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Response of actin microfilaments during phytochrome-controlled growth of maize seedlings

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Summary. In seedlings of maize (*Zea mays* L. cv. Percival), growth is controlled by the plant photoreceptor phytochrome. Whereas coleoptile growth is promoted by continuous far-red light, a dramatic block of mesocotyl elongation is observed. The response of the coleoptile is based entirely upon light-induced stimulation of cell elongation, whereas the response of the mesocotyl involves light-induced inhibition of cell elongation. The light response of actin microfilaments was followed over time in the epidermis by staining with fluorescence-labelled phalloidin. In contrast to the underlying tissue, epidermal cells are characterized by dense longitudinal bundles of microfilaments. These bundles become loosened during phases of rapid elongation (between 2–3 days in irradiated coleoptiles, between 5–6 days in dark-grown coleoptiles). The condensed bundles re-form when growth gradually ceases. The response of actin to light is fast. If etiolated mesocotyls are transferred to far-red light, condensation of microfilaments can be clearly seen 1 h after the onset of stimulation together with an almost complete block of mesocotyl elongation. The observations are discussed in relation to a possible role of actin microfilaments in the signal-dependent control of cell elongation.

Keywords: Actin; Cell elongation; Confocal microscopy; *Zea mays*; Microfilaments; Phytochrome.

Introduction

Actin microfilaments are essential elements of the plant cytoskeleton and participate in a variety of morphogenetic events, such as nuclear migration into the prospective division plane (Traas et al. 1987, Lloyd 1991), cytoplasmic streaming (Nagai and Fukui 1981), tip growth (Staiger and Schliwa 1987), nuclear RNA export (Barja and Turian 1994), gravitropic perception (Sievers et al. 1991), and establishment of cell polarity (Bouget et al. 1996). The close correlation of microfilaments with cellular morphogenesis is not surprising. Microfilaments form a highly dynamic scaffold that is capable of both force generation and transport, and they also embody both axiality and polarity. The impact of microfilaments on cell shape in yeast and animal cells has been studied in great detail (Zigmond 1996), and it is likely that microfilaments are also involved in the spatial control of cell expansion in plants.

Several observations indicate a microfilament role in the control of cell growth in plants. Inhibitors of the actin-myosin system cause stimulation of radial expansion in *Arabidopsis* roots (Baskin and Bivens 1995) and reorganization of the microfilament system seems to mediate the phototropic response of tip-growing moss caulonemata (Meske et al. 1995, 1996). In oat coleoptiles, auxin-induced cell elongation was shown to require intact actin microfilaments (Thimann et al. 1992, Thimann and Biradivolu 1994). To study the possible role of microfilaments in the control of cell growth, the behavior of actin filaments was analyzed during phytochrome-triggered cell elongation in the epidermis of maize seedlings. This system was chosen for the following reasons: (1) the response of the coleoptile (stimulation of cell elongation by phytochrome) is opposed to that of the mesocotyl (inhibition of cell elongation by phytochrome), (2) the response of cell growth can be induced with high precision and high specificity in intact plants, (3) the epidermis has been shown to be the tissue that

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limits and controls organ growth in coleoptiles (Kutschera et al. 1987). The response of microfilaments was followed over time in etiolated coleoptiles and compared to the response in coleoptiles that were cultivated under continuous far-red light activating the phytochrome system only. The results indicate close correlation between signal-dependent changes in the structure of the microfilament system and signal-dependent cell elongation.

Material and methods

Plant material

Seeds of *Zea mays* L. cv. Percival RX385 (Asgrow, Bruchsal, Federal Republic of Germany) were soaked for 2 h in running tap water and sown equidistantly, embryo up, on moist cellulose (Pehazell; Hartmann AG, Heidenheim, Federal Republic of Germany) in plexiglass boxes (300 × 200 × 70 mm) with a transparent plexiglass lid. Seedlings were cultivated at 25 °C, either under far-red light (λ_{max} 740 nm, fluence rate 3.5 W/m^2 or 8.2 μmol/m^2 · s, for details refer to Mohr et al. 1964) or in complete darkness, for which the cultivation boxes were placed in light-tight black boxes covered with black cloth. Seedlings were selected for straightness and homogenous length, more than 75% of the entire population could be used for the experiments.

