

THEORETICAL PAPER

Comparison of plant and fungal gravitropic responses using imitational modelling

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ABSTRACT

The mechanisms of gravity perception are still hypothetical, but there are sufficient data from experiments with plants to enable mathematical modelling to imitate the behaviour of gravitropic response systems. We have a much less complete picture of gravitropic kinetics in agaric mushrooms. However, some existing mathematical models which imitate plant responses are in principle universal because their conceptual components are not limited to any specific cellular entities. In this work we have used such models to compare plant and fungal gravitropism, using recently acquired kinetic data from the agarics *Coprinus cinereus* and *Flammulina velutipes*. The results show striking similarities between plants and fungi. First, it is evident that the basic assumptions of the plant models are logically applicable to fungi. Secondly, the mechanism of bending is the same (differential growth of opposite flanks of the growing organ). Thirdly, the distribution of growth seems very similar: in both plants and fungi growth of the organ is most intensive just behind the apex and is almost absent at the apex and at the base. Fourthly, in both fungi and plants the gravitropic response exhibits a substantial time delay suggesting that many time-consuming processes are involved in reception, transduction and realization of gravitropic stimuli. Important differences in plant and fungal gravitropism kinetics were: (i) the agaric stem apex always returned to the vertical, whereas some plant organs show stable plagio-gravitropic growth; (ii) inflections were usually seen in *C. cinereus* stem gravitropism time courses suggesting that a curvature compensation process delayed bending for a time; (iii) *C. cinereus* stems very rarely overshoot or oscillated around the vertical although many plant subjects oscillate and the (limited) data for *F. velutipes* showed a single, exaggerated overshoot and oscillation. In this latter case, experimental modelling with parameters characteristic of a low level of perception improved the fit to the *F. velutipes* data, indicating that the two fungi may differ in this factor. Application of the plant models focused future

research attention on the urgent need for data bearing on angle–response and acceleration–response relationships in fungi, and their detection-level thresholds for gravitational acceleration. Since the modelling also highlighted some fundamental kinetic differences between the only two fungi for which sufficient data are available at the moment, it is also clear that detailed observations need to be made of gravitropism kinetics in a larger number and wider range of fungi.

Key-words: *Coprinus cinereus*; *Flammulina velutipes*; computer simulation; development; fruit body; fungi; gravitropism; growth; kinetics; mathematical modelling; morphogenesis; mushroom.

INTRODUCTION

The gravitropic response is an important factor determining the optimal spatial orientation of axial plant and fungal organs as well as proper positioning of other organs such as leaves, flowers, fungal caps and gills. The Earth's gravitational field influences all (overground, underground and submerged) parts of an organism, and has acted continuously in this pervasive way over the entire period of biological evolution (Barlow 1995). A gravitropic response is present in all higher plants and in many taxa of algae and fungi (Merkys *et al.* 1989; Merkys 1990; Moore 1991).

Gravitropic responses in plants have been investigated for over a century and are still attracting attention because of the complexity of the phenomena. Our present knowledge of the mechanisms of the gravitropic response is still fragmentary and incomplete. The mechanisms of gravity perception are still hypothetical, and relations between different stages in gravitropism are essentially schematic. Nevertheless, there are sufficient data to enable us to postulate the chain of events which occurs when the orientation of a growing plant apex changes in the gravitational field. This cannot be said for fungi. There are various reasons (see Moore 1996) for the relatively late start which has been made on detailed investigation of the kinetics of fungal gravitropism (Hatton & Moore 1992, 1994; Kher *et al.* 1992; Haindl & Monzer 1994; Monzer *et al.* 1994). As a consequence, we have a very incomplete picture of what happens in such higher fungi as the agarics *Coprinus cinereus* and *Flammulina velutipes* when they receive gravitropic stimuli (Moore *et al.* 1996).

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Despite the amount of data we have about the behaviour of plant organs, there are few mathematical imitational models of plant gravitropism in the literature (Johnsson & Israelsson 1968; Barlow *et al.* 1991; Stočkus 1992, 1994c). On the other hand, given the paucity of information about fungal systems, it is not at all surprising that no attempt has ever been made to produce a mathematical model describing gravitropism in mushrooms. However, some existing mathematical models which imitate the behaviour of gravitropic response systems are in principle universal because their conceptual components are not limited to any specific cellular entities. These models can validly be used to compare plant and fungal gravitropism, even though some experimental data necessary for refinement of a model are still lacking. The intention is to use the better understood plant kinetics to aid in the first stage of development of a model of fungal gravitropism and to guide further experimentation.

Modelling gravitropism in plants

Mathematically, the gravitropic response is a very complex phenomenon, and two general strategies can be adopted in creating models. In one approach the specific characteristics of particular parts of the cell biological system are used as modelling parameters. For example, the detailed distribution of elemental growth rates along an organ and their changes after receiving the gravitropic stimulus have been used to derive mathematical models (Barlow *et al.* 1989, 1991), and observed auxin concentrations on opposite sides of an organ undergoing gravitropic bending have also been used (Larsen 1957; Johnsson 1971).

The alternative approach (Johnsson & Israelsson 1968; Brown & Chapman 1977; Stočkus 1992) differs in that the basis of the model is independent of the real processes, but dependent on the *informational content* of those processes for an organism. In other words, these imitational models use abstract terms such as 'physiological signal' rather than exact parameters like 'substance concentrations'. The advantage of such an approach is that it can mimic the overall picture of events in gravitropically responding organs without going into detail about how the gravitropic response is realized. The resultant model is an abstraction which can be applied to a wider range of subjects.

Development of gravitropic response models generally falls into three main stages, which could be characterized (Stočkus 1992) as: (i) separate formulae describing particular features of gravitropism, such as a particular mathematical relationship between angle of inclination and gravitropic response; (ii) analytically derived functional time-angle relationships based on very concrete assumptions such as distribution of auxin in an axial organ (which may be treated as 'static' models), and (iii) the stage which has been reached with the plant models, which could be characterized as the stage of dynamic modelling, formulated in terms of differential equations describing angular velocity or angular acceleration of apex angle. This parameter, the angle of the apex (of shoot or root as appropriate)

in relation to the gravity vector, is crucially important to plants because it predetermines the spatial orientation of the growing plant axis. The reasons for the use of differential equations rather than analytically obtained formulae are the greater biological adequacy of such models and their flexibility; various experimental conditions can be simulated by a single equation.

Deduction and improvement of the dynamic model is similar to the so-called hypothetic-deductive methodology, or system analysis (Fretwell 1972; Straskraba & Gnauck 1985). One of the most important advantages of this methodology is that it demands a holistic view of the investigated subject and is not limited to considering a restricted part or component, unlike the classical approach which limits mathematical treatment to a particular element which is selected at the outset. With the holistic approach, there is some hope that abstraction of the model may make the latter predictive or experimentally useful in ways not initially envisaged.

The main steps of model deduction, according to the methodology employed here, are (i) compilation of a verbal model, (ii) formalization of the verbal model leading to the mathematical model, (iii) derivation of checkable conclusions, (iv) verification of models and their conclusions and, if verification fails, (v) correction of the initial model. If verification succeeds, new conclusions are extracted and the cycle is reiterated.

The verbal model of gravitropic response used (Stočkus 1992, 1994a,c, 1996) consists of a basic scheme and general assumptions (Fig. 1) which are amenable to mathematical treatment, and were derived from Rawitscher (1932) and Merkys *et al.* (1972). The scheme shows changes of apex angle $d\alpha$ as a result of four consecutive stages — susception, perception, transduction and growth response. For simplicity, only one feedback relation, via changes of apex angle, was assumed to be essential. Susception is the physical change which occurs when the subject is disoriented. It may be a sedimentation, floatation, change in pressure or shear, but for the purpose of the model the nature of the change does not need be defined. Perception is the conversion of the physical change into a physiological change, again, of undefined nature. The transduction stage imposes some properties of an informational process which conveys the physiological signal to the undefined competent tissue, which then produces the (undefined) growth response which generates the apex angle. The feedback loop permits a simple regulatory step to be introduced (and modelled, of course).

