase; (ii) the secondary light-harvesting antenna complex of PS I (LHC I), which contains both chlorophylls *a* and *b* in a ratio of approx. 3.5 [3], may develop more slowly than the PS I core complex (core complex I); and (iii) PS I complexes may interact to a greater extent with LHC II and/or PS II complexes at later stages of development. In this paper we examine the changes in LHC I, core complex I and LHC II content of developing wheat thylakoids together with fluorescence emission spectra of the membranes at 77 K and the effects of preferential excitation of chlorophyll *a* and *b* and cation depletion on PS I photochemical activity in order to determine the changes in the antenna of PS I during chloroplast biogenesis. It is concluded that the initial absence and development of LHC I in the thylakoids play a major role in determining the light-harvesting characteristics of PS I at early stages of chloroplast development in wheat leaves.

Materials and Methods

Wheat leaf tissue containing chloroplasts at different developmental stages were grown as described previously [4]. A gradient of cellular and plastid development exists from the base to the tip of young wheat leaves [5]. Thylakoids were isolated from 1 cm sections cut from along the length of the first leaves of 5-day-old plants. Tissue was disrupted using a Polytron homogenizer. For the immunological analyses of thylakoid polypeptides an isolation medium comprising 300 mM sucrose/50 mM Tricine/10 mM NaCl/5 mM $MgCl_2$ (pH 7.6) was used. Homogenates from sections 0–3 cm from the leaf base were centrifuged for 5 min at $3000 \times g$, preparations from older tissues were spun for only 3 min. Pellets were resuspended in about 1 cm^3 of 50 mM Tricine/5 mM EDTA (pH 7.6) and the membranes were further purified by discontinuous density centrifugation using a method described previously [6]. For spectroscopic and photochemical activity studies, chloroplasts were isolated in a medium comprising 50 mM Hepes/300 mM sucrose/10 mM NaCl/5 mM $MgCl_2$/2% (w/v) poly(vinylpyrrolidone)/0.2% (w/v) bovine serum albumin. Pellets were resuspended in 50 mM Hepes/10 mM NaCl/5 mM $MgCl_2$ (pH 7.6) and centrifuged for 5 min at $3000 \times g$. The pellets were resuspended in about 1 cm^3 of the same medium except that 300 mM sucrose was omitted. For Mg^{2+} depletion experiments, the 5 mM $MgCl_2$ was removed from this resuspension medium.

Thylakoid polypeptides were fractionated by electrophoresis on polyacrylamide gels using the method of Chua [7], except that polypeptides were solubilized at 20 °C for 30 min in 50 mM Tris-HCl/50 mM dithiothreitol/2% (w/v) sodium dodecyl sulphate/5% (w/v) glycerol/0.004% (w/v) Bromophenol blue using an SDS/protein ratio of 4:1 and separated on linear 10–18% polyacrylamide gradient gels. Immunoblotting of fractionated polypeptides was carried out essentially as described by Montano and Lane [8]. Polypeptides were transferred onto nitrocellulose filter papers for 3 h at 200 mA. The filters after washing and incubation with phosphate-buffered saline blocking buffer were then incubated for 8 h at 20 °C with antiserum raised in rabbit against the apoproteins of LHC I, LHC II or the 60–70 kDa reaction centre and chlorophyll-*a*-binding polypeptides of core complex I. The filters were then washed and incubated with a peroxidase-conjugated goat anti-rabbit immunoglobulin for 4 h at 20 °C. The blot was then developed with a saturated 4-chloro-1-naphthol solution. Full details of the preparation and specificity of the antisera have been previously reported by Williams and Ellis [9].

Fluorescence emission spectra from isolated thylakoids were measured at 77 K using a fibre-optic scanning spectrofluorimeter [10]. 0.2 cm^3 aliquots of dark-adapted thylakoid preparations, containing 10 μg chlorophyll $\cdot$ cm^{-3}, were frozen to 77 K in a cuvette to produce samples of about 1 mm thick, which were excited from above via one branch of a bifurcated fibre optic with 100 μmol $\cdot$ $m^{-2} \cdot s^{-1}$ of broad band blue radiation (400–540 nm) produced from a quartz-halogen source and blue glass filters. Fluorescence emission from the sample surface was passed via the second arm of the bifurcated fibre optic to a scanning monochromator with a half-band-width of 2 nm and detected using a Hamamatsu R446 photomultiplier. Emission spectra were measured at the maximal level of fluorescence.