Determination of cell length

Coleoptile length was measured as the distance between tip and coleoptile node, the mesocotyl length as the distance between the node and base of the primary root. The length of epidermal cells was estimated from micrographs of epidermal strips with the autofluorescence of the cell wall as natural label. For the coleoptiles, epidermal strips were collected from the central regions of the coleoptile, avoiding regions close to the tip or to the node. In most cases, the strips were collected in two sites in the upper and the lower third of the coleoptile. Fluorescence images of these strips were obtained with an epifluorescence microscope (Axioplan; Zeiss, Oberkochen, Federal Republic of Germany) with excitation at 365 nm, beam split at 395 nm, and emission at 397 nm. The images were recorded on 400 ASA black-and-white film (Tri X Pan; Kodak, Rochester, MA, U.S.A.) and the negatives were projected onto a wall for the determination of cell length, cell width, and cell number. For calibration an object micrometer scale was photographed at the same magnification. For each time, epidermal strips from at least four different seedlings were analyzed; average values represent data from at least 100 cells.

Visualization of actin microfilaments

Various fixation protocols were tested at the beginning of this study. To try to preserve the cortical microfilaments described in cultured tobacco cells, segments were prefixed by chemical cross-linking (Sonobe and Shibaoka 1989). However, in three independent experiments no effect of chemical cross-linking could be observed (data not shown). The best results were obtained with mild conventional fixation in paraformaldehyde, similar to a protocol developed to stain actin in maize roots (Blancaflor and Hasenstein 1997). Fixation was included to exclude the possibility of rapid microfilament response to mechanical stress during tissue processing. Actin filaments were stained with fluorescent-labelled phalloidin. After fixation for 15 min in 1.8% (w/v) fresh paraformaldehyde in microfilament buffer (100 mM potassium phosphate buffer, 100 mM KCl, 0.25% (v/v) Triton X100, pH 7.3), tangential sections of 100 μm thickness were cut on a vibratome (Vibroslice VSL; World Precision Instruments Inc., Sarasota, FL, U.S.A.). The sections were collected in microfilament buffer, and then placed on a glass slide in a drop of 1.2% agar dissolved in microfilament buffer. After incubation with 130 nM fluorescein-isothiocyanate labelled phalloidin (Sigma, Neu-Ulm, Federal Republic of Germany) in microfilament buffer for 45 min in darkness at room temperature, sections were thoroughly washed five times for 5 min and then mounted in microfilament buffer. Slides were analyzed immediately by confocal microscopy.

