

Kinetics and mechanics of stem gravitropism in *Coprinus cinereus*

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Using video recordings we have completed the first kinetic analysis of mushroom stem gravitropism. The stem became gravireceptive after completion of meiosis, beginning to bend within 30 minutes of being placed horizontal. Stem bending first occurred in the apical 15% of its length, then the position of the bend moved rapidly towards the base, traversing 40% of stem length in 2.5 h. Meanwhile, the stem elongated by 25%, mostly in its upper half but also in basal regions. If the apex was pinned horizontally the stem base was elevated but overshoot the vertical, often curling through more than 300°. When the base was pinned to the horizontal (considered analogous to the normal situation), 90% of the initial bend was compensated as the stem brought its apex accurately upright, rarely overshooting the vertical. The apex had to be free to move for this curvature compensation to occur. Stems transferred to a clinostat after some minutes gravistimulation showed curvature which increased with the length of initial gravistimulation, indicating that continued exposure to the unilateral gravity vector was necessary for continued bending. Such gravistimulated stems which bent on the clinostat subsequently relaxed back towards their original orientation. Reaction kinetics were unaffected by submergence in water, suggesting that mechanical events do not contribute, but submerged stems bent first at the base rather than apex.

In air, the gravitropic bend appeared first near the apex and then moved towards the base, suggesting basipetal movement of a signal. In water, the pattern of initial bending was changed (from apex to base) without effect on kinetics. Taken together these results suggest that bending is induced by a diffusing chemical growth factor (whose extracellular propagation is enhanced under water) which emanates from the apical zone of the stem. The apex is also responsible for regulating compensation of the bend so as to bring the tip to the vertical. The nature of this latter stimulus is unknown but it is polarized (the apex must be free to move for the compensation to occur) and it may not require reference to the unilateral gravity vector.

Gravitational reactions of cells not obviously specialized for detecting acceleration is a poorly explored area of cellular sensory physiology. Many cells respond to altered gravitational acceleration (Gmünder & Cogoli, 1988; Gruener & Hoeger, 1990) and gravity perception of whole animals and plants is well studied, but no gravity-sensing apparatus has been identified in fungi though these organisms are good candidates for such cell biological studies.

In basidiomycete fungi the mechanism of spore discharge is intolerant of water so the spore-producing tissue (the hymenium) must be protected from rain. Mushrooms and toadstools, their most characteristic fruiting structures, are miniature umbrellas whose vertical orientation is crucial to successful spore distribution. Mushrooms have a very sensitive gravity detection system and if reoriented they regain the vertical by bending the stem. The gravitropic response is a simple developmental pattern forming process; its control demands that the organism has a gravity perception system and a means of coupling this to asymmetric distribution of resources and growth potential. It is important to appreciate that perception of gravity is probably quite different from perception of other stimuli. Asymmetric responses (that is, the

tronic bending) to light, wind, temperature or chemicals can all be ascribed to the effects of differential exposure to a unilateral impulse, e.g. one side of the organism is relatively shaded from the incident light, wind or heat so grows more or less than the other side. But gravity cannot be 'shaded' and over the scale of living things there is no gravitational gradient. The perception system must depend on gravity establishing an asymmetric distribution of mass within the organism. This must set up a new morphogenetic pattern to which the organ is caused to adjust by differential growth. Study of gravitropism is therefore a natural, non-invasive means of generating a particular morphogenetic change on demand in a specific location.

Gravitropism of the mushroom stem provides the coarse adjustment, its negative gravitropism determining the orientation of the whole fruit body, while the fine adjustment resides in the spore-bearing tissue which is positively gravitropic. These basic features of gravitropism were established during the nineteenth century (Schmitz, 1842, 1843; Sachs, 1865, 1877). More detailed experimental work was done in the early part of this century (Buller, 1905, 1909, 1922, 1924; Hasselbring, 1907; Knoll, 1909; Streeter, 1909)

and there have been a number of studies and reviews at regular intervals since (Ingold, 1953; Plunkett, 1961; Banbury, 1962; Badham, 1982; Gorovoj, Kasatkina & Klyushkina, 1987; Moore, 1991*a*), but the total volume of research work done is extremely small and the knowledge base correspondingly meagre. In particular, no attempt has ever been made to determine the kinetics of the gravitropic response of the stem from continuous photo- or video-records. This is the subject of this report.

