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EFFECT OF LIGHT QUALITY ON THE COMPOSITION AND FUNCTION OF THYLAKOID MEMBRANES IN *ATRIPLEX TRIANGULARIS*

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Light quality was shown to exert well-coordinated regulatory effects on the composition and function of the thylakoid membranes as well as on the photosynthetic rates of intact leaves from *Atriplex triangularis* grown in continuous blue, white and red lights (50 $\mu E \cdot m^{-2} \cdot s^{-1}$). The higher photosynthetic rates in plants grown in blue light, as compared to those in white and red lights, resulted from marked changes in both light-harvesting complexes and electron carriers. The concentrations of electron carriers such as atrazine binding sites, plastoquinone, cytochromes *b* and *f* and P-700 on a chlorophyll basis were markedly increased in *Atriplex* grown in blue light; and the apparent light-harvesting antenna unit sizes of Photosystems I and II were greatly reduced. Consequently, the electron transport capacities of Photosystems I and II were also increased as was the coupling factor CF_1 activity. *Atriplex* grown in red light had lower photosynthetic rates than those grown in blue or white light by incorporating changes in the composition and function of the thylakoids in a direction opposite to those caused by growth in blue light. When these regulatory effects of light quality were compared with those of light quantity [6,7], it is clear that Chl *a*/Chl *b* ratios, electron transport capacities of Photosystems I and II, concentrations of plastoquinone, atrazine binding sites, coupling factor CF_1 activity and the apparent antenna unit size of Photosystem II are more affected by light quantity, whereas light quality has a greater influence on the concentration of P-700, the apparent antenna unit size of Photosystem I and the overall photosynthetic rates of intact leaves.

Introduction

The quality of light used for the development of etiolated seedlings has a regulatory effect on plant growth, chloroplast structure and function [1–5]. When dark grown barley and radish seedlings were greened in continuous red or blue light of low and equal intensity, there was a much higher prenylquinone content, higher chlorophyll *a*/*b* ratios, and lower xanthophylls to carotene ratios in chloroplasts greened under blue light than those greened under red light [1]. Furthermore, the Hill reaction rate was higher in chloroplasts developed under blue than in those under red lights. These differences were accompanied by differences in the ultrastructures of the chloroplasts. Chloroplasts developed under red light exhibited a mich higher grana content than those developed under blue light [1]. Thus, Lichtenthaler proposed that the differences in thylakoid composition, photosynthetic activity and chloroplast structure of plants

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Abbreviations: Chl, chlorophyll; PS, Photosystem; CP1a[1], CP1a[2], CP1, chlorophyll-proteins of PS I; CPa, reaction centre complex of PS II; LHCP[1], LHCP[2], LHCP[3], Chl *a*/*b*-proteins of the main light-harvesting complex; Tes, 2-{[hydroxy-1,1-bis(hydroxymethyl)ethyl]amino}ethanesulfonic acid; Tricine, 2-amino-2-hydroxymethylpropane-1,3-diol.

adapted to low intensity blue light are similar to sun plants or to plants grown in high intensity white light [1,4]. In contrast, plants adapted to low intensity of red light resemble shade plants or plants grown under low intensity white light.

Our aim was threefold: to determine the regulatory effect of light quality alone on the stoichiometric relationship of the thylakoid components; to see whether the changes in composition of thylakoid membranes induced by light quality correlated with changes in the function of isolated thylakoid membranes and intact leaves; and, to compare the regulatory effects of light quality with those of light quantity [6–8] on the various thylakoid components.

We have recently shown that under constant light quality, the composition and functions of pea thylakoids were regulated by light intensities in such a way that more drastic changes were observed in the lower intensity regions [6,7]. Furthermore, changes in the stoichiometric relationships between the intrinsic protein complexes were found to correlate with the overall photosynthetic rates. Since it was also shown that random combinations of light quality and quantity exerted well coordinated changes in the composition and functions of pea thylakoids [8], it is important to ascertain the regulatory effects of light quality alone.

Most of the previous work on blue and red light effects were performed with developing chloroplasts from etiolated seedlings [1–4]. Since it is known that chloroplast development is a multistepwise process (see Ref. 9), we chose to examine the effects of light quality on fully developed leaves. First attempts with peas did not give any significant differences in the composition and functions of the thylakoid membranes. However, experiments on *Atriplex triangularis* grown in blue, white and red light of the same intensity show that there were marked differences in the photosynthetic rates due to changes in the stoichiometric amounts of intrinsic protein complexes of the thylakoids, but most importantly, to significant differences in P-700 concentrations and in the apparent antenna unit size of Photosystem I.

