Coordinated cell elongation alone drives tropic bending in stems of the mushroom fruit body of *Coprinus cinereus*

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Abstract: During tropic bending in the stem of the mushroom fruit body of *Coprinus cinereus* the majority of extension occurred in the upper 20–30% of the stem. By attaching inert markers to the stem, it was shown that the outer flank of the bend initially has a faster rate of extension, although the inner flank matches this growth rate later in the response. Thus bending results from differential enhancement of growth rate rather than sustained differences. Large voids, up to 85 μm in diameter, observed in tropically bent stems showed no significant difference in number between inner and outer flanks but are implicated in bending because of their absence from unbent stems. Such voids may prevent the propagation of cracks through the stem tissue during bending. Creases at the external and lumen surfaces were also peculiar to bent stems and could represent constrictions caused by localized accumulation of stresses. Cell morphometric analysis of transverse sections of both flanks of the bend revealed no significant differences in hyphal diameter, distribution, or populations of cell types, but cells of the outer flank were four to five times longer than those of the inner. Thus, tropic bending requires only an increase in length of pre-existing inflated hyphae in the outer flank tissue.

Key words: *Coprinus cinereus*, fungi, hyphae, tropism, differential growth.

Résumé : Au cours de la courbure tropique de la tige des basidiomes du *Coprinus cinereus*, la majorité de l'extension survient dans les 20–30% de la partie supérieure de la tige. En attachant des marqueurs inertes sur la tige, les auteurs ont montré que le côté externe de la courbure s'allonge plus vite, bien que le côté interne atteigne la même vitesse de croissance, plus tard au cours de la réaction. Ainsi la courbure résulte d'une accélération différentielle du taux de croissance plutôt que d'une différence constante. Les grands espaces vides, atteignant jusqu'à 85 μm en diamètre, observés dans les tiges tropiquement courbées, ne montrent pas de différences significatives dans leurs nombres entre le côté interne et le côté externe, mais sont impliqués dans la courbure puisqu'ils sont absents dans les tiges non courbées. Ces espaces vides pourraient prévenir le fendillement dans la tige au cours de la courbure. Des replis observés sur les surfaces externes et du lumen sont également limités aux tiges courbées et pourraient représenter des constriction causées par l'accumulation de stress. L'analyse morphométrique des cellules sur sections transverses des deux côtés de la courbure ne montre aucune différence significative dans le diamètre des hyphes, la distribution ou les populations des cellules, mais les cellules de la face externe sont 4–5 fois plus longues que celle de la face interne. La courbure tropique ne nécessite que l'élongation de cellules gonflées pré-existantes dans les tissus du côté externe.

Mots clés : *Coprinus cinereus*, champignon, hyphes, tropisme, croissance différentielle.
[Traduit par la rédaction]

Introduction

Tropic bending is a simple developmental, pattern-forming process. Its control demands that the organism has a perception system and a means of coupling this to control differential tissue growth. Bending mechanisms in plants have been studied extensively, but because of the early confusion with plants, very little work has been carried out on fungi. Although distinct from plants, fungi have structurally similar cylindrical organs involved in tropisms. It seems reasonable to believe, therefore, that parallels may exist in mechanisms used to achieve bending. A variety of growth rate patterns during tropic bending in plants have been reported. Plant roots are characteristically positively gravitropic, whereas stems and shoots are usually negatively gravitropic. The direction of tropic bending is irrelevant to discussion of mechanisms.

In the following descriptions, work on the different plant organs is put into context by referring to events in the outer flank (tissues on the outside circumference of the bending curvature) in contrast to those occurring in the inner flank (tissues on the inside circumference of the bend). Carrington and Firn (1) showed that differential growth involved complete, or almost complete, cessation of growth in certain segments of the inner flank, and normal or slightly accelerated growth of the outer flank of sunflower (*Helianthus annuus* L.) hypocotyls. Jaffe et al. (2) reported that the rate of extension of the inner flank of the maize (*Zea mays* L.)

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seedling shoot did not change after reorientation, while the outer flank accelerated. Later in this response, there was a slowing in the rate of extension of the outer flank. In *Xanthium*, it has been suggested that a slight contraction in the inner flank of the stem may be responsible for production of the bend (3). Berg et al. (4) also pointed to a shrinkage in the inner flank with a rapid increase in growth rate of the outer flank of the sunflower hypocotyl. "Shrinkage" due to mechanical compression has not been excluded in these studies. Interestingly, a resumption of growth was observed in the basal regions of the hypocotyl that had ceased to elongate in the vertical seedlings (4). This reaction was delayed, the movement of the bend being basipetal. An initial slight positive gravitropic reaction in maize roots was discussed by Ishikawa et al. (5) in a similar study to the one presented here. They measured surface extension in zones and also reported a phase in the later stages of gravicurvature where the overall bending pattern was reversed, i.e., growth was more rapid in the inner flank of the root, resulting in the root straightening and preventing overshoot of the vertical. Similar observations have been made with roots of *Lepidium* (6).