Photosystem-I-mediated electron transport by isolated thylakoids from reduced TMPD to methyl viologen was determined polarographically in a Clark oxygen electrode. Oxygen uptake was monitored at 20 °C in a 2 cm^3 reaction chamber containing 50 mM HEPES/10 mM NaCl/0.2 mM TMPD/3 mM sodium ascorbate/0.1 mM methyl viologen/0.5 mM sodium azide/20 μM DCMU and 20 μg chlorophyll. Monochromatic irradiation at 440 and 470 nm (half-band-width 10 nm) was produced from a 900 W xenon arc source fitted with a high irradiance monochromator and attenuated with neutral density filters.

Results

As the profiles obtained by electrophoretic separation of solubilized thylakoid polypeptides did not allow satisfactory resolution of the constituent polypeptides of LHC I and PS I, Western immunoblot analyses were used to identify these polypeptides (Fig. 1). Probing the polypeptide profiles of developing thylakoids with antisera against both LHC I and the chlorophyll-*a*-binding polypeptides of core complex I (Fig. 1) demonstrated the appearance of the core complex I polypeptides prior to those of LHC I. In thylakoids from the leaf tip core complex I runs as two bands at apparent molecular weights of 100 000–110 000 and 67 000–70 000, whilst at earlier stages of development only the 67 000–70 000 band is observed (Fig. 1). The 100–110 kDa component is visible as a green band on unstained gels and is presumably the non-denatured core complex I chlorophyll-protein, whilst the 67–70 kDa band does not bind chlorophyll and is the fully denatured core complex I polypeptide. In thylakoids isolated from 0–1 cm and 1–2 cm segments (distances taken from the base of the leaf) the core complex I polypeptide was evident as a faint band at 67–70 kDa, but no bands could be detected in the 19 000–25 000 apparent molecular weight range where the LHC I polypeptides are found (Fig. 1). These data demonstrate that core complex I develops prior to LHC I in the thylakoids during chloroplast biogenesis in wheat leaves. On challenging thylakoid polypeptide profiles with antisera to LHC I and LHC II polypeptides, LHC II polypeptides were found to be present in large amounts from the leaf base, whereas LHC I polypeptides could not be detected until much later stages of development, i.e., 3–4 cm from the leaf base (Fig. 1). Thus, although both the LHC I and LHC II polypeptides bind chlorophylls *a* and *b*, are nuclear gene products and can be expressed under light control [11–13], their accumulation in the developing wheat thylakoid is not co-ordinated.

