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Adaptation of the thylakoid membranes of pea chloroplasts to light intensities. II. Regulation of electron transport capacities, electron carriers, coupling factor (CF_1) activity and rates of photosynthesis

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Abstract. The electron transport rates of photosystems II and I, amounts of electron carriers, coupling factor activity and photosynthetic rates were investigated in thylakoids isolated from pea plants grown under a wide range of light intensities (16 h light–8 h dark). The electron transport rates of PS II and PS I, as partial reactions or in whole chain, and coupling factor activity on a unit chlorophyll basis, all increased as the light intensity available for growth was altered from a very low intensity of 10 μE $m^{-2}s^{-1}$ to a high intensity of 840 μE $m^{-2}s^{-1}$. Similarly, there were increases in the amounts of atrazine binding sites, plastoquinine, cytochrome f and P700 per unit chlorophyll; significantly, the amounts of reaction centres of PS II and PS I were not equal at any light intensity. The rate of change of all parameters with respect to light intensity could be represented by two straight lines of different slopes which met at a transition point corresponding to approximately 200 μE $m^{-2}s^{-1}$ during growth. These photoadaptations were similar to those observed for both the relative distribution of chlorophyll in chlorophyll-protein complexes and the chl a/chl b ratios [Leong and Anderson, 1984, *Photosynthesis Research* 5:117–128]. Since these thylakoid components and functions were affected in the same direction by light intensity during growth and all show linear relationships with chl a/chl b ratios, it indicates that they are closely regulated and markedly well co-ordinated. Plants compensate for the limited amount of low light intensities by drastically increasing the light-harvesting antenna unit size of photosystem II and to a lesser extent that of photosystem I. Changes in the composition of the thylakoid membranes exert a regulatory effect on the overall photosynthetic rate up to approximately 450 μE $m^{-2}s^{-1}$.

Introduction

Light is one of the major environmental factors regulating plant growth (cf. [3]). To effectively utilize the amount of light available, higher plants [8, 9] and green algae [21] adapt to light intensity during growth by regulating leaf morphology, the composition, structure and function of thylakoid membranes and the overall rates of photosynthesis, so as to maintain maximal photosynthetic yields. Thus plants grown at higher light intensities generally have higher photosynthetic capacities than those grown at lower light intensities [8, 9].

Abbreviations: chl = chlorophyll, cyt = cytochrome, PQ = plastoquinone, PS = photosystem

It has been reported in a previous article that when pea plants were grown at different light intensities [13], the chl a/chl b ratios together with the relative amounts of chlorophyll-protein complexes in the thylakoid membranes showed a response to light intensity which could be represented by two intersecting straight lines. In view of this regulatory effect of light intensity on the distribution and amounts of pigments of the light-harvesting assemblies of photosystems I and II, it seemed important to also establish whether the electron transport and ATP synthase capacities are similarly affected by light intensity and in a manner consistent with the adaptation of the relative distribution of chlorophyll in the chlorophyll-protein complexes in the thylakoid membranes. An attempt was also made to establish the relationship between such adaptations and overall photosynthetic performance including the rate of CO_2 fixation in intact leaves.

The study reported here with peas grown at different light intensities indicates that the core reaction centre of photosystem II, electron transport capacities of photosystems II and I, plastoquinone and cytochrome f content as well as coupling factor (CF_1) activity photoadapt in a manner closely related to concurrent changes in chlorophyll-protein complexes and hence chl a/chl b ratios. Furthermore, since the light intensity variation during growth caused the same bilinear response in these components of the thylakoid membranes, there is a well regulated and co-ordinated synthesis of thylakoid complexes. Thus, as predicted [3], it appears that overall photosynthetic performance is closely related to the relative proportions of the intrinsic complexes of thylakoid membranes adapted to different light intensities.

Materials and methods

Pea (*Pisum sativum* L.) seedlings were grown in vermiculite in growth cabinets at 20 ± 0.5 °C under conditions described in the previous paper [13]. Chloroplasts and thylakoid membranes were isolated as reported [12].

Oxygen uptake/evolution assays on freshly isolated thylakoids (unwashed) were carried out polarographically using a Hansatech electrode at 20 °C with the following different electron acceptors in the media: (a) 50 mM sodium phosphate, pH 6.5, 12 μM 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 and 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 for the whole chain (PS II + PS I) electron transport rate, in the absence or presence of 2 mM NH_4Cl as uncoupler.

