

Adaptation of the thylakoid membranes of pea chloroplasts to light intensities. I. Study on the distribution of chlorophyll-protein complexes

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Abstract. The effect of light intensity (16 h white light and 8 h dark) during growth of pea plants at 20 °C on the chlorophyll composition and on the relative distribution of chlorophyll amongst the various chlorophyll-protein of pea thylakoids was studied. The chl a/chl b ratios increased from 2.1 to 3.2 as light intensity during growth varied from 10 to 840 $\mu\text{E m}^{-2} \text{s}^{-1}$. This function can be described by two straight lines intersecting at a transition point of approximately 200 $\mu\text{E m}^{-2} \text{s}^{-1}$. Similar discontinuities in the responses were observed in the changes in the relative distribution of chlorophyll amongst the various chlorophyll-protein complexes. This demonstrates that the chl a/chl b ratio of the various thylakoids is a good indicator of changes in the relative distribution of chlorophyll. As the chl a/chl b ratio decreased, the amount of chlorophyll associated with photosystem I complexes decreased, that with photosystem II core reaction centre complex was halved, and that with the main chl a/b-proteins of the light-harvesting complex was markedly increased.

Introduction

It is well established that higher plants adapt to different light intensities during growth in such a way that plants grown under high light intensities have a greater efficiency of photosynthetic quantum conversion than plants grown under low light intensities. This photoadaptation is accompanied by specific changes in composition, structure and function of the chloroplasts [10, 11, 12, 18]. Part of the functional change is associated with measurable changes in the chemical composition of the thylakoid membranes including varying chl a/chl b ratios, varying xanthophylls/ β -carotene ratios, changing amounts of electron carriers such as plastoquinone, cytochromes f, b_6 and b-559, and changes in ribulose-1,5-bisphosphate carboxylase concentrations. High light grown plants have higher chl a/chl b ratios, lower xanthophyll/ β -carotene ratios, and higher levels of electron carriers per unit chlorophyll [11, 12, 17, 22, 27]. Changes in the pigment composition are well documented but the changes in the relative amounts of chlorophyll-protein complexes in the thylakoid membranes during photoadaptation are less well

Abbreviations: chl = chlorophyll, PS = photosystem, SDS = sodium dodecyl sulphate, Tricine = N-tris (hydroxymethyl) methylglycine.

understood [13] mainly because, prior to 1978, only two main chlorophyll-proteins were resolved by gel electrophoresis and the amounts of free chlorophyll were relatively high [27].

Recent developments in mild SDS polyacrylamide gel electrophoresis procedures have led to high resolution of chlorophyll-protein complexes with the liberation of very little free chlorophyll and carotenoid [1, 2, 14, 24]. However, studies on changes in the distribution of chlorophyll in the various chlorophyll-protein complexes during photoadaptation have been limited to two studies with plants adapted to only two light intensities, namely, high and low light intensities [19, 20, 23]. These studies showed that the chloroplasts from low-light grown plants have more light-harvesting chl a/b-proteins and less photosystem I-chlorophyll a-protein complexes than chloroplasts from high-light grown plants [13, 19, 20]. However, it is not clear whether these changes are linear with respect to light intensity during growth since only two light intensities were investigated.

In this study, pea seedlings were grown at different light intensities. Analyses of the chlorophyll-protein complexes in the isolated thylakoid membranes show that the changes in the chlorophyll composition, as reflected by the chl a/chl b ratio and relative amounts of chl-proteins, with respect to light intensity can be represented by two straight lines with a transition point at about $200 \mu\text{E m}^{-2} \text{s}^{-1}$.

Materials and methods

Pea (*Pisum sativum* L.) seedlings were grown in vermiculite in growth cabinets at $20 \pm 0.5^\circ\text{C}$. The light source was a bank of white fluorescence tubes supplemented with tungsten incandescent lamps (the spectral property of the light source was as published [15]), operated on a 16 hour light/8 hour dark regime. Light intensities, measured with a Li-Cor Quantum Photometer (model LI-185A), were regulated by adjusting the distance between the seedlings and the light source as well as by using neutral density screens.

Chloroplasts were isolated as previously reported [15]. Thylakoids were washed in glass-distilled water, followed by two washes and resuspension in 50 mM Tricine (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 [8].

