

# Quantification of curvature production in cylindrical organs, such as roots and hypocotyls

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## Summary

- Differential growth curvature rate (DGCR), defined as the spatial derivative of the tropic speed, was derived as a measure of curvature production in cylindrical organs. Its relation to usual concepts, such as curvature ( $\kappa$ ), rate of curvature ( $d\kappa/dt$ ) and differential growth profiles, was determined. A root gravitropism model, testing the hypothesis of one and two motors, exemplified its capabilities.
- DGCR was derived using cylindrical geometry and its meaning was obtained through a curvature conservation equation. The root gravitropism model was solved using a discrete difference method on a computer.
- DGCR described curvature production independently of growth, and was superior to  $d\kappa/dt$ , which underestimated production. Moreover, DGCR profiles were able to differ between one and two motors, while profiles of  $\kappa$  and  $d\kappa/dt$  were not.
- The choice of the measure of curvature production has a large impact on experimental results, in particular when spatial and temporal patterns of differential growth need to be determined. DGCR was shown to fulfill the accuracy needed in the quantification of curvature production and should thus serve as a helpful tool for measurements.

**Key words:** curvature, gravitropism motor, gravitropism, hypocotyl, model, root.

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## Introduction

Differential growth in cylindrical organs, such as roots and hypocotyls, is a complex process that involves changes in transcription and dynamic alteration of protein expression patterns (Muday, 2001; Friml & Palme, 2002; Friml *et al.*, 2002; Blilou *et al.*, 2005; Teale *et al.*, 2005). Quantitative analysis of growth and differential growth is a prerequisite to understand the molecular organization of this process. Several concepts have been used to characterize the curvature of cylindrical organs, the three most notable being the differential relative elemental growth rate (REGR) distributions (Silk & Erickson, 1978; Silk, 1989; Ishikawa & Evans, 1993; Zieschang *et al.*, 1997; Mullen *et al.*, 1998a), the curvature ( $\kappa$ ) (Silk & Erickson, 1978; Selker & Sievers, 1987; Silk, 1989; Zieschang & Sievers, 1991) and distributions of the

curvature angle (Mullen *et al.*, 1998b; 2000; Wolverton *et al.*, 2002a,b). Differential REGR distributions and the rate of change of curvature ( $d\kappa/dt$ ) have been shown to be equivalent (Silk & Erickson, 1978; Silk, 1989; Zieschang *et al.*, 1997). However, differential REGR profiles are prone to errors because the traditional method used to measure REGR distributions relies on a relatively small amount of markers, and interpolation schemes need to be applied (Peters & Bernstein, 1997). Moreover, the determination of curvature production through differential REGR profiles is critical, because the coordinates of the profiles have to be matched correctly (nontrivial, for example, for curved root geometry and easily resulting in artifacts). As will be shown in the 'Description' section,  $\kappa$  and  $d\kappa/dt$  are not suited to describe the change of orientation of an organ and do not quantify sufficiently the production of curvature. However, quantitative relations of curvature production

