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Chloroplast Distribution in *Arabidopsis thaliana* (L.) Depends on Light Conditions during Growth[1]

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Chloroplasts of *Arabidopsis thaliana* move in response to blue light. Sensitivity to light and the range of fluence rates to which the chloroplasts respond were found to be comparable to those of other higher plants studied. We investigated typical chloroplast distributions in Arabidopsis grown under three different light conditions: standard-light conditions, similar to natural light intensities; weak-light intensities, close to the compensation point of photosynthesis; and strong-light intensities, close to the saturation of the light-response curve of photosynthesis. We observed a striking difference in chloroplast arrangement in darkness between plants grown under weak- and strong-light conditions. There was a slight difference after weak-light pretreatment, and the arrangements of chloroplasts after strong-light pretreatment in both plant groups were very similar. These results support the ecological significance of chloroplast movements.

Chloroplast movement is a phenomenon commonly observed throughout the plant kingdom (see reviews: Zurzycki, 1980; Haupt and Scheurelein, 1990; Wada et al., 1993). In most plants studied so far, the movement is controlled by a blue UV-absorbing system (Zurzycki, 1980; Galland and Senger, 1980). Only in a few cases are red light and phytochrome also involved: *Mougeotia* (Haupt, 1959), *Adiantum* (Yatsuhashi et al., 1985), and *Mesotaenium* (Haupt and Thiele, 1961). Chloroplast rearrangements in cells are induced and maintained by irradiation and depend on light direction, wavelength, and irradiance.

There are two extreme chloroplast positions: (a) face position (low fluence rate arrangement), with chloroplasts at the cell walls perpendicular to light; and (b) profile position (high fluence rate arrangement), with chloroplasts at the walls parallel to light. In D, the chloroplasts are distributed either randomly around all of the cell walls, or their position depends on local factors inside the cell (Haupt and Scheuerlein, 1990). These three arrangements are typical of species with multichloroplast cells like *Funaria, Lemna,* and *Tradescantia.* There are some differences in chloroplast movement in plants with cells containing one large chloroplast (e.g. *Hormidium, Mougeotia,* and *Mesotaenium*) or for coenocytes (e.g. *Vaucheria*) (see review: Schönbohm, 1980). Although movement patterns differ in their detail in various species, the common result of these patterns is greater exposure of chloroplasts to wL and reduced exposure under sL conditions.

The conventional interpretation of the ecological role of chloroplast movements is that they result in optimizing light utilization in photosynthesis. However, little is actually known about the significance of chloroplast movements, and only a few studies have been devoted to this problem. Zurzycki (1955) was the first to ask if there was a correlation between the level of photosynthesis and chloroplast response. He carried out experiments on the green alga *Mougeotia sp.*, the moss *Funaria hygrometrica,* and the duckweed *Lemna trisulca,* all of which have the ability to displace chloroplasts. For comparison, he also examined the green alga *Spirogyra nitida,* which lacks chloroplast movement.

Comparison of time courses for photosynthesis and chloroplast displacements under changing light intensities showed that there was a correlation between these two processes under low-fluence-rate conditions. These observations were true for all species exhibiting chloroplast movements. However, there was no such relationship in *Spirogyra,* whose assimilation rate reached a constant level immediately after new light conditions had been set. In *Lemna* at low fluence rates, there was a gradual increase in the rate of photosynthesis, which was correlated with the chloroplast displacement from the dark to the face arrangement. Over the range of high fluence rates (for which light was not a limiting factor for photosynthesis), the level of photosynthesis was high. Under these conditions, the quick movement of chloroplasts to the full profile position resulted in the marked reduction of their exposed surface but did not influence photosynthesis in any way.

According to Zurzycki's hypothesis, the low-intensity arrangement ensures maximum light absorption by the chloroplasts in the range of fluence rates below the saturation point for photosynthesis. The high-intensity arrangement is believed to protect chloroplasts from photodamage (Zurzycki, 1957). These findings were supported by the results of similar experiments on multilayer leaves of the terrestrial plants *Ajuga reptans* and *Syringa vulgaris* (Lechowski, 1974). In the latter, chloroplasts did not move,

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Abbreviations: $\Delta T(-)$, amplitude of the dark-to-profile response; $\Delta T(+)$, amplitude of the dark-to-face response; ΔT_{imp}, amplitude of the whole response; D, darkness; sL, strong light; stL, standard light; wL, weak light.

and a new level of photosynthesis was reached immediately after changing light intensity.