Thylakoid membranes (50 μg chl) were solubilized without prior lipid extraction in a solution (100 μl) containing 50 mM Tris (pH 8.0), 10% (v/v) glycerol and SDS to give an SDS/chl ratio of 7.5 (w/w). Samples equivalent to 17.5 μg chl were immediately applied to SDS polyacrylamide tube gels (4% stacking and 8% separation gels, 6 mm in diameter), as previously described [2]. The gels had been pre-electrophoresed at 3 mA per tube for 15 min, electrophoresis was for 45 min at 4°C [2]. Immediately after electrophoresis, these 'green' gels were scanned at 675 and 650 nm on a Varian 635 spectrophotometer fitted with a gel-scanning attachment. The relative distribution of chlorophyll on the gels was estimated as previously described

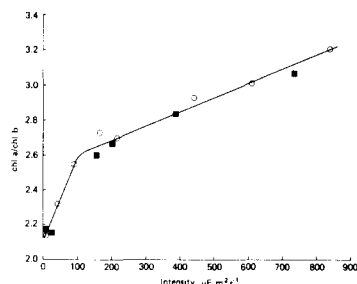


Figure 1. Effect of light intensity during growth on the chl a/chl b ratio in pea thylakoids isolated from plants grown at different light intensities. Circles represent data from one lot of plants, and squares represent data from another lot grown a few weeks apart.

[1] and were averages of three experiments each with duplicates. Standard deviations were within $\pm 7\%$.

Results

Photoadaptation of chl a/chl b ratio

The chl a/chl b ratios of pea thylakoids adapted to different light intensities ranged from 3.2 to 2.1 (Figure 1). The plot of light intensity during growth against chl a/chl b ratios shows clearly that the chl a/chl b ratios increase sharply in a linear manner at low light intensity in the region below $200 \mu\text{E m}^{-2} \text{s}^{-1}$, but increase gradually and linearly at higher light intensities between 200 to $840 \mu\text{E m}^{-2} \text{s}^{-1}$. While it is well known that plants grown under low intensity light and shade plants have lower chl a/chl b ratios than plants grown under high intensity light and sun plants [10, 11, 12, 17, 22], this experiment with pea thylakoids is the first evidence showing that there is a bilinear response of chl a/chl b ratios to light intensity with an unexpected transition point at about $200 \mu\text{E m}^{-2} \text{s}^{-1}$.

Distribution of chlorophyll between the chlorophyll-protein complexes

The pea thylakoids from plants adapted to different light intensities were solubilized at 4°C with an SDS/chl weight ratio of 7.5/1 and subjected to discontinuous SDS polyacrylamide gel electrophoresis at 4°C . Eight chl-containing bands were resolved (Figure 2) which were identified by their previously characterized spectral properties [1]. They are (in order of increasing mobility): CP1a¹, CP1a², CP1, LHCP¹, LHCP², CPa, LHCP³ and free chlorophyll. Three of these chl-protein bands are associated with PS I: CP1 is the β -carotene-P700-Chl a-protein and CP1a¹ and CP1a² are partially dissociated PS I complexes which include CP1, the antenna chl a/b-proteins of PSI (LHC-I) and other polypeptides. The other four chlorophyll bands are associated with PS II: CPa is the presumed reaction centre complex of PS II and LHCP¹, LHCP² and LHCP³ are three chl a/b-proteins with chl a/chl b

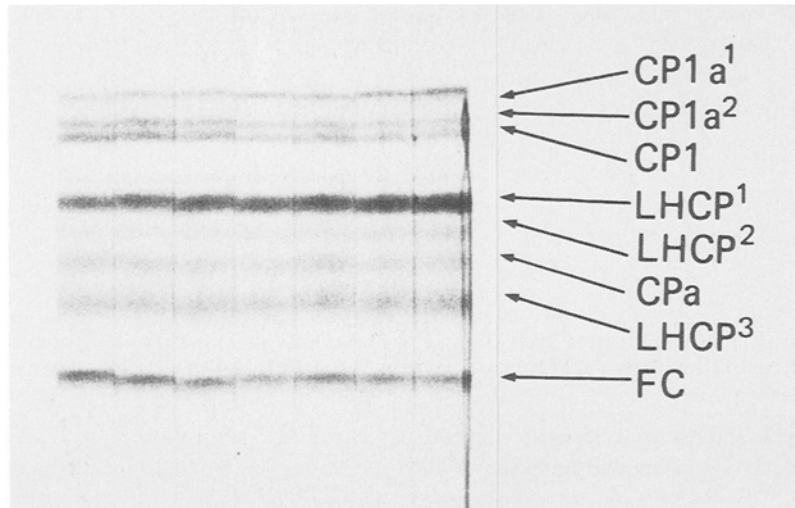


Figure 2. Unstained SDS-polyacrylamide gels after electrophoresis of chloroplast thylakoids from peas grown under different light intensities. Light intensities during growth are (from left to right) 840, 610, 440, 215, 165, 93 and $42 \mu\text{E m}^{-2} \text{s}^{-1}$. The designation of the chlorophyll-proteins resolved is referred to in the text.