Mathematical description of all the stages of the scheme in Fig. 1 can be divided into four relatively independent descriptions of the consecutive stages. The mathematical function describing each stage is effectively the input to the subsequent stage modified by the characteristics of that stage and, ideally, for the sake of realism, by random deviation. Since each successive stage depends on those which precede it, the overall mathematical representation is a set of nested function descriptions. The combined equation of the gravitropic response can thus be represented in the fol-

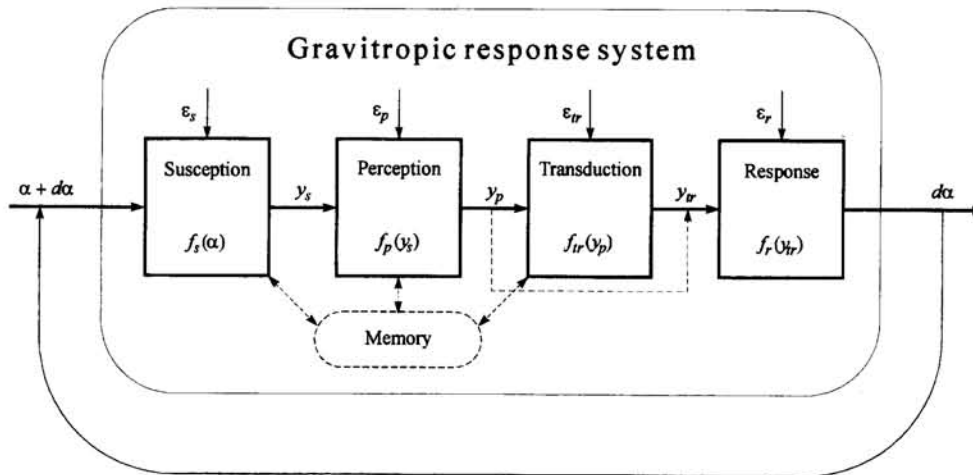


Figure 1. Basic scheme of an abstract gravitropic response system. The angle of the apex is represented by α , and symbols in and around the boxes represent component stages: f_s to f_r are functions describing each stage; y_s to y_{tr} are the outcomes of those stages; ϵ_s to ϵ_r provide for random deviations; $d\alpha$ is the final outcome of the gravitropic response system, the change of apex angle. In the equation shown in the text, the additional symbols represent: g = acceleration due to gravity; t = time; T = temperature.

lowing form (symbols are identified in the legend of Fig. 1):

$$d\alpha = f_r \{ f_{tr} \{ f_p \{ f_s [\alpha, g, t, T, \dots] + \epsilon_s, t, T, \dots \} + \epsilon_p, t, T, \dots \} + \epsilon_{tr}, t, T, \dots \} + \epsilon_r$$

For the sake of simplicity, the random deviations can be omitted and all the conditions (environmental and physiological) assumed to be constant. Then the mathematical model can be reduced to a form simple enough to operate using conventional mathematical and computer programming approaches.

It must be pointed out that the scheme presented here, and models based on it, can be applied only to freely responding subjects, in which storage of information in a memory can be assumed to be negligible (or instantly retrieved). Delayed retrieval of memorized information significantly changes the kinetics of gravitropic response through a process known as induction (Merkys *et al.* 1989; Merkys 1990).

The next step, formalization of the model, needs some additional assumptions to be made about the processes occurring in each stage of the scheme. The following main assumptions were used in the models shown here.

- (i) The difference of growth rates between opposite flanks of an axial organ is the cause of gravitropic curvature. In fact, such a specific definition is generally not necessary. For modelling purposes, it is usually enough to assume that curvature just *occurs* in response to some signal. The factor or factors which code the direction and intensity of this curvature in the modelling were considered to be the 'physiological signal' for tropic bending.
- (ii) The physiological signal is generated in the perception stage and then carried to the site of its realisation, where it is used to generate the growth differential. During this transduction the usual paths for signal transduction are used (i. e. no special constraints are imposed by the model).

- (iii) The time required for transduction of a physiological signal is the main reason for a time delay between the onset of gravitropic stimulation and start of tropic bending. However, this time may include the time delays required for signal perception and realisation as well; at the present stage of modelling these times are not separable.

- (iv) The physiological signal decays during its transduction. The rate of its decay was assumed to be proportional to the initial magnitude of the signal. Solution of the equation based on this assumption for time gives a formula showing exponential decay of the signal.

- (v) The magnitude of the physiological signal at the stage of perception is proportional to the sine of the apex angle with the gravity vector and to various modifiers (see 'Discussion' below).

Application of imitational models to plant responses

Four modifications of the gravitropism model based on the aforementioned scheme and assumptions have been derived so far. Their component parts and final formulae are summarised in Table 1.

In each model the susception function is set to be proportional to the acceleration due to gravity. The major difference between the models is in the perception function. This describes the basic parameters for the orientation of the apex, namely the relationship between the apex angle, the gravity vector and the polarity of the effective physiological signal. Consequently, most other features of the models depend on these attributes of the perception function. Except in the third model, other stages only change how the final (so-called liminal) angle is achieved without influencing its value. Model 1 is the simplest model in which the perception function is proportional to the sine of the apex angle, α . It has been shown (Stočekus 1992, 1996)

Table 1. Summary of gravitropic response models. The symbols used represent the following (but see text for discussion and explanations): g = acceleration due to gravity; α = angle between the apex and the direction of the gravity vector; β = the liminal angle (an internal reference angle); t = time delay; γ = distance from apex; v = velocity of physiological signal transmission; f_c = competence function (see Fig. 2); k with various indices represents different coefficients

Model No.	Susception f_s	Perception f_p	Transduction f_{tr}	Response f_r
1	$y_s = k_s \cdot g(t)$	$y_p = k_p \cdot \sin(\alpha(t)) \cdot y_s$	$y_{tr} = k_{tr} \cdot y_p(t - \tau)$	$\alpha'' = k_r \cdot y_{tr} - k_w \cdot \alpha'$
2	$y_s = k_s \cdot g(t)$	$y_p = [k_o \cdot \sin(\alpha) - k_d \cdot \cos(\alpha)](t) \cdot y_s$	$y_{tr} = k_{tr} \cdot y_p(t - \tau)$	$\alpha'' = k_r \cdot y_{tr} - k_w \cdot \alpha'$
3	$y_s = k_s \cdot g(t)$	$\begin{cases} y_p = [k_p \cdot \sin(\alpha - \beta)](t) \cdot y_s \\ \beta' = k_a \cdot y_p(t) \end{cases}$	$y_{tr} = k_{tr} \cdot y_p(t - \tau)$	$\alpha'' = k_r \cdot y_{tr} - k_w \cdot \alpha'$
4	$y_s = k_s \cdot g(t)$	$y_p = [k_o \cdot \sin(\alpha) - k_d \cdot \cos(\alpha)](t) \cdot y_s$	$y_{tr} = y_p \left(t - \frac{\lambda}{V} \right) \cdot \exp \left(- \frac{k_w \cdot \lambda}{V} \right)$	$\alpha' = \int_0^{\lambda_{max}} f_c(\lambda) \cdot y_{tr}(\lambda) \cdot d\lambda$