We have studied *Coprinus cinereus* (Schaeff:Fr) S.F. Gray sensu Konr. because of its ease of cultivation and reliable and rapid tropic response. Normal extension in vertical stems of *C. cinereus* was investigated by Hammad et al. (7) who described two phases of growth. The first phase was a period of relatively slow extension rate, which was followed by a rapid period of extension correlated to the onset of meiosis in the maturing cap. Most of the rapid phase extension, at an average rate of 6.6 mm $\cdot$ h^{-1}, occurred in the upper 20–30% of the stem. This rapid growth was attributed solely to an increase in cell size. Further studies (8) showed that the stem of *C. cinereus* contains two populations of hyphae: narrow and inflated. During normal vertical growth of *Coprinus* stems, there is evidence that inflated hyphae inflate further and that the proportion of narrow hyphae declines as the stem grows from 45 to 70 mm, indicating that stem extension involves both an increase in cross-sectional area of inflated hyphae and recruitment of narrow hyphae into the inflated population. Cell size distribution across the stem of *C. cinereus* also changes as the stem increases in length, cells becoming on average larger towards the central lumen (7, 9).

More recently, tropic responses of mushroom fruit bodies have been characterized in detail using gravitropism as a noninvasive means of investigating this developmental process. By attaching inert markers to the stem, asymmetric extension between the inner and outer flank of gravitropically bent stems was demonstrated and measured. Cytological studies of gravitropism were carried out to determine the morphometric patterning that achieved the gravitropic curvature, greatly amplifying previous reports (10, 11).

Materials and methods

Organism

For all experiments the basidiomycete fungus *C. cinereus* was used. The vegetative dikaryon was grown on complete medium (12) at 37°C in the dark for 3 days. Fruit bodies were obtained by inoculating sterilized horse dung with the dikaryon, incubating at 37°C for 3–4 days in the dark, and then transferring the cultures to a 27°C incubator with a 16 h light : 8 h dark photoperiod (average illuminance 800 lx).

Asymmetric stem extension

Inert glass beads of approximately 1 mm in diameter were attached to opposite sides of vertical *Coprinus* stems. No adhesive was necessary as the moist, fibrous stem held beads in place adequately. Stems were secured at the base in a horizontal orientation and positioned so that beads were on the extreme inner and outer flank of the gravitropic bend. Each stem was photographed using a Nikon FE camera with a 150-mm zoom and Kodak 160 Tungsten slide film. Photographic records were taken every 10 min from the start of the experiment for at least 3 h, or until the stem had reached the vertical. Measurements were made by projecting the positives onto a wall and measuring distances between beads by hand. Distances could be measured to an accuracy of at least $\pm$ 0.1 mm.

Microscopy

Stem material was taken from gravistimulated stems at the region that showed the greatest degree of gravitropic bending (invariably in the upper 20–30% of the stem). In gravistimulated stems used for transverse sectioning, the outer flank of the bent stem was removed from the inner flank by cutting longitudinally down the axis using a very sharp blade. Material was labelled with code numbers and the study was carried out blind (i.e., the identity of each section measured was not known during the measurement procedures), ruling out experimental bias. Where material was to be used for radial longitudinal sections the bent region was kept whole. By attaching a blade of grass to the outer flank of the bend prior to fixation, it was possible to identify the correct orientation of the stem during and after sectioning.

Stem sections approximately 3 mm in length were fixed in formacetic alcohol before being dehydrated in an alcohol series (see method in 7). The tissue was embedded in glycolmethacrylate resin using a Historesin embedding kit (Reichert-Jung). Sections were cut using an LKB 2218 Historange microtome using disposable glass knives. Sections between 2 and 4 μm thick were used and were stained using toluidine blue. Light micrographs were taken using a Leitz Diaplan microscope with a Wild Photoautomat MP545 camera and Kodak technical pan 2415 film. Cell measurements were made using Skye S1730 image analysis software (Skye Instruments Ltd., Unit 5, Ddole Industrial Estate, Llandrindod Wells, Powys, Wales, U.K.) or a Measure Mouse Computer system (Analytical Measuring Systems, Pampisford, Cambridge, U.K.). Transverse sections were measured in transects running from the exterior of the stem to the lumen and data recorded in strict order. This allowed a profile of cells running to the centre of the stem to be plotted. In longitudinal sections, only inflated hyphae were measured as narrow hyphae weave through the stem.