The fluorescence emission spectra at 77 K of

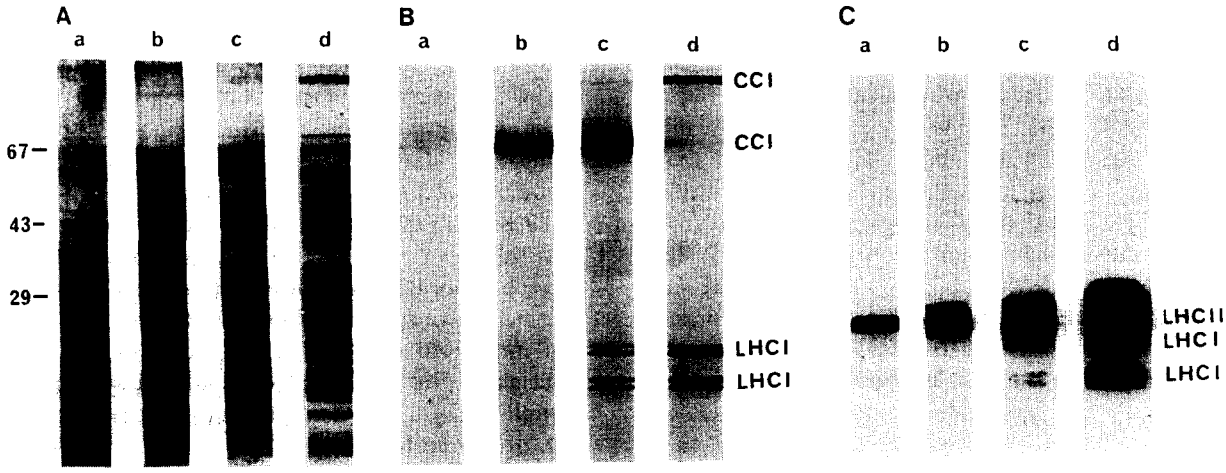

Fig. 1. (A) Polypeptide profiles of thylakoids isolated from segments taken from (a) 0–1 cm, (b) 1–2 cm, (c) 3–4 cm and (d) 5–6 cm from the base of the wheat leaves. The numbers on the left of the gel correspond to markers of known M_r expressed in thousands. (B) Immunoblot analyses of core complex I and LHC I polypeptides in the thylakoid polypeptide profiles shown in (A). (C) Immunoblot analyses of LHC I and LHC II polypeptides in the thylakoid polypeptide profiles shown in (A).

thylakoid preparations isolated from tissue taken 0–1 cm and 4–5 cm from the leaf base are shown in Fig. 2. With chloroplast development a large enhancement of the 740 nm peak relative to the 686 nm peak is observed. Although the absorption spectra of the thylakoid preparations demonstrate that there is a small increase with development in absorption at the longer wavelengths of the red absorption band (data not shown), it is unlikely that an increase in the reabsorption of the fluorescence at 686 nm could account for such a large enhancement of the 740 nm relative to the 686 nm fluorescence emission; it should be noted that the chlorophyll content of both samples used for measurement of the fluorescence emission spectra was 10 $\mu g \cdot cm^{-3}$. It has been argued from studies of isolated and fractionated PS I complexes [14–16] and from intermittent light-grown or mutant plants which lack chlorophyll *b* [17,18] that the 740 nm fluorescence emission peak originates from LHC I, whilst the primary antenna of the core complex I emits a considerably smaller signal at about 720–725 nm. In the 77 K emission spectrum of thylakoids from the leaf base, distinct emission peaks at about 720 and 740 nm are observed (Fig. 2), suggesting that core complex I is present in considerably greater amounts than LHC I. Since chlorophyll *a* associated with PS II and LHC II is the major contributor to emission below 700 nm [19–21], the enhancement of 740 nm relative to 686 nm emission with development can be attributed to the low concentration of LHC I relative to PS II and LHC II in the thylakoids during early stages of development and the relatively more

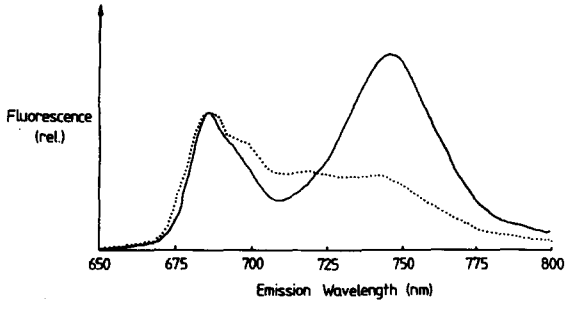

Fig. 2. Fluorescence emission spectra measured at 77 K for thylakoids isolated from segments taken 0–1 cm (·····) and 5–6 cm (———) from the base of the wheat leaves. The spectra are normalised on the 686 nm peak.

rapid accumulation of LHC I at later stages.

