Planta (2001) 212: 184–189

Planta

Gravitropic microtubule reorientation can be uncoupled from growth

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Received: 23 November 1999 / Accepted: 10 May 2000

Abstract. The causal relationship between gravitropic growth responses and microtubule reorientation has been studied. Growth and microtubule reorientation have been uncoupled during the gravitropic response of maize (*Zea mays* L.) coleoptiles. Microtubule orientation and growth were measured under three different conditions: (i) a gravitropic stimulation where the growth response was allowed to be expressed (intact seedlings were displaced from the vertical position by 90°), (ii) a gravitropic stimulation where the growth response was suppressed (coleoptiles were attached to microscope slides and kept in a horizontal position), (iii) suppression of growth in the absence of gravitropic stimulation (coleoptiles were attached to microscope slides and kept in a vertical position). It was found that (i) gravitropic stimulation can induce a microtubular reorientation from transverse to longitudinal in the upper (slower growing) flank of the coleoptile, and an inhibition of growth; (ii) the reorientation of microtubules precedes the inhibition of growth; (iii) the gravitropic response of microtubules is weaker, not elevated, when the inhibition of growth is artificially enhanced by attaching the coleoptiles to a slide; and (iv) artificial inhibition of growth in the absence of gravitropic stimulation cannot induce a microtubular response. Thus, the extent of microtubule reorientation is not correlated with the extent of growth inhibition. Moreover, these findings demonstrate that microtubules do not reorient passively after growth changes, but actively in response to gravitropic stimulation.

Key words: Coleoptile (gravitropism, growth) – Gravitropism – Growth (coleoptile) – Microtubule reorientation – *Zea* (gravitropism)

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Introduction

Cortical microtubules are thought to regulate the shape of plant cells by directing the movement of cellulose synthase complexes in the plasma membrane (Giddings and Staehelin 1988, 1991). The way in which the cellulose microfibrils are laid down determines the direction of cell expansion. Microtubules adopt different alignments when the direction of cell expansion changes. For example, in response to phototropic and gravitropic stimulation of plant organs such as coleoptiles and stems, the cortical microtubules underneath the outer epidermal wall reorient (Nick et al. 1990). In cells that undergo rapid elongation, cortical microtubules are generally found to be transverse, whereas in non-growing or slowly growing tissue they are often oriented longitudinally. In the case of the gravitropic bending of maize coleoptiles, microtubules on the faster growing lower flank of the coleoptile are transverse, while microtubules on the slower growing upper flank assume a longitudinal orientation with respect to the long axis of the cell (Nick et al. 1990). This gradient of reorientation seems to be related to a lateral transport of auxin that is observed in response to gravitropic stimulation (Dolk 1936; Parker and Briggs 1990). The lateral auxin transport causes a depletion of endogenous auxin in the upper coleoptile flank, whereas auxin accumulates in the lower flank. Auxin depletion causes a longitudinal orientation of microtubules, whereas they become transverse in response to addition of auxin (Bergfeld et al. 1988; Nick et al. 1990; Zandomeni and Schopfer 1993). The time course and spatial pattern of gravitropically induced microtubule reorientation are compatible with a model in which a gravitropic stimulus induces gravitropic bending via: (i) triggering lateral auxin transport towards the lower coleoptile flank, (ii) a reorientation response of cortical microtubules to the local concentration of auxin, and (iii) a shift in the orientation in which microfibrils are laid down, controlled by the underlying microtubule template.

However, microtubule reorientation also occurs in response to mechanical stimulation and tissue bending

(Zandomeni and Schopfer 1994). Mechanical extension or compression of the epidermis causes cortical microtubules to reorient perpendicular to the direction of the effective force. This observation and further investigations (Fischer and Schopfer 1998) led to the hypothesis that microtubule reorientation, rather than being a mediator of stimulus-triggered growth changes, might be regarded as a response to these stimulus-triggered growth changes.

In this article we focus on the reorientation of microtubules and growth changes induced by gravitropic stimulation. By means of microinjection studies, different steps during microtubule reorientation (on the upper coleoptile side) from transverse to longitudinal in gravitropically stimulated maize coleoptiles could be observed (Himmelspach et al. 1999). For these experiments, maize coleoptiles were mounted onto microscope slides with adhesive. This attachment prevents coleoptiles from bending and inhibits growth. We approach the question of whether this growth inhibition affects microtubule reorientation.