Results

Macroscopic stem extension

Figure 1 is a plot of elongation of the inner and outer flanks of horizontal stems bending over a 4.5-h period. All stems in the study increased in length about 25%. The majority of this extension occurred in the apical region (although the extreme apex grows less). In fact, 78% of the measured extension occurred in the apical 16 mm of the stem. Extension occurred throughout the stem, however, and was consistently greater on the outer flank than the inner in the ratio 3:2, measured over the entire length of the stem.

Despite the difference in the overall length of the stem, the inner and outer flanks of the bending stem eventually

Fig. 1. Extension of *Coprinus* stems during gravitropic bending shown as the extension of inner (hatched bars) and outer (open bars) flanks in successive 4-mm zones along the entire length of the stem after 260 min of gravistimulation. Apex is at position zero.

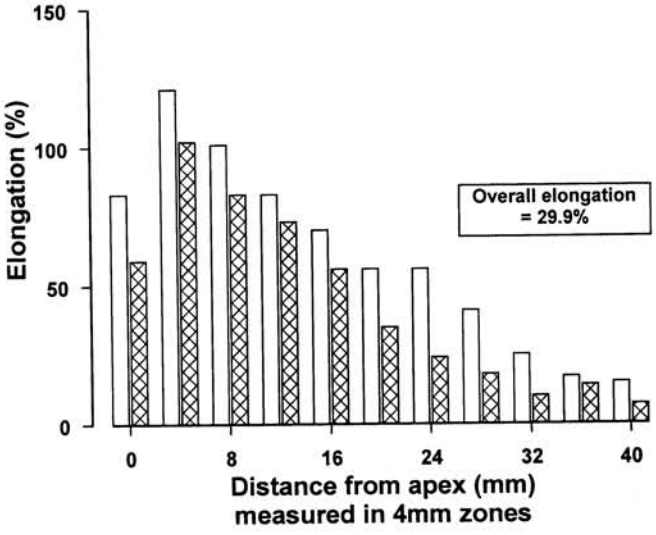


Table 1. Differential elongation rates of the inner and outer flanks of a horizontal stem of *Coprinus cinereus*.

	Time interval (min)			
	0–30	50–100	150–200	210–260
Upper side	0.14	0.13	0.34	0.49
Lower side	0.12	0.33	0.34	0.49

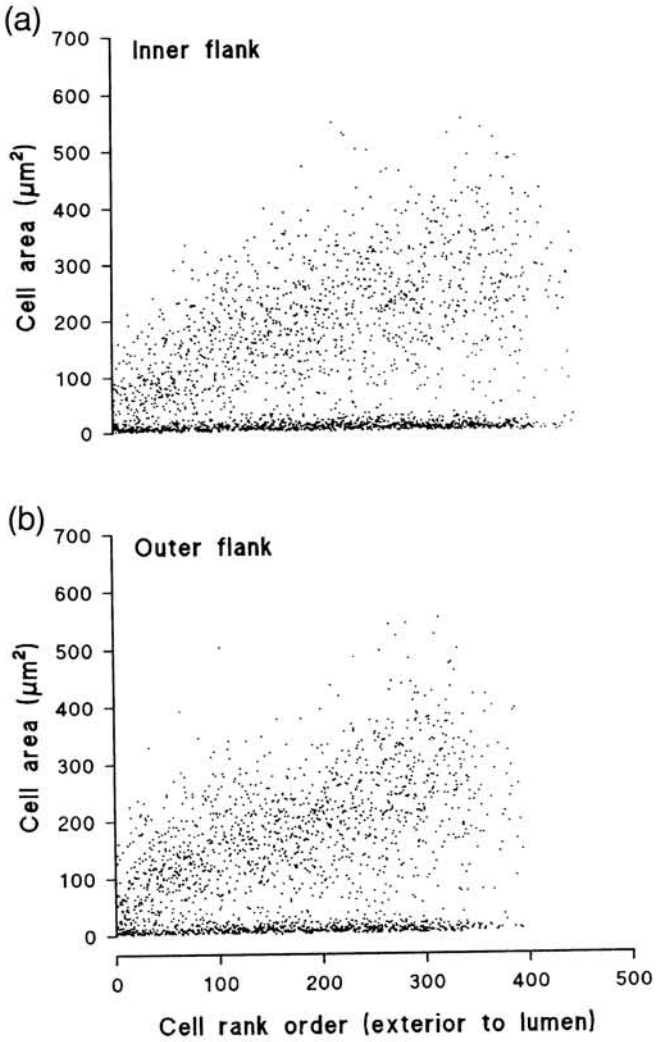
Note: Values are the slopes of linear regressions calculated over the indicated time intervals.