P700 was assayed from ferricyanide-oxidized minus ascorbate-reduced difference spectra [15] and cytochrome f was estimated from hydroquinone-reduced minus ferricyanide-oxidized difference spectra [6].

Plastoquinone was extracted from ethanol-treated thylakoids (400 μg chl) preparations with methanol-chloroform-heptane (1:1:1, v/v) and assayed as described [5].

Herbicide-binding analysis was performed according to the method of Tischer and Strotmann [22]. Binding reactions were initiated by vortexing 1 ml suspensions of thylakoids (50 μg chlorophyll/ml) in 400 mM sucrose, 50 mM N-tris (hydroxymethyl)methyl-2-aminoethanesulfonic acid, 10 mM NaCl, 5 mM $MgCl_2$, pH 7.5, 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 [22]. Atrazine (16 mCi/mmol) was purchased from Amersham.

The Mg^{++}-specific ATPase activity in chloroplast coupling factor CF_1 was assayed in the presence of octyl glucoside as described [19]. Pi was assayed according to the ascorbic acid-reduction method [2].

Leaf photosynthesis was excited by white light of various intensities (mercury vapour lamp). Measurements were made in air of normal CO_2 and O_2 partial pressures at a leaf temperature of 20 °C.

Results

In the previous paper [13], it was shown that light intensity had a regulatory effect on the chl a/chl b ratios and relative distribution of chlorophyll between the chl-proteins of PS II and PS I of thylakoids isolated from peas adapted to different light intensities. Changes in both the chl a/chl b ratios or the chlorophyll-protein complexes with respect to light intensity were represented by two straight lines of different slopes, which met at a transition point corresponding to approximately 200 μE $m^{-2}s^{-1}$.

Effect of light intensity during growth on electron transport rates of PS II and PS I

The rate of electron transport of PS II, measured as O_2 evolution with phenyl-*p*-benzoquinone as electron acceptor [1], increased as the light intensity available during growth was increased. Similarly, the rate of electron transport of PS I, measured as O_2 uptake in the presence of 2,6-dichlorophenolindophenol and methylviologen, also increased as the light intensity increased (Figure 1a). In turn, the rate of whole chain electron transport by PS II and PS I measured with water as electron donor and methylviologen as electron acceptor also increased with increasing light intensity, both in the absence and presence of uncoupler (Figure 1b). These results are in agreement with other studies where both PS II and PS I electron transport rates are lowered by decreasing light intensities during growth [10, 17, 21]. It is clear that changes in light intensity during growth had a greater effect on the uncoupled whole chain electron transport rates than on those of coupled

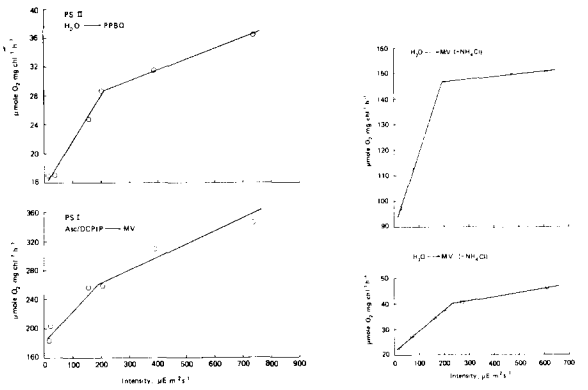

Figure 1. Effect of light intensity during growth on the (a) partial rates of electron transport of PS II and PS I and (b) whole chain electron transport rates, in freshly isolated thylakoids of photoadapted peas.

electron transport (Figure 1b), due perhaps to the fact that uncoupled rates are generally known to be higher than the coupled rates.

In all the electron transport rates reported in this study (Figures 1a and b), there is a bilinear response to light intensity during growth with a greater change of electron transport rates at the lower light intensities compared to the rates at the higher light intensities above the transition point.

Effect of light intensity during growth on the amounts of PS II and PS I reaction centres and electron carriers

In view of the close co-ordination in the electron transport rates of photosystems II and I, it is important to investigate the concentration of P680 or Q, the primary electron acceptor of PS II, and the relationship of this with electron carriers such as plastoquinone and cytochrome f, as well as P700, the reaction centre of PS I, with respect to light intensity during growth.