Materials and Methods

Atriplex triangularis plants were grown in pots of soil inside growth cabinets at 22 ± 1°C. The light sources were banks of fluorescence tubes shielded with neutral glass filters. The seedlings were positioned in such a way as to maintain the same continuous quantum flux densities of 50 $\mu E \cdot m^{-2} \cdot s^{-1}$ in the blue (band width 400–550 nm, emission maximum at 430 nm), white (band width 400–700, emission maximum at 575 nm) and red (band width 600–740 nm, emission maximum at 660 nm) cabinets. Emission spectra of the light sources were recorded with a Techtum Spectroradiometer, QSM 2500. The following Philips fluorescence tubes were used as light sources: TL 40 W/15 (red), TL 40 W/18 (blue) and TL 65/80 W 33 RS (white).

Chloroplasts were isolated from leaves of 2–3-month-old plants as described previously [8] except that 0.1% bovine serum albumin was added to the homogenization buffer. Thylakoids were washed in glass-distilled water, followed by two washes and resuspension in 50 mM Tricine-NaOH (pH 8.0) (1–4 mg Chl/ml) prior to storage in liquid nitrogen. Total Chl and Chl *a*/Chl *b* ratios were determined in 80% acetone [10]. Chloroplasts were counted with a bacteria counter.

Thylakoid membranes were solubilized and the chlorophyll-proteins resolved in SDS polyacrylamide gels at 4°C as previously described [6]. The relative distribution of chlorophyll on the gels was estimated as described previously [11], and are averages of five experiments. Standard deviations were within ±6%.

Measurements of oxygen evolution or uptake on freshly isolated thylakoids (unwashed) were carried out polarographically using a Hansatech oxygen electrode at 20°C. Saturating red light was from a slide projector fitted with a red filter. Different electron acceptors and donors were used in media composed of (a) 50 mM sodium phosphate (pH 6.5)/12 mM NaCl/0.5 mM phenyl-*p*-benzoquinone as a measure for PS-II electron-transport rate (b) 50 mM Tricine (pH 8.5)/35 mM NaCl/2 mM NaN_3/10 μM 3-(3′,4′-dichlorophenyl)-1,1-dimethylurea/2 mM NH_4Cl/150 μM methylviologen/4 mM ascorbate/0.2 mM 2,6-dichlorophenolindophenol as a measure for PS-I electron-transport rate; and (c) 50 mM sodium phosphate (pH 7.5)/50 mM NaCl/2 mM methylviologen as a measure of whole chain (PS-II + PS-I) electron-transport rate, in the absence or presence of 2 mM NH_4Cl as an uncoupler.

P-700 was assayed from (ferricyanide-oxidized)-minus-(ascorbate-reduced) difference spectra [12]. Cytochrome *f* was estimated from (hydroquinone-reduced)-minus-(ferricyanide-oxidized) difference spectra in the presence [13] or absence of Triton X-100 [14]. Both methods gave comparable results. Cytochrome *b*-559_{HP}, cytochrome *b*-559_{LP} and cytochrome *b*-563 were assayed as in [13]. Plastoquinone was extracted from ethanol-treated thylakoid preparations with methanol/chloroform/heptane (1 : 1 : 1, v/v) and assayed as previously described [15].

Atrazine-binding analysis was carried out according to the method of Tischer and Strotmann [16]. Binding reactions were initiated by vortexing 1 ml suspensions of 50 μg Chl/ml in 400 mM sucrose/50 mM Tes (pH 7.5)/10 mM NaCl/5 mM $MgCl_2$, with 30 μl of [*ethyl*-1-^{14}C]atrazine dissolved in ethanol to give various concentrations of atrazine. Data presentation and calculations were as described [16]. Atrazine (16 mCi/mmol) was purchased from Amersham.

The Mg^{2+}-specific ATPase activity of chloroplast coupling factor CF_1 was assayed in the presence of octyl glucoside as described [17].

Leaf photosynthesis was measured in white light of various intensities from a mercury vapour lamp, using neutral density filters. Measurements were made in air of normal CO_2 and O_2 partial pressures at a leaf temperature of 22°C.

