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# Review

# Actin-based photo-orientation movement of chloroplasts in plant cells

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**Summary**

**In photosynthesizing plant cells, chloroplasts change their arrangements and/or positions in response to light irradiation. These photo-orientation movements of chloroplasts are believed to play important roles in optimizing the photosynthetic activity of plant cells. We have been investigating the roles of the actin cytoskeleton in the intracellular movement and positioning of chloroplasts using the aquatic monocot *Vallisneria gigantea* Graebner and the terrestrial dicot *Spinacia oleracea* L. (spinach). In *Vallisneria* epidermal cells, chloroplasts accumulate on the cytoplasmic layer facing the top surface (outer periclinal layer) under dim red light, whereas they move to the cytoplasmic layer perpendicular to the outer periclinal layer (anticlinal layer) under strong blue light. Concomitant with these responses, actin filaments exhibit dramatic changes in their configurations. The possible modes of action of the actin cytoskeleton to regulate the movement and positioning of chloroplasts are briefly summarized, together with our recent analysis of the association of actin filaments with chloroplasts isolated from spinach leaves.**

Key words: chloroplast, photosynthesis, photo-orientation movement, actin cytoskeleton, *Vallisneria gigantea*, *Spinacia oleracea*.

## Photo-orientation movement of chloroplasts

Chloroplasts, which are cell organelles specifically differentiated for photosynthesis, change their intracellular arrangements and/or positions in response to irradiation with light (Senn, 1908; Haupt and Scheuerlein, 1990; Wada and Kagawa, 2001). These movements are widely observed in a variety of plant species and are designated as the photo-orientation movement of chloroplasts. Typical examples of such movements are schematically shown in Fig. 1. Basically, chloroplasts move to expose their ‘faces’ to incident dim light and their ‘profiles’ to strong light. These movements are believed to play important roles in the maximization of photosynthetic activity (Zurzycki, 1955) and the minimization of photo-damage (Zurzycki, 1957; Park et al., 1996) in plants under fluctuating light conditions.

In most cases studied to date, blue light specifically induces chloroplast movement under both dim and strong light (Zurzycki, 1980; Haupt and Scheuerlein, 1990). Recently, in the model plant *Arabidopsis thaliana*, flavoprotein phototropins (phot1 and phot2) were identified as blue-light photoreceptors that function in the light-induced relocation of chloroplasts (Kagawa et al., 2001; Jarillo et al., 2001; Sakai et al., 2001). On the other hand, the involvement of phytochromes, another photo-morphogenic photoreceptor family in plants (Furuya, 1993), in the orientation movement of chloroplasts has been demonstrated in algae (Haupt et al., 1969), mosses (Sato et al., 2001), ferns (Yatsuhashi, 1996), and angiosperms (Dong et al., 1995). From the effects of linearly polarized light (Zurzycki, 1967) and microbeam irradiation (Haupt et al., 1969), both blue-light photoreceptors and phytochromes are postulated to be orderly arranged in the vicinity of the plasma membrane to regulate the photo-orientation movement of chloroplasts (Haupt and Scheuerlein, 1990; Yatsuhashi, 1996).

Actin filaments are involved in the intracellular movement of chloroplasts (Takagi, 2000). The anti-actin drug cytochalasin inhibits the light-dependent movement of chloroplasts in many kinds of plant cells, including those of algae (Wagner et al., 1972), mosses (Sato et al., 2001), ferns (Kadota and Wada, 1992b) and angiosperms (Witztum and Parthasarathy, 1985; Izutani et al., 1990; Tlałka and Gabryś, 1993). Although the direct interaction of putative myosin molecules with chloroplasts was suggested in a couple of plant species based on immunolocalization studies (La Claire, 1991; La Claire et al., 1995, Liebe and Menzel, 1995), it has been generally accepted that chloroplasts participate only passively in the movement of the cytoplasmic matrix (Haupt and Schönbohm, 1970). Most of the plant myosins examined in the DNA sequences to date belong to either class VIII or XI (Liu et al., 2001), and the possible interaction of biochemically identified myosins from the alga *Chara* (Yamamoto et al.,