Since technically it was not possible in this study to measure P680 or Q spectrophotometrically [16], we have measured instead the concentrations of ^{14}C-atrazine binding sites. It has been proposed that the mode of action of atrazine is via high-affinity binding to the PS II complex [22]. Indeed, a 32 kilodalton polypeptide in the PS II core complex has been identified as the atrazine binding protein [18, 20]. Thus, the concentrations of atrazine binding sites would be a measure of the reaction centre of PS II, and an indication of the amounts of P680 and Q.

There is almost a 4-fold increase in the concentrations of atrazine binding sites when light intensity during growth is increased from 25 to 750 μE $m^{-2}s^{-1}$, again with a transition point at approximately 200 μE $m^{-2}s^{-1}$ (Figure 2a). This is the largest difference observed in this study, with respect to light intensity during growth, indicating that the PS II reaction centre is greatly affected by light intensity during growth.

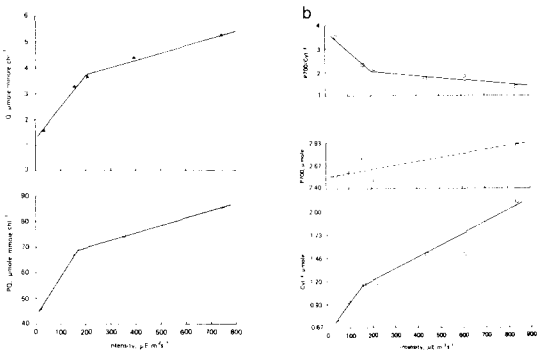

Figure 2. Effect of light intensity during growth on the amounts in μmoles per mmole chl of (a) Q, measured as atrazine binding sites, and plastoquinone; and (b) cytochrome f, P700 and P700/cytochrome f ratio, in the various photoadapted pea thylakoids.

Plastoquinone is the bulk electron carrier between PS II complex and the cytochrome b/f complex. The amount of cytochrome f is an indicator of the amount of cytochrome b/f complex, which contains 1 molecule of cytochrome f, 2 molecules of cytochrome b-563 and 1 molecule of the Rieske Fe-S centre [11]. Both the amounts of plastoquinone and cytochrome f on a chlorophyll basis increased as the light intensity during growth increased, again in a bilinear manner (Figure 2a and b).

The amount of P700 on a chlorophyll basis also increased generally as light intensity during growth increased, but this increase was not as marked as that of cytochrome f. The P700/cytochrome f ratios did not vary much in the high light intensity range (above 200 $\mu E\ m^{-2}s^{-1}$), but they increased greatly at lower light intensities (Figure 2). At 42 $\mu E\ m^{-2}s^{-1}$ (Table 1), the P700/cytochrome f ratio of 3.51 is even greater than that observed for a shade plant (i.e. 2.38 for *Alocasia* [10]). The P700/cyt f ratios reported here show a greater difference between thylakoids isolated from peas grown in high and low light intensity than was the case for thylakoids isolated from peas grown in different light climates [12].

The results on PS II and PS I reaction centres and electron carriers indicate

Table 1. Amounts of cytochrome f and P700 in thylakoids of light-adapted peas

Light intensity during growth, $\mu E\ m^{-2}s^{-1}$	cyt f, μmole mmole^{-1} chl	P700 μmole mmole^{-1} chl	$\frac{chl}{cyt\ f}$	$\frac{chl}{P700}$	$\frac{P700}{cyt\ f}$
840	2.12	2.91	472	344	1.38
610	1.52	2.87	659	350	1.88
440	1.52	2.67	659	376	1.75
215	1.16	2.49	867	401	2.15
165	1.16	2.75	867	370	2.34
93	0.97	2.60	1030	386	2.67
42	0.73	2.56	1374	392	3.51

not only that their changes with respect to light intensity during growth are in concert, but also that the photosynthetic unit sizes of PS II and I may be changing too.

Effect of light intensity during growth on the apparent light-harvesting antenna unit sizes of PS II and PS I

The apparent light-harvesting antenna unit sizes of PS II and PS I of light-adapted pea thylakoids were calculated by taking the ratios of the relative chlorophyll contents of PS II and PS I determined from mild polyacrylamide gel electrophoresis [13] to the concentrations of atrazine binding sites and P700, respectively (Table 2). As light intensities during growth increase from 75 to 750 $\mu E\, m^{-2}\, s^{-1}$, there is almost a 3-fold decrease in the apparent light-harvesting antenna unit sizes of PS II (Table 2), with a transition point again at approximately 200 $\mu E\ m^{-2} s^{-1}$. On the contrary, there is only a slight decrease in the apparent light-harvesting antenna unit sizes of PS I as light intensities increase.