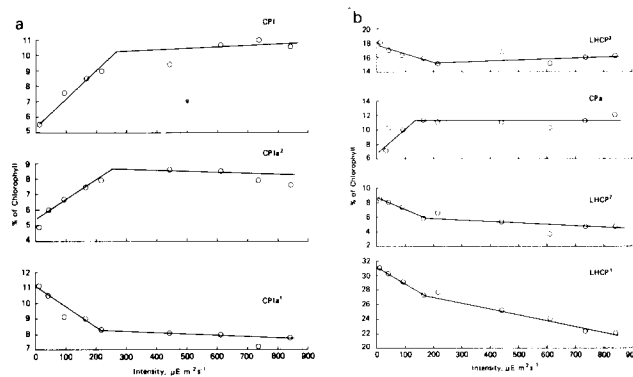


Figure 3. Relative distribution of chlorophyll in the chlorophyll-protein complexes as a function of light intensities during growth.

ratios of 1.3–1.1 belonging to the main light-harvesting complex of PS II (LHC-II) [1–3].

Inspection of the green gels (Figure 2), suggests that the amount of chlorophyll associated with CP1a¹ and LHCP¹ increases as light intensity during growth decreases. The reverse is true for the amount of chlorophyll associated with CP1. This was confirmed when the gels were scanned at 650 and 675 nm to determine the average relative amounts of chlorophyll associated with each of the chl-protein bands. The relative distribution of chlorophyll in the chl-protein complexes with respect to light intensities during growth (Figure

3) shows clearly that as light intensity during growth increases the relative percentage of chl associated with CP1a¹ decreases sharply until the light intensity is above 200 $\mu\text{E m}^{-2} \text{ s}^{-1}$. At intensities above approximately 200 $\mu\text{E m}^{-2} \text{ s}^{-1}$, the relative amount of CP1a¹ remains quite constant. This bilinear type of response towards light intensity with a transition point at about 200 $\mu\text{E m}^{-2} \text{ s}^{-1}$ is observed in the relative distribution of chlorophyll in all of the chl-protein complexes (Figure 3). As light intensity during growth increases, the relative amount of chlorophyll associated with CP1a¹, LHCP¹, LHCP² and LHCP³ decreases while that associated with CP1a², CP1 and CPa increases in a bilinear manner.

In higher plants, most of the PS II complexes and their associated chl a/b-proteins (LHC-II) are located in the appressed membranes of grana partitions, whereas PS I complex is mainly located in stroma-exposed thylakoids [4, 7]. Hence the domains of PS II and PS I chlorophyll are largely separated. However, there is still the possibility of some sharing of light energy between PS I and PS II in non-appressed membranes, and it is reported that part of the LHCP pool may be mobile under phosphorylated conditions [cf. 9]. Nevertheless, it is of interest to compare the amounts of chlorophyll associated with the chlorophyll-proteins of PS II and PS I. Since there is some free chlorophyll in the SDS polyacrylamide gels and the value is not constant, it should be noted that the comparisons between the PS I and PS II chlorophyll contents are relative only.

The relative amount of chlorophyll associated with PS I (sum of CP1a¹, CP1a² and CP1) (Table 1, Figure 4) is not markedly affected by light intensity during growth above the 200 $\mu\text{E m}^{-2} \text{ s}^{-1}$ transition point. Below this point PS I is influenced by light intensity changes. On the other hand, there is a decrease in the relative amount of chl associated with PS II (sum of CPa, LHCP¹, LHCP², and LHCP³) at higher light intensity during growth; thus PS II is more sensitive to light intensity changes. This is also reflected in PS II/PS I chlorophyll content ratio. However, it is clear that in all cases, the bilinear response is observed.

The ratio of chlorophyll content associated with light-harvesting chl-proteins of PS II [LHC-II] to that of the PS II core reaction centre complex, i.e. the LHCP¹⁺²⁺³/CPa ratio varies from 3.5 at high light to 8.6 at low light intensity (Table 1, Figure 5), showing again the bilinear response and a transition point at about 200 $\mu\text{E m}^{-2} \text{ s}^{-1}$. This indicates again that the light-harvesting chl-proteins of PS II are most sensitive to high light intensities than other chl-protein complexes. The marked increase in the LHCP¹⁺²⁺³/CPa ratio from 3.5 to 8.6 with decreasing light intensities occurs because of an increase in LHCP¹⁺²⁺³ and a concomitant decrease in CPa. These changes result in significantly greater amounts of chl b in PS II as the light intensity is decreased. Similar increases in the total amount of chlorophyll associated with the main chl a/b-proteins, LHCP¹⁺²⁺³, as well as a concomitant two-fold decrease in CPa were observed in pea thylakoids isolated from plants grown