Materials and methods

Plant material

Caryopses of maize (*Zea mays* L. cv. Percival; Asgrow, Bruchsal, Germany) were rinsed in tap water for 1 h and then sown on moist paper towels. The seedlings were cultivated at 25 °C under continuous red light (0.2 Wm^{-2}) for 2.5 d followed by 1 d in darkness. Directly before the start of the experiment they were again kept in red light for 1 h, resulting in a predominantly transverse microtubule orientation. The gravitropic stimulation and growth measurements were carried out in the red light used for cultivation. For gravitropic stimulation, seedlings were positioned horizontally with the flat side of the coleoptile adjacent to the caryopsis facing upwards. In the experiments where growth was inhibited, coleoptiles were mounted onto microscope slides with medical adhesive (B-401; Factor II Incorp., Lakeside, Arizona, USA), well supplied with water, and kept either in a horizontal or in a vertical position.

Immunolocalization and evaluation of microtubule orientation

Coleoptile segments (1.5 cm) were excised and fixed for 1 h at room temperature in 3.7% (w/v) paraformaldehyde in microtubule-stabilising buffer [MSB: 50 Pipes, 5 mM EGTA, 1 mM $MgSO_4$, 1% (w/v) glycerol and 0.5% (v/v) Triton-X 100, pH 6.9]. For gravitropically stimulated seedlings the upper coleoptile flank was marked by an incision. Following fixation, epidermal strips were peeled from the coleoptile segments and mounted on microscope slides with the outer side of the epidermis facing upwards. The strips were then blocked for 20 min at room temperature with normal goat serum (Sigma) diluted 1:20 in Tris-buffered saline [TBS: 150 mM NaCl, 20 mM Tris-HCl, and 0.25% (v/v) Triton-X 100, pH 7.4] and then incubated with mouse monoclonal antibodies against α- and β-tubulin (Amersham) diluted 1:100 in TBS for 1 h at room temperature. The epidermal peels were washed three times for 5 min each in TBS before incubation with a fluorescein-isothiocyanate-conjugated secondary antibody (anti-mouse immunglobulin G from goat; Sigma) diluted 1:50 in TBS for 1 h at room temperature. After final washing of at least 5 times for 5 min in TBS the strips were mounted in anti-fade medium (Moviol containing 0.1% *p*-phenylenediamine) and microtubules were imaged with a confocal laser microscope (DM RBE; Leitz) using an Argon-Krypton laser at 488 nm excitation, a beam splitter at 510 nm and a 515-nm emission filter. For areas of microtubules twice as long as the cell width, the orientation of microtubules adjacent to the outer cell wall of epidermal cells was classified into the following five groups: randomly oriented, transverse (0°), 30° oblique (30°), 60° oblique (60°) and longitudinal (90°).

Measurement of growth and gravitropic curvature

The coleoptiles ($n > 30$) were marked by two small dots of black ink at a distance of 10 mm. In the case of gravitropically stimulated seedlings both coleoptile flanks were marked. The distance between the two dots was measured with a flexible ruler at different time points, and the length as a percentage of the original length interval (100%) was plotted against time. Gravitropic curvature was determined according to Nick and Schäfer (1988).

Results

In order to investigate the correlation between microtubule reorientation and growth during the gravitropic response of maize coleoptiles, we examined these two parameters for three different coleoptile treatments (see Fig. 1): (i) a gravitropic stimulation with unimpaired growth response, (ii) a gravitropic stimulation where the growth response was prevented, (iii) suppression of growth in the absence of gravitropic stimulation.

Microtubule reorientation during unimpaired gravitropic bending

The time course of microtubule reorientation after gravitropic stimulation was followed in populations of freely growing, unattached coleoptiles (Fig. 1a) by immunocytochemistry and subsequently used as reference for the microtubule response in coleoptiles attached to slides. Figure 2 shows frequency distributions of microtubule reorientation on the upper and the lower flanks of coleoptiles that had been gravitropically

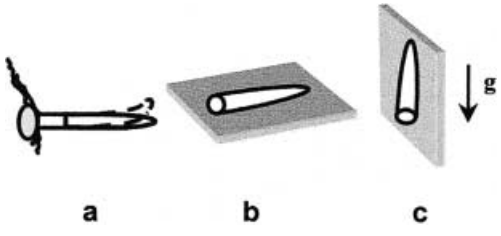

Fig. 1a–c. Scheme of the three different coleoptile arrangements used in this study. **a** Gravitropic stimulation with expression of the growth response allowed, leading to coleoptile bending: intact seedlings were displaced from the vertical position by 90°. **b** Gravitropic stimulation but growth response prevented: coleoptiles were attached to microscope slides, kept in a horizontal position (displaced from the vertical position by 90°; gravitropic stimulus of 1 *g*) and supplied with water. **c** No gravitropic stimulation and growth suppressed: coleoptiles were attached to microscope slides, kept in a vertical position (no gravitropic stimulation) and supplied with water. *g*, gravity vector