Furthermore, the ratio of atrazine binding sites to P700, an indication of the reaction centres of PS II and PS I, is not constant, but increases as light intensity during growth increases (Table 2), again with a transition point at approximately 200 $\mu E\ m^{-2} s^{-1}$. The Q/P700 ratios are shown to be higher in *Phaseolus* and *Atriplex* chloroplasts adapted to high sunlight intensities than those adapted to low sunlight intensities [17].

These results (Table 2) show that the amounts of PS II and PS I reaction centres are not necessarily equal, but vary dramatically with light intensity, confirming previous results of Melis et al. [16, 17]. These variations are important, in view of the discrepancy in the amounts of Q per unit chlorophyll in the literature for spinach chloroplasts where several studies report equal amounts of P680 and P700.

Table 2. Effect of light intensities during growth on the apparent light-harvesting antenna unit sizes of photosystems II and I of pea thylakoids

Light intensity $\mu E\ m^{-2} s^{-1}$	Apparent light-harvesting antenna unit sizes		*Atrazine binding sites*
	*PS II Chl**	*PS I Chl**	P700
	atrazine binding site	P700	Arbitrary units
	Abitrary units		
75	291	126	1.20
110	240	141	1.54
180	173	130	1.82
280	153	130	1.96
370	140	119	1.92
550	120	123	2.22
750	105	116	2.33

*The relative PS II and PS I chlorophyll content were determined by SDS polyacrylamide gel electrophoresis [13].

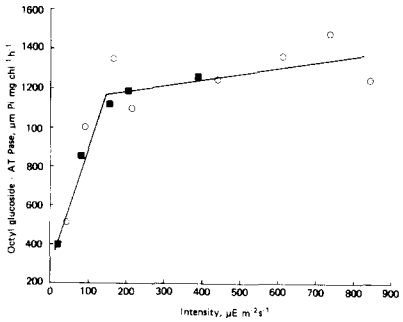

Figure 3. Effect of light intensity during growth on the octyl glucoside activiated Mg^{++}-ATPase in pea thylakoid membranes. Squares represent data from one lot of plants and circles represent data from another lot grown a few weeks apart.

Photoadaptation of coupling factor CF_1. The octyl glucoside-stimulated ATPase activity of CF_1 in thylakoid membranes again shows a bilinear response towards changes in light intensity during growth (Figure 3). There is a sharp increase up to 200 μE m^{-2} s^{-1} and a more gradual response at higher light intensities. Thus, the response of CF_1 activity to light intensity parallels that of chl a/chl b ratio, resulting in a linear relationship between CF_1 activity and chl a/chl b ratio (Figure 4). We found that the CF_1 activity of the thylakoid membranes on a mg chl basis (Figure 3) remained unaltered from that of the original chloroplast preparation, even after extensive washings of isolated thylakoids with glass-distilled water and 50 mM Tricine, pH 8.0 during the preparation of thylakoids. It was briefly reported [23] and later shown by Berzborn et al. [7] that the concentration of CF_1, used as a marker for ATP synthase in spinach, depended on light intensity during growth and was found to be about 3 times higher on a chlorophyll basis in spinach grown under high light intensity compared to low light intensity. This

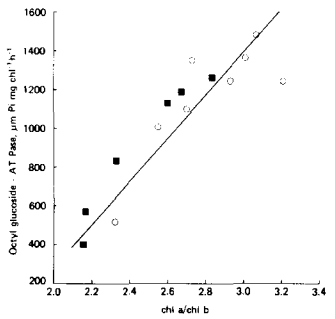

Figure 4. Relationship between octyl glucoside activiated Mg^{++}-ATPase in the thylakoid membranes of photoadapted peas and the chl a/chl b ratio. Squares represent data from one lot of plants and circles represent data from another lot grown a few weeks apart.

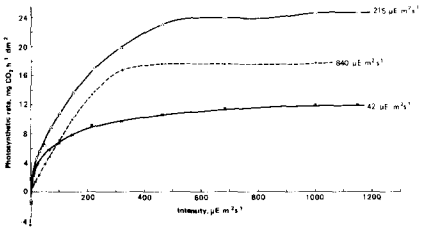

Figure 5. Rates of net photosynthesis as a function of incident light intensity for peas grown at 42, 215 and 840 μE $m^{-2} s^{-1}$.

is in agreement with the difference in octyl glucoside-stimulated ATPase activity between peas grown under high and low light intensities reported here (Figure 3).