Results

Physiological difference

Under the growth conditions used in this study, *Atriplex* grows into healthy, leafy plants under white or blue light within two to three months after germination. However, under red light, the plants grow much taller but develop much smaller and curly leaves, usually about a quarter of the size of those developed under blue or white lights. The number of leaves on each plant grown under red light is much lower than those grown under white or blue light. *Atriplex triangularis* grows best in blue light, less in white light and very poorly in red light.

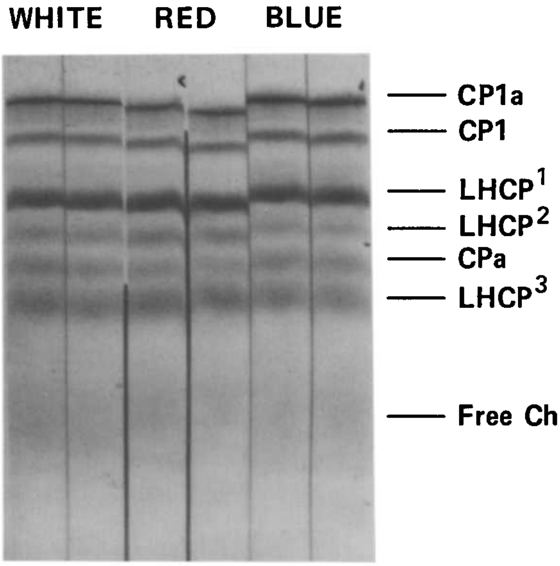

Fig. 1. Unstained SDS-polyacrylamide gels after electrophoresis of chloroplast thylakoids from *Atriplex triangularis* grown in white, red and blue light.

Despite these marked differences in growth, there was no significant difference in either the total content of chlorophyll or fresh weights on a leaf area basis in plants grown in blue, white or red light (Table I). When the amounts of chlorophyll per chloroplasts were compared, chloroplasts of plants grown in white and red lights have 11%

TABLE I

PHYSIOLOGICAL DIFFERENCES IN *ATRIPLEX TRIANGULARIS* GROWN IN CONTINUOUS BLUE, WHITE OR RED LIGHT OF THE SAME INTENSITY

	Total chl/leaf area (μg/cm^2)	Fresh wt./leaf area (mg/cm^2)	Total chl/chloroplast ($\times 10^{-6}$ μg)	Chl *a*/Chl *b*
Blue	37.3	14.8	0.94	2.85
White	30.3	15.1	1.04	2.91
Red	31.7	17.3	1.37	2.63

TABLE II

THE RELATIVE PERCENTAGE DISTRIBUTION OF CHLOROPHYLL IN THE CHLOROPHYLL-PROTEINS OF THYLAKOID MEMBRANES OF *ATRIPLEX TRIANGULARIS* GROWN IN CONTINUOUS BLUE, WHITE OR RED LIGHT OF THE SAME INTENSITY

Quality of light	Percentage chlorophyll in chlorophyll-proteins						
	CPIa	CPI	LHCP^1	LHCP^2	CPa	LHCP^3	FC
Blue	23.1	11.9	26.9	4.7	9.4	12.3	11.8
White	21.7	8.4	28.4	6.2	8.5	14.8	12.1
Red	19.1	8.4	28.7	7.1	7.7	16.4	12.8

and 46% more chlorophyll per chloroplast, respectively, than those grown in blue light. Therefore, plants grown in red light may be behaving like shade plants since it is known that chloroplasts from shade plants have higher chlorophyll content [18]. The chlorophyll-*a*-to-chlorophyll-*b* ratios in *Atriplex* grown under blue, white or red light varied, with plants grown under red light having the lowest value (Table I). Leaves from shade plants have even higher chlorophyll *b* relative to chlorophyll *a* contents [19] and low Chl *a*/Chl *b* ratios of 2–2.2 [18] compared to sun plants.