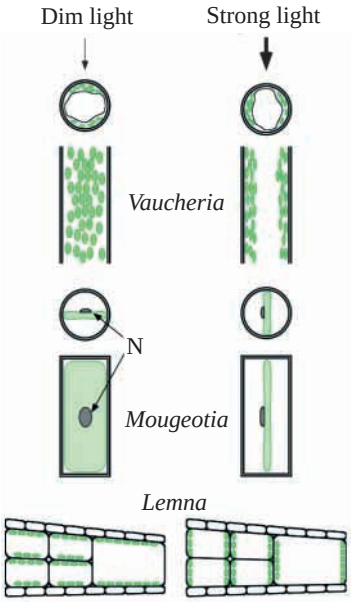


Fig. 1. Schematic demonstration of photo-orientation movement of chloroplasts in various types of plant cells. Typical intracellular distributions of chloroplasts observed under dim or strong light in the coenocytic alga *Vaucheria*, the green alga *Mougeotia* and the angiosperm *Lemna* are shown. N, nucleus. Modified from Senn (1908).

1995) and the angiosperm lily (*Lilium longiflorum*; Yokota et al., 1995) with cell organelles has been investigated. The exact localization and roles of myosins in the regulation of chloroplast movement remain to be clarified.

Concomitant with the light-dependent redistribution of chloroplasts, the spatial reorganization of actin filaments has been shown in the coenocytic alga *Vaucheria* (Blatt and Briggs, 1980; Blatt et al., 1980), the green algae *Caulerpa* (Menzel and Elsner-Menzel, 1989) and *Mougeotia* (Mineyuki et al., 1995) and the pteridophytes *Selaginella* (Cox et al., 1987) and *Adiantum* (Kadota and Wada, 1992a). Chloroplast movement in the green alga *Dichotomosiphon* is microtubule-dependent (Maekawa and Nagai 1988); however, chloroplasts that accumulated in cell apices after photo-orientation movement were found to be associated with numerous fine bundles of actin filaments (Fig. 2). Also, in vascular plants, actin filaments surrounding chloroplasts have frequently been observed by light microscopy (Kobayashi et al., 1987; Kadota and Wada, 1992a; Dong et al., 1996; Kandasamy and Meagher, 1999). In *A. thaliana*, disruption of the actin filaments by the anti-actin drug latrunculin B led to the disruption of the intracellular arrangement of chloroplasts (Kandasamy and Meagher, 1999). These studies have pointed out the possibility that actin filaments not only provide tracks for the movement of chloroplasts but also function to anchor the chloroplasts at proper intracellular positions. The different roles of the actin filaments may have resulted from the different signalling pathways from the photoreceptor systems functioning under different light conditions. We are investigating these aspects in higher plants, using the monocotyledonous aquatic plant *Vallisneria gigantea* Graebner and the dicotyledonous terrestrial plant *Spinacia oleracea* L. (spinach).