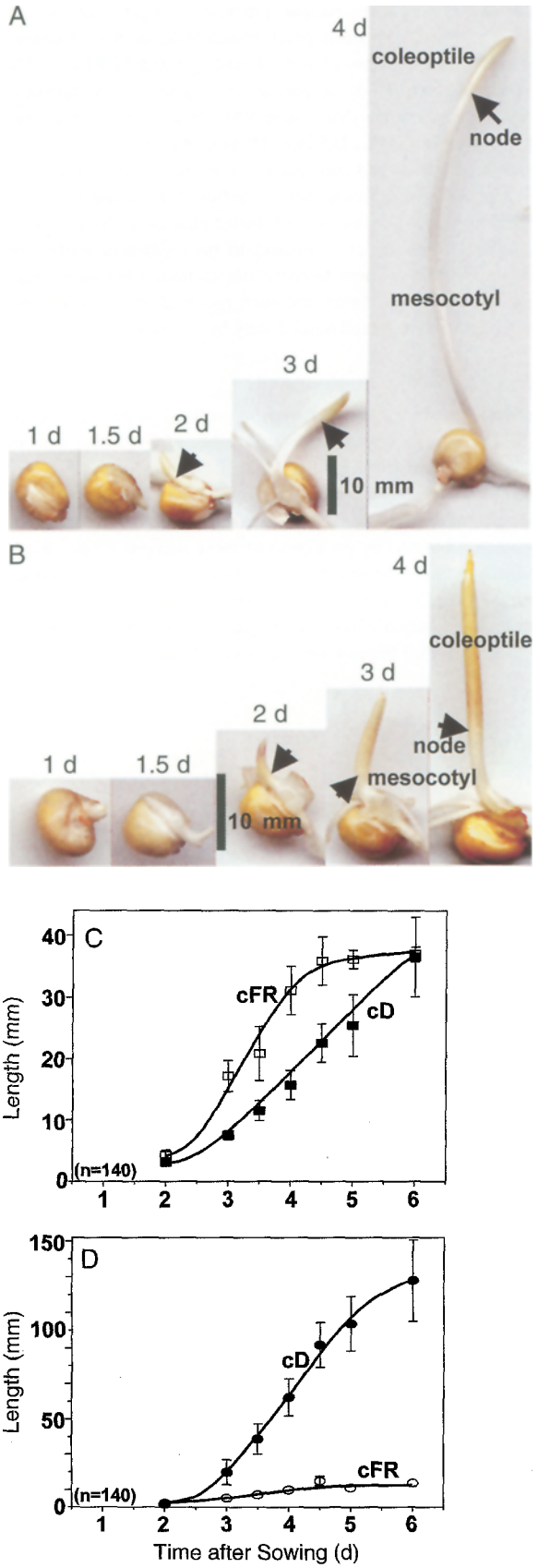
Confocal microscopy

Microfilaments were analyzed with a confocal laser microscope (DM RBE; Leitz, Bensheim, Federal Republic of Germany) with an argon-krypton laser at 488 nm excitation, a beam splitter at 510 nm, and a 515 nm emission filter. A series of 8 optical sections covering the diameter of the observed cell layer in the z-axis were scanned and images were obtained by projection of these sections ("line" average). Pictures were recorded with a Focus Imagecorder (Focus Graphics, Foster City, CA, U.S.A.) or with a Contax 167MT Camera from a high resolution Color Monitor, using 100 ASA Fuji Sensia color slide film (Fuji Photo Film Co, Tokyo, Japan).

Results

Elongation of maize coleoptile and mesocotyl is under phytochrome control

When maize seedlings are grown in complete darkness, they are characterized by hypertrophic elongation of the mesocotyl and reduced development of the coleoptile and primary leaves (Fig. 1 A). Upon induction of the phytochrome system by continuous far-red light, growth of the mesocotyl is suppressed, whereas the growth of coleoptile and primary leaf is promoted (Fig. 1 B). The growth time course reveals that the light responses of mesocotyl and coleoptile differ qualitatively (Fig. 1 C, D). Light causes an acceleration of coleoptile growth without altering the final length (Fig. 1 C). Whereas under far-red light the coleoptile reaches a final length of about 40 mm within four days, it requires six days to complete elongation in darkness. In contrast in the mesocotyl, dramatic light-induced reduction of final length is observed (Fig. 1 D). A similar response can be induced by pulses of red light (Kunzelmann and Schäfer 1985) demonstrating that phytochrome is the photoreceptor responsible. The strong response to far-red light shows that the response is a very-low-fluence-rate type of phytochrome response, consistent with earlier findings (Vanderhoef et al. 1979, Kunzelmann and Schäfer 1985).



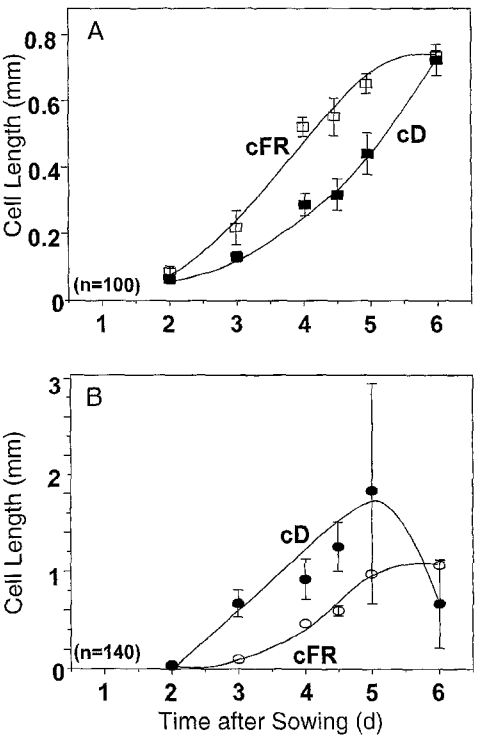


Fig. 2 A, B. Response of cell elongation to continuous far-red light. Epidermal-cell length over time in darkness (■, ●) and under continuous far-red light (□, ○) in the coleoptile (**A**) and in the mesocotyl (**B**). Error bars indicate standard errors

Elongation of epidermal cells can account for the light response of the coleoptile but not of the mesocotyl

To analyze the light response of coleoptile and mesocotyl growth at the cellular level, the length of epidermal cells was measured in the epidermis of both organs. In the coleoptile, epidermal cells elongate slowly but steadily in the dark between 3 and 6 days after sowing, and elongation is even slower between 2 and 3 days (Fig. 2 A). Under continuous far-red light, cell elongation is promoted between 2 and 4 days, but elongation rate declines 5 days after sowing (Fig. 2 A). For both dark-grown and far-red irradiated coleoptiles, the time course of cell elongation mimics the time course observed for elongation of the entire coleoptile (Fig. 1 C). Moreover, the number of epidermal