The role of chlorophyll-*b*-containing antennae complexes in determining the increase in light-harvesting by PS I during thylakoid development can be assessed by comparing the apparent quantum yields of PS I electron transport on excitation with 440 and 470 nm radiation; 440 nm radiation preferentially excites chlorophyll *a* relative to chlorophyll *b*, whilst 470 nm will preferentially excite chlorophyll *b*. Fig. 3 shows the light intensity response curves for excitation with 440 and 470 radiation of PS I electron transport from reduced TMPD to methyl viologen for thylakoids isolated from tissue taken 0–1 cm and 4–5 cm from the leaf base. The light response curves of the older thylakoids of the leaf tip for 440 and 470 nm were similar. However, this was not the case for thylakoids isolated from the leaf base; 440 nm radiation produced greater activities than similar photon flux densities of 470 nm radiation. The gradient of the initial linear portion of the light dosage response curve estimates the apparent quantum yield of PS I electron transport. It was difficult to obtain sufficient satisfactorily reproducible data points in this region of the light response curve due to the low rates of electron transport at the low photon flux densities, thus the apparent quantum yields were estimated from the reciprocals of the gradients of Lineweaver-Burk plots (electron transport rate)$^{-1}$ vs. (photon flux density)$^{-1}$, which equate to V_{max}/k_I, where V_{max} is the maximal rate of electron transport and k_I is the photon flux density at which the half-maximal electron transport rate is observed. Assuming electron transport to be a rectangular hyperbolic function of photon flux density, V_{max}/k_I estimates the apparent quantum yield of electron transport. The Lineweaver-Burk plots in Fig. 3 show that the apparent quantum yield of PS I electron transport is lower at the leaf base than at the leaf tip. Also the quantum yields for excitation at 440 and 470 nm are both the same for tip thylakoids, but for thylakoids from the leaf base the quantum yield was reduced by about 30% on changing excitation wavelength from 440 to 470 nm. This lower quantum yield observed in base thylakoids with 470 nm radiation can be attributed to the absence, or decreased level, in these membranes, relative to tip thylakoids, of a chlorophyll-*b*-containing antenna

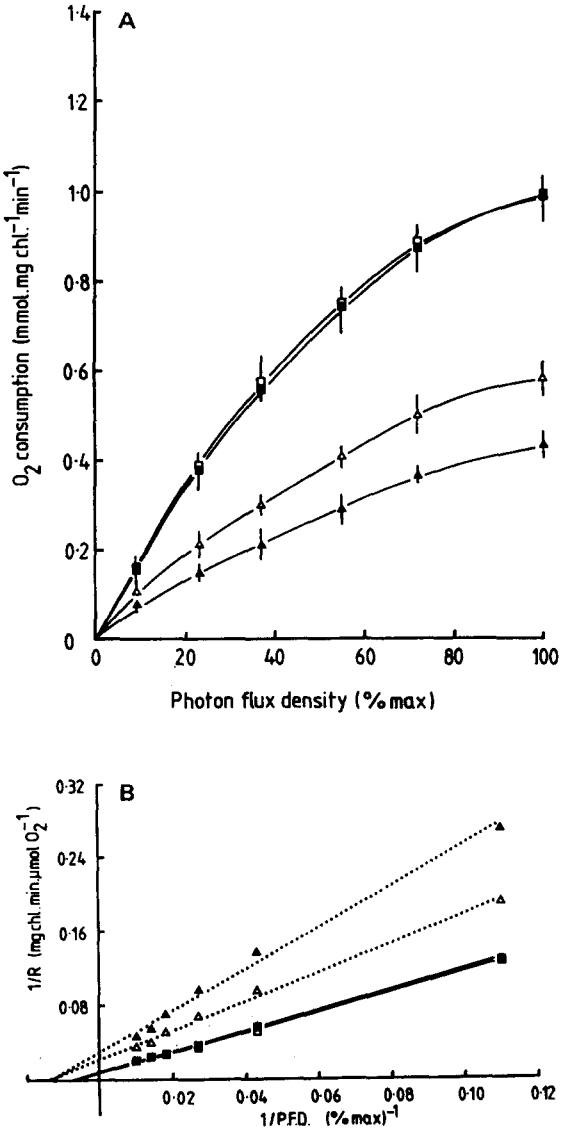

Fig. 3. (A) Light intensity response curves for PS I electron transport from reduced TMPD to methyl viologen in thylakoids isolated from segments taken from 0–1 cm (△, ▲) and 5–6 cm (□, ■) from the base of wheat leaves and excited at 440 nm (△, □) or 470 nm (▲, ■). Each point represents the mean of four independent measurements, and standard errors are given. 100% photon flux density was 164 μmol·m^{-2}·s^{-1} at both excitation wavelengths. (B) Lineweaver-Burk (double reciprocal) plots of the data shown in (A). Regression lines were determined and the apparent quantum yields were estimated from the reciprocal of the slope of the lines. The symbols used are defined above in the legend for (A).

complex which is capable of transferring excitation energy to P700.

