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REGULATION OF PHOTOSYSTEM STOICHIOMETRY, CHLOROPHYLL *a* AND CHLOROPHYLL *b* CONTENT AND RELATION TO CHLOROPLAST ULTRASTRUCTURE

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The structural-functional organization of higher plant chloroplasts has been investigated in relation to the particular light conditions during plant growth. (1) Light intensity variations during growth caused changes in the Chl *a*/Chl *b* ratio, in the light-saturated uncoupled rates of electron transport to a Hill oxidant and in the distribution of the chloroplast volume between the membrane and stroma phases. (2) Light quality differences during growth had an effect on the PS II/PS I reaction center ratio and on the chloroplast membrane phase differentiation into grana and stroma thylakoids. Plants grown under far-red-enriched (680–710 nm) illumination contained higher (20–25%) amounts of PS II and simultaneously lower (20–25%) amounts of PS I reaction centers. They also showed a higher grana density along with thicker grana stacks in their chloroplasts. (3) The size of the light-harvesting antenna pool of PS II centers was estimated from the fluorescence time course of 3-(3′,4′-dichlorophenyl)-1,1-dimethylurea-poisoned chloroplasts and was found to be fairly constant (±10%) in spite of the variable PS II/PS I reaction center ratio. The results are compatible with the hypothesis that the structural entities of grana facilitated the centralization and relative concentration increase of a certain group of PS II reaction centers.

Introduction

The use of a sensitive spectrophotometric method has recently allowed determinations of the stoichiometric ratio of PS II and PS I reaction centers in different photosynthetic membranes [1]. It was found that considerable differences in this ratio existed between membranes from the grana and stroma regions of chloroplasts. Grana membranes contained most of the Chl *b*, PS II centers and plastoquinone of the chloroplast. Stroma membranes contained primarily PS I reaction centers. Preliminary observations [1] also indicated seasonal changes in the relative concentration of PS II and PS I reaction centers which might occur in response to environmental light conditions. The correlation of structural and functional parameters in higher plant chloroplasts has been studied by different investigators [2,3] in relation to the particular light habitat of the plants. In the present investigation, we used different treatments of light intensity and light quality during plant growth as the means of probing the relationship between certain chloroplast structural and functional parameters. We found that intensity and quality of light variations produced distinctly different effects on the chloroplast ultrastructure and function. The intensity of the absorbed light apparently controlled the relative Chl *a* and Chl *b* content, the photosynthetic electron-transport capacity and the relative volume of the stroma and membrane phases in the chloroplast. The quality of the absorbed light controlled the concentration of PS II and PS I reaction center complexes and, in

Abbreviations: PS, photosystem; Chl, chlorophyll; *P*-700, primary donor of PS I; Q, primary acceptor of PS II; DCMU, 3-(3′,4′-dichlorophenyl)-1,1-dimethylurea; Tricine, *N*-tris-(hydroxymethyl)methylglycine.

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addition, the chloroplast membrane differentiation into grana and stroma lamellae. Neither treatment exerted any obvious effect on the functional antenna size of PS II which remained fairly constant during the various experiments.

Materials and Methods

Chloroplasts were isolated from leaves of the sun-adapted plants, *Atriplex triangularis* Wild., *Pisum sativum*, L. (pea) var. Alaska and *Phaseolus vulgaris*, L. (bean) var. Hawkesbury Wonder, and from the shade plants, *Asarum caudatum* Lindl. (wild ginger), *Polystichum munutum Presl.* (sword fern), and *Tolmiea menziesii* (Pursh) T and G. *Atriplex, Phaseolus* and *Pisum* leaves were ground in a Waring blendor for 30 s at low speed in a buffer containing 0.4 M sucrose, 50 mM Tricine, pH 7.8, 10 mM NaCl and 5 mM $MgCl_2$. *Asarum, Polystichum* and *Tolmiea* leaves were ground in the same buffer containing 10% (w/w) poly(ethylene glycol) 6000 to prevent phenolic compounds in these species from interacting with the chloroplasts. After filtration and centrifugation, the pellet was resuspended in the same buffer (poly(ethylene glycol) excluded) for the fluorescence measurements. For absorbance change measuements the suspending buffer contained the same ingredients minus sucrose.