Fig. 1 A–D. Response of maize seedlings to continuous far-red light. **A** Appearance of seedlings during etiolated growth, **B** appearance of seedlings during growth under continuous far-red light; arrows indicate the position of the coleoptilar node. **C** Time course of coleoptile elongation in darkness (■) and under continuous far-red light (□), **D** time course of mesocotyl elongation in darkness (●) and under continuous far-red light (○). Error bars indicate standard errors, n = 140

Table 1. Number of epidermal cells in coleoptiles cultivated in darkness or under continuous far-red light

Age (d)	Dark	Far-red
2	59 ± 16	81 ± 23
3	85 ± 10	95 ± 16
4	64 ± 10	69 ± 12
4.5	93 ± 14	75 ± 10
5	72 ± 17	69 ± 5
6	53 ± 11	55 ± 3
Av.	71 ± 15	74 ± 13

cells did not increase during growth and there was no significant difference between dark- and light-grown coleoptiles (Table 1).

This suggests that the light response of coleoptile growth can be understood entirely in terms of light-induced changes in the elongation of individual cells. However, the situation in the mesocotyl appears to be more complex. Under continuous far-red light the time course of epidermal elongation parallels elongation of the entire mesocotyl (Fig. 2 B), suggesting that the mesocotyl grows exclusively by cell elongation. In the dark, a similar parallelity is observed up to five days after sowing. From day 5 to day 6 average cell length declines dramatically (Fig. 2 B) and pairs of adjacent short cells can simultaneously be observed in the epidermis. This suggests that at least the second phase of etiolated-mesocotyl growth involves cell division. This conclusion is confirmed by a dramatic increase in the number of epidermal cells in mesocotyls, from 63.6 ± 23 (days 2–5) to 224 ± 41 (day 6). In light-grown mesocotyl, the cell numbers were much lower (33.6 ± 10) and did not increase over time. These observations demonstrate that the growth response of the mesocotyl cannot be understood in terms of cell elongation alone. There is a significant