The possibility of changes in the contribution of light captured by LHC II to PS I electron transport during chloroplast development was examined by studying the effects of Mg^{2+} depletion on the apparent quantum yield of PS I electron transport. Removal of Mg^{2+} from the medium in which the thylakoids are suspended results in a detachment of LHC II from PS II and a randomization of LHC II, PS II and PS I complexes within the plane of the membrane with the consequent increase in excitation energy transfer from LHC II and PS II to PS I [22–28]. The light response curves for PS I electron transport, and the associated Lineweaver-Burk plots, for base and tip thylakoids excited with 440 nm radiation after incubation in the presence or absence of Mg^{2+} are shown in Fig. 4. Mg^{2+} depletion has negligible effect on the apparent quantum yield of PS I electron transport in the base thylakoids compared to those isolated from the tip, where an enhancement in yield of about 60% is observed (Table I). Analyses of light response curves of PS I electron transport for base and tip thylakoids incubated in the presence and absence of Mg^{2+} but excited with 470 nm radiation (Fig. 5) demonstrate that Mg^{2+} depletion produces increases in the quantum yield of both base and tip thylakoids when activity is generated by 470 nm light; the increase for tip thylakoids was about 100%, whilst that for base thylakoids was about 35% (see Table

TABLE I

RELATIVE APPARENT QUANTUM YIELDS OF PS I ELECTRON TRANSPORT OF THYLAKOIDS ISOLATED FROM THE BASE (0–1 cm) AND THE TIP (5–6 cm) OF THE WHEAT LEAVES DETERMINED IN THE PRESENCE AND ABSENCE OF 5 mM Mg^{2+} AND USING 440 nm AND 470 nm EXCITATION RADIATION

Relative apparent quantum yields estimated by V_{max}/K_1, which is calculated from the reciprocal gradients of the regression lines calculated for the Lineweaver-Burk plots shown in Figs. 3–5. The standard errors (S.E.) are given in parentheses. All of the linear correlation coefficients for the plots were greater than 0.99.

Mg^{2+} (+/−)	Excitation wavelength (nm)	V_{max}/k_1 (S.E.)	
		base	tip
+	440	0.64 (0.017)	0.93 (0.008)
+	470	0.46 (0.026)	0.93 (0.010)
−	440	0.64 (0.013)	1.48 (0.024)
−	470	0.62 (0.016)	1.87 (0.018)