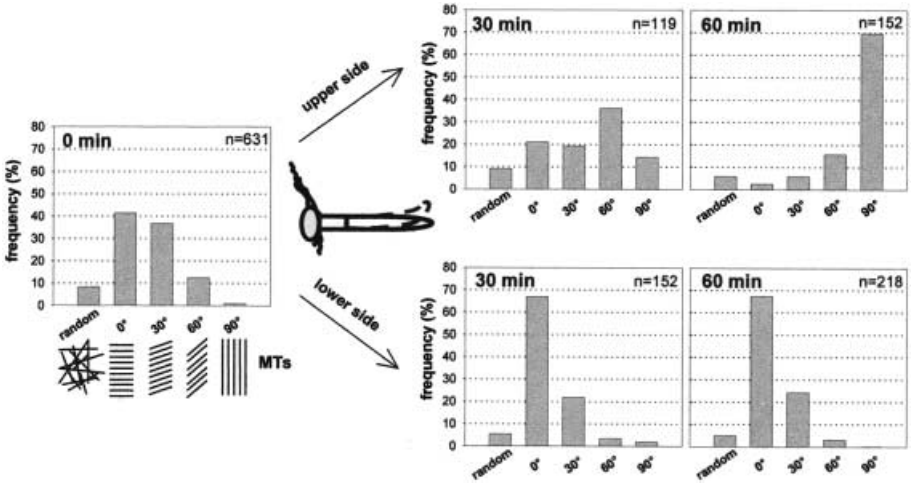

Fig. 2. Time course of microtubule reorientation during the gravitropic response: frequency distribution of microtubule orientation (determined by immunocytochemistry) on the upper and lower coleoptile flanks prior to (0 min) and following gravitropic stimulation (30 or 60 min of stimulation at 90°). The angles are defined with respect to the short axis of the cell (see Nick et al. 1990), discriminating between transverse (0°), slightly oblique (30°), steeply oblique (60°), longitudinal (90°) and randomly oriented microtubules. Note that microtubules become predominantly longitudinal on the upper side and transverse on the lower side. n = number of microtubule areas counted

stimulated. On the lower side microtubules changed their orientation from slightly oblique to predominantly transverse. This reorientation process was completed by 30 min. For the upper coleoptile flank, microtubules changed their orientation from slightly oblique to longitudinal. The time to reach this final longitudinal orientation of microtubules was somewhat longer (60 min). In contrast to this relatively fast response of the microtubules, only small effects could be detected for gravitropic bending (Fig. 3a) and changes of growth rate within the first 30 min (Fig. 3b). Thus, microtubule reorientation was initiated and completed faster than differential growth. During gravitropic bending, growth was redistributed from the upper towards the lower flank of the coleoptile (Fig. 3b).

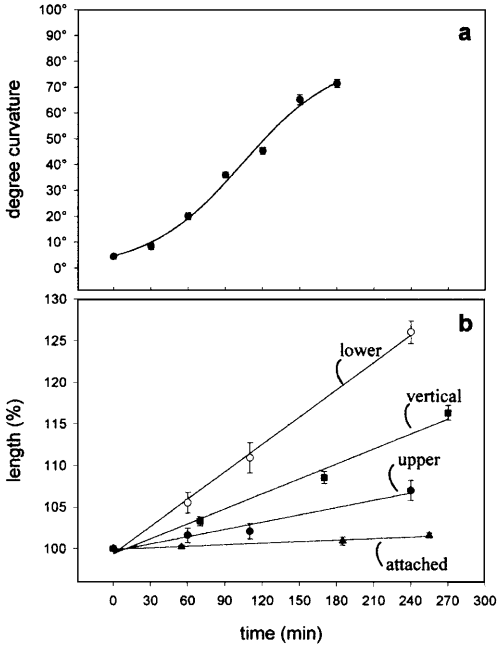

Fig. 3a,b. Time course of the gravitropic response. **a** Coleoptile bending induced by continuous gravitropic stimulation (displacement from the vertical by 90°). **b** Coleoptile growth, measured simultaneously, on the upper (*closed circles*) and lower (*open circles*) coleoptile flanks, as well as growth of vertical, unstimulated controls (*closed squares*). Growth was also measured on the upper side of isolated coleoptiles that were attached to microscope slides, kept in a horizontal position (gravitropic stimulus of 1 *g*), and supplied with water (*closed triangles*; for coleoptile treatment see Fig. 1b). Attachment of the coleoptile to the slide blocks growth almost completely. Mean values ± SE (n = ■–■)