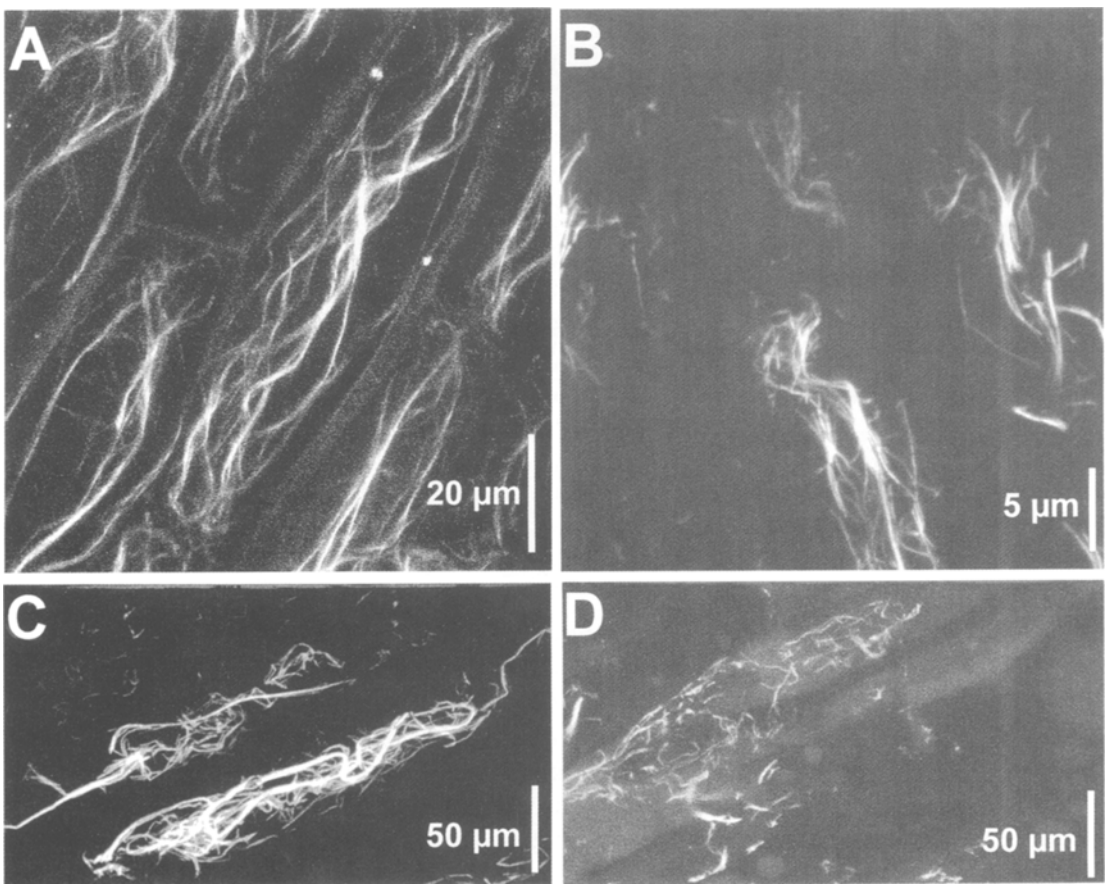


Fig. 3 A–D. Microfilament arrays observed in maize coleoptiles. **A** Loose epidermal array (coleoptiles, grown for 4 days in the dark). **B** Meshwork of fine actin filaments near the cell pole in elongating cells (coleoptiles, grown for 4 days in the dark). **C** Epidermal cells with condensed microfilament arrays (coleoptiles, grown for 2 days in the dark). **D** Subepidermal cells subtending the cells in **C** lack condensed microfilament arrays