MATERIALS AND METHODS

All experiments were done with the 'Meathop' dikaryon of *Coprinus cinereus* (Schaeff.: Fr.) S. F. Gray; this was originally isolated from a dung heap in Lower Meathop Hill farm in Cumbria. The Meathop vegetative dikaryon was grown on Complete Medium (Moore & Pukkila, 1985) in 9 cm Petri dishes in the dark at 37 °C. Vegetative cultures of the dikaryon were maintained by serial transfer. Fruit bodies were produced by inoculating sterilized horse dung with pieces of dikaryon taken from the Petri dish cultures. The dung cultures were incubated in the dark for 3 days at 37° to allow the mycelium to establish itself before being transferred to a 27° incubator with a 16 h light/8 h dark photoperiod to induce production of fruit bodies. Illumination was provided by white fluorescent lights which gave an average illuminance of 800 lx.

Some of the gross characteristics of gravitropism can be demonstrated by simply turning fruiting cultures on their side (for illustrations see Moore, 1991*a, b*) but the presence of the cap, parental mycelium and substrate is a complication and a hindrance to experimental manipulation. It has been known for many years that stem growth and gravitropic bending proceed in isolated, decapitated stems (Jeffreys & Greulich, 1956; Gooday, 1974; Cox & Niederpruem, 1975) and although this procedure clearly represents a severe injury we have adopted it as a standard technique. Fruit bodies were removed from their cultures and cap tissue was stripped away. The stems were then placed horizontally, pinned through their basal bulb to a horizontal balsa wood platform, in a perspex chamber. Humidity was kept high with a free water layer assisted by 'curtains' of chromatography paper, and room temperature was used (and measured with a resident thermometer). Fruit bodies of a wide range of developmental ages were examined. They were chosen first on the basis of stem length, but their 'physiological age' was established by microscopic analysis of the stage of development of their basidia using silver staining (Pukkila & Lu, 1985) for observations of meiotic stages. VHS Video recordings were made of stem behaviour under low-intensity red light to avoid phototropic effects. Throughout the preparative procedures the stem was maintained in a vertical orientation. Video recording was started during the preparation phase while the specimen was still upright so that the exact time of horizontal placement was recorded. For photographic illustrations (like Fig. 1), video frames were digitized with a Screen Machine real-time video digitizer card and software (Magnifeye, Studio 6, Walmer Studios, 235-239 Walmer Road, London W11 4EY) and transferred to film with a Polaroid Image Recorder. For

kinetic analyses video images were brought into an Opus PC computer using a Skye S1733 video digitizing card and Skye S1730 image analysis software (Skye Instruments Ltd, Unit 5, Ddole Industrial Estate, Llandrindod Wells, Powys LD1 6DF). Parameters measured are shown in Fig. 2. Images were sampled routinely at 10 min intervals and at shorter intervals when graphical analysis required intermediate data points.

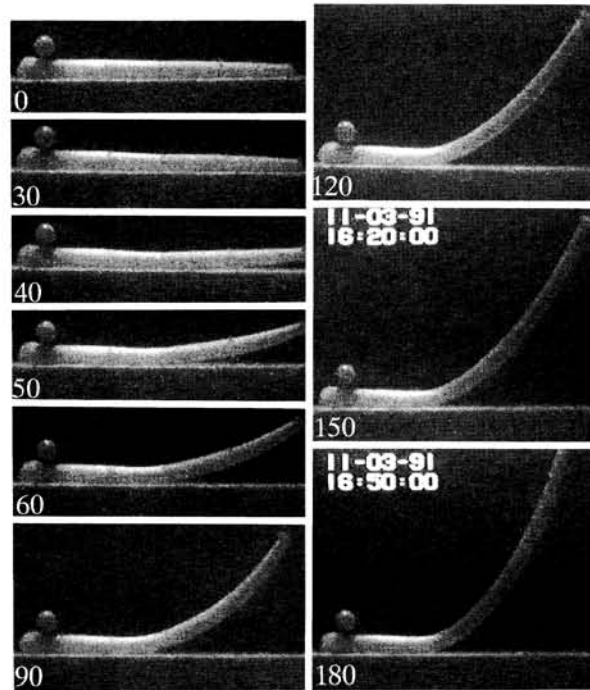


Fig. 1. The gravitropic reaction in air, shown in a panel of stills from a video recording of a stem of *Coprinus cinereus* which was 64 mm long at the start of the experiment. The stem was pinned through its basal bulb (on the left) to a horizontal balsa wood support using a map pin with a 5 mm diameter head (= size marker). Numerals show elapsed time in minutes.