The rate of photosynthesis of the brown alga *Dictyota dichotoma* (Nultch et al., 1981) measured in nonsaturating light depended on the light pretreatment. Photosynthesis rates of the same thallus for weak blue light (1.2 W m^{-2}) were more than three times higher when chloroplasts were in the face position than when they were in the profile arrangement. These results seemed consistent with those of Zurzycki and Lechowski. However, the kinetics of movements on a switch to high or low fluence rates and the changes in the rate of photosynthetic oxygen production did not match: in both cases the final photosynthesis rate for a given light intensity was reached earlier than the final chloroplast position. Strong blue light caused inhibition of photosynthesis, but the same effect was obtained for strong red light, which did not induce chloroplast rearrangement. In the brown alga *Alaria esculenta*, similar depression of photosynthesis in high intensity light was recorded, although this species did not exhibit chloroplast movements. Thus, the movements cannot regulate the level of photosynthesis in the brown algae that were studied. These findings question the assertion that chloroplast movements can be viewed as a general adaptive factor for photosynthetic conditions in a plant cell, even though other experiments speak in favor of their ecological significance.

In this work, we examined the effect of different growth conditions on chloroplast distribution in *Arabidopsis thaliana*. We characterized chloroplast movements in plants grown under light intensities similar to natural light conditions (stL), under wL intensities close to the compensation point for photosynthesis (wL), and under sL intensities that do not cause photodamage in cells (sL). We observed a dependence of both chloroplast movements and their final positions on light conditions during growth in these plants.

MATERIALS AND METHODS

Plant Material

All experiments were performed on *Arabidopsis thaliana* L. (Columbia race). The plants were germinated from commercial seed sown on a 1:1 mixture of sphagnum and sand in 7 × 7-cm pots. The surface was overlain with a layer of pure sand (about 2 mm thick). The support medium was thoroughly presoaked with distilled water. The pots with sprinkled seeds were placed in a growth chamber at 22°C. Germinating and growing plants were supplied with a nutrient solution (Somerville and Ogren, 1982) and distilled water every other day. Philips lamps (Eindhoven, The Netherlands) TL MF 140W/33RS were used as a white light source.

To get as complete a pattern of chloroplast movements as possible, three illumination cycles were applied: (a) stL plants were grown in a standard illumination cycle of 1 h of wL (15–20 μmol m^{-2} s^{-1})/12 h of stL (130–200 μmol m^{-2} s^{-1})/1 h of wL/10 h of D; (b) sL plants were grown in a cycle of 12 h of sL (300 μmol m^{-2} s^{-1})/12 h of D. The intensity of sL was chosen to ensure high levels of photosynthesis but to cause no photodamage in plants. Photosynthesis in *A. thaliana* is 86% of the maximum obtainable level at this irradiance; under these conditions, functional and structural parameters of leaf photosynthesis remain unaltered even under prolonged exposure (Russel et al., 1995); and (c) wL plants were grown in a cycle of 12 h of wL (15–20 μmol m^{-2} s^{-1})/12 h of D. The intensity of wL was close to the compensation point of photosynthesis. Irradiance was varied by changing the distance to the lamps and by using neutral density filters. Photon fluence rates were measured with a quantum photometer (Sonopan, Cracow, Poland) equipped with a sensor that detects radiation within PAR, i.e. from 400 to 700 nm.

In cases b and c, germinating seeds were first kept at the stL conditions for 2 weeks and then transferred to one of the two extreme light cycles. After 4 weeks of extreme light treatment, the plants were tested to find out if interactions between chloroplast movements and light conditions of growth could be observed.