Effects of light quality on the relative amounts of chlorophyll-proteins

When thylakoids from leaves of *Atriplex* grown in different light quality were solubilized at 4°C with an SDS/Chl weight ratio of 7.5 : 1 and subjected to discontinuous gel electrophoresis at 4°C, seven chlorophyll-containing bands were resolved (Fig. 1). They were identified and listed in order of increasing mobility as CPIa, CPI, LHCP^1, LHCP^2, CPa, LHCP^3 and free chlorophyll. Cpla is an undissociated PS-I complex which includes CPI, the Chl *a*/*b*-proteins of PS I (LHC I) [20] and colourless polypeptides, CPI is the β-carotene-P-700-Chl-*a*-protein complex, CPa is the presumed reaction centre complex of PS II and the three Chl *a*/*b*-proteins (LHCP^1, LHCP^2, LHCP^3) with Chl *a*/Chl *b* ratios of 1.3–1.1 belong to the main light-harvesting complex of PS II (LHC II) [11,21,22]. Since the amounts of free chlorophyll were roughly constant, a valid comparison can be made of the relative chlorophyll distribution between the various chlorophyll-protein complexes (Table II). When compared to those grown in white light, thylakoids from plants grown in blue light have higher relative amounts of chlorophyll in CPIa and CPI as well as in CPa, whereas those from plants grown in red light have higher relative amounts of chlorophyll in LHCP^1, LHCP^2 and LHCP^3 (Table II).

These differences between the effects of blue, white and red light are substantiated when the relative amounts of chlorophyll associated with LHC II, PS I and PS II are compared (Table III).

TABLE III

COMPARISON OF THE RELATIVE CHLOROPHYLL DISTRIBUTION IN THE CHLOROPHYLL-PROTEINS OF PS I AND PS II IN THYLAKOIDS OF *ATRIPLEX TRIANGULARIS* ADAPTED TO CONTINUOUS BLUE, WHITE OR RED LIGHT OF THE SAME INTENSITY

Quality	LHCP^{1+2+3} (%)	PS I * Chl content	PS II ** Chl content	LHCP^{1+2+3}/CPa	PS II **/PS I *
Blue	43.9	35.0	53.3	4.7	1.52
White	49.4	30.1	57.9	5.8	1.93
Red	52.2	27.5	59.9	6.8	2.18

* PS I Chl = CPIa + CPI.

** PS II Chl = CPa + LHCP^1 + LHCP^2 + LHCP^3.

The relative amount of chlorophyll associated with PS I is higher in plants grown in blue light than in red light; on the other hand, those associated with LHC II and PS II are higher in plants grown in red than in blue light. Because of these differential responses, the PS-II/PS-I chlorophyll content ratios (Table III) are different; the value for red-light-grown *Atriplex* is 40% higher than that of blue-light-grown plants.

The data on LHC-II, PS-I and PS-II chlorophyll contents (Table III) support the idea that chloroplasts of plants grown in low-intensity blue light resemble those grown in high-intensity white light or those from sunplants; while those grown in low-intensity red light resemble those grown in low-intensity white light or those from shade plants [1,3–7,18,19]. However, the Chl-*a*/Chl-*b* ratio of red light grown *Atriplex* is not as low as that of shade plants, probably because Chl-*a*/Chl-*b* ratios are influenced to a greater extent by the quantity rather than by the quality of light [23].

Effect of light quality during growth of Atriplex on the electron-transport system

Freshly prepared thylakoids from plants grown in blue, white or red light were assayed for partial reactions of PS I and PS II as well as whole-chain electron-transport capacity at saturating light intensities (Table IV). Clearly, thylakoids from plants grown in blue light have the higest rates of partial PS I and PS II reactions as well as coupled or uncoupled whole-chain electron-transport, those from plants grown in red light the lowest rates, while those from plants grown in white light have intermediate rates. The results obtained with thylakoids from plants grown in blue and red light are in agreement with those previously reported for barley seedlings where the Hill activity of chloroplasts is higher in blue than in red light illuminated seedlings [1]. On the other hand, it is reported that there is no significant difference in the PS I electron-transport rates of chloroplasts from pea plants grown in blue and red light [24].

Since these changes in electron transport capacity probably arise from changes in amounts of electron carriers, we determined the relative amounts of some of these carriers. Since it was technically not possible to measure the primary electron acceptor Q of PS II spectrophotometrically [25], the atrazine binding sites in the thylakoids were assayed. It has been proposed that the mode of action of atrazine is via high-affinity binding to the PS-II core complex [16,26]. Indeed, the presence of an atrazine-binding protein (32 kDa) has been demonstrated in the PS-II core complex [27]. Thus, the atrazine binding site should give an indication of the size of PS-II core reaction centre and hence P-680 and Q. Such measure-

TABLE IV

EFFECT OF LIGHT QUALITY ON THE FUNCTIONS AND COMPONENTS OF *ATRIPLEX* THYLAKOIDS

MV, methylviologen.