The concentrations of the primary electron acceptor Q of PS II and of the primary electron donor *P*-700 of PS I were measured by absorbance difference spectrophotometry in the ultraviolet (ΔA_{325}) and red (ΔA_{700}) regions, respectively. The apparatus and procedure for such measurements have been described [1,4]. Rates of CO_2 uptake were measured on the basis of leaf area per unit time with an open-flow gas-exchange system [5]. Rates of electron transport were measured with a Clark-type oxygen electrode in the presence of 1 mM potassium ferricyanide and were expressed as μequivalents (4 μequiv. = 1 μmol O_2)/mg Chl per h.

Atriplex, Phaseolus and *Pisum* plants were grown in natural daylight under three different light intensity regimes. The high intensity-grown plants remained under full sunlight and received in the 400–700 nm region a photon fluence rate of 51 mol/m^2 per day. Intermediate (17 mol/m^2 per day) and low (6 mol/m^2 per day) light intensity environments were created by placing the plants into cages made from neutral density screening. Other growth conditions were as previously described [6]. Light intensity was measured with a quantum sensor (Licor, Lincoln, NE) connected to an integrator (Campbell Scientific Co., Logan, UT).

Pisum plants were also grown in a growth chamber under continuous light of varying qualities. Far-red-enriched light was obtained by 100 W GE incandescent lamps while far-red-deficient light was obtained by 20 W GE cool-white fluorescence tubes. In both cases, the light intensities (measured between 400 and 700 nm) received by the plants were approx. 7 mol/m^2 per day. Shade plants grown in a shaded habitat received on the average intensities less than 2 mol/m^2 per day.

Chlorophyll determinations were made in absolute methanol or 80% acetone. The equations of Holden [7] were used for methanol and those of Arnon [8] for acetone extractions. For electron microscopy, leaf tissues were fixed in 0.1 M sodium phosphate buffer containing 2.5% glutaraldehyde and 1% paraformaldehyde. The tissues were postfixed with 1% OsO_4. The material was stained in Epon-Araldite blocks with 1% uranyl acetate, sectioned (600–900 Å thickness) and stained with lead citrate. Mounted sections were viewed with a Hitachi (HU-11E-1) electron microscope.

Results

Acclimation of higher plants under different light intensities of the same spectral distribution causes functional and structural changes at the leaf, cell and chloroplast levels [9–12]. The light-response curves of photosynthesis for leaves of *Atriplex* grown under different light intensities (Fig. 1) confirm that high intensity-grown plants support 4-times higher rates of CO_2 assimilation than low intensity-grown plants [2,3]. Similar results were obtained with leaves of *Phaseolus* grown under different light intensities (not shown, see Ref. 13). The above functional difference persist at the chloroplast level and are clearly manifested in the light-saturation curve of electron transport from H_2O to dichlorophenol-indophenol [3,10] or to potassium ferricyanide [13].

Two factors possibly limiting the light-saturated

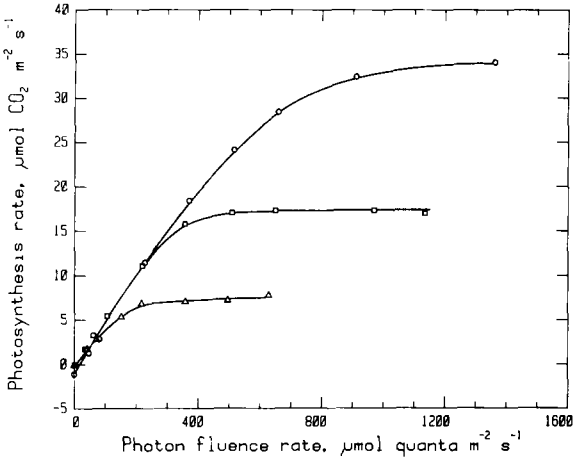

Fig. 1. Light-saturation curves of photosynthesis by leaves of *Atriplex* grown under high (○), intermediate (□) and low (△) light intensities. Photosynthesis was excited by white light of different quantum flux. Leaves were exposed to a CO_2 partial pressure of 460–510 μbar at 25°C.