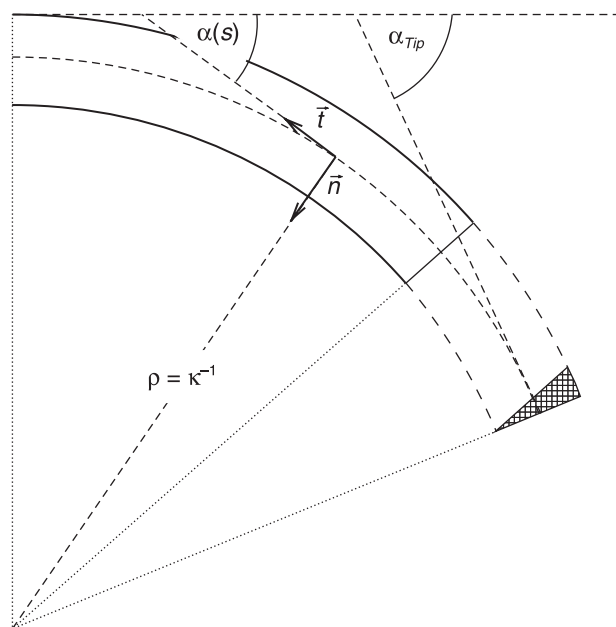
at specific regions need to be established to elucidate differential growth and organ curvature in gravitropism, phototropism and hydrotropism (Blancaflor & Masson, 2003; Epen *et al.*, 2005; Esmon *et al.*, 2005). Therefore, the concept of the curvature angle distribution (Mullen *et al.*, 1998b; 2000; Wolverton *et al.*, 2002a,b) was extended here to find a suitable measure of curvature production [differential growth curvature rate (DGCR)]. Theoretical calculations presented below, show, for curvature occurring in a plane, the relation of the DGCR to  $d\kappa/dt$  and to differential REGR profiles. This concept is extended to describe curvature and torsion processes in three dimensions, and, in addition, the DGCR is applied in a simple model of root gravitropism and used to simulate two different cases of curvature production in root gravitropism (one and two sites of production). The recent proposal of the existence of two motors in root gravitropism is tested therewith (Wolverton *et al.*, 2002a). The simulations presented here show that a suitable measure of curvature production is essential to be able to separate two motors that are located so closely as proposed [in the distal elongation zone (DEZ) and in the central elongation zone (CEZ); Ishikawa & Evans, 1993; Wolverton *et al.*, 2002a], and confirm the need for a suitable measure of curvature production (DGCR).

## Description

Plant organs seek, through curvature, to attain a certain direction in space. Root tips and hypocotyls, for example, tend to grow towards and against the gravity vector, respectively. These organs use their orientation to control the phytohormones/signals behind the curvature process (the basis of the root gravitropism model; reviewed by Muday, 2001; Friml & Palme, 2002; Perbal & Driss-Ecole, 2003). The curvature,  $\kappa$ , alone, does not measure the direction of such an organ; for example, a gravitropically stimulated root may have a high  $\kappa$ , but still be far from pointing downwards. Therefore, the curvature angle,  $\alpha$ , seems to be a more natural parameter for using to describe curvature processes than  $\kappa$  (Sachs, 1882). However, if the length of the organ is known in time,  $\alpha$  can be determined through the integral of  $\kappa$  over distance (Zieschang *et al.*, 1997):

$$\alpha(s,t) = \int_0^s \kappa(\sigma,t) d\sigma, \quad (1)$$

( $s$ , the arc length along the organ axis;  $\alpha(s,t)$ , the angle between the horizontal and the tangent  $\vec{t}$  at distance  $s$  from the organ apex and at time  $t$ ) (Fig. 1). The tropic speed  $\omega = d\alpha/dt$  is the angular velocity by which  $\vec{t}$  and the normal  $\vec{n}$  change orientation in time. The change of orientation at a specific location is a consequence of differential growth and manifests itself as an asymmetry in volume increase across the organ (shown as a hatched area in Fig. 1 for the whole organ).



**Fig. 1** Cylindrical organ which grows and curves.  $\rho$  and  $\kappa$  denote the curvature radius and the curvature at distance  $s$  from the organ apex, respectively.  $\alpha(s)$  is the curvature angle at position  $s$ , while  $\alpha_{Tip}$  denotes the tip's curvature angle. The tangent  $\vec{t}$  and normal  $\vec{n}$  at position  $s$  are shown (binormal is perpendicular to these and points out of the figure's plane). The dashed circle segments on the upper and lower sides have the same arc length, and the hatched area depicts the gradient in volume increase produced by differential growth.

Although Eqn (1) gives a relationship between the spatial and temporal distributions of curvature and curvature angle, it does not provide information on how local growth gradients affect orientation of the organ apex. Moreover, it does not allow determination of the amount of curvature angle contributed at a specific location of the organ. Both are, however, essential for understanding the signals and processes involved in organ curvature. A measure of curvature production is needed and should characterize the amount of curvature angle produced per unit time and unit length. Two possibilities arise from Eqn (1): the rate of change of curvature  $d\kappa/dt$ , and the DGCR (proposed here). Both have the same units, but differ substantially in growing organs (Eqn 4).  $d\kappa/dt$  gives the rate of change of curvature of a selected segment of the organ (material property), while DGCR is defined as the local derivative of  $\omega$  (local property). A calculation will be presented which shows that DGCR, in contrast to  $d\kappa/dt$ , accurately determines curvature production in growing organs (Eqns 4 & 5).