1. The simplistic systemic model
 $\alpha'' = [k \cdot \sin(\alpha) \cdot g](t - \tau) - k_w \cdot \alpha'$

2. Model with diagravitropic component
 $\alpha'' = [(k_o \cdot \sin(\alpha) - k_d \cdot \cos(\alpha)) \cdot g](t - \tau) - k_w \cdot \alpha'$

3. Adaptational model
 $\begin{cases} \alpha'' = [k \cdot \sin(\alpha - \beta) \cdot g](t - \tau) - k_w \cdot \alpha' \\ \beta' = k_a \cdot [k \cdot \sin(\alpha - \beta) \cdot g](t) \end{cases}$

4. Growth response simulation
 $\alpha' = \int_0^{\lambda_{max}} [(k_o \cdot \sin(\alpha) - k_d \cdot \cos(\alpha)) \cdot g] \left(t - \frac{\lambda}{V} \right) \cdot \exp \left(- \frac{k_w \cdot \lambda}{V} \right) \cdot f_c(\lambda) \cdot d\lambda$

that improved modelling of the gravitropic response of most subjects requires additional components in the formulae. Model 2 introduces a 'diagravitropic' component (cosine α) which attempts to reflect the common observation that roots more often grow downwards at angles of 10° to 30° away from the vertical than they do exactly vertically. Model 4 uses the same perception function, but models 2 and 4 differ in their transduction and response functions (discussed below). A second way of accounting for a plagiogravitropic growth mechanism is used in model 3 and assumes an adaptational process in the graviperception system (Stočkus 1996). In this model the perception function depends on the sine of the difference between the apex angle and some internal reference angle (β , called the liminal angle) and, in addition, the liminal angle changes (adapts) during the gravitropic response at a rate which is proportional to the gravity stimulus.

In all models, the third stage (transduction) introduces a time delay (t), and in the final stage the response function introduces signal decay. The response function of model 4 introduces angular velocity instead of angular acceleration (modelling angular acceleration is the unique feature of models 1 to 3). The resultant angular acceleration (or velocity) is proportional to the received physiological signal. Models 1 to 3 have the same transduction and response functions and bending is assumed, for ease of calculation, to occur at a theoretical mathematical point. Model 4 is a revision which attempts to model a more realistic development of curvature by integrating transduction and response along the length of the growth zone of the root (Stočkus 1994c). This model also incorporates the concept that the ability to respond to the gravitropic signal varies along the length of the growth zone, for which a new term, the *competence function* (f_c), was introduced. The competence function describes the degree of competence to realize the incoming physiological signal of the tissues along the plant

axis. At each segment along an axis the local bending rate, which, by analogy with the relative elemental growth rate of Erickson (1976), can be called the relative elemental bending rate, is the product of the physiological signal at that segment and the value of the competence function (or, in a *single* segment, the coefficient of competence) (Fig. 2).

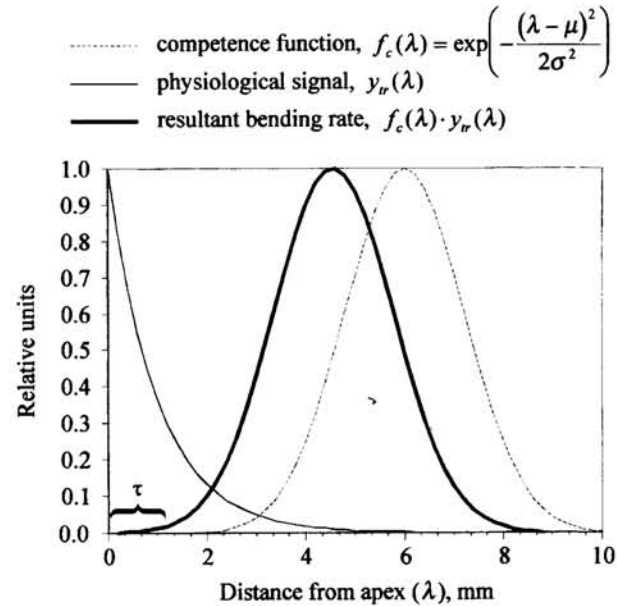


Figure 2. Explanation of the competence function and how it defines the local bending rates and time delay. The solid line is the physiological signal passing through the tissue, the dotted line is the competence function, and the bold line is the relative elemental bending rate (the product of the physiological signal and the competence function). The time delay (τ) is caused by the non-competent tissue zone through which the physiological signal must first pass (the transporting direction is basipetal, i.e. from left to right in the figure).

The integration of all local bending rates gives the angular velocity of an apex. The time delay, according to the third main assumption, was omitted because the shape of the competence function assures the required delay while the physiological signal moves through the incompetent tissues near the apex (Fig. 2). Also, the degree of response function in this model changes as the physiological signal adapts, as described in the previous paragraph.

Analysis indicates (Stočkus 1994c) that improvement and/or verification of model 4 depends on more detailed observational data becoming available. Thus, with the data

to hand, this model offers no advantage in description of tip angle kinetics during gravitropic response, but it is an intermediate step to more highly developed, and more naturalistic models.

Examples of how the models presented in Table 1 fit experimental data from a standard experiment with corn roots are shown in Fig. 3. Clearly, models 2 to 4 fit the data almost identically; this makes it impossible to verify the models on the basis of goodness of fit. Additional data and/or experiments are needed for verification. We emphasize that the models discussed here only describe changes