Microtubule reorientation in response to gravity when gravitropic bending is suppressed

Isolated coleoptiles were attached to microscope slides, kept in a horizontal position (thus administering a gravitropic stimulus of 1 *g*), and supplied with water (Fig. 1b). With this treatment, growth was rapidly and almost completely inhibited to an extent that even exceeded the growth inhibition observed in the upper flank of gravitropically stimulated, but freely bending coleoptiles. Whereas the length increment was reduced to 50% in the upper flank of the freely bending coleoptiles within 3 h of stimulation, it was inhibited down to a value of 14% in case of the attached coleoptiles (Fig. 3b). The orientation of microtubules in epidermal cells of the upper coleoptile flank was examined at different time points after the onset of the treatment. The reorientation from transverse to longitudinal was almost complete after 60 min (Fig. 4). A compelling difference between attached and freely growing coleoptiles is observed for the final state of microtubule orientation. Ninety minutes after the onset of gravitropic stimulation, the number of longitudinally oriented microtubules was only about 50% when coleoptiles were bound to the slide (Fig. 4). However, when coleoptiles were allowed to bend freely in response to the gravitropic stimulus, after 60 min about 70% of the microtubules had already adopted a longitudinal orientation (Fig. 2). This shows that microtubules in the upper flank of freely bending coleoptiles respond to a stronger extent than the microtubules in attached coleoptiles. In contrast, the growth inhibition was much more pronounced in the attached coleoptiles than in the freely bending coleoptiles (Fig. 3b). Thus the extent of microtubule reorientation was not correlated with the

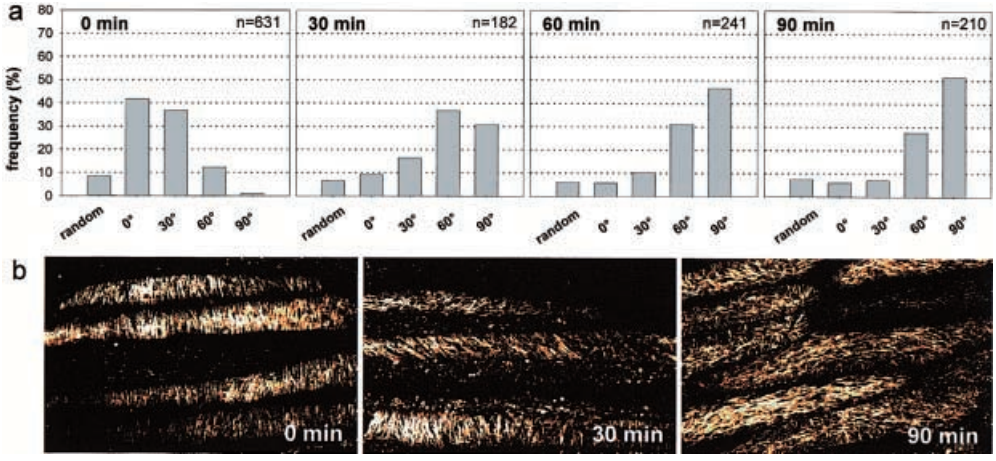

Fig. 4a,b. Microtubule reorientation in response to gravity under suppression of bending. **a** Frequency distribution of microtubule orientation at different times after the onset of gravitropic stimulation in the upper coleoptile flank. Isolated coleoptiles were mounted onto microscope slides, held in a horizontal position (gravitropic stimulus of 1 *g*), and supplied with water (for coleoptile treatment see Fig. 1b). Despite tissue attachment, microtubules in the upper flank of attached coleoptiles still undergo a significant gravitropic response. However the response is weaker as compared to microtubule reorientation in freely growing coleoptiles (see Fig. 2). **b** Images of immunofluorescence-stained microtubules in epidermal peels at time points 0, 60 and 90 min. n = number of microtubule areas counted

inhibition of growth. The gravitropic response of microtubules is even weaker when the inhibition of growth is artificially enhanced.