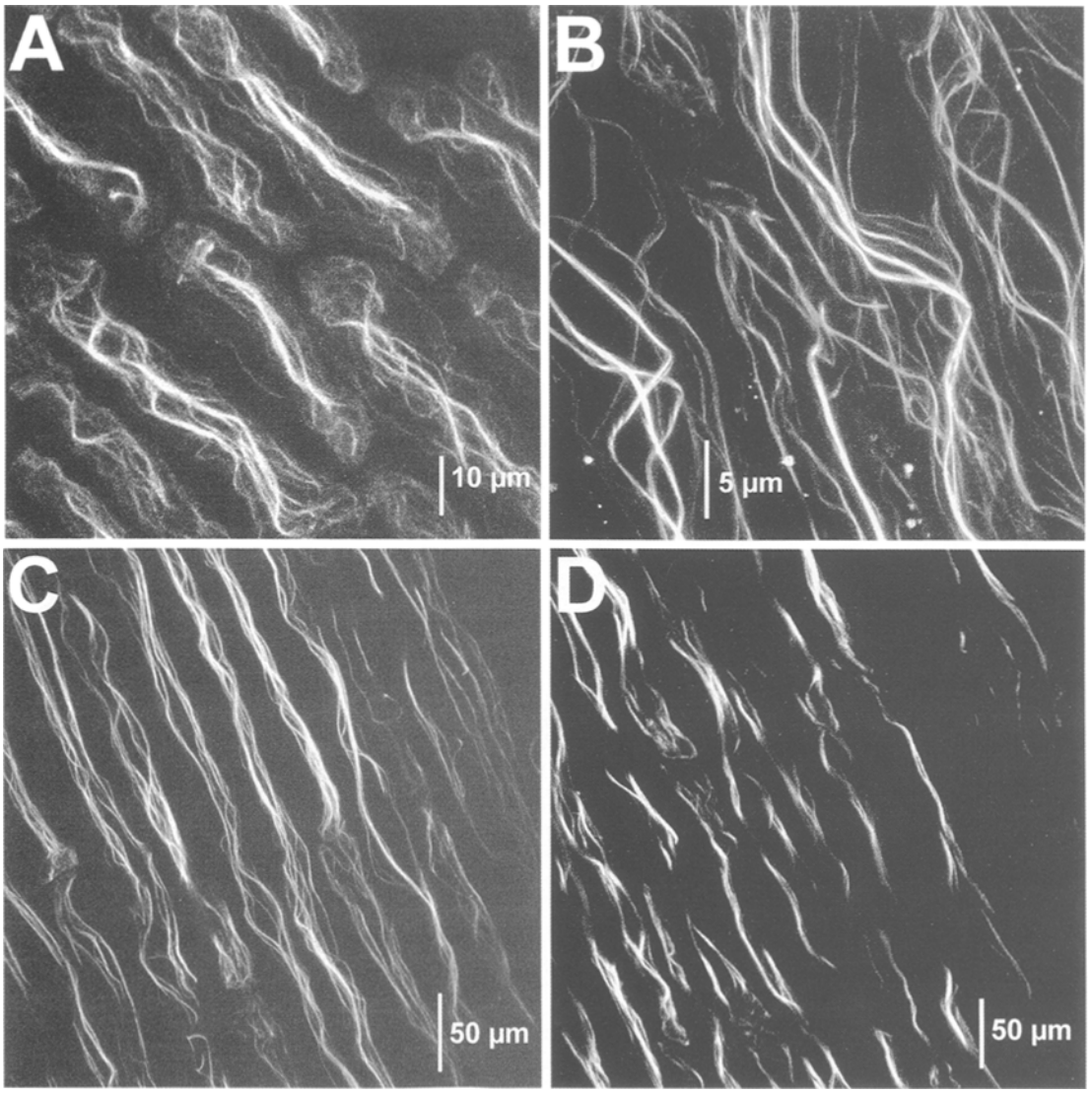


Fig. 4 A–D. Response of epidermal microfilament arrays to light. **A** Condensed array prior to elongation (darkness, 2.5 days after sowing). **B** Longitudinal arrays with numerous fine microfilaments in elongating cells (continuous far-red light, 2.5 days after sowing). **C** Loose arrays in elongating cells (darkness, 5 days after sowing). **D** Condensed arrays with evidence of microfilament degradation in cells that have completed elongation (continuous far-red light, 5 days after sowing)

contribution from cell division, and cell division is suppressed by continuous far-red light.

Reduced cell elongation is correlated with condensation of epidermal microfilaments

Actin microfilaments were visualized by fluorescent-labelled phalloidin in epidermal and subepidermal cells of maize coleoptiles and mesocotyls, and their light response was followed during seedling development. The appearance of microfilaments in epidermal cells was qualitatively different to microfilaments in subepidermal cells (Fig. 3). Epidermal cells are characterized by long strands of actin that are clearly aligned with the long axis of the cell (Fig. 3 A, C). Two different arrays could be observed in these longitudinal strands: a loose array of numerous longitudinal fine strands of actin accompanied by a meshwork of fine filaments near the cell poles (Fig. 3 A, B), and a condensed array with few thick actin cables spanning the entire cell length, accompanied by a reduction in the polar fine meshwork (Fig. 3 C). In contrast, in subepidermal cells, even if they are subjacent to epidermal cells with condensed actin cables (Fig. 3 C), microfilaments are arranged as a meshwork of

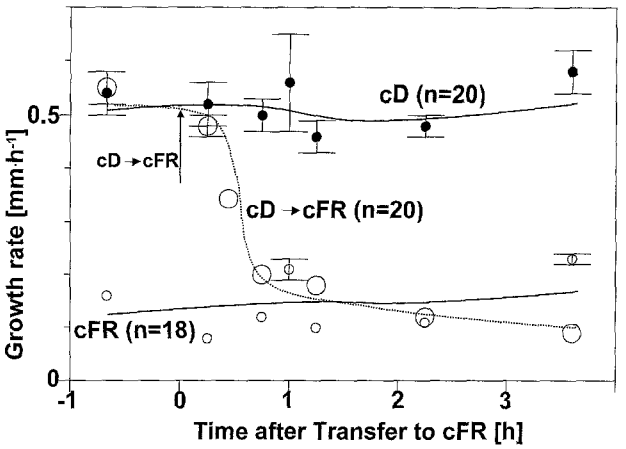


Fig. 5. Time course for the inhibition of mesocotyl growth after transfer from darkness to continuous far-red light. Seedlings were cultivated for 3 days in darkness and transferred at time 0 to continuous far-red light. Solid dots, mesocotyl growth-rate for seedlings that remained in darkness; small open circles, growth rate for seedlings grown for 3 days under continuous far-red light; large open circles, growth rate for seedlings that were transferred from darkness to continuous far-red light at time 0

very fine filaments that are difficult to visualize (Fig. 3 D). Although these filaments are preferrentially oriented parallel to the long axis of the cell, many filaments deviate from this orientation. There were no significant changes in the appearance of these subepidermal microfilaments in response to light and development (data not shown).

In seedlings that were grown in the dark, the condensed array was predominantly observed early in development, up to 3 days (Figs. 3 C and 4 A), after which the condensed array was gradually replaced by the loose array (Figs. 3 A, B and 4 C). From day 6 condensed arrays again became frequent (data not shown). In seedlings that were grown under continuous far-red light, the young epidermal cells were characterized by loose arrays, up to 3 days after sowing (Fig. 4 B). In older cells condensed arrays dominated (data not shown), and 5 days after sowing, when the primary leaves had already pierced the coleoptiles, condensed arrays with some microfilament degradation were observed (Fig. 4 D).