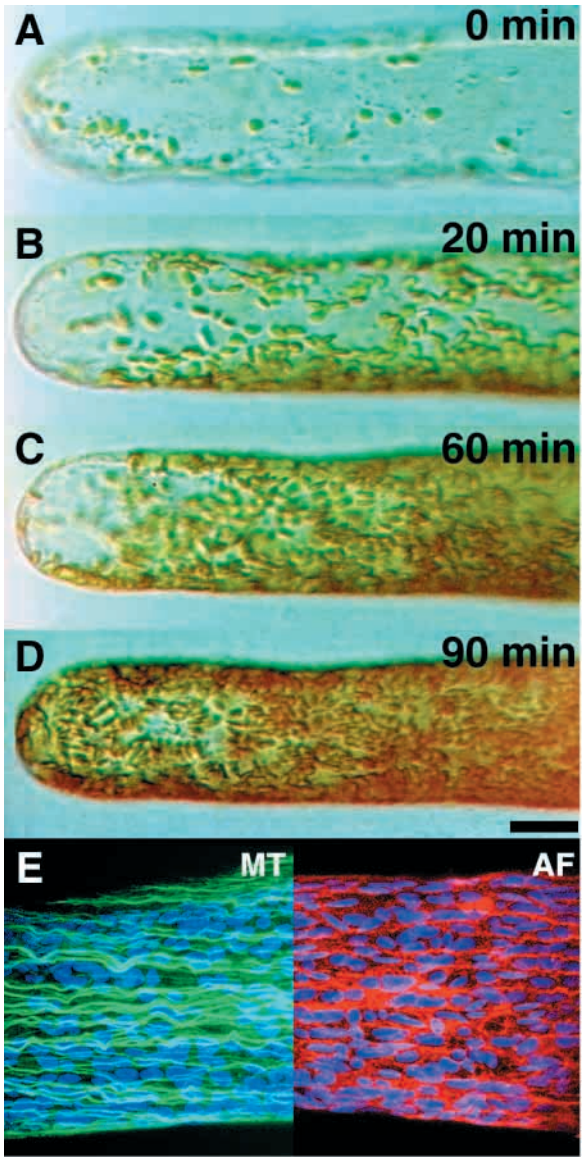


Fig. 2. Accumulation of chloroplasts in the cell apex of the coenocytic green alga *Dichotomosiphon*. (A–D) Dim blue light induced the accumulation of chloroplasts in the apical region of a cylindrical cell of *Dichotomosiphon* over a period of 0–90 min. (E) Microtubules (MT; green) and (F) actin filaments (AF; red) in the apical region filled with chloroplasts (blue) were visualized using fluorescence-labelled probes. Scale bar: 20 μm.

### Accumulation response of chloroplasts in *Vallisneria*

In leaf epidermal cells of *Vallisneria*, chloroplasts accumulate on the cytoplasmic layer facing the top surface (outer periclinal layer; P side) under dim light (accumulation response; Fig. 3A). We frequently observed that mitochondria also gather on the P side with the accumulated chloroplasts

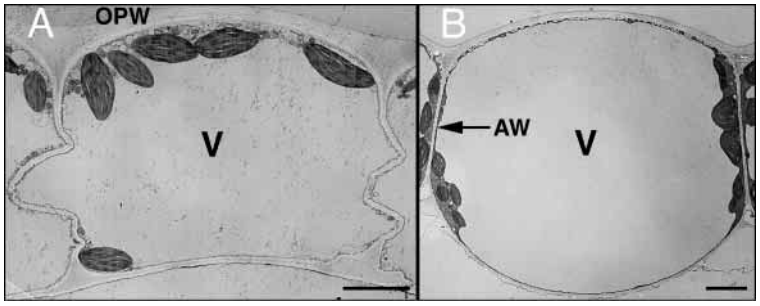


Fig. 3. Photo-orientation movement of chloroplasts in the aquatic angiosperm *Vallisneria gigantea* epidermal cells. Cross-sections of leaf epidermal cells, in which chloroplasts accumulated along the outer periclinal wall (OPW) under dim light (A) or along the anticlinal walls (AW) under strong light (B). V, central vacuole. Scale bar: 5 μm.