We conclude this short mathematical introduction with a remark to remind the reader of the difference between material and local derivatives. The material derivative of a function  $f = f[s(t), t]$ , of time  $t$  and arc length  $s = s(t)$ , is given by (compare Silk, 1989):

$$\frac{df}{dt}[s(t),t] = \partial_t f[s(t),t] + v\partial_s f[s(t),t], \quad (2)$$

( $v = ds/dt$ , the velocity at position  $s(t)$  and time  $t$ ). The first term on the right represents the local derivative, in the sense that it measures the change occurring at a certain fixed distance of the organ apex. The second term on the right is the contribution of advection/convection, in other words the contribution of movement of the organ segment taken into consideration (movement in relation to the organ apex). The notation used in Eqn (2) to differ between material,  $d/dt$ , and local derivatives,  $\partial_s$  and  $\partial_t$ , will be maintained in the sequel.

### Curvature production

In some situations, the center curve of curving organs can be approximated by a plane curve  $\varphi$  (i.e. the organ behaves essentially as two dimensional and lacks torsion). This is a usual approximation of the gravitropic reaction of roots (Sachs, 1882), while hypocotyl twining occurs in three dimensions (Silk, 1989). Here, we assume curvature in a plane, while the case in three dimensions will be treated in the 'Curvature in three dimensions' section. The natural coordinate system of a sufficiently smooth curve  $\varphi[s(t),t]$ , where  $s$  is arc length and  $t$  is time, is given by (Smirnow, 1990, compare Fig. 1):

$$\begin{aligned} \vec{t} &= \partial_s \varphi \\ \vec{n} &= \frac{\partial_s \vec{t}}{\kappa} = \frac{\partial_{ss}^2 \varphi}{\kappa} \\ \vec{b} &= \vec{t} \times \vec{n}, \end{aligned}$$

( $\vec{t}$  is the tangent,  $\vec{n}$  is the normal and  $\vec{b}$  is the binormal of  $\varphi$ ;  $\kappa = \|\partial_s \vec{t}\|$  is the curvature; and  $\times$  denotes the vector product.) [No confusion should arise between the tangent  $\vec{t}$  and time  $t$ , as one is a vector (denoted throughout the text with an overarrow.)] The curvature vector  $\vec{N}$  is defined as (Smirnow, 1990):

$$\vec{N} = \partial_s \vec{t} = \kappa \vec{n},$$

and gives a measure of the intensity and direction of curvature. Here, the midline  $\varphi$  of the organ depends on  $t$  because it deforms as a result of the curvature process as a consequence of asymmetrical growth. The rate of change of  $\vec{N}$  can be used to determine the rate of change of  $\kappa$ :

$$\begin{aligned} \frac{d\vec{N}}{dt} &= \frac{d\partial_s \vec{t}}{dt} = \partial_s \partial_t \vec{t} + \partial_{ss}^2 \vec{t} \frac{ds}{dt} \\ &= \partial_s (\partial_t \vec{t} + \partial_s \vec{t} v) - \partial_s \vec{t} \text{REGR}, \end{aligned}$$

where velocity,  $v = ds/dt$ , and  $\text{REGR} = \partial_s v$ , and the chain-law of differentiation were used. However, because  $\vec{t} = \vec{t}[s(t),t]$ :

$$\frac{d\vec{t}}{dt} = \partial_t \vec{t} + \partial_s \vec{t} v,$$

so that

$$\frac{d\vec{N}}{dt} = \partial_s \frac{d\vec{t}}{dt} - \partial_s \vec{t} \text{REGR}.$$