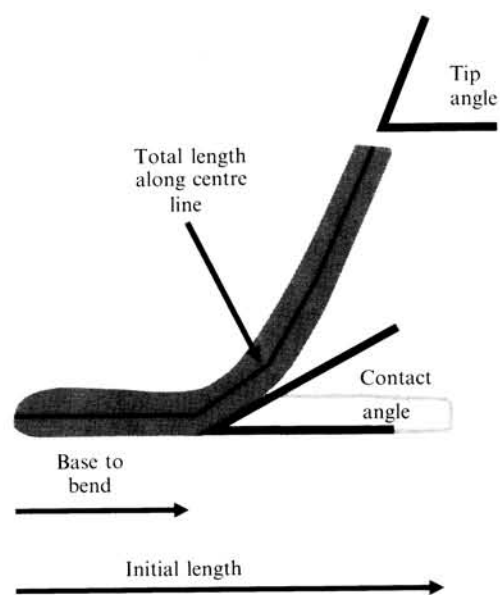


Fig. 2. Diagram showing the parameters routinely measured for analysis.

RESULTS AND DISCUSSION

Image analysis software was used to analyse frames from the video recordings to determine: (a) the angle of the stem tip, (b) the angle of contact between the bent stem and its horizontal support, (c) the overall length of the stem, and (d) the distance from the stem base to the position of the bend (Figs 1 & 2). In the initial series of experiments this sort of analysis was done for 18 stems varying in initial length between 20 and 64 mm. Data for each stem were plotted individually (Fig. 3), the reaction time and rate of response being extracted by regression analysis of data covering the early stages (Fig. 4). Results are summarized in Table 1 and allow the following generalizations.

(a) Response of stems to gravity is rapid; the mean reaction time being 25.4 ± 13.1 min.

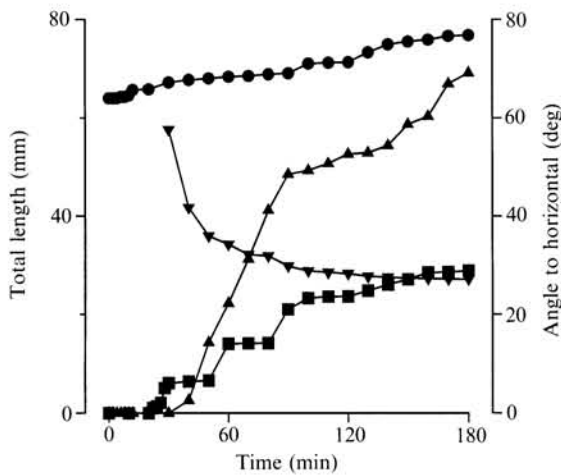


Fig. 3. Numerical data for the stem shown in Fig. 1. Combined plot showing contact angle (■), tip angle (▲), distance from base to the position of the bend (▼) and total length of the stem (●).

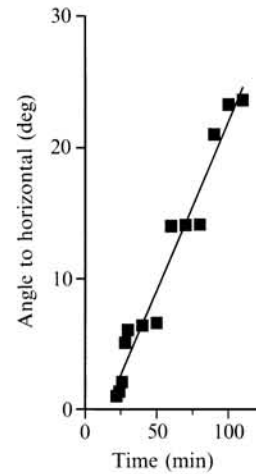


Fig. 4. Numerical data for the stem shown in Fig. 1. Regression analysis of contact angle measurements over the first 100 minutes which was used to calculate reaction time (as the intercept on the time axis) and rate of response (slope). Both of these values are shown in the last line of data in Table 1.

(b) There was no correlation between reaction time and stem length (coefficient of determination, $r^2 = 0.12$) or rate of response and stem length ($r^2 = 0.14$) which together suggest that the stems were equally competent over the whole range of sizes from 20 to 64 mm. Importantly though, only fruit bodies which had completed meiosis (average height 16 mm [$n = 7$]) before being placed horizontal were graviresponsive. Fruit bodies at earlier stages of development were not gravitropically competent.

(c) There was no correlation between rate of response and reaction time ($r^2 = 0.05$), suggesting that these two features are independent of one another (i.e. the factor that determines how soon the stem will bend is independent of that which determines how fast it bends).