Photometric Method

A recording double-beam photometer (Walczak and Gabryś, 1980) was used for measuring the amplitude and kinetics of chloroplast displacements occurring in response to light. Actinic light was provided by halogen lamps (100W, 12V). Blue light was obtained by a combination of filters: BG23 (2 mm), BG (2 mm), GG13 (2 mm), and a far-red absorbing filter, C805 (3 mm). Actinic red light was obtained by combining a long-pass RG1 filter (2 mm), a short-pass dichroic filter (PZO, Warsaw, Poland), and a C805 filter (3 mm). This filter combination gave broad-band red light with a maximum at 640 nm and a half-band width of 75 nm. Neutral glass filters were used to reduce actinic light intensity. Unless otherwise stated, all filters were produced by Schott (Cologne, Germany). The actinic light intensities were measured in the energetic units (W m^{-2}) with a calibrated silicon photodiode. Equivalent quantum flux densities were counted if necessary.

Upon illumination with actinic light, chloroplasts undergo rearrangements in the cells that result in changes in the light transmitted through the leaf tissue. Transmission changes were measured with monochromatic 660-nm radiation of 0.05 W m^{-2} modulated with a frequency of 800Hz (Gabryś and Walczak, 1980).

Before the measurements, whole plants were adapted in darkness for about 12 h. Samples were prepared in a completely light-proof room in dim green or weak red light. A leaf detached from a dark-adapted plant was placed on a special plexiglass ring mounted in the photometer chamber. The blade of the leaf was covered with a gas-permeable membrane, and the petiole was wrapped in a piece of wet cotton, which supplied the whole leaf with water during the measurements. The actinic and measuring light were applied as concentric beams perpendicular to the dorsal side of the leaf. The diameter of the irradiated area was 5 mm, and a diaphragm placed on the ventral side of the leaf limited the diameter of the signal collection to 4 mm.

Microscopy

Detached leaves of wL and sL plants were divided into three groups, and each group was preadapted to different light conditions—strong-white light (300 μmol m^{-2} s^{-1}), weak-white light (20 μmol m^{-2} s^{-1}), and D—to induce three typical chloroplast arrangements, namely the high-intensity, low-intensity, and dark arrangements, respectively. After the light pretreatment, the leaves were cut into pieces and vacuum-infiltrated with 25% glutaraldehyde and 2% formaldehyde, and the samples were fixed for 2 h. The next steps were dehydration in an alcohol series and embedding in Technovit 710 (Heraeus, Hanau, Germany). The microscopic preparations were obtained according to the standard Technovit procedure. Leaf cross-sections were cut with a microtome and stained with methylene blue. Leaf cells (100) from each sample were chosen (no more than 10 cells per cross-section), and the numbers of chloroplasts in the profile and face position were counted under an optical microscope. Statistical significance between groups of results was tested using Student's *t* test, assuming that differences between SD values are statistically nonsignificant (F-Snedecor test).

RESULTS

Continuous Light

Preliminary experiments were carried out with *A. thaliana* grown under stL conditions to find out if red light could stimulate chloroplast movements in this species. For this purpose, detached leaves were illuminated with continuous blue light of 0.1 and 30 W m^{-2} or with continuous red light of equivalent quantum flux density (wL, 0.38 μmol m^{-2} s^{-1} = 0.07 W m^{-2}; sL, 112.8 μmol m^{-2} s^{-1} = 20.3 W m^{-2}). The results showed that red light was completely ineffective in the induction of chloroplast movements (Fig. 1).

Fluence Rate Response Curve

The fluence rate response curve for continuous blue light was recorded using the photometer (Fig. 2). Leaves of stL plants were irradiated with a stepwise increase in blue light, starting from 0.02 to 40 W m^{-2}. Consecutive increases in fluence rate led to changes in chloroplast arrangement lasting approximately 1 h and subsequently to steady-state transmission levels for each step. Chloroplast movement started upon irradiation of 0.02 W m^{-2}. The saturation of the low-fluence-rate response was reached at about 0.1 W m^{-2}. The turning point of the curve was reached slightly above 1 W m^{-2}. The high-fluence-rate response was near saturation at 40 W m^{-2} of blue light. The minimum value of transmission corresponded to chloroplasts in the complete face arrangement, whereas the maximum value corresponded to the complete profile position. The fluence rate response curve for *A. thaliana* was similar to that obtained for *L. trisulca* and *Tradescantia albiflora*, as described by Gabryś and Walczak (1980).