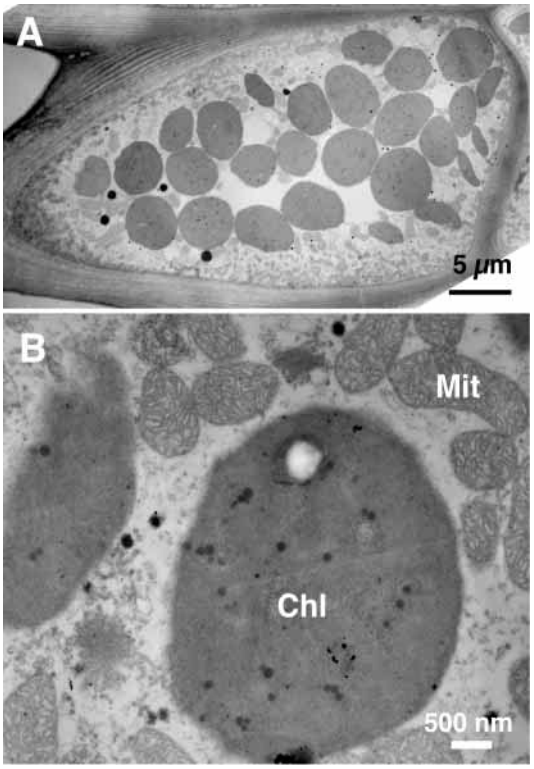


Fig. 4. Accumulation of mitochondria with chloroplasts in *Vallisneria* epidermal cells. Paradermal sections of *Vallisneria* epidermal cells under dim light, in which mitochondria (Mit) accumulated along the outer periclinal wall together with chloroplasts (Chl).

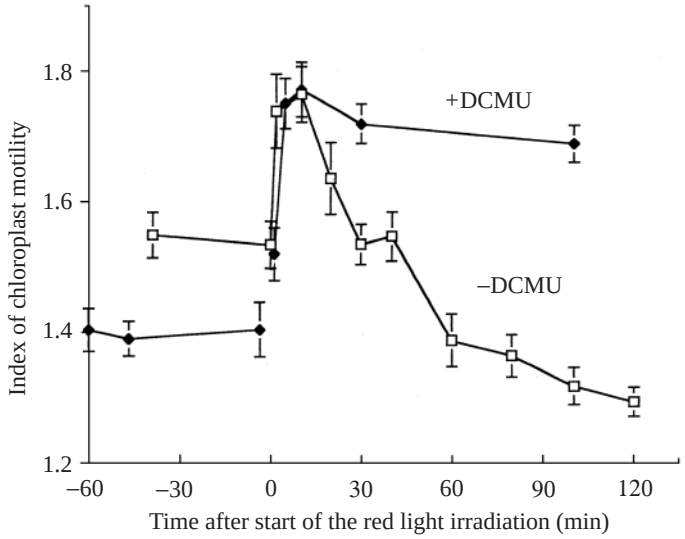


Fig. 5. Light-dependent changes in motility of chloroplasts in *Vallisneria* epidermal cells. The motility of individual chloroplasts was determined after digitization of images obtained by video microscopy of *Vallisneria* epidermal cells under dim red light in the presence (filled symbols) or absence (open symbols) of dichlorophenyl dimethylurea (DCMU), an inhibitor of photosynthetic electron transport. Modified from Dong et al. (1996).

(Fig. 4), suggesting mutual metabolic interactions (Raghavendra et al., 1994). Using video microscopy, we analysed the mode of movement of chloroplasts during the accumulation response semi-quantitatively (Dong et al., 1995). In the dark, the chloroplasts slowly migrated between the P side and the cytoplasmic layers perpendicular to the P side (anticlinal layers; A sides) at a constant rate. The number of chloroplasts that migrated from the A sides to the P side was almost the same as that migrating in the opposite direction. Within several minutes of irradiation with dim red light, the rate of migration of chloroplasts in both directions increased. After approximately 20 min, however, the rate of migration of chloroplasts from the P side to the A sides decreased compared with that in the opposite direction, leading to a gradual increase in the number of chloroplasts on the P side (Dong et al., 1995). Thus, red light appeared to initially enhance the motility of each chloroplast and to later suppress the motility of chloroplasts on the P side but not on the A sides (Fig. 5).