rates of photosynthesis (expressed on a chlorophyll basis) are: (a) the light-harvesting antenna pool size for the reaction centers of PS II and PS I, i.e., the number of chlorophyll molecules harvesting and transferring excitation to each particular reaction center and (b) the electron-transport capacity of the chloroplast, i.e., the relative concentration of the electron-transport intermediates (such as plastoquinone, cytochromes, and plastocyanin) with respect to the concentration of the reaction centers. Fig. 2 shows the variable part of the fluorescence kinetics of DCMU-poisoned chloroplasts, isolated from *Phaseolus* plants grown at different light intensities. The fluorescence time course is a measure of the photoreduction rate of the primary electron acceptor Q of PS II [14,15] and, in the presence of DCMU, it depends only on the exciting light intensity and the effective absorption cross-section of PS II [16]. There is only a small difference in the half-time of the fluorescence rise kinetics between the three samples of Fig. 2 (of the order of 10–30%), suggesting that acclimation of these plants to different intensities caused only small changes in the number of chlorophyll molecules servicing the PS II reaction centers.

Fig. 3 compares the fluorescence induction curves in the absence of DCMU from *Phaseolus* chloroplasts developed under different light intensities. In this example, the time required to reach the maximal fluorescence level (normalized to 1.0 for all samples) is the time needed to reduce the intermediate compounds between PS II and the terminal electron acceptor of the Mehler reaction [17] with electrons originating from PS II. Since no significant differences in the light-harvesting antenna pool size

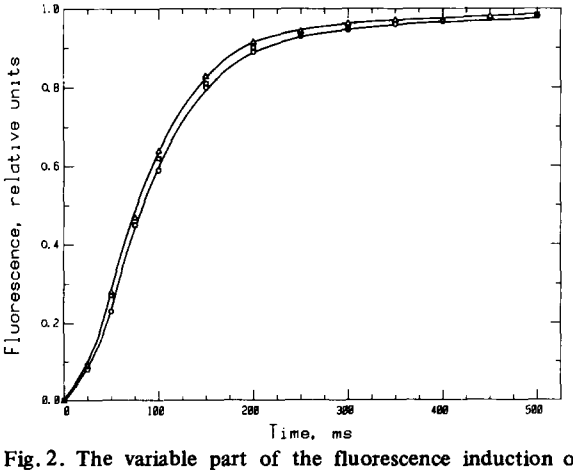

Fig. 2. The variable part of the fluorescence induction of *Phaseolus* chloroplasts developed under high (○), intermediate (□) and low (△) light intensities. The sample contained 15 μM DCMU. The variable fluorescence kinetics have been normalized between the values zero and one.