Concentration of components and functions	Light quality		
	Blue	White	Red
Electron transport rates (μmol O_2 per h per mg Chl) PS I, ASC/DCIP → MV	221	161	154
PS II, $H_2O \rightarrow p$-PBQ	61	57	48
PS I + PS II, $H_2O \rightarrow$ MV, $-NH_4Cl$	39	29	24
PS I + PS II, $H_2O \rightarrow$ MV, $+NH_4Cl$	108	76	52
Amounts of electron transport components (μmol per mmol Chl)			
Atrazine binding sites	2.94	2.67	1.96
Plastoquinone	49.0	48.0	37.6
Cyt *f*	1.67	1.55	0.89
Cyt b-559$_{HP}$	2.84	2.66	2.02
Cyt b-559$_{LP}$	1.53	1.48	0.87
Cyt *b*-563	1.91	1.88	1.31
P-700	3.44	2.16	1.88
Coupling factor, CF_1 activity (μmol Pi per mg Chl per h)	147	98	85

ments show that when compared to *Atriplex* grown in white light, those grown in blue light have 10% more whereas those grown in red light have 25% less atrazine binding sites (Table IV). A similar trend was observed in the contents of electron carriers between PS II and PS I on a chlorophyll basis (Table IV). There is, however, a markedly greater difference in the contents of P-700: when compared to *Atriplex* grown in white light, those grown in blue light have 60% more, while those grown in red light have 23% less P-700; i.e., there is an 83% difference in the P-700 content of thylakoids between plants grown in blue and red light (Table IV). A 73% difference in coupling factor CF_1 activity of the thylakoids is observed between plants grown in blue and red light (Table IV), in line with changes in electron transport rates and relative concentrations of electron carriers.

The fact that these differences in electron transport rates as well as in the contents of electron carriers occur in the same direction, with respect to light quality during growth, indicates that the regulations exerted by light quality are well coordinated.

Effect of light quality on the relative apparent photosynthetic unit sizes of PS I and PS II

Since the relative amounts of chlorophyll proteins associated with PS II and PS I in the thylakoids are changed by light quality, it is also important to measure the light-harvesting antenna unit sizes of PS I and PS II [23]. Thus, by comparing the relative amount of chlorophyll associated with PS I (Table III) with P-700, and that of PS II with atrazine binding sites (Table V), it is possible to obtain information on the apparent light harvesting antenna unit size of PS I and PS II, respectively. It is clear that the apparent antenna unit sizes of both PS I and PS II are larger in plants grown in red light than those grown in blue light. Furthermore, the ratios of the reaction centres of PS I and PS II are not constant; those from *Atriplex* grown in blue and red light are lower than those in white light and those in red light are 20% higher than those in blue light (Table V).

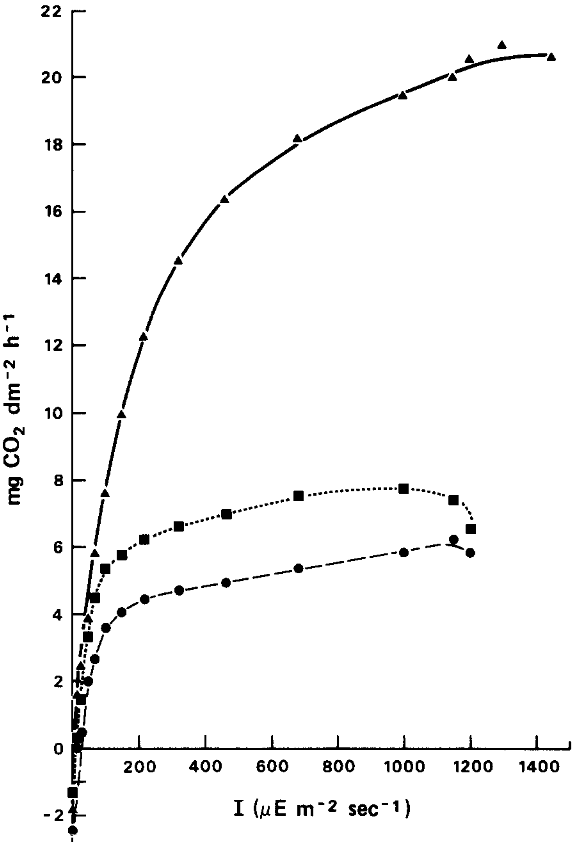

Fig. 2. Rates of net photosynthesis as a function of incident light intensity for *Atriplex triangularis* grown in blue (▲), white (■) and red (●) light.