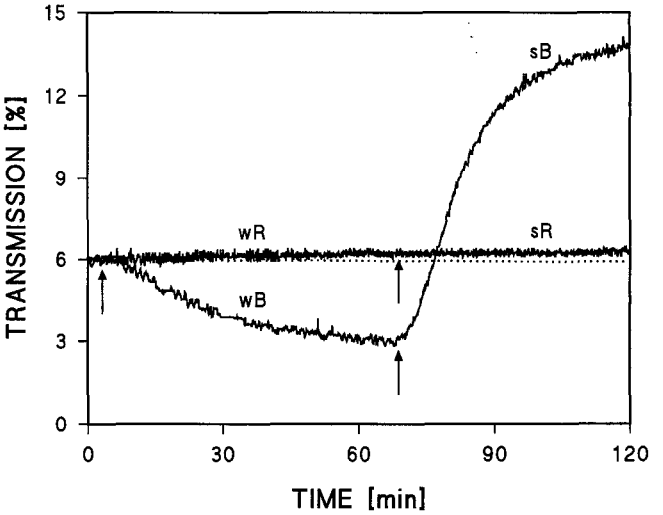

Figure 1. Response of chloroplasts in a leaf of stL *A. thaliana* to continuous blue and red light. The plant was dark-adapted for 12 h. wB, Weak blue light (0.38 μmol m^{-2} s^{-1} = 0.1 W m^{-2}); sB, strong blue light (112.8 μmol m^{-2} s^{-1} = 30 W m^{-2}); wR, weak red light (0.38 μmol m^{-2} s^{-1} = 0.07 W m^{-2}); sR, strong red light (112.8 μmol m^{-2} s^{-1} = 20 W m^{-2}).

Light Pulses

Stimulation of stL plants of *A. thaliana* with a 20-s light pulse induced first a partial face-to-profile response of chloroplasts with a concomitant increase in transmission (Fig. 3a). After attaining a maximum at about 5 to 6 min, the transmission decreased below the initial level. This phase corresponded to the chloroplast rearrangement toward the face position. After approximately 45 min, chloroplasts started a slow return to the dark position.

Parameters of the chloroplast response to light pulses, such as ΔT_{imp} and $\Delta T(-)/\Delta T(+)$ (Fig. 3a), were used for comparison of these responses in plants grown under different light conditions (Table I).

Plants from Nonstandard Light Conditions

Plants grown under two extreme light regimes were investigated. They differed both in developmental features and chloroplast rearrangement.

sL plants grown under the illumination cycle of 12 h sL and 12 h D were well developed, and the surface area of leaves was large. The amount of light received by plants was never limiting for their development. As a result, the level of photosynthetic productivity was high enough to provide the plants with ample amounts of structural material.

wL plants grown under the illumination cycle of 12 h wL and 12 h D were small, and their leaves were thin. They started blooming very late, about 50 d after sowing. The light intensity during growth was close to the compensation point of photosynthesis, and it was a strong limiting factor for the plant's growth. The overall photosynthetic production was used mainly to support the basic functions of plants, and little was left to build tissues. The results of photometric measurements (Table I; Fig. 3, a and b)

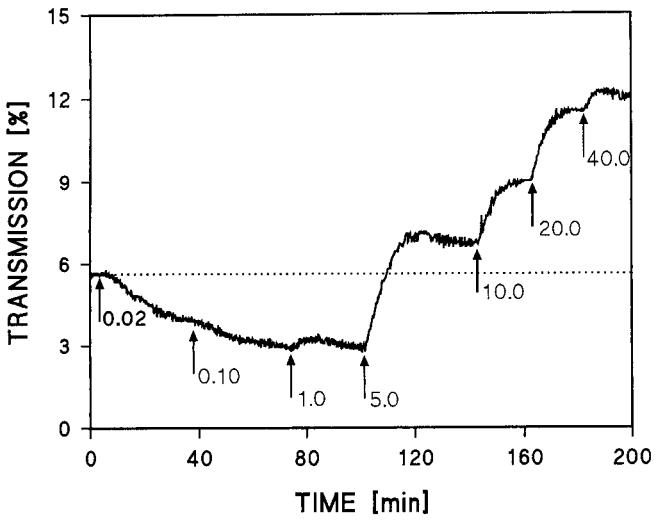

Figure 2. Fluence rate response curve. Response of chloroplasts in a leaf of stL *A. thaliana* (dark-adapted for 12 h) to low and high intensities of continuous blue light (given in W m^{-2}) measured as percentage transmission at 660 nm as a function of time.

showed differences in chloroplast responses to blue light pulses between plants from the stL, wL, and sL cycles.