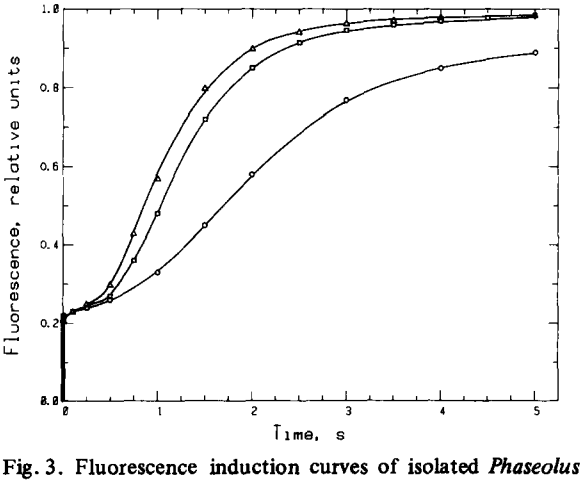

Fig. 3. Fluorescence induction curves of isolated *Phaseolus* chloroplasts in the absence of any electron-transport inhibitor. The maximum fluorescence yield was arbitrarily normalized to unity ($F_{max} = 1$). For the high light intensity sample, F_{max} was reached after about 20 s of illumination. For other details see legend of Fig. 2.

of PS II were detected (Fig. 2), variations in the fluorescence induction kinetics among the three samples must be explained in terms of different electron capacities in the three types of chloroplasts. High light intensity-grown plants exhibited a significantly slower time course, indicating an increased electron-transport capacity in these samples relative to the chloroplasts from low intensity-grown plants. A relative measure of the electron-transport capacity is obtained by comparing the areas over the fluorescence induction curves in Fig. 3 (see also Ref. 18). The measured area values were 27.6 for the high, 14.4 for the intermediate and 12.1 for the low light intensity-developed chloroplasts. In general agreement with the results of Fig. 3, the light-saturated uncoupled rates of electron transport from H_2O to ferricyanide were different in chloroplasts from the three samples [3,10]. Chloroplasts developed under high intermediate and low light intensity sustained rates of approx. 1 200, 700 and 400 μequiv./mg Chl per h, respectively.

Table I shows that *Phaseolus* and *Atriplex* grown at different light intensities have Chl *a*/Chl *b* ratios ranging from 2.6 in the low intensity to 3.7 in the high intensity samples. This observation is in agreement with earlier results [10] and points to the regulatory effect light intensity may have on the chloroplast Chl *a*/Chl *b* ratio. Table I also shows the amounts of the primary electron acceptor Q of PS II and of the primary electron donor *P*-700 of PS I occurring per 100 μmol of chlorophyll (*a* + *b*) in the above samples. Acclimation to low light intensities caused a decrease (of the order of 10–30%) in the Q and *P*-700 content on a chlorophyll basis. In this experiment, variations in Q and *P*-700 content occurred in parallel and the ratio of Q/*P*-700 varied by only 10–15%.

A separate group of experiments was conducted by using *Pisum* plants grown under continuous illumination of different spectral qualities. Table II compares the results obtained with *Pisum* chloroplasts developed in the greenhouse (control), under far-red-deficient (cool-white fluorescent) light, or far-red-enriched (incandescent) light. In this experiment, the intensity in the 400–700 nm region was

TABLE II

Chl *a*/Chl *b* RATIOS, Q AND *P*-700 CONTENT IN *Pisum sativum* CHLOROPLASTS

The amounts of Q and *P*-700 in μmoles correspond to 100 μmol chlorophyll (*a* + *b*). The chloroplasts were developed either in the greenhouse, by far-red-deficient cool-white fluorescent, or by far-red-enriched incandescent light.

	Chl *a*/ Chl *b*	Q (μmol)	*P*-700 (μmol)	Q/*P*-700
Greenhouse	2.50 ± 0.05	0.42 ± 0.06	0.23 ± 0.01	1.83
Fluorescent	2.96 ± 0.05	0.40 ± 0.06	0.22 ± 0.01	1.82
Incandescent	2.64 ± 0.05	0.49 ± 0.06	0.17 ± 0.01	2.83

TABLE I

Chl *a*/Chl *b* RATIOS, Q AND *P*-700 CONTENT IN DIFFERENT CHLOROPLAST SAMPLES

The amount of Q and *P*-700 in μmoles, correspond to 100 μmol of chlorophyll (*a* + *b*) in the chloroplasts. *Phaseolus vulgaris* and *Atriplex triangularis* chloroplasts were developed under high, intermediate and low sunlight intensities.