Effect of light intensity during growth on the photosynthetic rates of 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 (Figure 5). The leaves tested in this investigation all attained maximal photosynthetic rates at about 1000 μE $m^{-2} s^{-1}$. When this maximal photosynthetic rate is plotted against the light intensity during growth, the curve shown in Figure 6 is obtained. It is expected that the photosynthetic rates would stay constant at higher light intensity during growth. However, our results suggest that the optimal light intensity for pea growth is around 450 μE $m^{-2} s^{-1}$ (on a 16 h day basis as used in this study).

The photosynthetic rates reported here are expressed on a unit leaf area basis. No significant differences were found in the total amounts of chlorophyll per unit leaf area, for seedlings grown under various light intensities (results not shown). Thus, if the photosynthetic rates are expressed on the basis of total amount of chlorophyll, the same shaped curve as shown in Figure 6 is obtained.

Part of Figure 6 can be viewed in terms of the 'bilinear' response as seen in

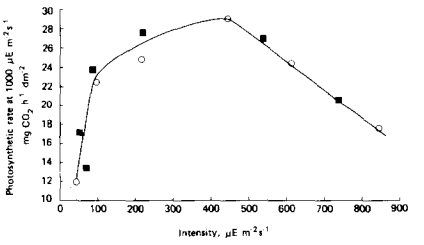

Figure 6. Effect of light intensity on maximal photosynthetic rates of peas. Squares represent data from one lot of plants and circles represent data from another lot grown a few weeks apart. Measurements were taken at random times during the light cycle.

the changes in the composition and function of thylakoid membranes (Figures 1–3). Indeed, it is possible to draw a straight line from 25 to 125 μE $m^{-2} s^{-1}$ and another one from 125 to 550 μE $m^{-2} s^{-1}$, with another one from 550 to 840 μE $m^{-2} s^{-1}$.

Discussion

Light intensity during growth clearly influences not only the relative proportions of the chlorophyll-protein complexes seen in the changes in chl a/chl b ratios [13], but also the electron transport capacities of both PS II and PS I, the concentrations of electron carriers and reaction centres of photosystems II and I, and the ATP synthase activity. Thus, as light intensity during growth increases, there is an increase in the relative amounts of chlorophyll associated with PS I [13] and in the concentrations of P680 and P700 as well as electron carriers per unit chlorophyll resulting in increased electron transport rates and coupling factor activity. However, this increase is counter-balanced by a decrease in the relative amounts of chlorophyll in PS II particularly that of the light-harvesting complex, leading to a decrease in the apparent light-harvesting antenna unit sizes of PS II and PS I with increasing light intensity available for growth.

The striking and unexpected 'bilinear response' of both chlorophyll-proteins, electron carriers and ATP synthase activity per unit chlorophyll [Figures 1, 3 and 4 of Ref. 13; Figures 2 and 3 of this study] with respect to light intensity, demonstrate that light intensity is regulating the relative amounts of all of the multisubunit thylakoid complexes. Significantly, the same transition point from the higher linear rates of change below 200 μE $m^{-2} s^{-1}$, to the lower linear rate of change above 200 μE $m^{-2} s^{-1}$, is seen in all cases.

It should be pointed out that since the amounts of the various thylakoid components were related to chlorophyll, the 'bilinear response' may just reflect such responses in the amounts of chlorophyll observed in the preceding paper [13]. However, when the effect of the amount of chlorophyll was cancelled out by taking the ratios of Q/P700, PS II chl/atrazine binding sites (Table 2), PQ/P700, electron transport rates/PQ or atrazine binding sites/cyt f (results not shown) these ratios all show such bilinear response. Further, the amounts of atrazine binding sites, P700, Cyt f, plastoquinone, electron transport rates (results not shown) as well as coupling factor CF_1 activity (Figure 4), all show linear relationships with respect to chl a/chl b ratios. Thus, these results constitute the first evidence that these components must be closely regulated and markedly well co-ordinated.