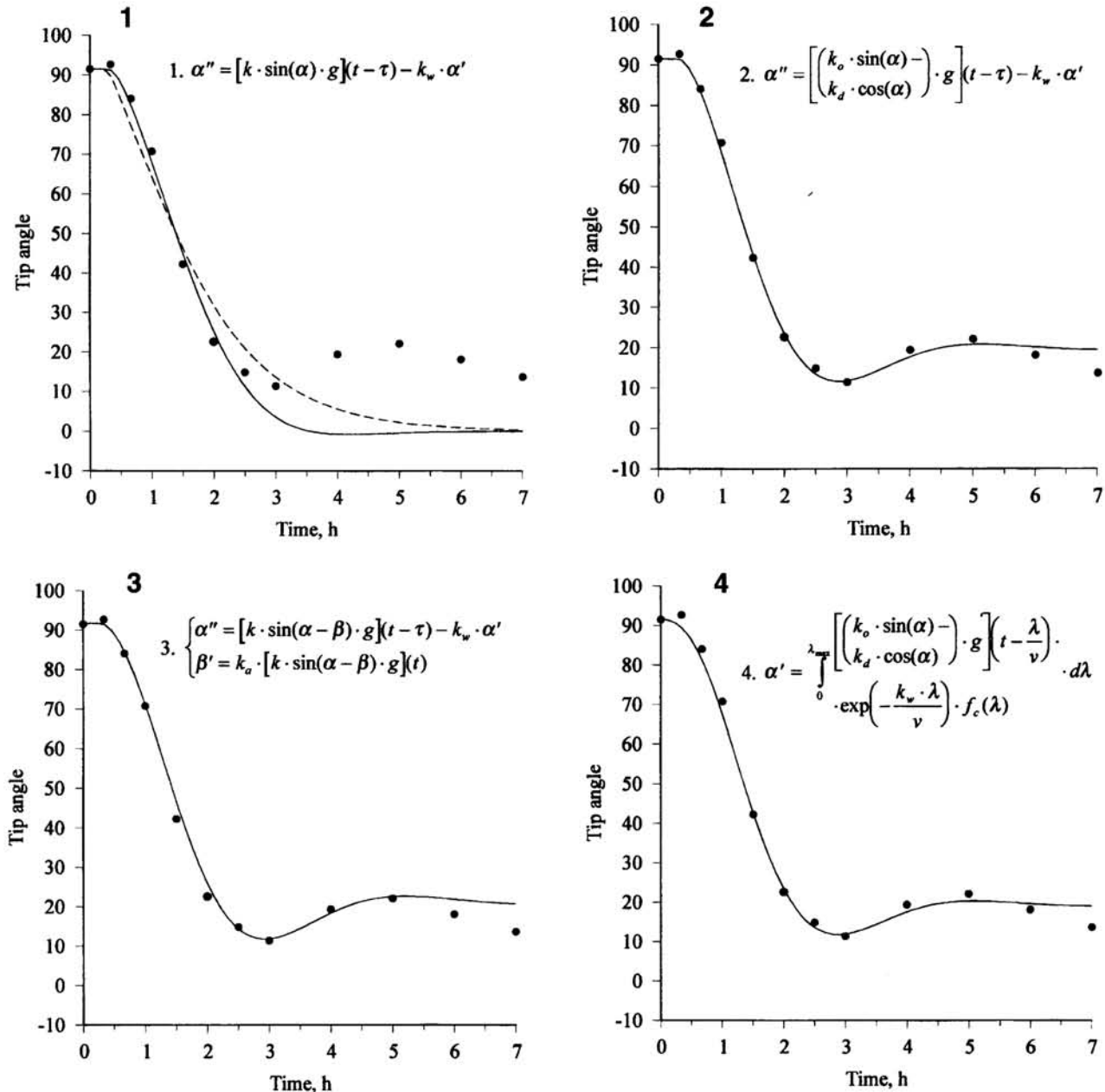


Figure 3. Examples of the way various models fit the same experimental data (corn primary roots, standard gravitropic stimulation by 90° under constant 1 g, solid circles). Parameters: 1. Fit to first 2.5 h (solid curve): $k = 208.0$, $\tau = 17.3$, $k_w = 4.31$; fit to all data (dashed curve): $k = 977.9$, $\tau = 15.7$, $k_w = 24.9$; 2. $k_o = 66.6$, $k_d = 59.4$, $\tau = 17.5$, $k_w = 2.83$; 3. $k = 120.0$, $k_a = 0.154$, $\tau = 15.9$, $k_w = 1.91$; 4. $k_o = 185.6$, $k_d = 63.7$, $k_w = 2.45$, $\mu^{\#} = 1.91$, $\sigma^{\#} = 0.857$, $v = 2.0^*$, $\lambda_{\max}^* = 5.0^*$ ($\mu^{\#}$, parameter from f_c ; * , arbitrarily fixed parameter).

in tip angle or elemental bending rates. Growth of axial organs is not considered by these models.

Application of plant gravitropism models to fungi

Although there are a few exceptions, orientation of growth of fungal mycelial hyphae is usually independent of the gravity vector, but fruit bodies of the higher fungi become oriented in the gravitational field, and particularly striking gravitropic reactions occur in mushroom fruit bodies. Results from both clinostat and space-flown experiments indicate that the basic form of the mushroom (overall tissue arrangement of stem, cap, gills, hymenium and veil) is established independently of gravitational stimulation although maturation, and especially commitment to the meiosis-sporulation pathway, requires the normal gravity vector (Moore 1991). During the course of development of a mushroom, different tropisms operate at different times; the young fruit body primordium is positively phototropic, but negative gravitropism predominates later.

Although mushrooms and plants belong to different Kingdoms, tropic bending of mushroom stems seems likely to be mechanically similar to tropic bending of plant roots or shoots. In both plants and fungi, the organ is essentially a cylinder composed of a community of interacting cells which have inelastic cell walls. Obviously, actions at the molecular and cell biological levels must be very different because of the hyphal structure of the fungal tissues. Nevertheless, the latest results of experiments on mushroom gravitropism show that it is a morphogenetic change resulting from differential tissue growth on the two sides of the mushroom stem, and that the gravity perception mechanism in agaric mushrooms probably depends on disturbance of cytoskeletal microfilaments (with nuclei possibly being used as statoliths), Ca^{2+} -mediated signal transduction being involved in directing the growth differentials (Moore *et al.* 1996); statements which are not far removed from what might be said about gravitropism in plants.

Justification for examining the applicability of plant mathematical models to fungal gravitropism hinges on the presumed mechanical similarities and can only be attempted with imitational models which do not require input of mechanism or substance-specific parameters. Mathematical modelling of tropic reactions has never been attempted in fungi. On the other hand, mathematical modelling of plant stem and root gravitropism is more highly developed. Here, we make the attempt to fit the plant models to fungal data in the hope of more easily deriving an accurate mathematical description of the process of mushroom stem bending. We hope to use the mathematical model to establish how best to proceed with experimental kinetic analyses specifically tailored to the needs of defining and testing a kinetic model of gravitropism in fungi.

However, present knowledge puts some restrictions on the usage of the models. First, there is no evidence about involvement of any kind of 'diagravitropic component', 'adaptation' or anything else that causes plagiogravitropic apex orientation of mushroom stems. As far as is known,

the apex of stems of fungal fruit bodies *always* reaches the vertical position if conditions are satisfactory and there is enough time for a response. Secondly, the results obtained should be interpreted with caution because not all of the assumptions used for deriving the models have yet been verified in fungi. For example, there are no data about the angle-response relationship (all fungal experiments to date have involved rotating the subject to the horizontal). Thus the sine-based perception function may not be appropriate.

Because of the first restriction, the only acceptable experimental data are those for stems which reach the vertical position during the observation period. Otherwise, the model fit is meaningless because the model fitting routine attempts to find unrealistic parameters (such as k and k_w) to make the modelled curve match the incomplete observational data. After evaluating the available data we chose 26 stems of *C. cinereus* from two different experiments which satisfied the modelling purposes: a relatively long time period which allowed all the stems to adjust to a near-vertical apex position, coupled with uniform and satisfactory experimental conditions (see 'Materials and methods'). The routine of fitting model 1 was then applied and the results analysed.

MATERIALS AND METHODS

Experimental material

Video recording and computer-based video-image analysis has been used for kinetic analysis of the gravitropism of the stems of the agaric fruit bodies of *Coprinus cinereus* (Schaeff. ex Fr.) S. F. Gray (Kher *et al.* 1992). Fruit bodies were obtained from *in vitro* cultures. The vegetative dikaryon was cultured on complete medium (Moore & Pukkila 1985) in 9 cm Petri dishes in the dark at 37 °C for 3–4 d. Fruiting bodies were obtained by inoculating the dikaryon onto sterilized horse dung in crystallizing dishes, incubating at 37 °C for 3–4 d in the dark and then transferring the dung cultures to a 26–28 °C incubator with a 16 h light/8 h dark illumination cycle (white fluorescent lights, average illuminance 800 lx). Similar observations have been made on *Flammulina velutipes* (M. A. Curtis ex Fr.) Singer using serial photographic records (Monzer *et al.* 1994). The standard assay in *C. cinereus* involves removal of the cap followed by continuous video recording of the stem secured on a horizontal platform housed in a humidity chamber at room temperature. Video records give no evidence for rotation of the fruit body stem during either vertical growth or tropic bending. In studies with *F. velutipes*, the cap was sometimes left in place, though stems were trimmed to a uniform 25 mm length and then secured to the top of a pin for observation. In all cases, low-intensity red light was used for illumination to avoid phototropic effects. The results obtained in the two laboratories have been reviewed (Moore *et al.* 1996).

Primary roots of *Zea mays* L. hybrid GK26 × DK501 (Institute of Corn, Dnepropetrovsk, Ukraine) were used for plant gravitropism experiments (Stočkus 1994b). Roots

were grown in water vapour-saturated air for 48 h at 25 °C in the dark. Seedlings with 10–30 mm straight roots were transferred into plastic experimental boxes, fixed in position through their caryopses with a piece of plasticine and covered with moist filter paper, leaving roots free. Operations were carried out under continuous mist spraying, using dim dark-green illumination (530 ± 25 nm, ≤ 5 lx). Gravitropic stimulus was applied by rotation of boxes to a required angle, and gravitropic response was recorded from time lapse photographs which were made using the same dark-green filter.