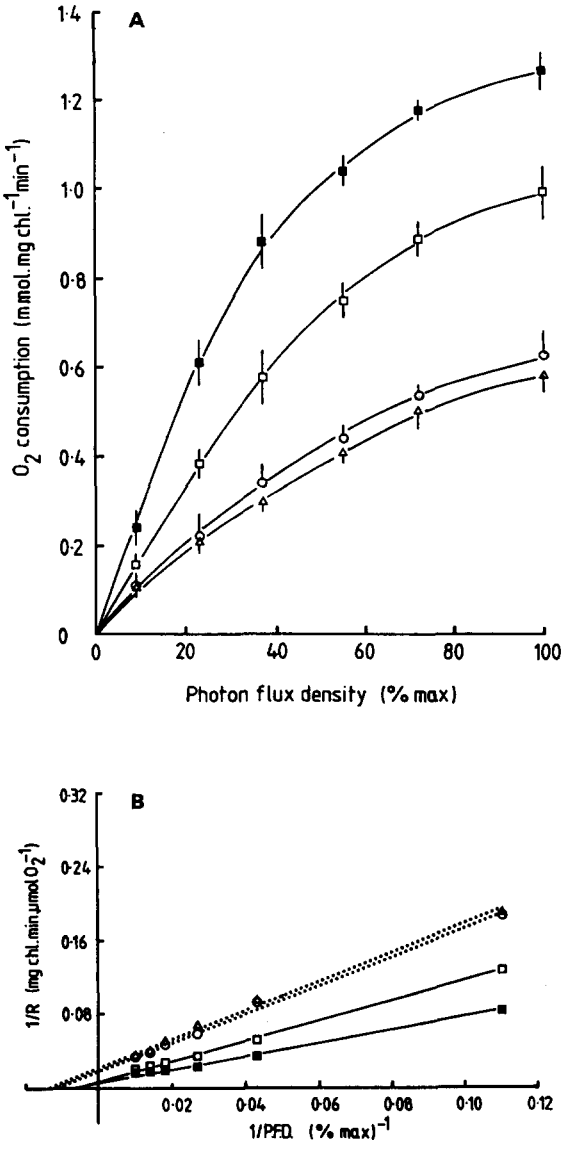

Fig. 4. (A) Light intensity response curves for PS I electron transport from reduced TMPD to methyl viologen in thylakoids isolated from segments taken from 0–1 cm (△, ○) and 5–6 cm (□, ■) from the base of wheat leaves. Measurements were made on thylakoids which had been incubated in the presence (△, □) and absence (○, ■) of 5 mM Mg^{2+} and using 440 nm excitation. Each point represents the mean of four independent measurements and standard errors are given. (B) Lineweaver-Burk (double-reciprocal) plots of the data shown in (A). Regression lines were determined and the apparent quantum yields were estimated from the reciprocal of the slope of the lines. The symbols used are defined above in the legend for (A).

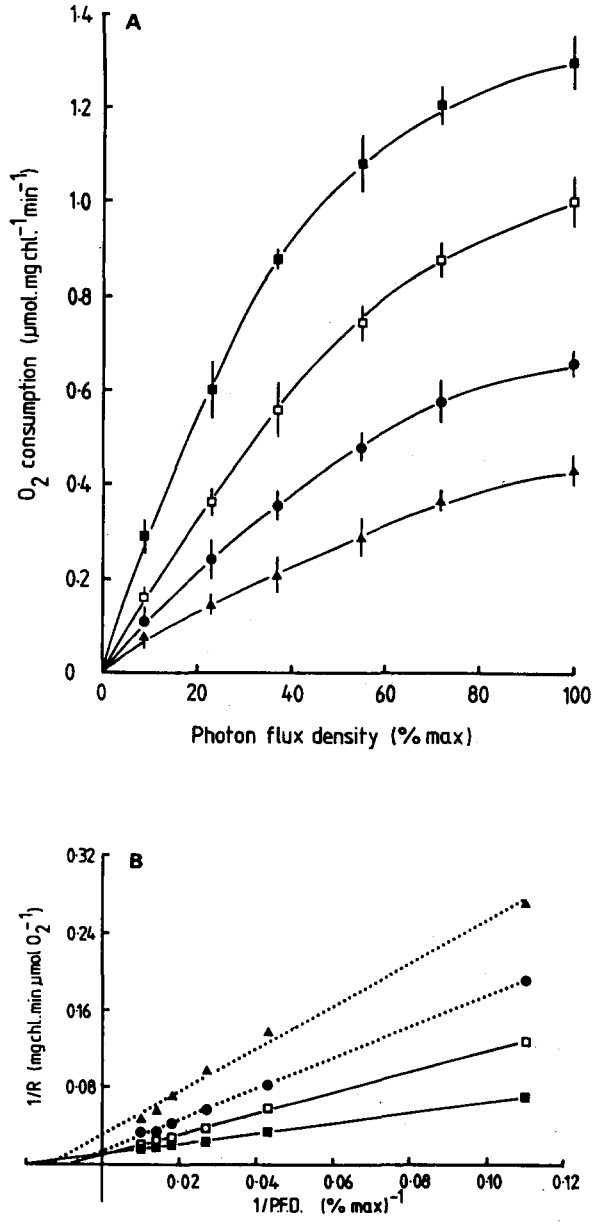

Fig. 5. (A) Light intensity response curves for PS I electron transport from reduced TMPD to methyl viologen in thylakoids isolated from segments taken from 0–1 cm (▲, ●) and 5–6 cm (□, ■) from the base of wheat leaves. Measurements were made on thylakoids which had been incubated in the presence (▲, □) and absence (●, ■) of 5 mM Mg^{2+} using 470 nm excitation. Each point represents the mean of four independent measurements, and standard errors are given. (B) Lineweaver-Burk (double-reciprocal) plots of the data shown in (A). Regression lines were determined and the apparent quantum yields were estimated from the reciprocal of the slope of the lines. The symbols used are defined above in the legend for (A).