Both far-red light and inhibitors of photosynthesis [dichlorophenyl dimethylurea (DCMU), atrazine and tetraphenyl boron] antagonized the red-light-induced accumulation of chloroplasts on the P side. However, the modes of inhibition were completely different. Far-red light rapidly suppressed the initial red-light-induced increase in the motility of chloroplasts. The rates of migration of chloroplasts between the P side and the A sides promptly returned to the dark control level. By contrast, in the presence of DCMU, there was hardly any decline in chloroplast motility after the initial increased motility of chloroplasts by red light (Fig. 5). In fact, the increased migration of chloroplasts between the P side and the A sides continued for

a long time and did not decrease as it did after dim-red-light irradiation in the absence of DCMU. Thus, in either case, the number of chloroplasts on the P side did not change because no imbalance in the rates of migration of chloroplasts between the P side and the A sides occurred. We consequently succeeded in distinguishing the effects of dim red light on the motility of chloroplasts. Firstly, there is the rapid, red-light and far-red-light reversible effect. Red light accelerates the motility of chloroplasts, whereas far-red light inhibits this increased motility. This effect is thought to be mediated by photoreceptor phytochromes. The other effect is a much slower, photosynthesis-dependent suppression of the motility of chloroplasts. We clarified that the reorganization of actin filaments is involved in the latter photosynthesis-dependent process. Although we identified a $Ca^{2+}$-sensitive motor protein activity that interacts with actin filaments in *Vallisneria* leaves (Takagi 1997), its intracellular localization has not been determined yet. The possible involvement of the motor protein activity in the regulation of the motility of chloroplasts remains to be investigated.

### Actin-dependent anchoring of chloroplasts

In *Vallisneria* epidermal cells after incubation in the dark, actin filaments on the P side formed a loose network (Dong et al., 1996) composed of thin bundles (Yamaguchi and Nagai, 1981). Concomitant with the dim-red-light-induced decrease in motility of chloroplasts on the P side, the configuration of the actin filaments markedly changed to a honeycomb array, as if the filaments surrounded each chloroplast (Fig. 6A). Importantly, DCMU suppressed the red-light-induced reorganization of actin filaments, as well as the decrease in motility of chloroplasts (Fig. 5). The chloroplasts themselves seemed to produce signals to regulate the configuration of actin filaments so that they could settle into the proper position under dim red light.

After accumulation on the P side under dim red light, the chloroplasts became considerably resistant to centrifugal force (Takagi et al., 1991; Dong et al., 1998). This effect was antagonized by treatment with cytochalasin, which simultaneously brought about the complete fragmentation of the honeycomb array of the actin filaments surrounding the chloroplasts (Dong et al., 1998). Therefore, in *Vallisneria*, we demonstrated for the first time that actin filaments not only drive the movement of chloroplasts but also anchor the chloroplasts after the photo-orientation movement.

### Avoidance response of chloroplasts in *Vallisneria*

Under strong light, chloroplasts in *Vallisneria* epidermal cells accumulate on the A sides (avoidance response; Fig. 3B). As seen in other plant species, blue light specifically induces the avoidance response of chloroplasts (Izutani et al., 1990). Under video microscopy, chloroplasts on the P side, which had been apparently motionless, began to sway randomly within a few minutes of blue light irradiation. Then, the chloroplasts commenced to move more directionally and migrated towards the A sides. The chloroplasts that moved to the A sides did not