These findings demonstrate that loose arrays of epidermal microfilaments are characteristic of elongating cells (Figs. 3 A, B and 4 B, C), whereas condensed arrays are typical of cells resting prior to elongation (Fig. 3 C) or which have already elongated (Fig. 4 D).

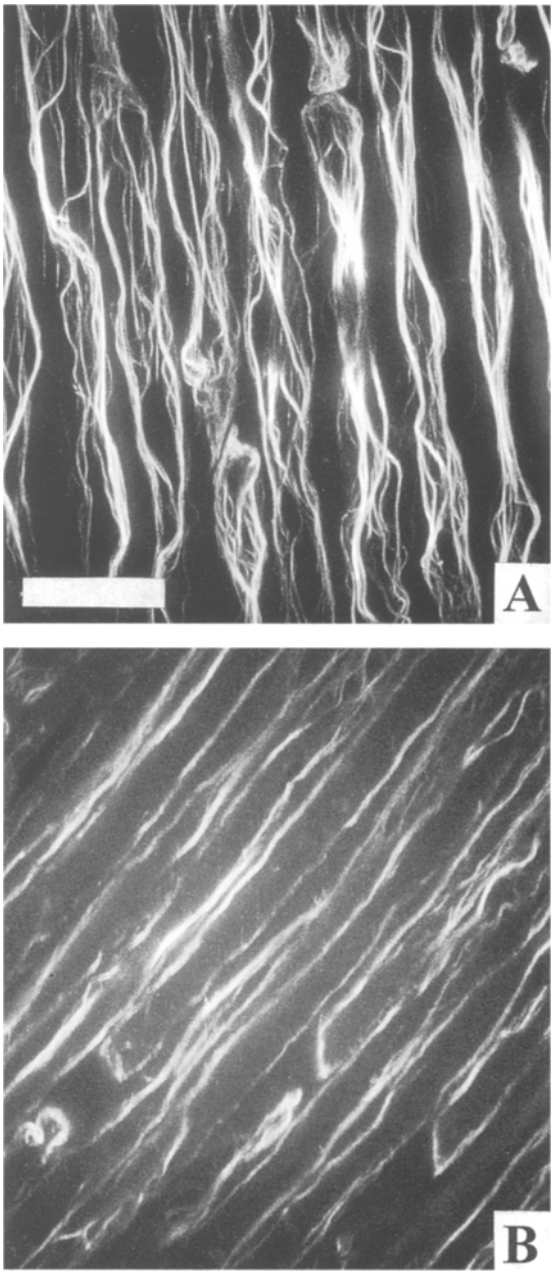


Fig. 6 A, B. Response of actin filaments in mesocotyl epidermal cells upon transfer from darkness to continuous far-red light. **A** Microfilaments in etiolated control mesocotyls, **B** microfilaments 1 h after transfer to continuous far-red light. Bar: 40 μm

The response of microfilaments to light is fast

The most dramatic growth response to light is observed in the mesocotyl. When, three days after sowing, etiolated seedlings are transferred to continuous far-red light, a strong and rapid decrease in growth rate is observed in the mesocotyl (Fig. 5). 30 min after the onset of irradiation, conspicuous

inhibition of growth is observed, and within 1 h growth rate is reduced to that observed in seedlings that had been kept under continuous far-red light throughout their development.

This fast response was chosen to check for fast light responses of microfilaments (Fig. 6). The appearance of microfilaments was dramatically altered after 1 h of far-red light. In the controls kept in the dark, microfilaments formed numerous fine longitudinal strands that fan out into a fine meshwork of cortical filaments near the cell poles (Fig. 6 A). Following transfer to continuous far-red light, microfilaments assumed the condensed array and approached the lateral cell walls (Fig. 6 B). At this time, most of the fine filaments had merged into the thick actin cables that are also characteristic for mesocotyls that had been cultivated in continuous light.

This analysis of mesocotyl growth and microfilament appearance in response to phytochrome reveals close temporal correlation between the formation of condensed microfilament arrays and inhibition of cell elongation.