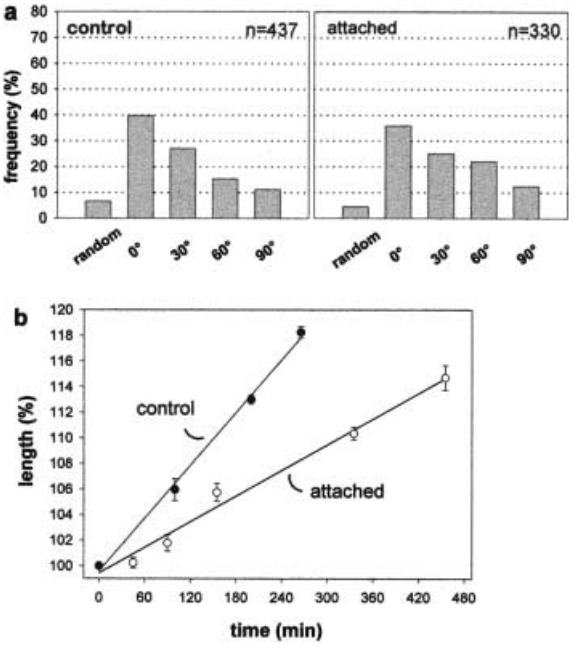

Fig. 5a,b. Inhibition of growth does not induce microtubule reorientation. **a** Coleoptiles were excised, mounted onto slides with adhesive, held in a vertical position (i.e. without a gravitropic stimulus) and supplied with water (for coleoptile treatment see Fig. 1c). After 1 h (in red light) the tissue was fixed and microtubules in epidermal peels (from the unglued side) were stained by immunocytochemistry in order to determine the microtubule orientation. In controls, epidermal peels of untreated seedlings were also immunostained. **b** In addition, growth was measured for the attached coleoptiles (*open circles*) and for the non-attached coleoptiles (*closed circles*). The attachment of the coleoptiles slowed growth to less than 25% of the control value (**b**), whereas microtubule orientation was not affected (**a**). n = number of microtubule areas counted; mean values ± SE

Microtubule reorientation during impaired growth without gravitropic stimulation

In order to test whether inhibition of growth produced by the attachment per se could induce a reorientation of microtubules in the absence of gravitropic stimulation, the experiment of Fig. 4 was varied such that the attached coleoptiles were oriented in a vertical position (Fig. 1c). Again, growth was inhibited dramatically by the attachment (down to 25% of unattached controls during 3 h, see Fig. 5b), but not completely. This can be explained by the elasticity of the coleoptile, which allows the free side of the coleoptile to expand to some degree. In contrast to this pronounced growth reduction (Fig. 5b), microtubule orientation remained essentially unaltered (Fig. 5a). Thus, growth inhibition alone, i.e. in the absence of gravitropic stimulation, does not induce a microtubular response. This result demonstrates that growth and microtubule orientation can be uncoupled.

Discussion

What is the trigger for microtubule reorientation?

It has been debated for several years whether microtubule reorientation is causally linked to changes in growth. Phototropism and gravitropism are excellent processes for addressing this question because they are fast responses, can be triggered by signals, and are exclusively brought about by a response of cell expansion. For the gravitropic response of coleoptiles a model was proposed (Nick et al. 1990) that includes redistribution of auxin as a consequence of graviperception. According to this model the auxin redistribution causes a reorientation of cortical microtubules in the epidermal cells leading to a transverse microtubule orientation in

the lower coleoptile flank and the formation of longitudinal microtubule arrays in the upper flank. This gradient of microtubule reorientation was proposed to be responsible for a growth gradient: enhancement of growth on the lower coleoptile side and suppression of growth on the upper side. Finally, the differential growth of the two flanks causes bending of the coleoptile.