Table 1. Comparison of the relative distribution of chlorophyll in the chl-proteins associated with PS I and PS II in thylakoids from peas adapted to light intensities

Intensities during growth ($\mu\text{E m}^{-2} \text{ s}^{-1}$)	$\frac{\text{chl } a}{\text{chl } b}$	PS I* chl (%)	PS II* chl (%)	$\frac{\text{PS II}^*}{\text{PS I}}$	$\frac{\text{LHCP}^{1+2+3}}{\text{CPa}}$
840	3.21	26.0	55.0	2.12	3.55
735	3.07	26.1	54.1	2.07	3.60
610	3.01	27.2	53.2	1.96	4.16
440	2.93	26.1	58.4	2.24	4.26
215	2.70	25.5	60.6	2.38	4.46
165	2.73	25.0	60.5	2.42	4.31
93	2.55	23.4	63.0	2.69	5.24
42	2.32	22.6	65.8	2.91	5.39
10	2.13	21.5	64.4	3.00	8.61

$$\text{PS I}^* = \text{CP1a}^1 + \text{CP1a}^2 + \text{CP1}; \text{PS II}^* = \text{CPa} + \text{LHCP}^1 + \text{LHCP}^2 + \text{LHCP}^3$$

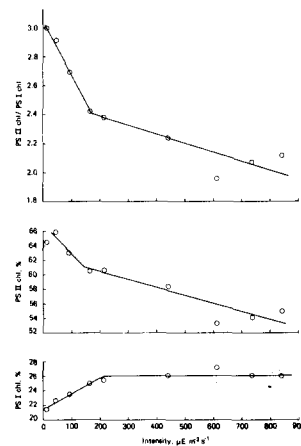


Figure 4. Relative distribution of chlorophyll content in PS I and PS II as a function of light intensity during growth.

under different light regimes which varied not only in intensity but also in quality [15].

Relationship between chl a/b ratio and chlorophyll-protein complexes

Since all chlorophyll and carotenoid molecules are non-covalently bound in stoichiometric amounts to a few specific intrinsic proteins which are organized as light-harvesting assemblies of PS I and PS II [5, 27], the changes in chl a/chl b ratios as a result of photoadaptation should also be reflected in the amounts of chlorophyll associated with the main chl-proteins. Although exact measurements of the amount of chlorophyll associated with the two photosystems is not yet feasible by these methods, approximate values may be obtained as stated by summing CP1a^1 , CP1a^2 and CP1 for PS I, and summing CPa , LHCP^1 , LHCP^2 , and LHCP^3 for PS II. When these relative

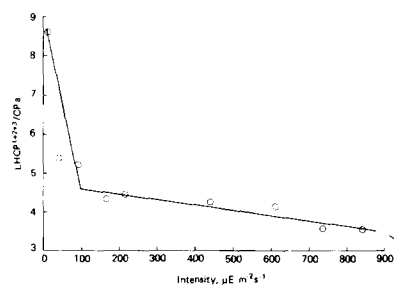


Figure 5. Effect of light intensity during growth on the $(LHCP^1 + LHCP^2 + LHCP^3)/Cpa$ ratio.

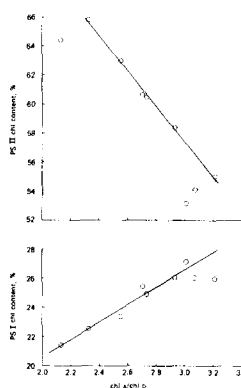


Figure 6. Relationship between chl a/chl b ratios and the relative chlorophyll content of PS II and PS I.

chlorophyll contents are plotted against chl a/chl b ratio (Figure 6) it becomes clear that the relationship between PS II chlorophyll content and chl a/chl b ratio is linear except for points scattered at the extreme ends, and, that between PS I chlorophyll content and chl a/chl b ratio is also linear (Figure 6).