The average dark transmission varied among the three groups of plants (Table I). The differences found could be easily explained by the morphological structure of the leaf, which reflected the conditions in which the plant was grown.

Differences in the ratio of the amplitude of the high-intensity phase to that of the low-intensity phase [$\Delta T(-)/\Delta T(+)$] were remarkable; the ratio for wL plants was about 1.0, whereas for those grown in both sL and stL conditions the ratios were much lower and had similar values of approximately 0.4 (Table I). In four cases out of 14 measurements, responses to light pulses in wL plants could not be included in the overall result because the response had only the first phase, i.e. an increase of transmission, and the second phase was not observed. Even the return to the initial dark transmission level was very small (Fig. 3b).

Direct microscopic observations of leaf cross-sections (Table II; Fig. 4) confirmed the Figure 4 photometric estimations. After preparation for microscopy, chloroplast position in the cell was evaluated in leaf cross-sections from each group. The results showed a striking difference in the dark arrangement and only slight differences in the wL arrangement. In darkness, about 63% of chloroplasts in mesophyll cells of wL plants were in the face position, whereas in sL plants, only 29% of chloroplasts were in this arrangement. There was a slight difference in the chloroplast arrangement after wL pretreatment. Approximately 10 and 17% of chloroplasts were still in profile in wL and sL plants, respectively. The results obtained for sL pretreatment for both plant groups were effectively identical.

Figure 4 shows typical examples of chloroplast arrangements in cells of wL and sL plants after the three types of light pretreatment. After the dark pretreatment, chloroplasts in wL plants were close to the face position (Fig. 4b),

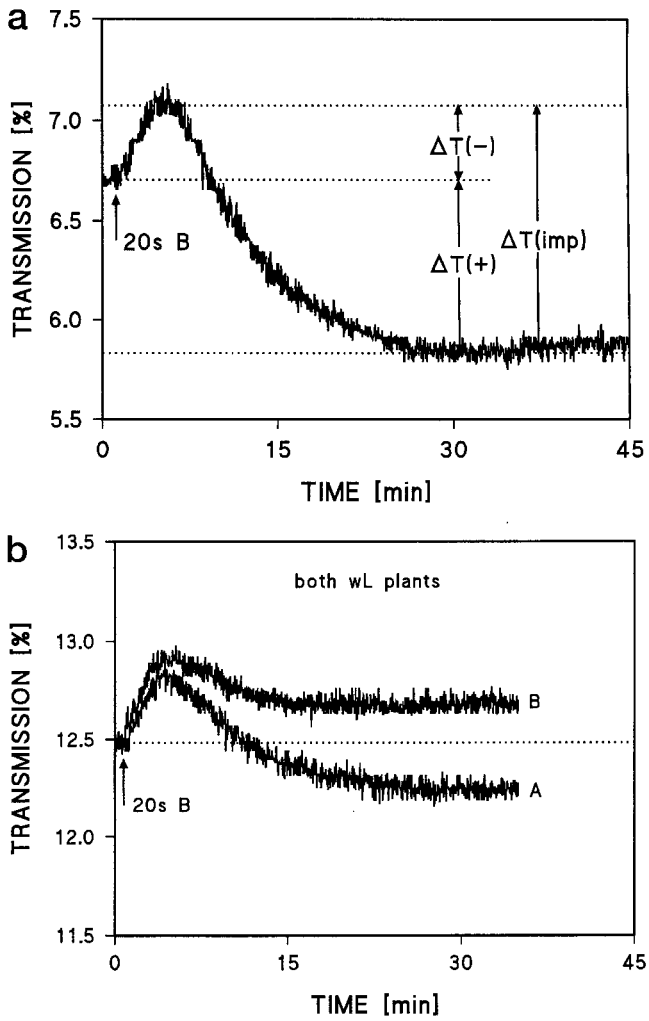

Figure 3. Responses of chloroplasts in dark-adapted (12 h) leaves of *A. thaliana* to a 20-s blue light pulse of 30 W m^{-2} ($\uparrow_{20s\ B}$) measured as percentage transmission at 660 nm as a function of time. a, Trace typical of plants grown under stL or sL conditions. b, Responses of chloroplasts in plants grown under wL conditions: A, a typical biphasic response; B, a response lacking the second phase.