Mathematical model fitting

Solution of differential equations, estimation of initial modelling parameters and fitting of the experimental data were accomplished using the programs written by A. Stočkus in the Borland Pascal 7.0 object-oriented language. The routine of fitting the model to experimental data consists of the following steps.

- (i) All data were transformed to a standard form: apex angles were represented in degrees from the gravity vector.
- (ii) Each data set used consisted of a number of replicate observations (up to $n=26$) of tip angle time courses, for which averages were calculated and used as initial data for modelling.
- (iii) These initial data were used for the fit adjustment using manual input with visual control of the resultant solutions to establish initial approximate parameters.
- (iv) The initial parameters were used as a starting point for the rest of the data for individual subjects and a program of minimization by the sum of squares was run for each data entry. The parameters obtained, resultant model curves and their deviations from data points were extracted and used for subsequent analysis.

The numerical methods used to solve differential equations and initial conditions were described in Stočkus (1992, 1994c). As a rule, 600 steps were used for solving models 1, 2 and 3, and 200 steps for model 4. A constrained method of minimization by sum of squares was programmed using the unconstrained Newton method as a basis (Dennis & Schnabel 1985), and the termination conditions were norm of gradient (≤ 0.01) and number of function calls (≤ 1000). Derivatives necessary for the Newton method were calculated using a second-degree numerical differentiation formula based on Newton interpolation formulae.

RESULTS

The averages of the experimental data used together with averages of model fits to each individual stem are presented in Fig. 4. These curves are typical of attempts to apply model 1 to *C. cinereus* data: there was an adequate fit to the initial stages of the response, but deviations in the middle and at the end of the response.

The fits to data of individual stems, however, show significant variations. We tried to classify the data used by

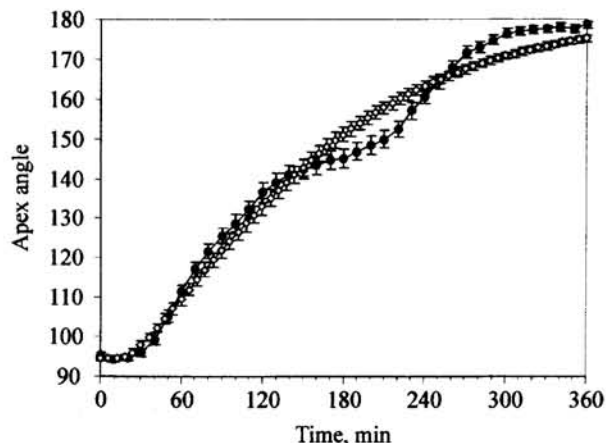


Figure 4. Averaged data of the *C. cinereus* tropic response to standard gravitropic stimulation at 90° (solid circles; means \pm SE, $n=26$ for each point) and the averages of model 1 fits (diamonds; means \pm SE) to each individual stem.

the following criteria: short or long lag period and 'smooth' or 'inflected' shape of response time course. These typical patterns, together with model 1 fits and graphs of deviations of fit from data, are shown in Fig. 5 and Table 2. In addition, two other types are included: rapid response (e) and 'hunting' type (f).

Deviation graphs are shown immediately above each response time course. Deviation graphs show the extent (and sign) of the difference at each observation point between the observed and modelled data. Their higher resolution aids in judging the fit between experiment and model. In the case of a good fit, the deviation graph should effectively represent stochastic variation or 'noise'. The illustrations in Fig. 5 show that there were no systematic deviations in stems of type (a), but deviations became larger when the lag period was long and especially when stems showed an inflected response (c and d).

Finally, the rapid response (e) was well imitated by the model, while the hunting type of response (f) obviously accentuated the frequency of change in the sign of the deviations.

Table 2. Parameters for the model 1 curves (see Fig. 5). The coefficient k defines the magnitude of the physiological signal resulting from the gravity perception, τ is time delay (min) and k_w is the coefficient of signal decay (k_w^{-1} indicates the half-time of signal decay, in h)

Sample	k	τ	k_w
(a)	-110	20.0	4.05
(b)	-257	41.2	11.1
(c)	-172	15.1	6.42
(d)	-182	15.2	8.84
(e)	-393	15.4	6.79
(f)	-21.2	20.0	0.766