	Chl *a*/Chl *b*	Q (μmol)	*P*-700 (μmol)	Q/*P*-700
Phaseolus				
High intensity	3.40 ± 0.05	0.55 ± 0.06	0.30 ± 0.01	1.83
Intermediate intensity	3.02 ± 0.05	0.45 ± 0.06	0.27 ± 0.01	1.67
Low intensity	2.70 ± 0.05	0.37 ± 0.06	0.23 ± 0.01	1.61
Atriplex				
High intensity	3.69 ± 0.05	0.58 ± 0.07	0.26 ± 0.01	2.23
Intermediate intensity	2.80 ± 0.05	0.52 ± 0.07	0.25 ± 0.01	2.08
Low intensity	2.63 ± 0.05	0.46 ± 0.07	0.24 ± 0.01	1.92

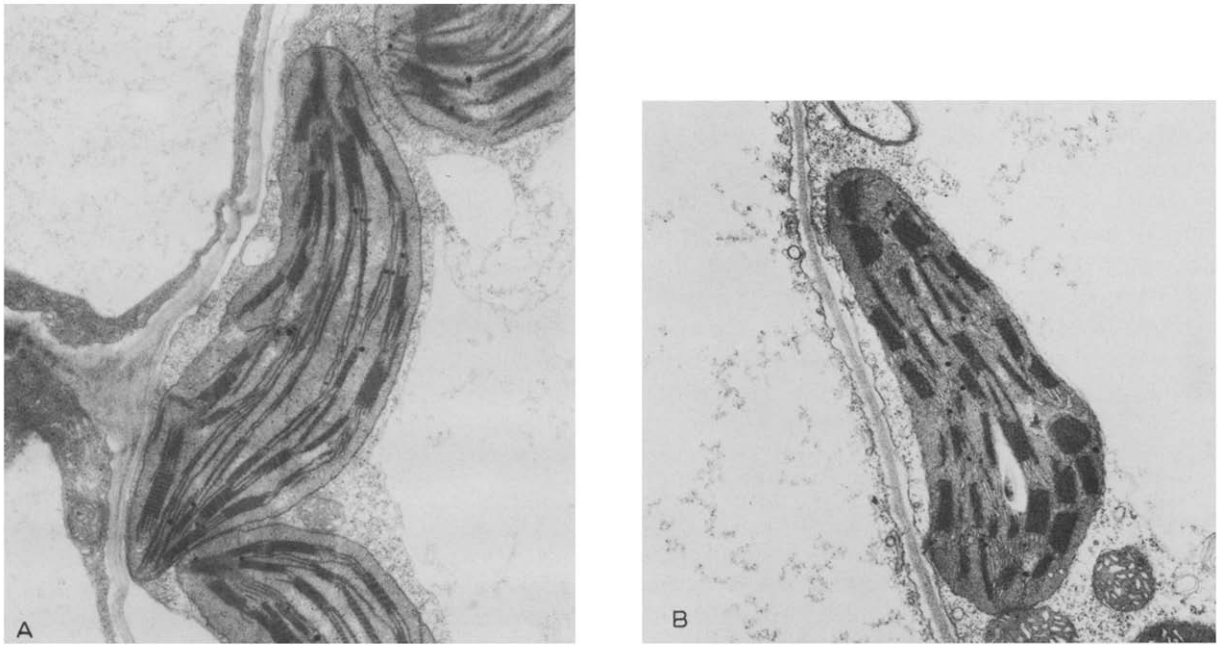

Fig. 4. Electron micrographs of *Pisum* chloroplasts greened under far-red-deficient (A) and under far-red-enriched light (B). Magnification, X 8 640.

kept at 7 mol/m^2 per day. Greenhouse and far-red-deficient plants showed minor quantitative differences in the Chl *a*/Chl *b* ratio, and Q and *P*-700 content. However, chloroplasts developed in far-red-enriched light showed a significant quantitative difference from those developed in far-red-deficient light in the Q and *P*-700 content: on a chlorophyll basis, we consistently measured an enrichment in the far-red-developed chloroplasts in the amount of Q present and a simultaneous decrease in the concentration of *P*-700. Such alterations shifted the Q/*P*-700 ratio from the average value of 1.8 to that of 2.8, representing an overall change by approx. 60%.