whereas in sL plants many of them were situated at the cell walls perpendicular to the leaf surface (Fig. 4a). Note that the cell walls adjacent to the epidermis are completely devoid of chloroplasts (Fig. 4, a and b), even though after wL pretreatment (Fig. 4, c and d) these walls become "populated." Chloroplasts of wL plants illuminated with wL reached nearly the full face position. Only occasionally were single chloroplasts visible at cell walls parallel to the

Table I. *Mean parameters of the light pulse response for stL, sL, and wL plants after 12 h of dark adaptation*

T_D, Dark transmission. The number of measurements is given in parentheses. Data shown are averages ± SD.

Parameter	stL Plants (17)	sL Plants (14)	wL Plants (10)
T_D	5.20 ± 1.05	4.31 ± 0.56	8.37 ± 3.64
ΔT_{imp}	0.66 ± 0.37	0.52 ± 0.32	0.54 ± 0.17
$\Delta T(-)/\Delta T(+)$	0.43 ± 0.15	0.42 ± 0.17	1.02 ± 0.35

Table II. *Chloroplast distribution in cells of wL and sL plants*

The results were obtained from direct counting of chloroplasts in 100 cells of each type. p_α, Significance level. Differences between the groups of results were considered to be statistically significant when $p_\alpha < 0.05$.

Type of Plant	Pretreatment	Percent of Chloroplasts in Profile Position	Percent of Chloroplasts in Face Position	SD	p_α
wL	wL	9.8	90.2	5.5	<0.05
sL		16.6	83.4	7.2	
wL	D	36.5	63.5	7.6	<0.001
sL		71.0	29.0	5.6	
wL	sL	90.7	9.3	3.8	>0.1
sL		90.0	10.0	3.3	

light direction. In the case of sL plants, some more chloroplasts were still in the profile position. As for the sL pretreatment, most chloroplasts were in the profile position in both types.

DISCUSSION

The experiments reported here show that chloroplast movement in *A. thaliana* is blue light sensitive. The responses can be induced either by pulses of blue light or by continuous irradiation. The fluence rate response curve is similar to those obtained for other blue-light-sensitive species, e.g. *Funaria hygrometrica* (Zurzycki, 1961), *L. trisulca* (Zurzycki, 1962), *Ajuga* (Lelątko, 1970), and *T. albiflora* (Gabryś and Walczak, 1980). However, in comparison to other higher plants studied to date, the range of fluence rates at which chloroplasts of *A. thaliana* attain the full face arrangement is broader. At high light intensities (about 40 W m^{-2}), chloroplasts of *A. thaliana* showed a normal response toward profile arrangement, whereas in *L. trisulca*, intensities higher than 10 W m^{-2} caused a decrease in light transmission as a result of their abnormal formation of clusters. In the latter species, chloroplasts gathered in haphazardly distributed groups in cell corners, unable to form the typical sL arrangement (Zurzycki et al., 1983).