Table 1. Gravitropic reactions of 18 stems of *Coprinus cinereus* to being pinned through the basal bulb to a horizontal support in air

Length at start (mm)	Reaction time (min)	Rate of response (degree min ⁻¹)	Tip angle after 3 h	Length increase in 3 h (mm)	Length increase [%]
20	13.9	0.062	7.9	3.1	[15]
24	36.4	0.049	24.6	3.4	[14]
25	50.8	0.239	30.0	2.7	[11]
26	41.3	0.091	24.6	5.1	[20]
31	16.6	0.111	35.2	13.5	[44]
32	44.8	0.155	42.5	12.7	[40]
34	25.5	0.292	55.9	13.7	[40]
35	26.2	0.136	45.0	16.4	[47]
36	22.2	0.353	58.7	6.7	[19]
36	24.6	0.062	11.5	6.1	[17]
36	11.8	0.553	73.8	8.6	[24]
44	21.2	0.371	65.5	13.9	[32]
44	9.2	0.198	64.4	14.3	[33]
46	38.8	0.391	53.3	8.0	[17]
48	15.2	0.322	64.8	11.2	[23]
50	7.6	0.237	88.9	11.8	[24]
52	36.4	0.083	31.6	8.5	[16]
64	14.8	0.258	69.2	12.8	[20]
Means	25.4 ± 13.1	0.22 ± 0.14	47.1 ± 22.6	—	25.3 ± 11.2

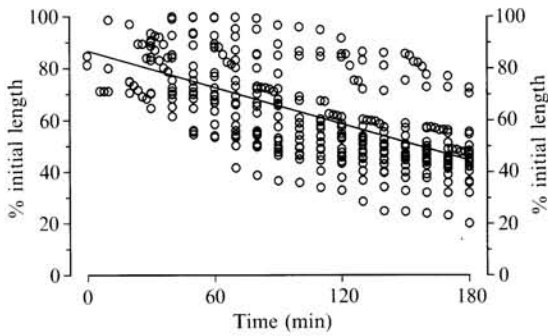


Fig. 5. Scatter diagram and trend line of base to bend measurements for all the gravitropically reacting stems represented in Table 1.

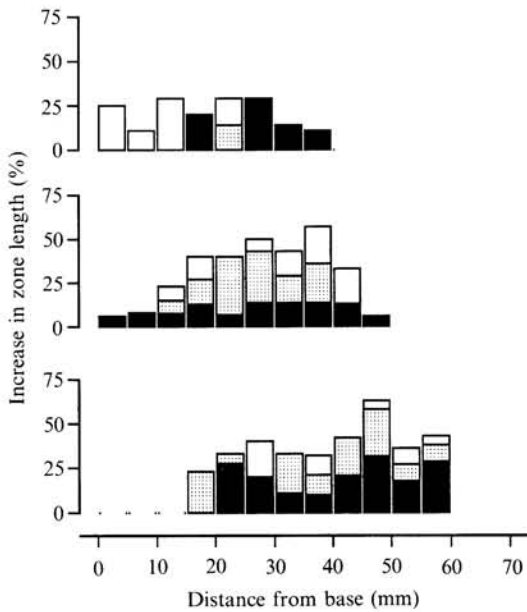


Fig. 6. Pattern of distribution of growth along the stem during gravitropic curvature. Drawing ink was used to mark stems at 5 mm intervals and the size of these segments was measured, on the lower side of the stem, at hourly intervals after stems were placed horizontal in air. The display shows data for three stems which were 45 (top), 50 and 65 (bottom) mm long at the start of the experiment. The percentage increase in the length of each segment after 1 h is shown as a solid bar, after 2 h as a shaded bar and after 3 h as an open bar. Note that most expansion occurred in the mid to upper region but some growth could occur along the entire length of the stem, even at the base.

(d) Bending first occurred towards the apex of the stem – on average within the apical 15% of the stem length but then the location of the bend moved steadily towards the base of the stem, traversing about 40% of the length of the stem (Fig. 5).

(e) All stems increased in length during the bending process, the mean increase in length being 25% (range 11 to 47%) but there was no correlation between initial stem length and percentage increase ($r^2 = 0.0004$).