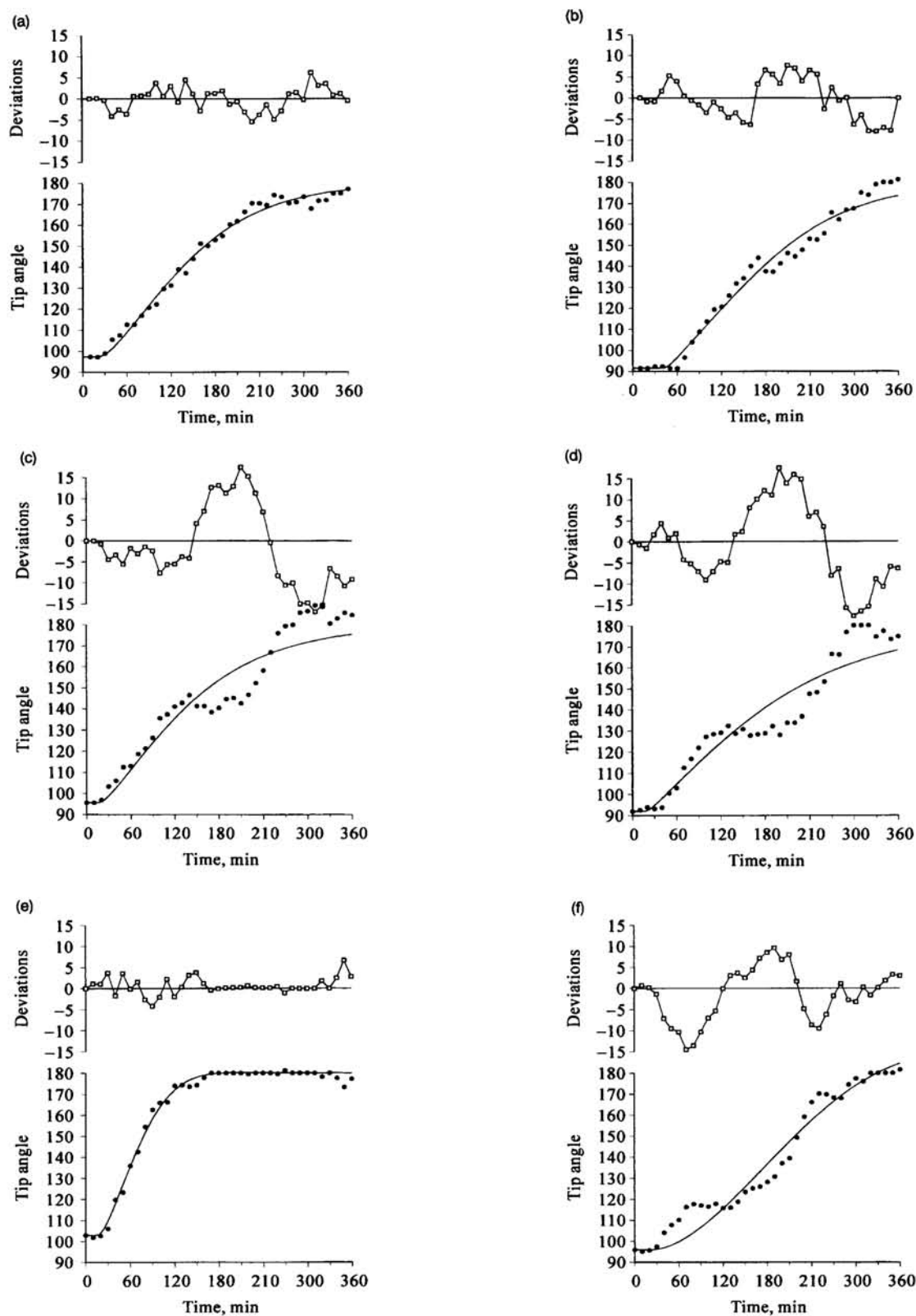


Figure 5. Gravitropic responses of various individual stems of *C. cinereus* (solid circles), model 1 fits to those data (solid line) and graphs of deviations, i.e. the differences between data and the fitted curve (squares). For the latter, the zero line represents experimental data. Stem types: (a) short lag period, 'smooth' response; (b) long lag-period, 'smooth' response; (c) short lag period, 'inflected' response; (d) long lag period, 'inflected' response; (e) one rapidly responding stem, possibly showing the optimum capabilities of the *C. cinereus* gravitropic response system; (f) response of the 'hunting' type, in which the apex angle seems to 'hunt' uncertainly for the response path. Parameters of the fits are presented in Table 2.

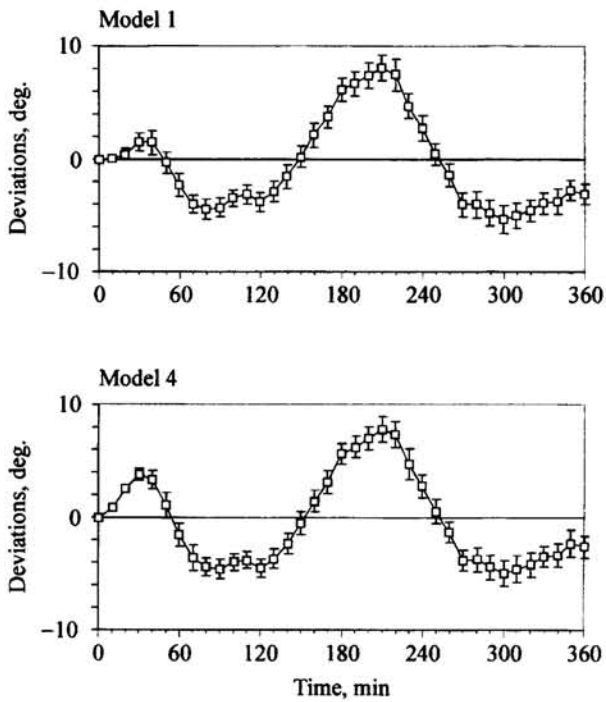


Figure 6. Averaged deviation graphs of two models fitted to individual *C. cinereus* gravitropic response data (26 stems from two experiments, standard gravitropic stimulation at 90°). Top panel, model 1; bottom panel, model 4 (means \pm SE). The zero line represents experimental data.

Figure 5 illustrates the behaviour of selected individual stems, but the deviations between time course plots and model predictions for all stems can be combined and averaged (Fig. 6). These plots clearly show that the fits between model predictions and *C. cinereus* stem gravitropism time courses are remarkably good; deviations rarely exceed 8%. Nevertheless, the deviations which do exist are also remarkably consistent, revealing:

- (i) a significant positive deviation at the beginning of the response, which indicates that model 1 fails to imitate the initial stages of gravitropic response; the model predicts a shorter time lag than is normally observed;
- (ii) that negative deviations between model fits and data at 1–2 h and at the end of time course are probably caused by the method of least squares, which adjusts the extremes but does not compensate the main deviation, which is
- (iii) that the model does not simulate the decreased bending rate which generally occurs at about 2.5 to 3.5 h in *C. cinereus* stems, causing the inflected response time course and a consequential positive peak of deviations on graphs in Fig. 6.

Comparison between model 1 and model 4 was accomplished by excluding the diagravitropic component from model 4 by zeroing parameter k_d . Since some parameters must be fixed to obtain comparable results (Stočkus 1994c), the parameter v (signal velocity) was set to 6 mm

Table 3. Analysis of variance of transformed sums of squares of two model fits to *C. cinereus* gravitropic response data

Source of variation	Sum of squares	d. f.	Mean square	F	P
Model	0.013	1	0.013	0.264	0.612
Stipe	36.70	25	1.468	29.76	0.000
Residual	1.233	25	0.049		

h^{-1} , which is similar to the mean value of the rate of bending front migration along the *C. cinereus* stem (Kher *et al.* 1992) and λ_{max} (maximal distance from the apex for integration) was set to 36 mm (assuming physiological signal migration at 6 mm h^{-1} for 6 h). The normal competence function f_c was used (Fig. 2; Stočkus 1994c).

The resultant sums of squares from both model fits were transformed to logarithms to normalize data and then were analysed by multifactorial analysis of variance (Table 3). Results indicate no significant differences in goodness of fit between the two models.

However, analysis of the averaged deviation graph showed that there was a significant difference between the two models in the pattern of deviations over the initial stages of the response time course (Fig. 6). Model 4 fits the initial stages generally less well; the same was true for plant data (A. Stočkus, unpublished results). Deviations over these stages were caused by the nature of the competence function. Most fits are adjusted by the reiterative modelling program to have competence functions which do not produce any time delay at all (Fig. 7), that is, the coefficient of competence was not equal to zero at the very tip of the 'theoretical' stem. This is inconsistent with experimental data since the first region in which curvature occurs is located at about 7–10 mm below the apex (Kher *et al.* 1992), and most observations show a delay (the

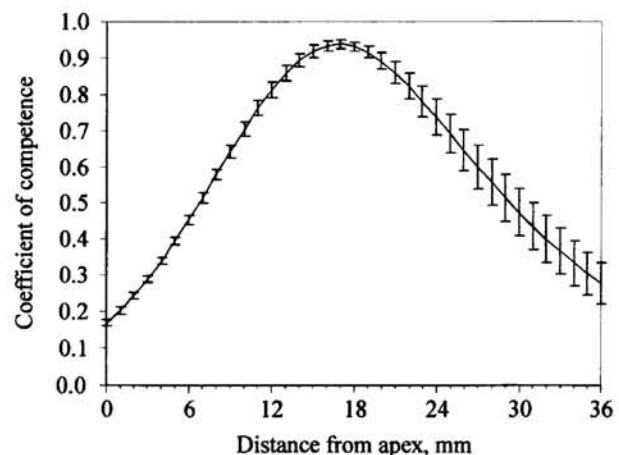


Figure 7. Averaged competence function obtained from model 4 fits to *C. cinereus* stems gravitropism data.

Parameter	Model 1				Model 4		
	k	τ (min)	k_w (h ⁻¹)	k_o	k_w (h ⁻¹)	μ (mm)*	σ (mm)*
Average	-285.0	16.53	11.21	-67.62	3.782	18.81	10.10
Minimum	-29.30	4.870	0.766	-19.72	1.293	13.22	6.638
Maximum	-881.8	23.22	40.91	-192.0	9.006	28.58	16.86
SD	244.3	4.071	11.02	44.63	2.245	4.203	2.933

*Parameters from f_c (see Fig. 3). μ represents the position of the maximum of the competence function (in mm from the apex), and σ is the width of the competence distribution (corresponds to standard deviation).

reaction time) of about 30 min. Obviously, this reflects the inability of this particular model to imitate properly the initial stages of the gravitropic response.