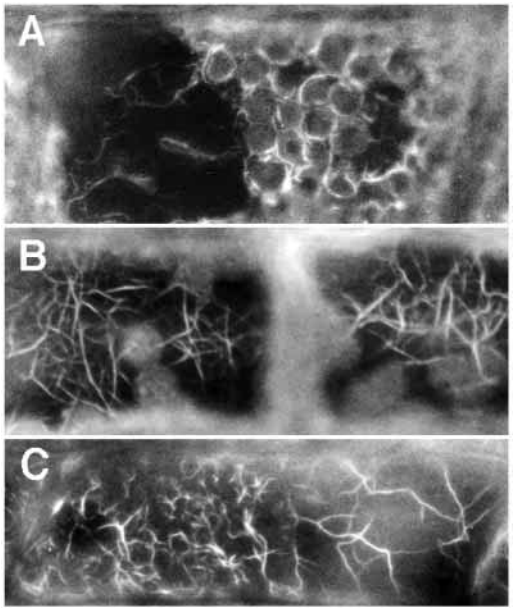


Fig. 6. Different configurations of actin filaments in *Vallisneria* epidermal cells. Actin filaments along the outer periclinal walls were visualized by fluorescence-labelled phalloidin in *Vallisneria* epidermal cells under dim red light (A), strong blue light (B) or microbeam irradiation with strong blue light (C).

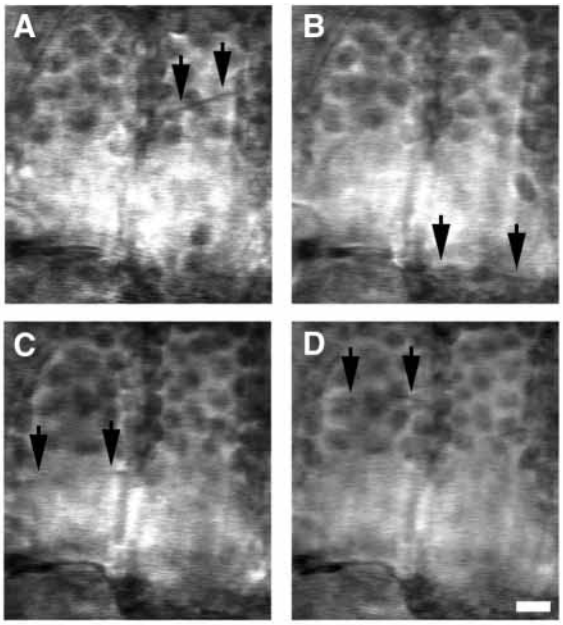


Fig. 7. Avoidance response of chloroplasts induced in partially irradiated *Spinacia oleracea* mesophyll cells over time: (A) 28 min, (B) 45 min, (C) 119 min and (D) 128 min. Partial irradiation of *Spinacia* mesophyll cells with strong blue light induced the localized avoidance response of chloroplasts, together with the formation of cytoplasmic strands (each pair of arrows) that moved freely in the irradiated cells. The lower half of the cells was irradiated. Scale bar: 10 μm.

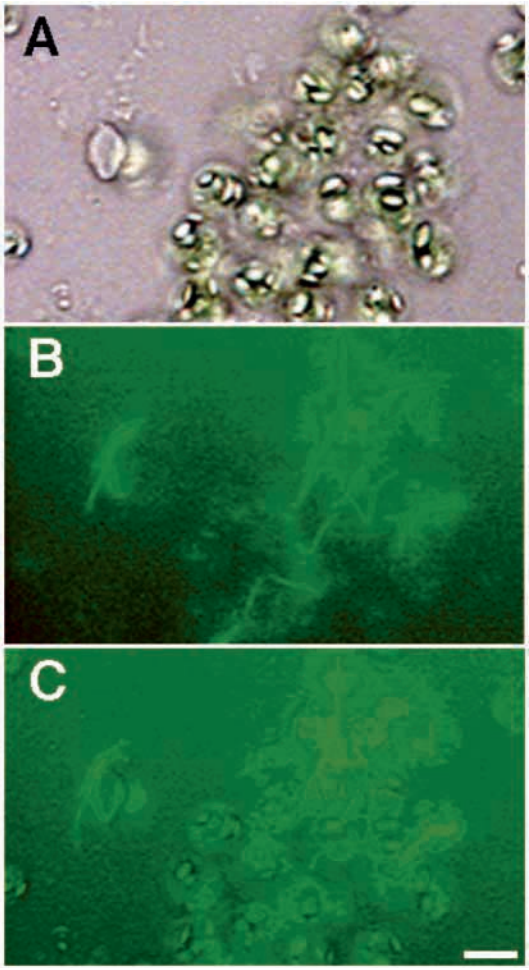


Fig. 8. Actin filaments associated with chloroplasts squeezed from spinach mesophyll cells. Chloroplasts squeezed out from manually dissected spinach mesophyll cells (A) were stained with fluorescence-labelled phalloidin (B), and the images were superimposed (C). Scale bar: 5 μm.