In *L. trisulca*, light pulses of 30 W m^{-2} induced transient changes in light transmission of a leaf in the subsequent dark period, which reflects chloroplast displacement in mesophyll cells. Duration of a light pulse has a strong influence on the chloroplast response. If the pulse lasts long enough (above 3–5 s), a typical bipolar response is generated. If it is shorter, the transient change in transmission reflects a partial response of chloroplasts toward the face arrangement (Gabryś et al., 1981). Chloroplast responses to light pulses in *A. thaliana* were consistent with this general pattern; the mean amplitude of the whole response was similar for stL, sL, and wL plants despite their different dark transmission levels (Table I). This suggests that the morphological structure of a leaf and, especially, its thickness and number of mesophyll layers did not affect the amplitude. However, parameters of the light pulse response differed between the plant groups. The ratio $\Delta T(-)/\Delta T(+)$ for stL and sL plants had the same value, whereas for wL plants the value was over twice as large (Table I). The ratio showed that, in wL plants, the amplitude of the partial rearrangement [$\Delta T(-)$] was much higher than the amplitude of the subsequent partial dark-to-face rearrangement [$\Delta T(+)$] and was more than twice as high as that of stL and sL plants (Fig. 3). These results suggested a possible difference in the starting dark arrangement of chloroplasts. The microscopic observation of cross-sections and counting of chloroplasts demonstrated that the majority of chloroplasts in the dark-adapted wL plants were in the face position. Therefore, they started their quick "flight" from light immediately after the light pulse. This led to a rapid and comparatively high increase in light transmission in the first phase of the response. However, in 30% of wL leaves, the second phase of the response did not occur (Fig. 3b). We do not have a clear explanation for this incomplete response.

The dark position in wL plants was so close to the face arrangement that the change of transmission between these two arrangements was much lower than for plants from the other two groups. This dark position of chloroplasts in wL plants resulted in the high value of the ratio $\Delta T(-)/\Delta T(+)$. wL plants were grown under conditions of limited light intensities, which barely supported their basic life functions. Therefore, any process that could facilitate light absorption might be expected to be promoted. The dark distribution of chloroplasts close to the face arrangement enabled an immediate high absorption of light as soon as it was switched on, without any waste of energy on chloroplast translocation to their optimal arrangement.

The dark position is probably not random, as is commonly assumed, but is generated by specific factors in cells, which, in turn, are induced by environmental conditions. The differences in dark arrangements in wL and sL plants of *A. thaliana* resulted from external light conditions. It is possible that the cytoskeleton and particularly actin-myosin filaments play an important role in this nonrandom dark preorientation, because they are directly involved in the chloroplast rearrangement (Malec, et al., 1996).

The observations of the different dark arrangement in wL and sL plants support the proposed ecological significance of chloroplast movements. In the case of light-limiting conditions, a distribution enabling immediate optimal light absorption is promoted. This result speaks in favor of Zurzycki's finding that, in the range of low fluence rates, chloroplast arrangement is closely parallel with the rate of photosynthesis. A slight difference in chloroplast distribution induced by the wL pretreatment was noticeable between wL and sL plants. In sL plants, more chloroplasts still remained at the side cell walls than in wL plants. Light had never been a limiting factor for their growth, so sL plants had not needed to optimize light absorption, and this tendency persisted over the temporary light conditions of the experiments. In contrast, sL caused a chloroplast distribution very close to the complete profile arrangements seen in both sL and wL plants. This result indicates that the avoidance response of chloroplasts to sL is of primary importance and dominates over any other long term orientation patterns. Our observation is consistent