Fig. 4 compares, in cross section, the ultrastructure of *Pisum* chloroplasts developed under far-red-deficient and far-red-enriched light. There is a considerable difference in the relative abundance and size of grana and stroma lamellae in the two samples. Under far-red-deficient light the chloroplasts appeared to have thinner grana stacks and more extended stroma thylakoids (Fig. 4A). Far-red-enriched light generally yielded a higher density of thicker grana (Fig. 4B). Since grana thylakoids are normally enriched in Q (PS II reaction centers) and stroma thylakoids are enriched in *P*-700 [1], the above structural changes are in agreement with the light quality-induced changes in Q and *P*-700 content.

The structural differentiation of the higher plant chloroplasts into grana- and stroma-exposed thylakoids apparently concurs with the functional differentiation of PS II into α centers that are exclusively located in the partition regions of the grana and into β centers located on stroma-exposed thylakoids [16,19]. We have reported on chloroplast developmental [20] and genetic [16] conditions that induce alterations in the chloroplast thylakoid membrane differentiation and, consequently, in the relative concentration of α and β centers. Here, it will be shown that corresponding changes in the relative amounts of α and β centers occur during the plant growth under far-red-deficient and far-red-enriched light. Fig. 5 compares the variable fluorescence kinetics of DCMU-poisoned chloroplasts isolated from *Pisum* plants grown in the greenhouse, under far-red-enriched, or under far-red-deficient light. We observed a small but

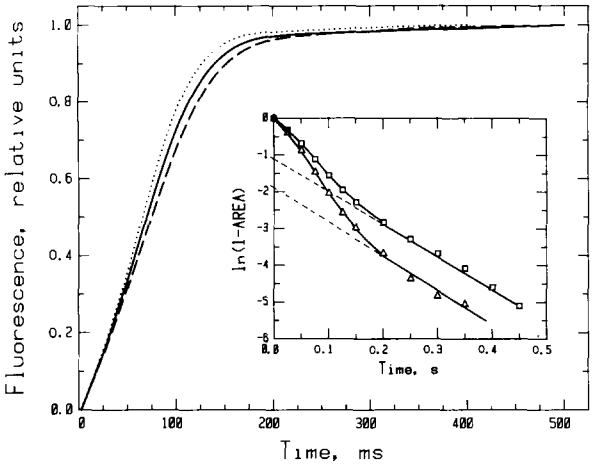

Fig. 5. The time course of variable fluorescence yield of *Pisum* chloroplasts in the presence of 15 μM DCMU. The chloroplasts were developed either by far-red-enriched light (△, also dotted curve), by direct sunlight (solid curve) or by far-red-deficient light (□, also dashed curve). The initial fluorescence yield was arbitrarily taken equal to zero and the maximum yield equal to 1.0. The area over the fluorescence induction curves was measured and plotted (insert) as in Ref. 15. Each curve is the average of four measurements.

consistent difference in the kinetic patterns of the three curves which is caused by the variable contribution of the slow β-phase [15] in the biphasic photoconversion kinetics of PS II [16]. Fig. 5 (insert) shows a first-order kinetic analysis of the data in which the exponential β-phase clearly appears from approx. 0.2 s until the end of the induction phenomenon. The intercept of the linear β-phase with the ordinate at zero time gave the relative concentration of the β-centers, about 35% of the total PS II in the far-red-deficient and 15% in the far-red-enriched plants. In agreement with earlier results [16], an increased granal partition area, induced by far-red-enriched light, is accompanied by a corresponding increase in the concentration of α centers.