The concomitant increase and decrease in the relative PS I and PS II chl contents, respectively, as light intensity during growth increases [13] might appear at first sight to contradict the increase in electron transport capacities of both PS I and PS II observed here. It should be emphasized that although the chl content of the light-harvesting complexes of PS II (LHC-II) decreases

as light intensity increases, the chl content of CPa, the core reaction centre of PS II, increases, being 2-fold greater at high light intensity [12, 13]. Furthermore, there is almost a four-fold increase in the atrazine binding sites, indicating that P680 and Q also increase as light intensities increase. Thus, the electron transport capacity of PS II is indeed correlated with the total amount of PS II reaction centres.

This study also demonstrates that there is no fixed stoichiometry between the electron transport complexes and ATP synthase. Interestingly, when the differences between the extreme light intensities are compared for the amounts of various thylakoid components, PS II reaction centre (measured as atrazine binding site) is the most affected by light intensity during growth, followed by cytochrome f, plastoquinone and P700. This is also reflected in the almost 3 fold increase in the apparent light-harvesting antenna unit sizes of PS II as compared to the 20% increase in those of PS I (Table 2). Furthermore, the ratios of the reaction centres of PS II/PS I are not constant, but increase as light intensity increases, indicating again that there is no fixed 1:1 stoichiometry between P680 and P700, as shown already by Melis et al. [16, 17].

It becomes clear that as light intensity during growth decreases, plants compensate for the limited amount of available light by increasing the apparent light-harvesting antenna unit sizes by as much as 3-fold in photosystem II, and to a much lesser extent in photosystem I (Table 2). This differential response in photosystems I and II is reflected also in the ratios of reaction centres of photosystems I and II, which do not stay constant, but increase as light intensity during growth increases.

The results reported here constitute the first evidence that there is a linear relationship between chl a/chl b ratio and CF_1 activity (Figure 4), cytochrome f, plastoquinone, atrazine binding sites, and electron transport capacities (results not shown). Investigations on two cultivars of sunflower grown at different temperatures also show that the levels of CF_1 activity follow closely the variations in the chl a/chl b ratios [14]. In this case since the chl a/chl b ratios ranged only from 2.7 to 3.2 in one cultivar and 3.0 to 3.4 in another, the variations were not marked; nevertheless, it is striking that the variations in CF_1 activity matched those of the chl a/chl b ratios [14].

The maximal photosynthetic rate at saturating light intensity in intact pea leaves as a function of light intensity during growth (Figure 6) is rather unusual compared to that of *Atriplex* [8], where the photosynthetic rate increased to a plateau as light intensity during growth was increased (Leong, unpublished result). The decrease in photosynthetic rate in plants grown above 450 $\mu E\ m^{-2}\ s^{-1}$ may be attributed to two factors. Firstly, the amount of carbohydrate accumulated during the long days (16 h light –8 h dark regime used here) would probably be supra-optimal at higher light intensities during growth and might decrease the overall photosynthetic rates by a feedback inhibition mechanism. Indeed, it was observed during the isolation of

chloroplasts that large deposits of starch were present in plants grown at higher light intensities, but no starch was observed in chloroplasts isolated from plants grown at low light intensities. Secondly, at higher light intensities, the net photosynthetic rates could be limited by nitrate nutrition [24]. Since no decrease was observed in the rate of PS II electron transport (Figure 1) the observed decrease at the higher light intensities could not be due to photoinhibition [8]. However, pea seedlings adapted to light intensities higher than 370 μE $m^{-2} s^{-1}$ have a slower growth rate (as measured by the height of the seedlings) than those adapted to 370 μE $m^{-2} s^{-1}$. Indeed, the average heights of 10 week-old seedlings grown at 370, 550 and 750 μE $m^{-2} s^{-1}$ are 175, 157 and 105 mm, respectively, indicating that the photosynthetic rates of intact leaves could be lower when seedlings are grown at higher light intensities. Thus, it can be concluded that changes in the composition of the thylakoid membranes do exert regulatory effects on the overall photosynthetic rate up to about 450 μE $m^{-2} s^{-1}$, but beyond that, other factors must have been rate limiting.

The reason for the transition point in the bilinear response curves with respect to light intensity during growth (Figures 1, 2 and 3) is still unknown. However, peas being sun plants may not need to incorporate drastic changes in the composition and function of their thylakoid membranes in the light intensity ranges similar to those encountered in their 'natural' habitat, i.e. light intensities above the transition point (approximately 200 μE $m^{-2} s^{-1}$). However, at light intensities below this level, peas may not adapt so readily without drastic changes, thus leading to a different response and the dramatic changes at lower light intensities.

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