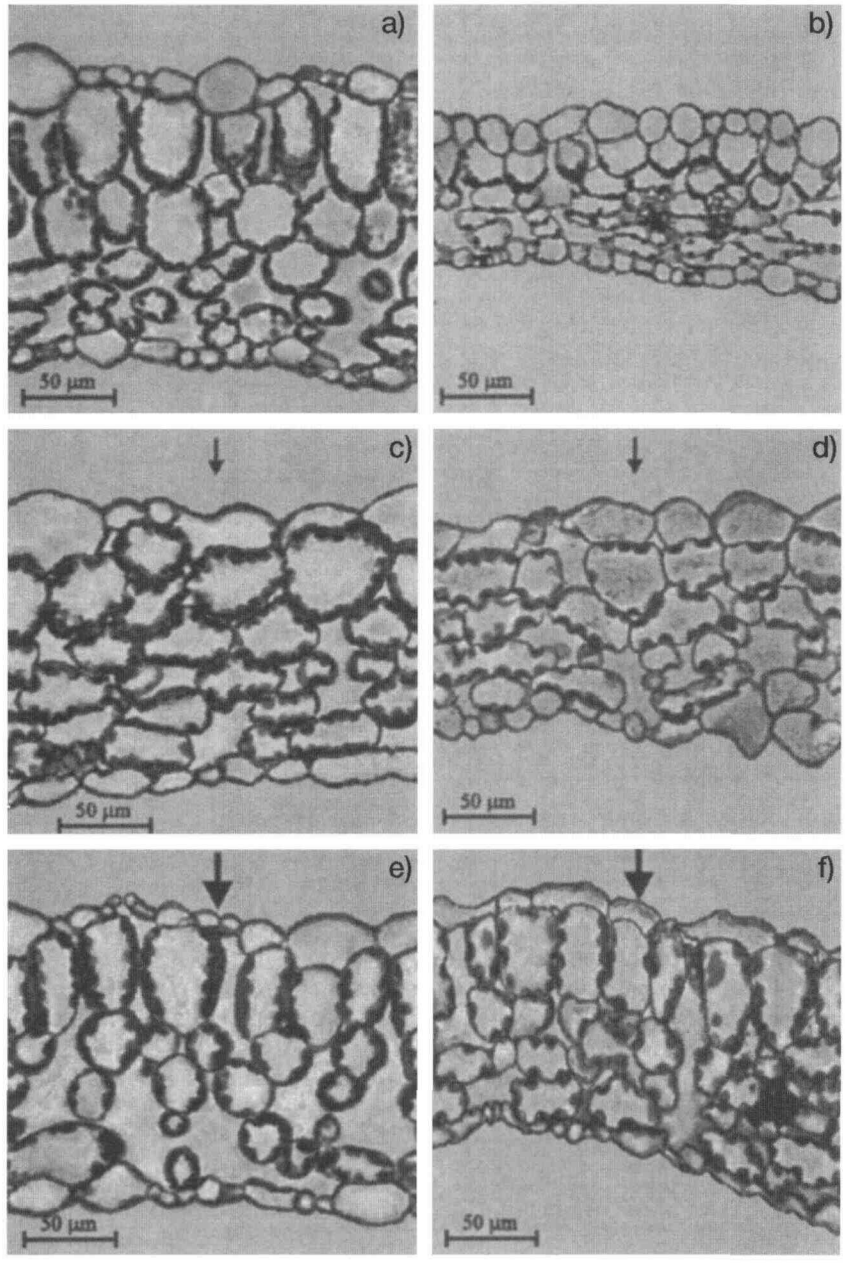

Figure 4. Chloroplast arrangements in cells after different light pretreatments. a, sL plant after dark adaptation; b, wL plant after dark adaptation; c, sL plant after wL irradiation (↓); d, wL plant after wL adaptation (↓); e, sL plant after sL adaptation (↓); and f, wL plant after sL adaptation (↓).

with Zurzycki's hypothesis that high-fluence-rate movement serves to protect chloroplasts from photodamage.

Chloroplast movement in higher plants is one of the blue light-controlled responses that constitute the so-called "blue light syndrome." Phototropic bending and inhibition of stem elongation are other important processes characteristic of this category of response that allow the plant to orient its growth with respect to the illumination conditions of its environment. Recently, major progress was achieved in characterizing the photoreceptor step of these responses, largely due to investigations carried out on *A. thaliana*. Consequently, this species, long favored for genetics and molecular genetics, also became the model plant for studying sensory physiology. A number of mutants have been isolated and characterized in Arabidopsis with alterations in hypocotyl elongation (Liscum, Hangarter, 1991) and phototropism (Khurana and Poff, 1989; Liscum and Briggs, 1995). Investigations carried out on these mutants recently led to two important discoveries: identification of a gene (HY4) encoding the blue light photoreceptor pigment mediating the suppression of hypocotyl elongation (Ahmad and Cashmore, 1993) and genetic separation of the signal transduction systems for this latter response and phototropism (Liscum et al., 1992; Liscum and Briggs, 1995).

We tested leaves of several hypocotyl elongation and phototropism mutants (*hy* and *blu* strains) and did not find any apparent abnormality in their chloroplast responses (H. Gabryś and A. Trojan, unpublished results). A detailed investigation is in progress to determine whether chloro-

plast movements in Arabidopsis use a separate photoreceptor or if the initial step of the sensory transduction leading to chloroplast rearrangements is shared with the other two blue-light-controlled responses.

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