TABLE V

EFFECT OF LIGHT QUALITY DURING GROWTH ON THE MOLAR RATIOS OF PS II/PS I REACTION CENTRES AND ON THE APPARENT ANTENNA SIZES OF PS I AND PS II IN *ATRIPLEX TRIANGULARIS*

Light quality	Atrazine binding sites/P-700	Antenna size of PS I PS I Chl/P-700 (arbitrary units)	Antenna size of PS II PS II Chl/atrazine binding sites
Blue	0.85	102	181
White	1.24	139	217
Red	1.04	146	306

Photosynthetic rates of intact leaves

The composition and function of thylakoids grown in blue, white and red light described alove indicate that chloroplasts from plants grown in blue light are photosynthetically more efficient than those grown in red light, with those grown in white light in between the two. This in vitro performance is compared with in vivo measurements on intact leaves. The net photosynthetic rates of intact leaves were compared by measuring the CO_2 fixation rates with an infrared gas analyzer at various light intensities (Sig. 2). Leaves tested in this investigation all attained maximal photosynthetic rates at about 1200 $\mu E \cdot m^{-2} \cdot s^{-1}$. Leaves from plants grown in blue light reached a maximal rate of 20 mg CO_2 per dm^2 per h, while those grown in red and white attained maximal rates of 5.7 and 7.7 mg per CO_2 dm^2 per h, respectively. The maximal rates on a total amount of chlorophyll basis were also in the same proportion (i.e., 4.3, 2.7 and 1.1 mg CO_2 per mg Chl per h for plants grown in blue, white and red light, respectively). Thus, the photosynthetic performance of the leaf is indeed correlated with the changes in composition and function of the thylakoid membranes.

Discussion

Light quality clearly exerts a well coordinated regulatory effect on the composition and function of chloroplasts from mature leaves of *Atriplex triangularis.* With respect to light-harvesting, the relative distributions of chlorophyll in the chlorophyll-protein complexes of PS I and PS II are changed in such a way that thylakoids from plants grown in blue light have higher content of chlorophyll in PS I and lower content in PS II as compared to those grown in red light. Concomitantly, the electron-transport rates of either PS II or PS I measured as partial or whole chain reactions at saturating light intensities, as well as coupling factor, CF_1 activity, are higher in the chloroplasts from plants grown in blue light than those grown in white or red light. Hence, these chloroplasts form more NADPH and ATP on a chlorophyll basis, and their leaves have a higher photosynthetic rate. The higher electron transport capacity of *Atriplex* grown in blue light is partly attained by relatively increased amounts of atrazine binding sites, plastoquinone, cytochromes *b*-559, *b*-563 and *f*, and P-700 on a chlorophyll basis.

It has been suggested that plants grown in blue light resemble sun plants or plants adapted to high intensity white light, and those grown in red light resemble shade plants or plants adapted to low-intensity white light [1,4]. While it may be true that blue light- or high-intensity white-light-adapted plants have greater photosynthetic rates compared to the red-light- or low-intensity-adapted plants, there are many significant differences in the composition of these thylakoid membranes. Firstly, the plant species is important. Since we had examined the effect of light intensity with pea plants [6,7], we first tried to grow pea plants under red, white and blue light of equal intensities, but found no significant differences in the composition, function and structure of these thylakoid membranes. Hence we turned to *Atriplex.* The regulatory effects of blue and red light on *Atriplex* reported here are not identical to those observed with pea plants adapted to a wide range of white light intensity [6,7]. While it is true that there are similarities in the chlorophyll content, the Chl *a*/Chl *b* and chl/cyt *f* ratios, there are many other differences. For example: the Chl/P-700 ratio of *Atriplex* grown in blue light is two-times-lower than that grown in red light (Table IV), whereas the Chl/P-700 ratios are not greatly different for peas grown at high or low light intensity [7]. Further, the Chl/P-700 ratios of sun and shade plants are not markedly different [9,28,29]. Moreover, there are significant differences in Chl/Q ratios: in *Atriplex* grown under blue light, this ratio is about 1.5-times-higher than that grown under red light (Table IV), while it is roughly similar in high- and low-light-grown *Atriplex* [23]. There are marked differences also in the Chl/Q ratios of sun and shade plants [23,30]. We, therefore, conclude that the effects of light quality and light quantity are different.