Now, taking into account that the tangential and normal vectors are rotated by an angular velocity,  $\vec{\Omega} = \omega \vec{b}$ , we find:

$$\frac{d\vec{t}}{dt} = \vec{\Omega} \times \vec{t} = \omega \vec{b} \times \vec{t} = \omega \vec{n}, \quad (3)$$

$$\frac{d\vec{n}}{dt} = \vec{\Omega} \times \vec{n} = \omega \vec{b} \times \vec{n} = -\omega \vec{t}$$

and

$$\begin{aligned} \frac{d\vec{N}}{dt} &= \partial_s (\omega \vec{n}) - \partial_s \vec{t} \text{REGR} \\ &= (\partial_s \omega) \vec{n} + \omega \partial_s \vec{n} - \kappa \text{REGR} \vec{n} \\ &= (\text{DGCR} - \kappa \text{REGR}) \vec{n} - \kappa \omega \vec{t}, \end{aligned}$$

( $\text{DGCR} = \partial_s \omega$  is denoted as differential growth curvature rate;  $\partial_s \vec{t} = \kappa \vec{n}$ ;  $\partial_s \vec{n} = -\kappa \vec{t}$  (Smirnow, 1990) and the chain-law of differentiation was used). Now, using  $d\vec{N}/dt = d\kappa/dt \vec{n} + \kappa d\vec{n}/dt$ , we finally obtain the material formulation:

$$\frac{d\kappa}{dt} = \text{DGCR} - \kappa \text{REGR}. \quad (4)$$

This shows that the rate of change of curvature,  $d\kappa/dt$ , is composed of a 'production' term DGCR and the term  $-\kappa \text{REGR}$ . The latter can be denoted as a dilution term, because it is negative for growing organs (as  $\kappa > 0$  and  $\text{REGR} > 0$ ). Equation (4) describes the evolution of curvature  $\kappa$  of a selected cell group (Lagrangian or material coordinates). The DGCR and the REGR are given, however, in relation to the quiescent center (Eulerian or local coordinates). Therefore, Eqn (4) could only be used to model a curvature process if the position of the cell group is known in time. Two methods are available to overcome this difficulty. Either the position of the cell group is determined through the ordinary differential equation:

$$\begin{aligned} \frac{ds}{dt} &= v[s(t),t] \quad \text{for } t > t_0 \\ s &= s_0 \quad \text{for } t = t_0, \end{aligned}$$

where  $s_0$  is the Lagrangian coordinate of the cell group (position at time  $t_0$ ), or a curvature conservation equation is

used instead of Eqn (4). A conservation equation is obtained through:

$$\frac{d\kappa}{dt} = \partial_t \kappa + \partial_s \kappa v = \partial_t \kappa + \partial_s (\kappa v) - \kappa \text{REGR},$$

so that comparison delivers the local formulation:

$$\partial_t \kappa + \partial_s (\kappa v) = \text{DGCR}. \tag{5}$$

In the context of a curvature conservation equation, DGCR is the source of curvature [compare, for example, the mass conservation equation  $\partial_t \rho + \text{div}(\rho \vec{v}) = 0$ ]. This shows that DGCR is exactly the concept sought for to characterize the production of curvature. Moreover, its calculation is simple through the angular velocity  $\omega$  (tropic speed):

$$\text{DGCR} = \partial_s \omega. \tag{6}$$

It is defined according to the REGR, as a divergence of a ‘velocity’. However, instead of representing the relative increase in length, it describes the amount of curvature angle produced per unit time and unit length. Therefore, the curvature angle can be obtained similarly to Eqn (1) by an integration:

$$\alpha[s(t), t] = \int_0^T \int_0^{s(t)} \text{DGCR} ds(t) dt. \tag{7}$$

Note that because the arc length  $s(t)$  changes in time, the integration over distance and over time do not commute.

### Differential growth

The term differential growth has to be defined carefully. A measure of growth could be the rate of change of length, of area or of volume or the relative growth rate (REGR, RGR). Thus, the term differential growth can be interpreted widely and lead to misunderstandings. REGR gradients may be interpreted as differential growth (Zieschang *et al.*, 1997; Mullen *et al.*, 1998a). However, although a REGR gradient may not exist, the organ can change its orientation owing to a gradient in rate of change of length. It becomes clear that orientation is determined by gradients in rate of change of length and not by gradients in REGR. (REGR measures the relative increase in length. For same REGR, a long-length element increases absolutely more than a short element, leading to a change of orientation.) Differential growth should be thus defined, in the context of tropisms, as the process behind changes in orientation.