elongated at about the same rate (which was higher than the rate of elongation prior to reorientation). What caused the bending was that the outer flank accelerated to that rate almost immediately, whilst the inner flank accelerated to the maximum rate over a period of 2 h (Table 1; and see Fig. 7 in Moore et al. (11)). The most rapid phase of increase in the apex angle coincided with the time interval over which the elongation rate of the outer flank was two- to three-fold greater than that of the inner.

Microscopic analysis of stem extension

The dramatic changes in the bending stem were examined by a microscopic study involving morphometric analysis of the cell patterning that led to the gravitropic curvature (preliminary results in 10). Initially, three gravistimulated stems were examined at the cellular level; the results are presented in Table 2. The image analysis programme used measures areas of hyphal profiles observed in the microscope sections. Initial examination confirmed the presence of two hyphal populations (narrow and inflated hyphae) described by Hammad et al. (8). In the three gravistimulated stems the analysis of inner and outer flanks of gravitropically responding cells at the point of maximum curvature revealed that cell cross-sectional areas were not significantly different in terms of their constituent narrow and inflated hyphae. In a similar study, C. Sánchez confirmed these results using a different

Fig. 2. Combined scatterplots comparing cell cross-sectional area with position in the stem in the six replicate transects (= rank order) for the inner flank (top graph) and outer flank (bottom graph) of stem 1.



method to measure cell diameter in an independent sample of five stems. In the original three stems measured, differences in the number of narrow hyphae (percentage of the total cells measured) between inner and outer flanks of the bend were not significant (Table 2). There was no differential packing density of hyphae between the two flanks.

Figure 2 shows typical rank-order plots of the cumulated data for the six transects in each inner and outer flank of one of the stems studied. The plots show the distribution of cell sizes from the exterior to the lumen and provide profiles of the inner and outer flanks of the bent stem. Both plots show a gradual increase in cell size towards the central lumen of the stem. The most striking feature of the plots is their similarity. In fact, the only differences found during the microscopic examination of tropically bent stems was in cell length (Table 2). Hyphae of the inner flank were short with contents that stained deeply with toluidine blue (Fig. 3*a*). The cytoplasm seems to be localized around the septa. In contrast, hyphae of the outer flank (Fig. 3*b*) were very long, containing large vacuoles, the cytoplasm located at the periphery of the cell, and consequently the staining was less

Table 2. Cell morphometric analysis of sections of gravitropically responding stems of *Coprinus cinereus* at the point of maximum curvature (adapted from Moore et al. 1996).

	Lower region of the bend		Upper region of the bend	
	n	Mean ± SE	*n*	Mean ± SE
Mean cross-sectional area of narrow hyphae (μm^2)	626	9.82±0.60	881	9.43±0.49
	803	8.93±0.79	625	8.95±0.43
	775	9.15±0.78	538	9.58±0.88
Mean cross-sectional area of inflated hyphae (μm^2)	1422	176.08±6.51	1442	183.00±7.62
	1152	185.96±9.24	1202	178.55±9.39
	1195	184.29±11.74	1203	189.71±15.38
Mean width of hyphae (μm)[a]	20	20.90±3.64	20	19.85±3.01
	20	19.74±4.67	20	16.25±3.06
	20	18.73±3.47	20	18.08±4.42
	20	19.25±3.85	20	18.86±5.71
	20	17.13±2.97	20	18.74±4.91
Narrow hyphae (%)	3[b]	30.5–39.1[c]	3[b]	28.8–41.5[c]
Packing density	3[b]	0.44±0.02	3[b]	0.47±0.28
Cell length (μm) of inflated hyphae in three different stems	34	542±35.0	34	116±7.4
	34	534±37.9	34	170±12.4
	34	698±50.6	34	107±5.7
Cell length (μm) of inflated hyphae in five different stems[a]	20	263.12±50.5	20	141.0±24.0
	20	439.74±153.2	20	133.16±22.1
	20	299.35±114.9	20	122.70±18.5
	20	385.30±107.8	20	137.36±27.5
	20	271.45±77.2	20	127.57±24.3

Note: Stems were fixed 3 h after reorientation and embedded in glycol methacrylate. Sections were cut 2 to 4 μm thick with glass knives on an ultramicrotome and observed by light microscopy, video images being processed by computer-aided image analysis. Means represent values of six replicate sections; the values shown represent the upper and lower regions of corresponding stems.