Under light-limiting conditions, electron transport capacity depends on the capacity of electron turnover in each photosystem. In turn, the electron transport capacity of each photosystem depends on (i) its relative concentration, (ii) its light-harvesting antenna unit size, i.e., the total number of chlorophyll *a* and chlorophyll *b* molecules transferring light excitation energy to the reaction centre, and (iii) the chlorophyll composition of the light-harvesting antenna. Clearly the relative amounts of total chlorophyll associated with PS II or PS I differ between the chloroplasts from plants grown under the three light qualities (Table II). The amounts of reaction centres, P-680, measured here as atrazine-binding site per unit chlorophyll, or P-700 per unit chlorophyll also differ (Tables III and IV). The apparent light-harvesting antenna unit size of PS II and PS I calculated by taking the ratios of the PS I or PS II relative chlorophyll content to the concentrations of P-700 and atrazine binding sites, respectively, are larger in thylakoids from plants grown in red light than those grown in either white or blue light. This in part accounts for the decreased rates of partial electron transfer in PS II or PS I, and their limited overall whole chain electron transport capacity relative to chloroplasts from plants grown in blue light.

The molar ratios of atrazine binding sites/P-700 (Table V) show some variation in the *Atriplex* grown under blue, white and red light, indicating that the PS-II/PS-I reaction centre ratios are not necessary constant as has been reported previously by Melis and Harvey [23]. However, the effects of light quality on the concentrations of PS-II and PS-I reaction centres (Table IV) contradict those reported on peas grown in far-red-deficient and far-red-enriched light conditions, where an increase in PS-II reaction centre content was accompanied by a decrease in the concentration of P-700. The discrepancy is perhaps due to the difference in light quality (far red enriched versus blue and red lights) and to plant species (peas vs. *Atriplex*), since it is well known that the photoreceptors for far-red and blue lights are different (Ref. 27 and also Ref. 31 for comprehensive coverage) and that under the present experimental conditions we did not observe any significant differences between pea plants grown in blue and red light (unpublished data).

A comparison between the effects of light quantity [6,7] and light quality (this study) on the composition and function of the thylakoid membranes indicates that the Chl *a*/Chl *b* ratio is more affected by light quantity than by light quality (Table III) [6,18], so are the apparent light-harvesting antenna size of PS II, electron transport capacity of PS I and PS II, concentrations of plastoquinone, atrazine binding sites and coupling factor CF_1 activity. On the other hand, light quality has a greater influence than light quantity on the concentration of P-700, the apparent light-harvesting antenna size of PS I and the overall photosynthetic rates of intact leaves.

It should be emphasised that when plants adapt to natural light conditions, they incorporate suitable changes in the composition and function of the thylakoid membranes in such a way that these changes are well balanced so as to provide an efficient performance in photosynthesis. This is but a natural outcome of economic optimization within the plants.

The coordinated regulation of the relative stoichiometries of the thylakoid supramolecular complexes which lead to the well-balanced rates of photosynthesis are controlled by both quality and quantity of light [6,7]. The molecular mechanisms underlying this remarkable regulation are as yet unknown. Both phytochrome [31,33] and a blue-light mediator [32] control the stepwise development of chloroplast function and structure, and chlorophyll synthesis itself is light dependent in most higher plants [34]. Phytochrome is implicated in the synthesis of the apoproteins of LHC II [35] encoded by the nuclear genome and in the 32 kDa herbicide-binding thylakoid protein encoded by the chloroplast genome (see Ref. 36). Do all of the supramolecular complexes contain at least one polypeptide encoded by a 'photogene' which senses the light environment and exerts a regulatory effect on the expression of the other components? Since each of the electron transport complexes and ATP synthase are made up of some polypeptides encoded by the nuclear genome and some by the chloroplast genome, each complex may indeed have at least two key polypeptides encoded by a nuclear and a chloroplast photogene.

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