The connection of the DGCR to REGR gradients is found by assumption of a cylindrical organ of radius  $r$  (compare Silk & Erickson, 1978; Silk, 1989; Zieschang *et al.*, 1997). At a

certain arc length, the midline and the upper and lower sides can be approximated by segments of a circle (Fig. 2). The curvature radius  $\rho$  of the midline curve can be determined through:

$$s = \beta \rho \Rightarrow \rho = \partial_\beta s,$$

( $s$ , arc length;  $\beta$ , opening angle of the segment). The difference in curvature radius between the upper and lower sides is:

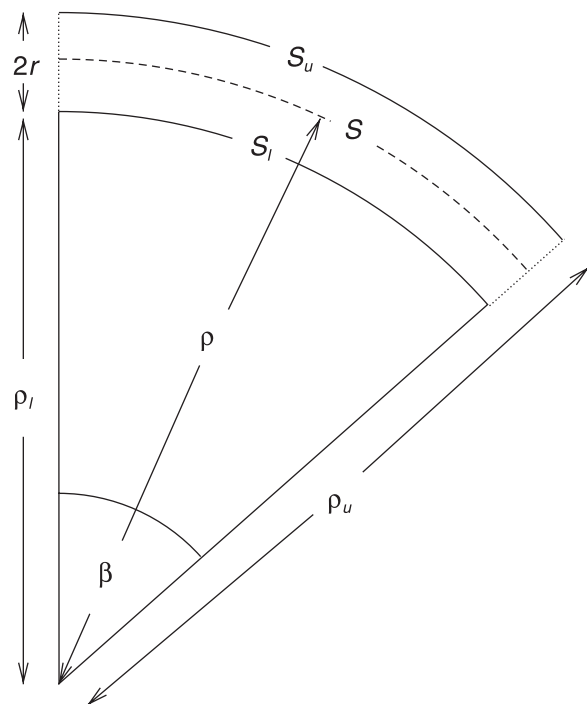
$$\rho_u - \rho_l = \partial_\beta s_u - \partial_\beta s_l = 2r. \tag{8}$$

The organ is assumed to have a constant radius,  $r$ , so that the time derivative of Eqn (8) is:

$$\frac{d}{dt} (\partial_\beta s_u - \partial_\beta s_l) = 0.$$

The partial derivative,  $\partial_\beta$ , and the total  $d/dt$  do not commute because  $\beta = \beta(t)$ , so that using the chain-law of differentiation and  $s_{u,l} = s_{u,l}[\beta(t), t]$ , the above equation is transformed into:

$$\begin{aligned} \partial_\beta \left( \partial_t s_u + \partial_\beta s_u \frac{d\beta}{dt} - \partial_t s_l - \partial_\beta s_l \frac{d\beta}{dt} \right) \\ - (\partial_\beta s_u - \partial_\beta s_l) \partial_\beta \frac{d\beta}{dt} = 0. \end{aligned}$$



**Fig. 2** Simplified geometry of a curved cylindrical organ.  $\rho$  is the curvature radius of the midline, while  $\rho_u$  and  $\rho_l$  are the curvature radii of the upper and lower sides.  $\beta$  is the opening angle of the arc segments  $s$ ,  $s_u$  and  $s_l$  (midline, upper and lower side, respectively), and  $r$  is the radius of the organ.

However,  $d\beta/dt = \omega$  is the angular velocity by which the tangent  $\vec{t}$  is rotated, so that:

$$\partial_\beta \frac{d\beta}{dt} = \partial_s \frac{d\beta}{dt} \partial_\beta s = \rho \partial_s \omega = \rho \text{DGCR},$$

where  $\text{DGCR} = \partial_s \omega$  and  $\rho = \partial_\beta s$  were used. Taking now into account Eqn (8) and that  $ds_{u,l}/dt = \partial_s s_{u,l} + \partial_\beta s_{u,l} d\beta/dt$  we find finally:

$$\text{DGCR} = \frac{\partial_s (v_u - v_l)}{2r}, \quad (9)$$

( $v_u = ds_u/dt$  and  $v_l = ds_l/dt$  are the rate of change of arc length of the upper and lower sides, respectively). Equation (9) can be transformed into an expression of an REGR gradient:

$$\text{DGCR} = \frac{\text{REGR}_u - \text{REGR}_l}{2r} + \kappa \frac{\text{REGR}_u + \text{REGR}_l}{2}. \quad (10)$$