Studies of normal (vertical) stem growth (references in Moore, Elhiti & Butler, 1979) show that the most active zone of vertical elongation is in the upper mid-region. Our

measurements show that much the same is true of horizontal stems. However, although most growth does occur in the upper half of the gravistimulated stem, considerable extension can occur throughout the entire length, even in basal segments (Fig. 6). Basal regions are also capable of gravitropic bending. Securing stems at their centre showed that both base and apex were apparently negatively gravitropic (Fig. 7). Such stems responded in a very particular way. The apical half reacted first, the bend curling back towards the central pin. As the bend reached the pin the basal half of the stipe reacted, first lifting off the horizontal support and then bending. We interpret these reactions to reflect apex to base progression of a bending impulse which pivots the bottom half of the stem upwards as it reaches the pin (= fulcrum) and then proceeds into the basal regions to cause the stem to bend.

Stems pinned at their centre would often bend into a U-shape, showing that the stem has very high potential for bending. Indeed, it has a much greater capacity to bend than can be revealed under normal circumstances, though there must be occasions when it has survival value. Moore (1991b) shows a video sequence in which a fruit body of *C. cinereus* that had elevated itself to a 45° angle 3 h after being placed horizontal fell back to the floor but had restored itself to the vertical by the time its spores were discharged 3 h later.

However, even under the simple circumstances of a stem pinned at the base on a horizontal support it can be argued that the capacity to bend to a greater extent than required to restore a horizontal stem to the vertical is revealed. Consider the stem illustrated in Figs 1 & 3. The position of the bend moved 30 mm towards the base between its appearance at about the 30 minute sample time and the end of observation at 180 minutes. During that time 15 measurements of the contact angle were made (which were consequently 2 mm apart); if each of these segments had maintained their original angle to the horizontal support the cumulative angle would have been 550°, but the final tip angle was 70°. The other stems shown in Table 1 reacted similarly. On average ($n = 18$) measurements of the contact angle accumulated to 405° as the bend moved 17 mm towards the base (average stem length = 40 mm); the final tip angle averaging 47°. These calculations imply that the stem has a much greater capacity to bend than is actually expressed in the angle of the stem apex. Almost 90% of the initial bend (as represented by the angle between the bottom surface of the stem and its horizontal support) may be reversed by subsequent events.

This effect was directly demonstrable by fixing stems to the horizontal support with a pin through their apex. Gravitropic bending causes such a stem to raise its base, but this is raised far beyond the vertical, often curling through 360° (Fig. 8). Thus, gravitropic bending and its compensation are separate phenomena and the stem is polarized; the apical region must be free to move for the stem to be adjusted to the vertical.

A plausible mechanism to account for the compensation process would be to assume that the mass of the raised apical portion of the stem provides a feedback regulator which causes growth to occur differentially in the most acutely bent upper part of the stem, so compensating for the initial bend; equalization of mechanical stress across the diameter of the stem would signal return to the vertical. Because of the

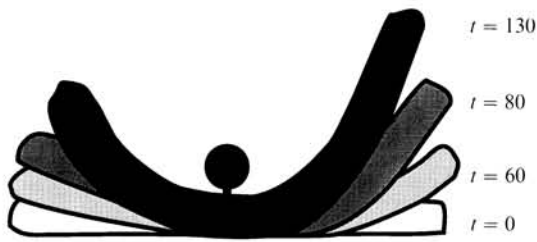


Fig. 7. Summary diagram of the reactions of stems pinned centrally. In this diagram the stem base is on the left.