[a]Measurements were made by C.S. 1 year later than the others, using different analysis methods. Cells were fixed for 4 h in Spurr's resin and 1 section was examined.

[b]Values are the number of stems.

[c]Values are ranges.

pronounced. Hyphae of the outer flank (Fig. 3*b*) were significantly longer than those of the inner flank (Fig. 3*a*) of the bend in a ratio of 4:1 to 5:1 (Fig. 4).

Figures 4 and 5 show light and fluorescent micrographs of two structures observed only in sections of gravitropically bent stems. Figure 4 shows creases on the surfaces of the stem, both external surfaces and the surfaces bounding the lumen in the region of the bend. Figure 5*a* shows a void 85 μm in diameter between normally inflated hyphae, with some flattened hyphae on the border of the void; a similar void is seen in longitudinal section in Fig. 5*b*. Neither of these structures have been described before in extensive cytological studies of the stem of *C. cinereus*, nor were they seen in sections of vertical stems. Table 3 shows measurements of the numbers of voids in inner and outer flanks of three stems. There were no significant differences in numbers of voids between inner and outer flanks of the gravitropic bend, and it is concluded that differential occurrence of voids does not contribute directly to gravicurvature. However, since such voids seem to occur only in gravitropically bent stems, it is reasonable to suppose that they have a role in stem bending. Voids were also observed in longitudinal section (Fig. 5) confirming that the structures were indeed voids and not channels through the stem.

Creases occurred throughout the exterior and the lumen of both inner and outer flanks of the bend and were numerous.

Table 3. Number of voids measured in inner and outer flanks of a gravistimulated stem of *Coprinus cinereus*.

	Outer region of the bend		Inner region of the bend		
	n	Mean±SD	*n*	Mean±SD	
Stem 1	6	37.7±3.7	6	40.2±12.4	ns*
Stem 2	6	53.8±6.1	6	58.0±14.1	ns
Stem 3	6	66.7±9.0	6	56.7±7.5	ns

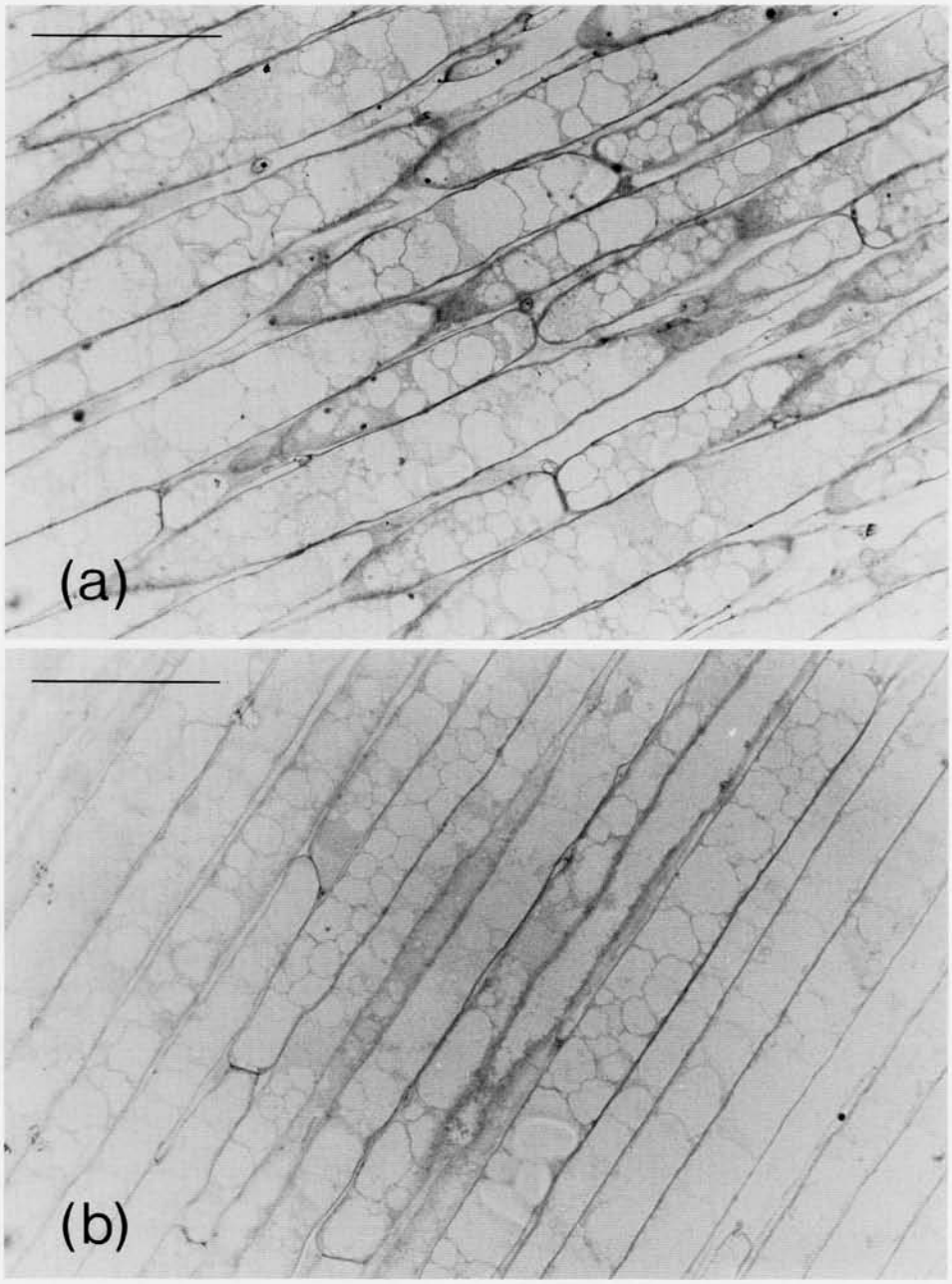
*ns, not significant (*t* test, $p > 0.05$).