Where  $\text{REGR}_u = \partial_s v_u$  and  $\text{REGR}_l = \partial_s v_l$  are the REGR of the upper and lower sides, respectively. The second term on the right of Eqn (10) arises from the change of variables  $s \rightarrow s_{u,l}$ . Note that in general:

$$\text{REGR} \neq (\text{REGR}_u + \text{REGR}_l)/2.$$

Silk & Erickson (1978) derived a similar expression to Eqn (10):

$$\frac{d}{dt} \ln(1 + 2r\kappa') = \text{REGR}_u - \text{REGR}_l, \quad (11)$$

where  $\kappa'$  is the curvature of the lower side. A simple but somewhat cumbersome calculation shows that Eqn (11) is consistent to Eqns (4) and (10) up to second order terms of  $\kappa$ . Silk & Erickson (1978) used another nomenclature:  $M(o) = \text{REGR}_u$ ,  $M(i) = \text{REGR}_l$  and in particular  $R = \rho - r$ . This results in a slightly different curvature than that used here:  $\kappa' = R^{-1} \neq \rho^{-1} = \kappa$ .

The determination of curvature production DGCR through Eqn (6) is superior to Eqn (10), as it uses the midline of the organ and is of particular advantage in root tips, where cell lineages have a complicated geometry near the quiescent center and the organ radius  $r$  cannot be assumed to be uniform along the axis (Hejnowicz & Hejnowicz, 1991).

### Curvature in three dimensions

In the Curvature Section above, we treated curvature production of organs in a plane. Nonetheless, curvature processes occur in a three-dimensional space. This opens new motion possibilities, in particular torsion of the organ.

Circumnutations of roots and hypocotyls are known to include torsion of the organ (Silk, 1989; Barlow, 1992). A description in plane is thus only a rough approximation. However, the plane case can be subsequently extended to describe curvature in three dimensions.

The calculations presented above are based on Eqn (3). Here, the rotation axis of  $\vec{t}$  and  $\vec{n}$  is not anymore necessarily  $\vec{b}$ ; the angular velocity  $\vec{\Omega}$  is instead a linear combination of the three vectors:

$$\vec{\Omega} = \omega_t \vec{t} + \omega_n \vec{n} + \omega_b \vec{b}, \quad (12)$$

where  $\omega_t = \vec{\Omega} \cdot \vec{t}$ ,  $\omega_n = \vec{\Omega} \cdot \vec{n}$  and  $\omega_b = \vec{\Omega} \cdot \vec{b}$ , and  $\cdot$  denotes the scalar product of two vectors:  $\vec{a} \cdot \vec{b} = \sum_i a_i b_i$ . Equation (12) shows that  $\vec{\Omega}$  acts also on the binormal  $\vec{b}$ , resulting in torsion of the organ. The time dependence of the natural coordinate system is determined by the ordinary differential equation:

$$\begin{aligned} \frac{d\vec{t}}{dt} &= \vec{\Omega} \times \vec{t} = \omega_b \vec{n} - \omega_n \vec{b} \\ \frac{d\vec{n}}{dt} &= \vec{\Omega} \times \vec{n} = \omega_t \vec{b} - \omega_b \vec{t} \quad \text{for } 0 < t \end{aligned} \quad (13)$$

$$\begin{aligned} \frac{d\vec{b}}{dt} &= \vec{\Omega} \times \vec{b} = \omega_n \vec{t} - \omega_t \vec{n} \\ \vec{t} &= \vec{t}_0, \quad \vec{n} = \vec{n}_0, \quad \vec{b} = \vec{b}_0 \quad \text{for } t = 0 \end{aligned}$$