On the other hand, the model parameters obtained seem more meaningful in the case of model 4 (Table 4). For example, the coefficient of signal decay, k_w , is less (and more uniform) in model 4 than in model 1, where in individual fits it varies from 0.766 to 40.9, while in model 4, the range was from 1.29 to 9.01. In physiological terms, the reciprocal of k_w is the half-life of the physiological signal (in hours). $1/40$ is therefore approximately 1.5 min and $1/0.766 = 1.3$ h, suggesting that in one stem the physiological signal would disappear in a few minutes while in another it would last for hours. This seems to be an unrealistic range and strongly suggests that model 1 is providing inadequate fits in many cases. Model 4 seems more adequate from this point of view, giving an average half-life of 16 min (range 7 to 46 min). Coefficient k_o , like k (see Table 2), indicates the magnitude of the physiological signal, and both k and k_o changed in accordance with k_w : the greater k_w , the greater k or k_o . The calculated time delay, τ , provides time delays of about half those extracted directly from experimental data (Kher *et al.* 1992, Table 4).

Since the motive of this work at the outset was to use models derived from plant experiments to examine fungal experimental data, it is interesting to compare model fitting to fungal data, particularly the deviation graphs, with similar data obtained from plant material. Figure 8 shows a deviation graph obtained from model 2 fits to gravitropism

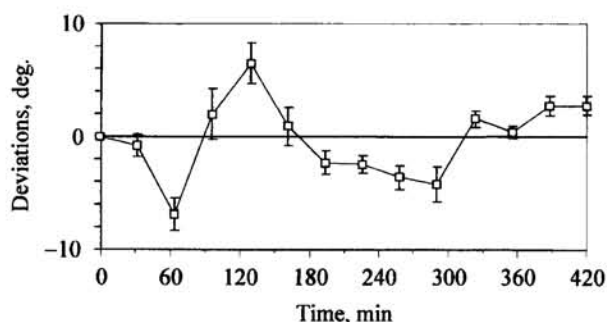


Figure 8. Deviation graph for model 2 fits to primary corn roots gravitropism data (A. Stočkus, unpublished results). Means \pm SE, $n = 7$ for each data point).

Table 4. Averages of two model parameters from fittings to a set of individual *C. cinereus* stipes

data obtained with corn primary roots. Generally, the fits were rather similar to those shown for fungal material. Deviations in the root data were smaller for most time intervals except for the first 2 h, where the variance of deviations also seems much higher.

However, the broad compatibility between, for example, Fig. 8 and Fig. 6 justifies the attempt to model the fungal response from a plant kinetic basis. It also encourages consideration of how the models might be improved to tailor them to the fungal response, and what the accuracy of the imitation might mean in terms of fungal mechanisms.

Stočkus (1992, 1994a) pointed out that the second-degree models used describe initial stages of gravitropic response well, though this inference was drawn from fits to averaged data and from visual estimation. The deviation graphs employed here allow us to reformulate this conclusion. The data presented in Fig. 8 show that initial stages actually contain the most pronounced deviations, although this is not obvious during visual inspection of fitted curves. The deviations in initial stages were also found in fits to fungal data (Fig. 6). If we restrict model fitting to the first 2 to 3 h of response, the minimization by sum of squares routine significantly improves the fit to the restricted data set, although the price is greater variance of the parameters obtained (Table 5).

Application of models 2 and 3 to the fungal gravitropism data seems pointless because these models feature the di-gravitropic component and, since most stems do adjust to the vertical, these two models would transform themselves to model 1 by zeroing coefficients k_d in model 2 and k_a in model 3. Preliminary runs did show these tendencies, confirming the theoretical prediction.

The fungal data examined here refer to *Coprinus cinereus*, for which the greatest amount of kinetic data are

Table 5. Summary of model 1 parameters from fittings to initial 2.5 h of individual *C. cinereus* stems data

Parameter	k	τ	k_w
Average	-339.3	17.17	12.40
Minimum	-35.09	0.34	2.054
Maximum	-1419	49.63	58.72
SD	306.5	11.78	12.72

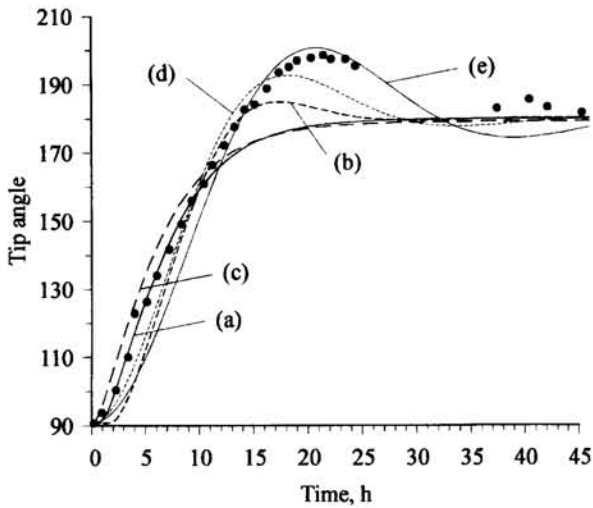


Figure 9. Fits of model 1 to *F. velutipes* gravitropism data. Closed circles are experimental data; (a) fit to initial 12 h, (b) fit to all the data; (c), (d) & (e), fits with fixed τ and k . Parameters are as follows:

Curve	k	τ	k_{ws}
(a)	-33.1	54.0	3.43
(b)	-7.26	101	0.677
(c)	-30	5	2.78
(d)	-3	5	0.227
(e)	-2	5	0.146

available. Similar experiments have been done with *F. velutipes* (Monzer et al. 1994). The major difference between *C. cinereus* and *F. velutipes* is a 6-fold difference in the initial rate of response (51° h^{-1} in *C. cinereus*, 9° h^{-1} in *F. velutipes*). The difference in initial rates means that, while the apex of the stem of *C. cinereus* attains the vertical within 3 to 4 h, stem segments of *F. velutipes* fruit bodies require 12 h to reorient to the vertical. However, this is not only a qualitative difference. Attempts to fit model 1 to numerical data extracted from published graphs (Kern 1994) showed that the model was unable to fit initial and final stages of gravitropic response with the same accuracy. Where fitting was restricted to the initial 12 h (Fig. 9a), the model did not show any overshoot or oscillation around the vertical. Instead, it produces an asymptotic curve. A fit to all data (Fig. 9b), on the other hand, resulted in a curve which overshoot slightly, but the fit deviated from the measurements at the beginning of the response. The method of least squares did not generate better fits. We can, however, fix some model parameters, and test other hypotheses. For example, by fixing the time delay, τ , to 5 min. and setting coefficient k to -30 (representing a high level of perception; Fig. 9c), then to -3 (Fig. 9d) and to -2 (representing a low level of perception; Fig. 9e), it is possible to improve the fit visually by making it follow the oscillation in the data points more accurately. A further decrease of k , however, does not provide a better fit: instead, it began to deviate from all the data. Interestingly,

one of the suggested differences between *C. cinereus* and *F. velutipes* is that the latter has much less gravity-perceiving tissue (Moore et al. 1996), an idea which is in accordance with the modelling results shown in Fig. 9.