The reasons for such structures is unclear, but they may be a product of the redistribution of hyphal associations caused during bending.

Discussion

The first detailed study of the kinetics of stem bending in an agaric was carried out by Kher et al. (13). Using *C. cinereus* and gravitropism as the model for tropic bending they showed that bending occurred usually within 20 min of exposure to the stimulus, the bend first occurred just below the apex of the stem and progressed down towards the base. Generally similar results were reported for the fruit body of

Fig. 3. Light micrograph of radial longitudinal sections of (*a*) the outer flank of the bend (upper panel) and (*b*) the inner flank of the bend (lower panel) stained with toluidine blue. Cells of the inner flank have short hyphal compartments with deeply stained contents in contrast to those of the outer flank of the bend, where hyphal compartments are very long with large vacuoles and cytoplasm is concentrated at the periphery of the cell. Scale bar = 100 μm.



Flammulina velutipes (M.A. Curtis: Fr.) Singer (14), although the rate of response of this fungus is much slower being $9° \cdot h^{-1}$, compared with the initial rate of bending of $51° \cdot h^{-1}$ in *C. cinereus*. This difference in bending rate is explained by the fact that so much less tissue is involved in *F. velutipes* where the response is limited to the apical few millimetres. This contrasts with gravitropism of *C. cinereus* where removal of over 50% of the apex did not affect the successful completion of the gravitropic response (15). Such results suggest that large parts of the stem are responsive and demonstrate that any graviperception mechanism is not confined to the apex in *C. cinereus*.

It would be foolish to ignore the structural similarities between mushroom stems and cylindrical plant organs. There is no difference in the conceptual basis of gravireception in fungi and plants, and thus it is reasonable to assume that some similarities in the mechanisms of tropic bending might exist. Stočkus and Moore (16) used plant-derived data to produce imitational mathematical models and applied these models to fungal data. They found that plant models do apply

Table 4. Different ways of producing tropic bending in a number of different organisms illustrating the variations and similarities with tropic bending in *C. cinereus*.

Tissue	Outer flank	Inner flank	Reference
Sunflower hypocotyl	Normal or slightly accelerated growth	Cessation of growth	1
Zea mays stem	Accelerated growth rate	Normal growth rate	2
Xanthium stem	Increased growth rate	Slight contraction	3
Sunflower hypocotyl	Rapid increase in growth rate	Shrinkage	4
Zea mays root	Enhanced growth rate	Shrinkage	5
Lepidium roots	Enhanced growth rate	Normal growth rate or slight contraction	6
Flammulina stem	Growth rate increases	Growth rate decreases	14
Coprinus stem	Rapid increase in growth rate	Increase in growth rate (delayed relative to outer flank)	10