return to the P side; thus, the number of chloroplasts on the P side rapidly decreased (Fig. 3B). Upon blue light irradiation, the configuration of actin filaments on the P side changed, this time from a loose network to a more stretched network composed of thick bundles (Fig. 6B).

Using microbeam irradiation, we found that the avoidance response of chloroplasts was induced locally only in the region exposed to blue light. Chloroplasts in the non-irradiated regions did not change their positions at all. The reorganization of the actin filaments was also induced only in the irradiated region, producing a 'hybrid' cell possessing both the actin filaments of a honeycomb array surrounding the motionless chloroplasts and the thick, straight bundles that did not come in contact with any chloroplasts (Fig. 6C). The thick, straight bundles of actin filaments most probably function as tracks for the unidirectional migration of chloroplasts from the irradiated region. The regulation of the configuration of actin filaments by blue light photoreceptors is under strict spatial control in individual epidermal cells.

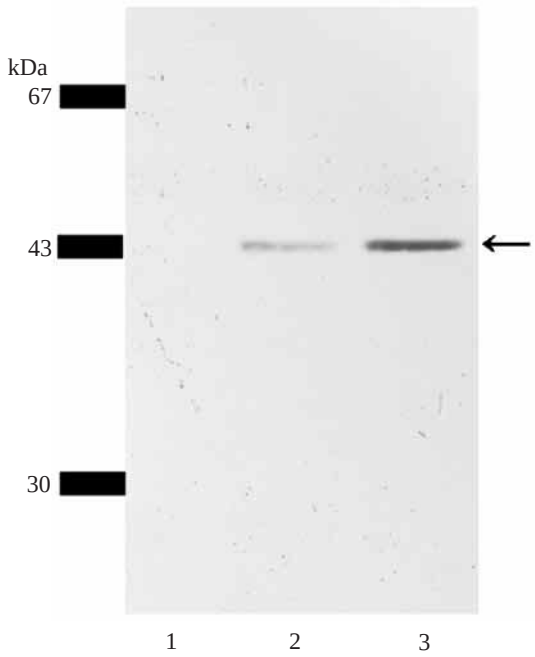


Fig. 9. Immunoblot analysis of actin associated with isolated chloroplasts from *Spinacia oleracea*. The association of actin with the isolated intact chloroplasts from spinach leaves was examined by immunoblotting of the chloroplasts immediately after isolation (lane 1), and incubation for 0 min (lane 2) and 30 min (lane 3) with exogenously added chicken skeletal muscle F-actin. The arrow indicates the position of the actin band. Molecular markers are indicated on the left.

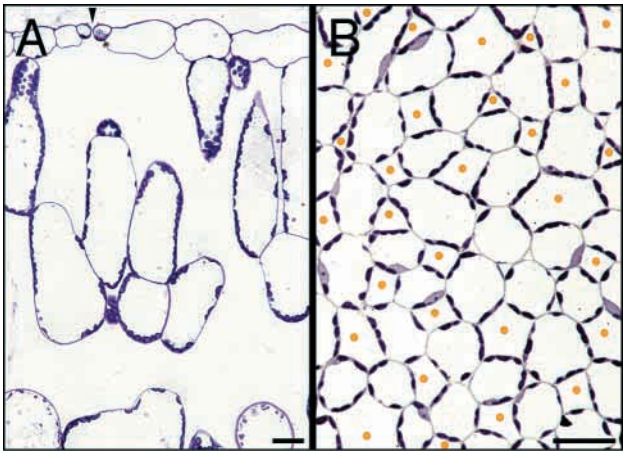


Fig. 10. Intracellular arrangement of chloroplasts in terrestrial plant leaves. Intracellular arrangement of chloroplasts is demonstrated in a cross-section of the adaxial part of a *Spinacia oleracea* leaf (A) and in a paradermal section of the parenchyma cells of *Maesa japonica* (B). Arrowhead in A indicates the stoma, while the yellow circles in B indicate intercellular spaces. Scale bars: 25 μm.