DISCUSSION

The results of gravitropic experiments carried out with stems of the agarics *C. cinereus* and *F. velutipes*, and comparison of the data with similar data obtained with plant subjects, show striking similarities between gravitropic response in these two groups. First, it is evident that the basic assumptions of the plant models (as summarized in Fig. 1) are logically applicable to fungi (i.e. we can accept them as a first approach without changes). Secondly, the basic mechanism of bending is the same, being caused by differential growth of opposite flanks of the growing organ. Thirdly, the distribution of growth seems very similar: in both plants and fungi growth of stems (roots) is most intensive just behind the apex and is almost absent at the apex and at the base. There is also a similar positively asymmetric distribution of relative elemental growth rates (Erickson 1976; Greening & Moore 1996). As a consequence, bending first occurs in the region near the apex in both groups, then migrates basipetally as the tissue matures. Fourthly, in both fungi and plants the gravitropic response is a process with a substantial time delay suggesting that many time-consuming processes are involved in the reception, transduction and realization of gravitropic stimuli. This feature is strikingly different from animal systems, where gravitational stimuli are processed by the nervous system. The time range of gravitropic response itself is also comparable in the two groups. Fifthly, the comparison of data from *C. cinereus* and *Zea mays* revealed variability amongst individuals in the kinetics of tropic response (Fig. 5 & Table 4; Stočkus 1989). Since genetically homogenous lines were used for experiments, the reason for such variability is not genetic. Clearly, the subjects (roots or mushroom stems) are sensitive to quite small physiological, structural and/or environmental differences. The only significant physiological factor influencing the variability of final apex angle during gravitropic response at 1 g identified is the biological age of stems or roots (Stočkus 1989; Kher et al. 1992).

Despite the similarities, this analysis has revealed some important differences in plant and fungal gravitropism kinetics. First, the inflections seen in many *C. cinereus* stem gravitropism time courses at about the time that curvature compensation has been suggested to begin (Kher et al. 1992) cannot be modelled, and additional assumptions may have to be included to account fully for *C. cinereus* stem gravitropism.

Secondly, the *C. cinereus* stems very rarely exhibited oscillations around the vertical tip angle position although plant subjects oscillate. This is, however, consistent with current models since they easily imitate this kind of response and there are some plant subjects which generally do not show oscillations as part of their gravitropic

response. The available data for *F. velutipes* gravitropism, on the other hand, did show such an exaggerated single oscillation that it was impossible to simulate adequately with these models. However, the lack of oscillation (in *C. cinereus*) may be the unusual feature. Buller (1905, 1909, 1922) describes oscillation occurring as mushroom fruit bodies adjust to the vertical, and Streeter (1909) shows a photograph of an *Amanita* fruit body with pronounced S-shaped curvature of the stem. Thus, more data from detailed kinetic observation of different species of mushroom are required to categorize possible differences in this respect.

Thirdly, the data obtained with *C. cinereus* indicate that the processing of gravitropic stimuli might be accomplished in an 'all-or-nothing' manner (Hatton & Moore 1994) which differs from what is observed in plants. Experimental data under 1 g indicate that plants probably do not show an 'all-or-nothing' response even at the level of individual cells (Merkys & Laurinavicius 1991). However, the validity of an 'all-or-nothing' response in fungi still needs more careful examination, since there are no data on their gravitropic response at low g levels.

Finally, it seems that neither of the agarics investigated ever grows stably at a plagiogravitropic tip orientation, which indicates that there are no adaptational or 'diagravitropic' processes in the gravireceptors of these subjects of the kind proposed to explain stable plagiogravitropic growth of some plant organs (Stočkus 1992, 1996).

Unfortunately, there are no data on angle–response or acceleration–response relationships in fungi, making it impossible to compare them with plants, where such relationships have been characterized. We also have no evidence about threshold acceleration forces for fungi; there is only one approximate estimation of perception time (i.e. time of 1 g stimulation required for initiation of gravitropic response) — approximately 7 min (Hatton & Moore 1994), which is approximately 1 order of magnitude greater than is common for plants which usually have a perception time of 2–3 min, though it can be as little as 12–30 s (Volkman & Sievers 1979).

To fill these gaps in the available data set should be the primary goal of further experimentation. It is absolutely necessary to obtain the angle–response and acceleration–response relationships for the derivation of improved mathematical model(s).

The next set of experiments which seems necessary to elucidate fungal gravitropism is suggested by the list of possible dissimilarities with plants. To ensure that we are not dealing with an artefact or species-specific feature, the factors causing inflection of the time course of *C. cinereus* stem gravitropism should be tested. This would include non-specific adaptational-stress responses, genetic factors (using various strains) and temperature. The same is true for oscillating–non-oscillating stems (more data from *F. velutipes* and other species would be especially welcome), and for justification of the 'all-or-nothing' response type (which may be combined with determination of more accurate dose–response relationships).

Finally, the absolute threshold values of the fungal gravitropic system for gravity acceleration and time of stimulation need to be refined. All the data we have at the moment dealing with threshold time were obtained using clinostats. However, their usage is based on extensive theoretical as well as experimental elaboration of plant research methods and needs to be carefully verified in fungi. Experiments like those performed for a few plant subjects (Halstead & Dutcher 1987) under true microgravity conditions are necessary to evaluate absolute threshold values validate the use of clinostats.

Model 4 failed to imitate properly the initial stages of the gravitropic response (Fig. 6), but, in contrast to conclusions from experiments using plant material (Stočkus 1994c), it was found that this model had some advantages in the description of *C. cinereus* data, providing parameters which seemed more realistic and less variable. This may indicate that fungal gravitropic kinetics is more dependent on how the curvature is realized along the stem. Kher *et al.* (1992) indicated that about 90% of initial curvature is compensated during the course of gravitropic bending, causing them to introduce 'curvature compensation' as a participant of the gravitropic response mechanism (logically, a similar phenomenon must be present in plant organs, too, although we have not found any similar calculations in the literature). The compensation mechanism cannot be independent of the pattern of curvature. Thus, for adequate description of any mechanism like this we need a model which provides curvature data in each stem segment. Only model 4 described here, or the model of Barlow *et al.* (1989, 1991), would serve as a basis for this. After curvature simulation, it would be possible to introduce the appropriate description of curvature compensation. This would need at least one additional loop and rearrangement of the basic scheme, as in that presented by Chapman *et al.* (1994). At the moment, we have two (not necessarily mutually exclusive) hypotheses about the mechanism of presumed curvature compensations, i.e. gravity-dependent and gravity-independent compensation. Kher *et al.* (1992) first interpreted curvature compensation as a gravity-dependent process, which begins as the apex is raised about 35° from the horizontal. Curling of apex-pinned stems into circles seems to support this point of view. Alternatively, curvature compensation may be a reaction to curvature, being dependent on the degree of curvature in the stems and gravity-independent. Similar gravity-independent straightening has been observed in plants (Leopold & Wettlaufer 1989; Chapman *et al.* 1994), and there is evidence for an autotropic-like reaction from clinostat experiments with stems of *C. cinereus* (Hatton & Moore 1994). Bend-dependent curvature compensation can explain the inflections in gravitropism time courses observed in *C. cinereus*, because when curvature reaches a maximum (for example, in the middle of the response), curvature compensation increases and the rate of bending will decrease. However, release of the 'tension' (unspecified) by the first burst of curvature compensation would lessen the demand for compensation (allowing bending to

increase again) even though the gravitropic signal had remained almost unaltered. If curvature compensation is gravity-dependent it is difficult to see how it could generate the inflection. On the other hand, the experiments showing that apex-pinned stems bend well beyond the vertical might suggest that stem polarity is important in permitting compensation to initiate. Clearly, this interpretation is speculative and more data are required.

The data for *F. velutipes* are particularly interesting for two reasons. First, this organism overshoots the vertical consistently, whereas in *C. cinereus* it is rare for a stem apex to overshoot. Secondly, attempts to fit the model to *F. velutipes* data indicated that some particular assumptions must be made in the model to adapt it to this subject. In this respect it is interesting that *C. cinereus* and *F. velutipes* possibly have some differences in the mechanism of curvature realization since differential growth in *C. cinereus* results from a difference in the rates of growth rate acceleration on the two sides of the stem, whereas in *F. velutipes* the growth of the upper side of the stem is reduced and that of the lower enhanced (Monzer *et al.* 1994). Such differences cannot yet be used for modelling purposes because we cannot relate them to the mechanical-informational properties of gravitropic response used in the models described here. More detailed information about a wider range of species is clearly required.

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