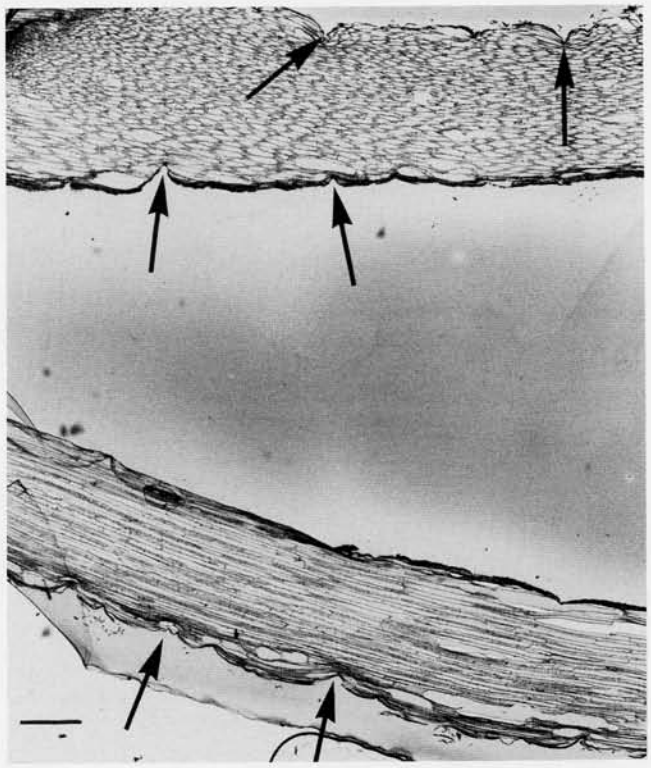
to the fungal system and suggest a basic underlying similarity between the kingdoms with relatively minor differences in the kinetics of the response.

In *Coprinus*, production of the bend is a result of the outer flank extending more and reaching a maximum rate of extension very close to the reaction time of 25 min (13), while the inner flank shows a period of acceleration before reaching a similar extension rate to the outer. Overall, the outer flank extends more than the inner by a ratio of 3:2. This is quite different from the bending mechanisms of *F. velutipes* (14) where the inner flank elongates very much less and at a slower rate than the outer flank. Examples of plant tropisms also contrast (Table 4), and production of the bend is attributed exclusively to a cessation of growth or even shrinkage in the inner flank of the responding organ (1, 2, 3, 4).

Dines and Bell (17) suggested that packing density of cells may be a factor in accommodating differential growth. Plant cells are so closely packed that they can build up elastic tension. Sliwinsky and Salisbury (18) restrained *Xanthium* stems for 48 h, which when released, bent immediately to about 130°. In *C. cinereus*, even when the inner flank is under compression during bending, the packing density remains unchanged (Table 2), perhaps reflecting the importance of maintaining organisation in the stem. Nevertheless, there do appear to be features that indicate a response to tensions in the *Coprinus* stem.