Our present data show that microtubule reorientation induced by gravitropic stimulation (Fig. 2) actually precedes changes in growth and gravitropic bending (Fig. 3) during the gravitropic response of maize coleoptiles. A similar redistribution of growth had previously been shown for the phototropic response of maize coleoptiles (Iino and Briggs 1984). It should be mentioned, however, that for the gravitropic response of maize roots, microtubule reorientation was found to be slower than gravitropic bending (Blancaflor and Hasenstein 1995). In addition, pharmacological studies have indicated that microtubules are not necessary for the differential growth response to root gravistimulation (Baluška et al. 1996). For maize coleoptiles it has been shown that gravitropism is strongly reduced by the use of the microtubule-disrupting drug ethyl-*N*-phenylcarbamate (Nick et al. 1991b). But this inhibition of the gravitropic response is probably due to a failure in perception of gravity, which also involves microtubules. This indicates that the correlation between the gravitropic growth response and microtubule organisation may be complex. Moreover, there are cases where differential growth or growth regulation does not always result in corresponding differences in microtubule alignment (e.g. Nick et al. 1991a). Nevertheless, cortical microtubules are usually oriented transverse to the longer axis of the cell in strongly growing cells (Williamson 1991; Cyr 1994; Cyr and Palevitz 1995; Hush and Overall 1996), and longitudinal in non-growing cells (Iwata and Hogetsu 1988; Laskowski 1990; Nick 1998). This led some authors to propose that microtubule reorientation could be just a secondary effect of growth changes (Fischer and Schopfer 1997, 1998). We therefore asked whether growth changes alone can induce microtubule reorientation. In our experiment this is not the case. Inhibition of growth by attaching the coleoptiles to slides is not sufficient to cause microtubule reorientation (Fig. 5). This finding is not consistent with a model where microtubules merely respond to changes in growth rate.

The time course of microtubule reorientation on the upper coleoptile side of gravistimulated and attached coleoptiles also does not show a simple correlation between growth rate and microtubule orientation (Fig. 4). Although growth was almost completely blocked (a length increment of only 1.4% over 3 h, Fig. 3b) the microtubule reorientation process was slower than for the unglued, gravitropically stimulated control (compare Fig. 4, 60 min, with Fig. 1, 60 min), where growth was almost three times faster (Fig. 3b). This indicates that a certain level of growth is required to allow microtubule reorientation or that there is a feedback loop between growth and microtubule orientation. It is also possible that mechanical forces caused by coleoptile bending, which is prevented in our experiment, usually reinforce the tendency of microtubules to adopt a longitudinal orientation. Alternatively, the gravitropically induced microtubule reorientation could be a systemic property of the whole plant organ such that reorientation on both flanks of the coleoptile would not proceed independently but in a co-ordinate manner. In such a case, mounting the lower part of the coleoptile onto the slide could inhibit growth on that side and presumably microtubule reorientation. This could co-ordinately inhibit the reorientation process on the upper coleoptile flank. For instance, redistribution of auxin from the upper to the lower flank could be impaired by the inhibition of growth on the lower flank caused by attachment of the coleoptile to the glass.

In summary, microtubule orientation can be uncoupled from growth. This finding is contradictory to the assumption that microtubule reorientation is just secondarily triggered by growth changes or tissue strains, as has been proposed by Fischer and Schopfer (1997, 1998). The results of the present study demonstrate that changes in growth rate are not sufficient to mimic the effect of gravitropic stimulation on microtubule orientation, even if they are more drastic than those occurring during gravitropic bending, and that artificial changes in growth rate do not support (but even weaken) gravitropic microtubule reorientation. Thus, microtubules must respond to gravitropic stimulation directly and not to changes in cell growth induced by gravity. Microtubule reorientation seems to be a primary part of the gravitropic response and not merely a secondary effect of the strains produced by bending. The most straightforward explanation is a gravitropically induced lateral transport of auxin (Cholodny 1927; Dolk 1936; Parker and Briggs 1990) causing a local auxin depletion in the upper coleoptile flank triggering the reorientation of cortical microtubules. This is consistent with recent results (Takesue and Shibaoka 1999) that have shown in azuki bean epicotyls that auxin can induce microtubule reorientation by a mechanism that does not involve changes in the rate of cell elongation. However, this does not exclude the possibility that growth can respond to tropistic stimulation by a mechanism independent of microtubules (Nick and Schäfer 1994). The relationship between microtubule orientation and growth is complex, because there appears to be feedback from the cortical microtubules to the cell wall (Fisher and Cyr 1998; for review, see Williamson 1991), and because growth can be regulated by several, and possibly numerous, independent pathways.

Although this study does not generally exclude the possibility that microtubules can respond to changes in growth rate (Fischer and Schopfer 1997), it demonstrates that the microtubular response to gravitropic stimulation can be separated from growth. For the molecular mechanism underlying the reorientation response it would be expected that molecules that mediate a coupling of auxin-triggered signal transduction to tubulin assembly/disassembly or microtubule movement are involved, as suggested by studies involving microinjection of fluorescence-labelled tubulin (Himmelspach et al. 1999).

This work was supported by a grant from the Landesgraduiertenförderung (Baden-Württemberg) to Regina Himmelspach.

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