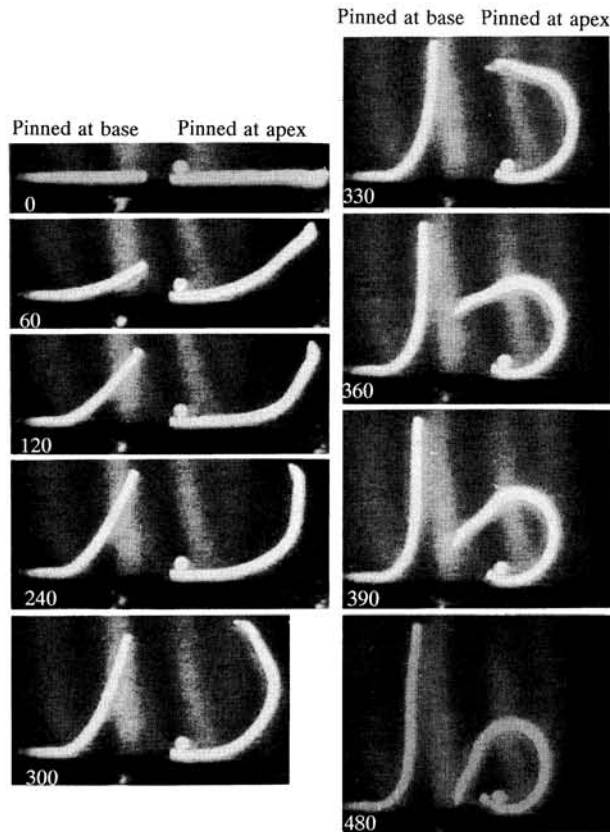


Fig. 8. Panel of stills from a video recording of an experiment comparing the gravitropic reactions of a stem pinned through the basal bulb (left) and one pinned through its apex (right). Numerals show elapsed time in minutes.

complex dynamics of the phenomena involved this is probably a gross oversimplification. However, Dennison & Roth (1967) showed a relationship between growth rate and mechanical tension in *Phycomyces* sporangiophores and mechanosensitive ion channels, which direct mechanical or stress-elicited deformation by changing ion permeabilities, are present in yeasts (Gustin *et al.*, 1988).

Dennison (1961) was able to differentiate between a transient mechanical response and a long-term intracellular response to acceleration stress in *Phycomyces* by experimenting with sporangiophores submerged in a dense fluid. We have emulated this approach by submerging stems in continuously aerated distilled water. The outcome was that submerged stems raised themselves from the horizontal by pivoting at the basal pin which secured them to the horizontal support.

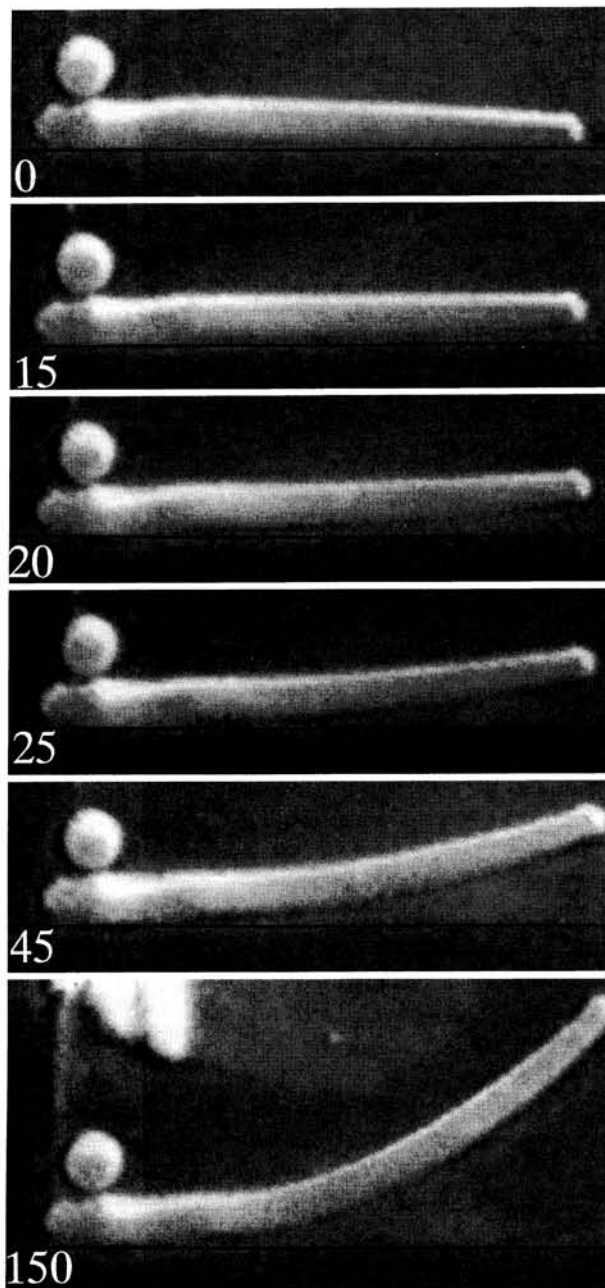
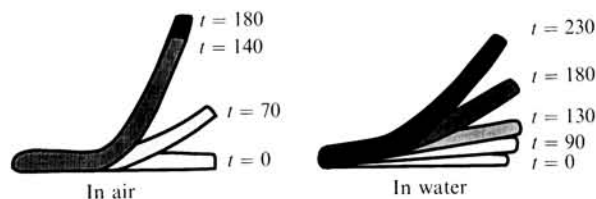


Fig. 9. The gravitropic reaction in water shown in a panel of stills from a video recording of a stem which was prepared as before and pinned through its basal bulb (on the left) but was then immersed in a tank of sterile distilled water. Numerals show elapsed time in minutes. The water was aerated with an aquarium pump for 2 h prior to preparation of the stem and aeration continued throughout the experiment.