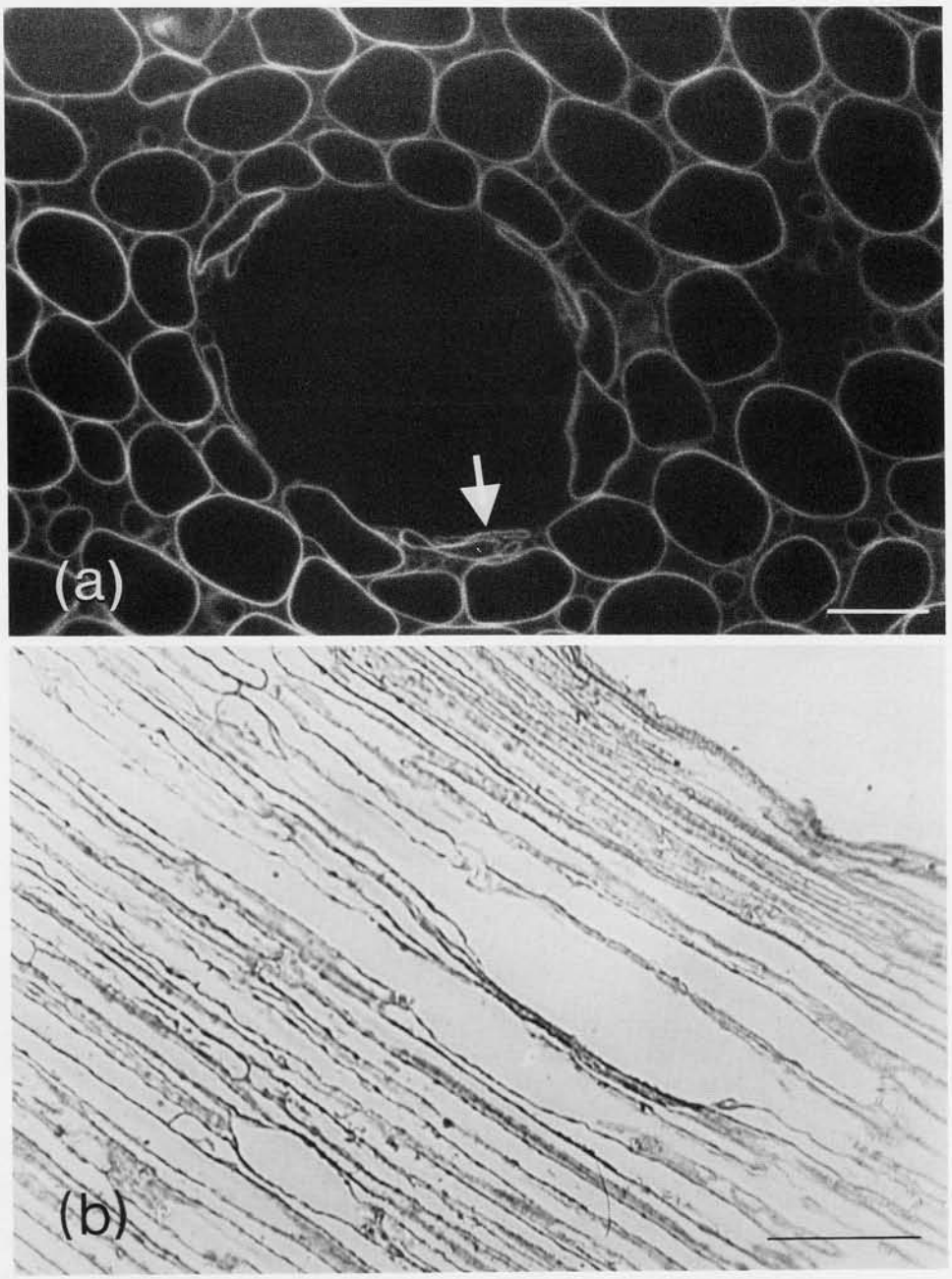
Differential growth, by its very nature, is designed to impose asymmetric stress so that the whole organ bends. It is inevitable that severe stresses will be imposed locally within the tissues yet it is essential that the whole organ does respond. Any structural failure that is likely to dissipate the strain must be contained and localized. Voids (Fig. 5, Table 3) in the stem may act as "crack stoppers." In a fibrous material, especially one in which the elements run in one direction, splits are common, but much more energy is required to maintain such a crack across a void (19). The presence of voids may, therefore, serve this mechanical function, maintaining the integrity of the stem during bending. Invaginations in the external regions of the stem tissue and lining the lumen may also be a consequence of curvature. Inflation of hyphae during bending may cause a redistribution of the network of narrow hyphae to points where they cause constriction. We have no clear evidence whether the creases are temporary or permanent (i.e., they may be transient during the bending process).

Fig. 4. Light micrograph of a radial longitudinal section of the stem showing both inner (uppermost) and outer (lowermost) flanks of the bend, stained with toluidine blue. There is a clear difference between hyphae of the inner and outer flanks. Arrows indicate creases. Scale bar = 1 mm.



Data in Table 2 shows that production of the gravitropic bend does not rely on a change in diameter of the hyphal compartment. Neither was any change in the proportion of narrow hyphae observed (narrow hyphae were not decreased in representation in the outer flank). In *C. cinereus* the bend is generated as a direct and unique result of an increase in

Fig. 5. Fluorescence micrograph of sections of a gravistimulated stem. (*a*) Void surrounded by flattened cells (arrow). The section was stained with calcofluor white. Scale bar = 20 μm. (*b*) Light micrograph of a longitudinal section, stained with toluidine blue, showing a large void in the stem tissue. Scale bar = 100 μm.



hyphal length only in the outer flank. Evidently, the intercalary wall growth that drives the four to five-fold increase in length, which is solely responsible for bending, is somehow regulated to lengthen the cells without increasing their girth. In this respect it may be relevant that, in stem cells of *C. cinereus*, the presence of left-handed chitin helices in the wall is unique (20), suggesting that helicity of the wall structure is of considerable importance. It may be that the growth pattern that characterizes tropic bending is to extend the helices without increasing their diameter. Whether this speculation is borne out or not will depend on further research into the cellular nature of growth during tropic bending.

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