I). The observed enhancements of PS I quantum yield on Mg^{2+} depletion when tip thylakoids are excited with either 440 or 470 nm radiation is as would be predicted for a Mg^{2+} depletion-induced increase in excitation energy transfer from LHC II and PS II to PS I. The reduced level of enhancement of PS I quantum yield induced by Mg^{2+} depletion in basal thylakoids, compared to that in tip thylakoids, when excited with 470 nm radiation is consistent with the hypothesis that at early stages of chloroplast biogenesis in wheat the lateral segregation of LHC II and PS II complexes from PS I complexes is considerably less than at the later developmental stages found in the leaf tip (see Refs. 1, 4, 29). However, the absence of any significant enhancement in PS I quantum yield on Mg^{2+} depletion from base thylakoids excited with 440 nm radiation suggests that after randomization of the thylakoid protein complexes the contributions to PS I photochemistry of the chlorophyll *a* molecules of LHC II and PS II, relative to that of the chlorophyll *a* of core complex I, are minimal. If during chloroplast biogenesis the excitation energy transfer from LHC II to PS I were increasing, then the stimulation of PS I quantum yield on Mg^{2+} depletion would be expected to be proportionally less at later stages than the early stages of development. Clearly, this is not found to be the case; thus, from these data it can be argued that an increased interaction between LHC II and PS I complexes does not occur during development and thus cannot account for the increased contribution of chlorophyll *b* to PS I activity at later stages of development.

Discussion

The data presented in this paper strongly support the hypothesis that the increase in the ability of PS I to capture light energy during chloroplast biogenesis is due to the development of LHC I after core complex I. The reduction in the apparent quantum yield of PS I electron transport of thylakoids isolated from the leaf base when measured with 470 nm radiation compared to that measured in 440 nm, which is not observed for tip thylakoids, indicates that at later stages of chloroplast development there is a greater contribution of a chlorophyll-*b*-containing antenna to PS I activity than there is at early stages. In addition, the immunological assays of polypeptides associated with LHC I, LHC II and core complex I and analyses of the 77 K fluorescence emission spectra of thylakoids demonstrate that LHC I appears in the thylakoids after core complex I and LHC II and implicate the lack of LHC I at early stages of chloroplast biogenesis as the major cause of the depressed PS I quantum yield. The possibility that an increase in interaction between LHC II and PS I during development could account for the increased contribution of chlorophyll *b* to PS I activity is untenable, not only because of the already existing evidence supporting a large increase in the degree of lateral separation of LHC II and PS II complexes from PS I that occurs concurrently with an increase in thylakoid membrane appression [1,4,28,29], but also because of the observed effects of Mg^{2+} depletion on the apparent quantum yield of PS I electron transport of base and tip thylakoids when measured with 440 and 470 nm radiation, which are reported above.

The accumulation of LHC I in the thylakoids of the developing wheat leaf does not appear to be co-ordinated with either the accumulation of core complex I or of LHC II; thus, this system may exhibit a differential expression of the genes coding for the polypeptides of LHC I, LHC II and core complex I. This being the case, then the system would be particularly useful in studies of the control of expression of the nuclear genes coding for the polypeptides of the two chlorophyll-*b*-containing light-harvesting complexes, LHC II and LHC I. Also the system has potential to provide information on the assembly of PS I particles, since LHC I becomes a major component of the PS I particles only after establishment of a large and photochemically functional core complex I.

Acknowledgements

The authors are grateful to Dr. Richard Williams and Professor John Ellis for providing the antibodies to LHC I, LHC II and core complex I used in this study. G.J.B. was the recipient of a research studentship from the U.K. Science and Engineering Research Council.

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