The significant increase in the stoichiometric ratio of PS II/PS I reaction centers in *Pisum* chloroplasts caused by far-red-enriched illumination was not followed by a decrease in the antenna size of PS II centers, i.e., it was not brought about by insertion of new PS II reaction centers in the existing chlorophyll pigment bed. From the semilogarithmic plots of Fig. 5 (insert) we have determined that the rate constants for the photoconversion of the two kinetic components were, within experimental error, identical. Based on the direct proportionality between photoconversion rate constant and effective absorption cross-section for a given reaction center [16], our results suggest that the antenna pool size of the α and β centers remained unchanged during the above light quality treatment. It must be concluded, therefore, that PS II organizational and PS II/PS I reaction center ratio changes in chloroplasts are not necessarily followed by antenna pool size changes, irrespective of the measured chlorophyll per Q and chlorophyll per *P*-700 values. On the basis of these results, the definition of the term photosynthetic unit is evaluated in the Discussion.

Such experiments were expanded to shade species, which in nature occur only in the lower vegetation level of densely shaded habitats. An important feature of shade plants is their chloroplast size and ultrastructure [2,10]. Fig. 6 shows the chloroplast ultrastructure of the typical shade species *Asarum*, revealing the large well developed grana stacks which in many cases extended across the entire chloroplast body. A concomitant decrease in

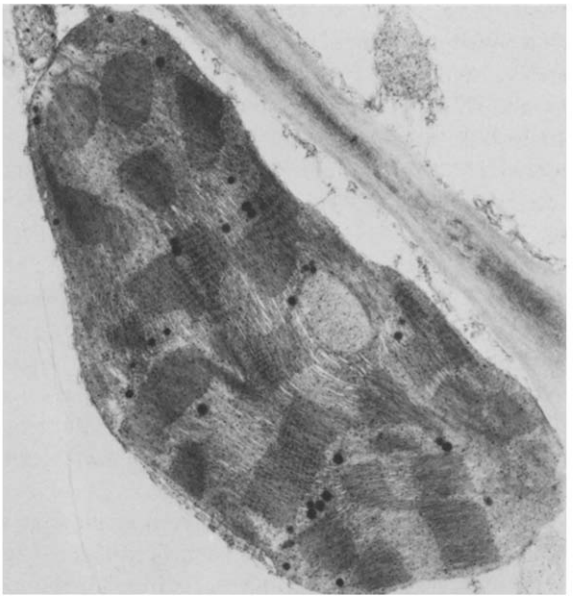

Fig. 6. Electron micrograph of *Asarum* chloroplast showing the extended grana stacks, high membrane density and decreased stroma volume, typical of shade-adapted plants. Magnification, × 8 640.

TABLE III

Chl *a*/Chl *b* RATIOS, Q AND *P*-700 CONTENT IN THE SHADE-ADAPTED SPECIES *ASARUM CAUDATUM, POLYSTICHUM MUNUTUM* AND *TOLMIEA MENZIESII*

The amounts of Q and *P*-700 in μmoles correspond to 100 μmol chlorophyll (*a* + *b*).

	Chl *a*/ Chl *b*	Q (μmol)	*P*-700 (μmol)	Q/*P*-700
Asarum	2.32 ± 0.05	0.52 ± 0.07	0.19 ± 0.01	2.74
Polystichum	2.29 ± 0.05	0.62 ± 0.07	0.16 ± 0.01	3.88
Tolmiea	2.31 ± 0.05	0.46 ± 0.07	0.19 ± 0.01	2.42