Discussion

Correlation of coleoptile and mesocotyl light response with that of actin microfilaments in epidermal cells

A comparative study of organ growth, cell elongation, and microfilament appearance produced the following correlations:

1. The light response of the coleoptile can be explained entirely in terms of a phytochrome-induced promotion of epidermal cell elongation (Figs. 1 and 2).
2. In the coleoptile, the time shift between cell elongation in the light compared to the dark is correlated with alterations in the appearance of epidermal actin microfilaments. Loose arrays of numerous microfilaments (Figs. 3 A, 4 B, C, for coleoptiles, and 6 A, for mesocotyls) accompanied by a fine cortical meshwork of actin near the cell poles (Fig. 3 B) were correlated with phases of strong cell elongation (Figs. 1, 2, and 5), whereas condensed arrays of thick actin cables accompanied by reduced polar meshworks (Figs. 3 C, 4 A, D, and 6 B) were characteristic for nonelongating cells (Figs. 1, 2, and 5).
3. The response of microfilaments seems to be confined to the epidermis (Fig. 3 C, D), the target tissue for control of growth in the coleoptile (Kutschera et al. 1987).
4. The phytochrome-induced transition from the loose to condensed microfilament array in the mesocotyl is correlated with the phytochrome-induced inhibition of mesocotyl elongation (Figs. 5 and 6).

The trigger for these changes is continuous far-red light. The only photoreceptor in higher plants that responds to far-red light is phytochrome. The high sensitivity of the responses to even short irradiation with far-red light (e.g., Figs. 5 and 6, for the mesocotyl response) suggests that a very-low-fluence-rate type of response is involved. This is consistent with previous findings reporting a failure to revert the effect of red-light pulses by subsequent irradiation with far-red light (Blaauw and Blaauw-Jansen 1975, Vanderhoef et al. 1979). Our data show that the photoequilibrium induced by far-red light alone is sufficient to trigger the response, explaining the problems with pulse induction and reversion experiments.

The correlations between microfilament arrays and cell elongation in terms of light response, timing, and tissue specificity strongly suggest actin microfilaments play a role in the phytochrome-triggered growth response to light.

Possible function of actin microfilaments in the signal response of cell growth

What is the functional significance of the observed correlations between microfilament arrays and growth response? The following possibilities exist and should be tested experimentally.

As condensation of microfilaments is correlated with phases of reduced growth and bundling might be the result of crosslinking between actin filaments, the mechanical properties of the longitudinal strands could be altered. Bundling of actin filaments has been shown to be important for their mechanical properties in animal cells (Edwards and Bryan 1995) and it is possible that they play a direct role in preventing longitudinal expansion. Longitudinal bundles that are connected with the plasma membrane at the cell poles could be stiffened by mutual crosslinking of actin filaments, or could generate a force via myosin-mediated sliding, holding the cell poles together. In *Avena* Thimann et al. (1992) have found that inhibition of coleoptile segment elongation by an osmoticum is accompanied by strong bundling of longitudinal actin filaments. Grabski and Schindler (1995) have shown that reduced growth of soybean root cells is associated with more rigid transvacuolar strands of actin filaments. Furthermore, auxin-induced growth promo-

tion is correlated with a release of tension in these strands in vivo, whereas growth inhibition by cytokinin has the opposite effect (Grabski and Schindler 1996).

In addition to a possible mechanical role, actin filaments might control growth via the intracellular transport of vesicles. They are known to be involved in cytoplasmic streaming (Nagai and Fukui 1981) and intracellular vesicle transport (Pope et al. 1979). Bundling of longitudinal filaments could prevent the pole-directed transport of vesicles containing cell-wall material or molecules that are required for wall loosening. When actin filaments are destroyed by Cytochalasin D, inhibition of coleoptile segment growth has been observed (Thimann et al. 1992, Wang and Nick unpubl.). These observations cannot be explained as a limitation of growth by bundled microfilaments, but seem to indicate that actin has a highly drug-sensitive, but growth-promoting function. In this context, the fine polar meshwork of actin microfilaments in the loose array, characteristic of elongating cells (Fig. 3 B), should be mentioned. These fine cortical actin filaments could be responsible for the spatially ordered distribution of membrane material (Meske and Hartmann 1995), enzymes enhancing cell-wall extensibility, or the distribution of membrane receptors (Cox and Muday 1994).

The observed changes in actin filament structure, the possible binding of actin filaments to the plasma membrane and other cellular components as well as mutual crosslinking between microfilaments is expected to involve actin-binding proteins. Future work will be directed to the identification and characterization of such proteins. In the meantime, a rice mutant (Yin-Yang) has become available, in which the response of microfilaments is disturbed in response to auxin (Nick et al. 1997). Analysis of this mutant should permit molecular approaches to the role of actin filaments in plant growth.

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