**Interaction of chloroplasts with actin filaments in spinach**

We used spinach to investigate the possible interaction of chloroplasts with actin filaments *in vitro* because the isolation procedures of chloroplasts from spinach are well established.

Moreover, the light-dependent redistribution of chloroplasts was suggested, based on measurements of light-induced absorbance changes of the spinach leaves (Inoue and Shibata, 1974). By video microscopy, we confirmed that blue light induced the directional migration of chloroplasts to avoid the incident light in mesophyll cells. Such movement was reversibly inhibited by cytochalasin, indicating the involvement of actin filaments. When the mesophyll cells were partially irradiated with strong blue light, the avoidance response of chloroplasts was induced only in the irradiated area (Fig. 7). Blue light often induced the formation of one or two thick cytoplasmic strands in each irradiated cell. These cytoplasmic strands moved freely from the non-irradiated area to the irradiated area and *vice versa* (Fig. 7). Although the nature of the light-induced formation of the cytoplasmic strands has not yet been characterized in detail, in this case, signals from the photoreceptors seem to be transmitted from the irradiated area to the surrounding non-irradiated areas.

Because we succeeded in visualizing the actin filaments associated with chloroplasts in spinach mesophyll cells under dim light, we attempted to isolate such chloroplasts from the cells. In the cytoplasm obtained by squeezing manually dissected cells, we occasionally observed chloroplasts associated with actin filaments (Fig. 8). This suggested a possible direct interaction of chloroplasts with actin filaments; however, when chloroplasts were isolated after homogenization of the leaves and Percoll centrifugation, we could not detect any actin by immunoblotting of the final fraction, which was rich in intact chloroplasts (Fig. 9; lane 1). Actin filaments might have been detached from the chloroplasts during the isolation procedure. Finally, using such isolated intact chloroplasts, which are apparently free of actin filaments, we examined the possible binding of the exogenously added skeletal F-actin. As expected, F-actin co-sedimented with the intact chloroplasts, depending on the incubation time (Fig. 9; lanes 2 and 3).

## Concluding remarks

The entire process involved in the photo-orientation movement of chloroplasts can be separated into photoperception, signal transduction, relocation of chloroplasts and anchoring of chloroplasts. The recent identification of blue-light photoreceptors for chloroplast relocation by mutant analysis in *A. thaliana* (Kagawa et al., 2001; Jarillo et al., 2001; Sakai et al., 2001) is undoubtedly a great breakthrough. On the other hand, by observing cytoskeletal organization, we surmise that actin filaments may play important roles in the relocation and anchoring of chloroplasts. From our study, we found that actin filaments can at least bind to chloroplasts *in vitro*. However, most parts of the signal transduction process, particularly the molecular basis for the regulation of the dynamic behaviour of actin filaments in plant cells (Staiger, 2000), remain unsolved.

Furthermore, as has already been pointed out by several eco-physiologists (Evans and von Caemmerer, 1996), chloroplasts are almost always positioned along the cell walls facing the intercellular spaces in the leaves (Fig. 10). Although this may be interpreted as indicating that chloroplasts have to capture much $CO_2$ even under spatially limited conditions (Terashima et al., 1995), we know nothing about the mechanism of this simple phenomenon. To obtain a much deeper insight into the photo-orientation movement of chloroplasts – one of the most precisely regulated cellular responses in plants to environmental stimuli – much more extensive collaboration among cell biologists and eco-physiologists is essential.

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