the relative number or length of the inter-grana stroma lamellae was not always apparent in the shade species we examined. However, the density of the membrane phase (grana and stroma thylakoids) was always higher than in chloroplasts from plants exposed to full sunlight, occupying almost the entire chloroplast volume and thus resulting in a drastic reduction of the relative stroma volume [10]. This result correlates with the decreased levels of ribulosebisphosphate carboxylase and other soluble protein [21] in such chloroplasts. Interestingly, in the three shade species we examined, the light-saturated uncoupled rates of electron transport were low, ranging between 100 and 250 μequiv./mg Chl per h [3,10]. Table III additionally shows that in the shade species *Asarum, Polystichum* and *Tolmiea,* the Chl *a*/Chl *b* ratios were considerably lower and the stoichiometric ratios of Q/*P*-700 were generally higher than that of sun-adapted plants (compare with data of Tables I and II). In these chloroplasts there is a parallel increase in Chl *b*, PS II content and thylakoid membrane density in the chloroplast volume.

Since a shade habitat is an environment of low light intensity but enriched in far-red light [2], it may be observed that chloroplasts from the above shade species show the combined effect of the low light intensity on the Chl *a*/Chl *b* ratio superimposed on the light quality effect on the reaction center ratio (Q/*P*-700).

Discussion

Under predominantly far-red-enriched illumination, PS I reaction centers turn over electrons faster than their PS II counterparts. The increased PS II/PS I ratio observed under these conditions may serve to offset this energetic imbalance and to maintain a balanced electron flow through the electron-transport chain [22]. Such a response is of particular importance, given the relatively limited ability of the chloroplast to adjust the antenna size of PS II and, presumably, of PS I. Our results agree with and give support to the concept of Myers et al. [23] involving a constancy of the light-harvesting antenna size of PS II and PS I in spite of the wide variations in the ratio of PS II/PS I reaction centers that may be observed. It may be concluded that in oxygen-evolving organisms, PS II and PS I constitute integral thylakoid membrane protein complexes that are structurally and, therefore, stoichiometrically independent of each other.

The varying PS II/PS I reaction center ratios introduce an uncertainty with respect to the use of the term 'photosynthetic unit'. As originally proposed by Gaffron and Wohl [24], this term had a functional meaning, referring to the number of chlorophyll molecules cooperating in the absorption of light for the evolution of one O_2 molecule [25]. Later, the photosynthetic unit size was often measured by the ratios of chlorophyll per *P*-700 or chlorophyll per cytochrome *f* [2,26–28]. Our results show that the latter definitions may be inadequate in describing the light-harvesting antenna pool of each photosystem. The complication arises from the fact that the ratio of PS II and PS I reaction centers in a chloroplast sample is not unity. An alternative concept recently proposed [29] may be the 'photochemical unit' referring to a specific reaction center and defining the number of antenna chlorophyll molecules that transfer their excitation energy to that reaction center. It is implicit in the definition that the photochemical unit of PS II may be different from that of PS I and must be determined separately.

The concept developed from this work is that light intensity and light quality may have different effects in terms of chloroplast structure and function. Light intensity apparently controls the chloro-

plast Chl *a* and Chl *b* content (Table I), the electron-transport capacity (Figs. 1 and 3) and the distribution of the chloroplast volume between the membrane and stroma phases (Fig. 6, see also Refs. 10 and 13 for electron micrographs of *Atriplex* and *Phaseolus*, respectively). The quality of light during chloroplast growth apparently controls the differentiation of the membrane phase into areas of grana stacks and stroma thylakoids and, in addition, the stoichiometric amounts of PS II and PS I reaction centers. Under our far-red-enriched light conditions, we observed a simultaneous increase in the amount of the α centers and in the grana partition region of the chloroplasts. The exclusive association of the α centers with the grana partition regions [16,19] is in agreement with the present results. We hypothesize that the structural differentiation of the chloroplast membranes into grana regions occurs, at least in part, in order to facilitate the centralization and relative concentration increase of this particular group of PS II reaction centers (α centers). The mechanism by which the above changes take place is not clear at this time. One may suggest the possible regulatory role of phytochrome and/or of a blue-light receptor in chloroplast biosynthesis [30]. Further work on the regulation of chloroplast structure and function by light quantity and quality may be needed.

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