Throughout the early parts of their response, submerged stems remained straight. Only after being raised from the horizontal did they begin to show evidence of bending anywhere other than at the point of attachment to the support (Fig. 9). Because submerged stems bent only after first lifting from the horizontal they generally required a longer time to restore their apices to the vertical (as the bend did not move, the bending increments did not accumulate). Nevertheless, none of the initial kinetic parameters was greatly different from those encountered with stems in air (Table 2) and the

Table 2. Gravitropic reactions of 7 stems of *Coprinus cinereus* to being pinned through the basal bulb to a horizontal support under water

Length at start (mm)	Reaction time (min)	Rate of response (degree min ⁻¹)	Tip angle after 3 h	Length increase in 3 h (mm)	Length increase [%]
25	38.8	0.140	29.7	5.2	[21]
28	6.2	0.230	9.2	5.1	[18]
31	29.4	0.069	19.3	8.7	[28]
41	10.0	0.426	52.2	13.4	[33]
46	8.8	0.413	52.6	16.3	[35]
50	20.6	0.368	39.1	11.5	[23]
58	9.8	0.089	36.9	18.2	[31]
Means	17.7 ± 12.4	0.25 ± 0.15	34.1 ± 16.1	—	27.0 ± 6.5

**Fig. 10.** Diagrams comparing the gravitropic reactions of stems in air and in water.

stems were all able to restore their apices to the vertical, suggesting that submergence caused no metabolic (respiratory) stress. *Coprinus* stems develop a central lumen as they extend so it is important to emphasize that at the conclusion of the observations the stems were unpinned and it was confirmed that they all sank in water.

Submergence in water affects neither the time, nor the rate, nor the extent of the gravitropic response, but it drastically changes the pattern of the response, concentrating it in the basal rather than apical region of the stem (Fig. 10). There seems little scope for an explanation of this effect in the 1000-fold difference in density between air and water. For example, if the mass of the raised stem apex acts as a feedback to compensate the initial bend then the magnitude of the feedback signal would be reduced in water, resulting in an excessively bent stem. On the other hand, if the mass of the horizontal stem provides a positive driving force in promoting bending (by activating a stretch or compression receptor) then a submerged stem might be expected to bend much less or much later than normal. None of this was observed and these lines of argument do not predict flexing at the base in water rather than the apical bending observed in air. It may be another property of water which is responsible.

An explanation based on an osmotic effect seems equally unlikely because of the specificity and uniformity of the response. All stems lifted upwards by flexing at their base but, initially, without bending anywhere else along their length (Fig. 9). If this reaction reflected the osmotic ingress of water causing some cell expansion it would be necessary to explain why, in every case, there was a much greater net expansion in those cells of the stem base which were closest to the horizontal support (i.e. those in the 'bottom' zone). Similarly, all subsequent bending occurred in the vertical plane and brought the stem apex towards the vertical. All of this points to the reactions being a genuine, though water-modified, expression of the gravitropic response.

It is quite clear from experiments in air that the gravitropic bend moves towards the stem base and this is likely to be a manifestation of the like movement of an inducing signal emitted by an apical graviperception mechanism. If this signal is an extracellularly transmitted chemical its route through the mucilage or liquid film over hyphal surfaces of a stem in air could be so tortuous under normal circumstances that its progress could be unnaturally facilitated by immersion in water, so enabling it to reach the base before any other part of the stem can react.