Discussion

Although it is well known that the chl a/chl b ratios of higher plants and some green algae increase with higher light intensity during growth [12, 19, 22, 25], it was not clear whether this rate of photoadaptation is linear. Since plants adapted to high light intensity have 'sun' type chloroplasts and those adapted to low light intensity have 'shade' type chloroplasts [11, 12, 19], it is possible that photoadaptation of a given species might be different at high and low light intensities. By studying peas grown at various light intensities, we have now shown for the first time that the photoadaptation of the photosynthetic units of PS II and PS I as reflected by the chl a/chl b ratio is not

simply linear with respect to light intensity, but bilinear with a transition point (Figure 1). That is, the rate of photoadaptation of the chl a/chl b ratio at higher light intensities is different from that at lower light intensities. This is also reflected in the relative distribution of chl-protein complexes in the thylakoid membranes (Figures 3, 4 and 5). The light intensity at which this transition point occurs varies from 150 to 250 $\mu\text{E m}^{-2} \text{ s}^{-1}$, reflecting perhaps variations in the measurement of the various parameters.

It is well known that chl a and chl b are present in almost equal amounts in the main LHCP (LHC-II) of PS II (chl a/chl b ratio of 1.1–1.3) [27]. However, there is also some chl b present in PS I, since recent evidence indicates that PS I has specific, minor chl a/b-proteins with chl a/chl b ratios greater than 1.3, and with apoproteins distinct from those of the main chl a/b-proteins of PS II light-harvesting complexes [6, 26, 29]. Most of the chl b present in thylakoid membranes is associated with LHC-II. In spinach thylakoids, LHC-I accounts for only 8% of the total chlorophyll content of thylakoids, and 14% of the total chlorophyll b [21]. Therefore it is possible from the chl a/chl b ratio to roughly predict the abundance of chlorophyll associated with PS II or PS I. Thus, a high chl a/chl b ratio would mean less LHC-II and thus lower PS II chlorophyll content and higher PS I chlorophyll content and *vice versa*. This is indeed observed in the present study (Figure 6 and Table 1); higher chl a/chl b ratios indicate higher PS I chlorophyll content and lower PS II chlorophyll content.

As light intensity during growth decreases, relatively more chl becomes associated with PS II (Figure 4) to ensure higher efficiency of light-harvesting in PS II. Furthermore, the chlorophyll composition of PS II changes since the ratio of LHCP¹⁺²⁺³/CPa increases dramatically when light intensity is decreased (Figure 5). There is strong evidence that LHC-II is essential for thylakoid stacking [4]. The immediate consequence of increased LHC-II should be more stacked thylakoid membranes, since PS II is localized mainly in stacked membranes [4]. This is indeed the case: a higher degree of stacking is found in low light intensity-adapted thylakoids than those adapted to high light intensity [17, 20].

The chl a/chl b ratios of pea plants grown at high light intensity (3.2 at 840 $\mu\text{E m}^{-2} \text{ s}^{-1}$) are comparable to 2.8 of normally grown spinach, a sun plant [3, 4]. On the other hand, the chl a/chl b ratio of pea plants grown at low light intensity (2.1 at 10 $\mu\text{E m}^{-2} \text{ s}^{-1}$) is comparable also to 2.2 of *Alocasia*, an extreme shade plant when grown in its natural habitat [3, 4]. Thus, it seems at least with regard to chl a/chl b ratios that pea plants have adapted efficiently to the light intensities used in the present study. However, while the ratio of PS II chlorophyll content to PS I chlorophyll content of 2.1 for peas grown at high light intensity of 840 $\mu\text{E m}^{-2} \text{ s}^{-1}$ is comparable to the value of 2.0 of normally grown spinach [3, 4], the value of 3.0 for peas grown at low light intensity of 10 $\mu\text{E m}^{-2} \text{ s}^{-1}$ is different from the value of 5.0 reported for the shade plant, *Alocasia* in natural habitat [3, 4].

Although it is shown that pea plants adapt very efficiently to light intensity during growth by changing their chl a/chl b ratios, thereby markedly changing the composition of the chl-proteins associated with PS I and PS II, these changes are limited and do not appear to reach the ultimate limits observed in shade plants where the light quality is also markedly different.

A possible explanation for the unexpected change in the linear rate of photoadaptation by pea plants is that they are sun plants which tend, therefore, to behave in a 'normal' way in the light intensity ranges similar to those encountered in their 'natural' habitat, i.e. light intensities above the transition point (approximately $200 \mu\text{E m}^{-2} \text{ s}^{-1}$). However, below approximately $200 \mu\text{E m}^{-2} \text{ s}^{-1}$, pea plants appear to be less able to cope with the lower light intensities that are more characteristic for shade plants, and so they have to incorporate more drastic changes in the relative distribution of chlorophyll in the various chlorophyll-protein complexes. Hence, the bilinear nature of the response curves.

In view of this unexpected regulatory effect of light intensities on the distribution of chlorophyll-protein complexes, we have also examined the effects of light intensities on the other photosynthetic components of the thylakoids. The results of that investigation are described in the following paper [16].

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