We are aware that these experiments may not truly reflect the *in vivo* situation. We have removed the cap (but initial experiments indicated that this had little effect, illustrated in Moore, 1991a) and removed the stem from its mycelium (though the main effect of this seems to be sensitivity to desiccation). We are also dealing with the most extreme situation – a horizontal stem. In nature the more frequently encountered response is likely to be a relatively small adjustment for a slightly dislodged fruit body and may be more a matter of control of the process we have described as curvature compensation. Nevertheless, these experiments provide *prima facie* evidence for apex-to-base transmission of a growth factor which could activate the growth potential of the bottom zones of a gravistimulated stem to cause it to bend upwards. Compensation of the gravitropic bend must involve preferential activation of the other (physically upper) zones of the stem but the nature of the regulator which controls this process is far from clear. It is evidently essential for the apical part of the stem to be free to move, which might mean that as the angle between the apex and the horizontal approaches some critical value the apical region begins to produce a growth factor which activates growth in those zones of the stem which had previously grown least. However, a complication is raised by experiments in which stems ($n = 13$) gravistimulated for 15 to 25 minutes were transferred to a 2 rpm clinostat. Whilst on the clinostat, these developed the gravitropic curvature expected as a result of their gravistimulation but they then relaxed their direction of growth so that the original orientation of the apex was restored by the conclusion of the experiment (Fig. 11). This shows that continued gravistimulation is necessary for continued gravitropic bending. But more enigmatically, it shows that the apex can be restored to its original orientation in the absence of a unilateral gravitational reference. If the apical region produces a curvature compensation signal as it approaches the vertical, what is it sensing if it is not dependent

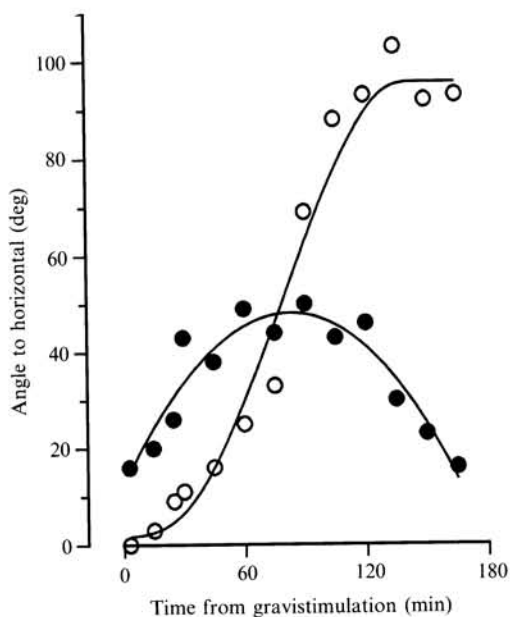


Fig. 11. Gravitropic reaction (expressed as the tip angle) of a stationary stem (open symbols) and a stem transferred to a clinostat rotating at 2 rpm after 25 minutes gravistimulation. Note that the apex of the stationary stem returns to the vertical (i.e. 90° to the horizontal support) and that the apex of the stem on the clinostat reaches an angle of approximately 45° but then relaxes back to its original orientation.

on the normal gravitational field? On the other hand, if the initial curvature builds up some sort of 'tension' (using that word figuratively – it may be a mechanical tension or it may be a matter of asymmetric distribution of metabolic reserves) which is subsequently released to provide curvature compensation as soon as the gravitropic signal is removed, why is it polarized? Why does a stem pinned through its apex not show curvature compensation? Experiments are continuing with the clinostat (which randomizes the signal vector that produces the initial gravitropic reaction) to establish the degree of dependency on a unilateral gravitational field and the nature of this reaction.

For the moment we would summarize the gravitropic reaction of a horizontally placed *C. cinereus* stem as follows. Completion of meiosis in the cap coincides with the stem becoming competent to react to disorientation. Within 30 min of disorientation the negatively gravitropic bend initially appears within the apical 15% of its length. The bend then becomes more acute as it progresses basally, traversing 40% of the initial length of the stem. Gravitropic bending is most likely the result of asymmetric distribution of growth, although whether it is due to cell expansion alone is unclear as even in the most acute bends (as in Fig. 8) the ratio between inner and outer circumference, which is the most extreme measure of the asymmetry, is only 2:3. Gravitropic bending may be stimulated by a diffusing, extracellular growth factor which is produced by the apical region of the stem. Since stems from which the apex has been removed are still able to respond (see illustrations in Moore, 1991a), the phrase 'apical region' does not refer to the structural apex of the whole stem but to the apically placed extremity of the stem or stem segment.

Bending raises the apex and as this approaches an angle of about 45° to the horizontal, curvature compensation begins to adjust the degree of bending so that the apex can be brought exactly vertical. Curvature compensation requires that the apical region is free to move towards the vertical. The mechanism involved is uncertain as an apparently similar process occurs on the clinostat.

Further work will concentrate on the nature of the signalling processes, biochemical, structural and ultrastructural aspects of curvature and curvature compensation, and sensitivity to gravitational acceleration.

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