Through a calculation analogous to the plane case, but taking Eqn (13) and  $\partial_s \vec{n} = -\kappa \vec{t} - \tau \vec{b}$  (Smirnow, 1990) into account, we find:

$$\frac{d\kappa}{dt} = -\omega_n \tau + \partial_s \omega_b - \kappa \text{REGR}, \quad (14)$$

$$\frac{d\tau}{dt} = \omega_n \kappa + \partial_s \omega_t - \tau \text{REGR}.$$

Equation (14) is a coupled ordinary differential equation system, which, when solved gives  $\kappa$  and  $\tau$  of a selected organ segment at any time (material coordinates). Equation (14) can be transformed into conservative form to obtain a local formulation:

$$\begin{aligned} \partial_t \kappa + \partial_s (\kappa v) &= -\omega_n \tau + \partial_s \omega_b, \\ \partial_t \tau + \partial_s (\tau v) &= +\omega_n \kappa - \partial_s \omega_b, \end{aligned} \quad (15)$$

yielding the sources of curvature and torsion:

$$\begin{aligned} \text{DGCR} &= -\omega_n \tau + \partial_s \omega_b, \\ \text{DGTR} &= \omega_n \kappa - \partial_s \omega_t, \end{aligned} \quad (16)$$

where DGTR denotes the differential growth torsion rate. Note that the DGCR in Eqn (16) is consistent with Eqn (6), because  $\tau = 0$  for organs that curve in a plane.

### Root gravitropism model

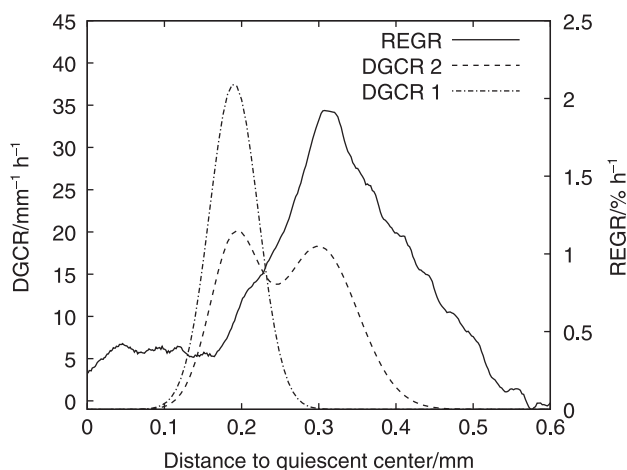
The proposed measure DGCR is applied here in a simple model of the gravitropic reaction of roots. Equation (5) can be used to simulate two cases of curvature production: one and two sites of production. These cases are conceivable in root gravitropism, as the existence of two motors have been proposed recently (Wolverton *et al.*, 2002a). These motors have been assumed to be located at the distal and central elongation zones (DEZ and CEZ; Ishikawa & Evans 1993), which are centered around the elongation maximum (CEZ) and apically of the elongation maximum where growth attains 30% of the maximal REGR (DEZ; compare Fig. 3).

Let a gravitropism motor be given by a bell-shaped curve:

$$M(s, \beta) = A \sin(\beta) \exp\left(-\frac{s - s_0}{\sigma^2}\right), \quad (17)$$

( $s$ , arc-length;  $\beta$ , stimulation angle;  $A$ , an amplitude;  $s_0$ , center position of the motor;  $\sigma^2$ , extension of the motor). The factor  $\sin(\beta)$  models the dependence on the stimulation angle,  $\beta$ , and was chosen in terms of the Sine-Law (Sachs, 1882).

Because the DGCR is the source of curvature (compare Eqn 5), and sources are additive, it can be described as a sum over the motors:



**Fig. 3** Root growth and model of gravitropism motors. The solid line denotes a measured relative elemental growth rate (REGR) distribution/profile of an *Arabidopsis thaliana* root (average over the first 3 h of the gravitropic reaction; provided by K. A. Nagel, Forschungszentrum Jülich). Dashed and dashed dotted lines denote the differential growth curvature rate (DGCR) assumed for two gravitropism motors and one gravitropism motor, respectively. The gravitropism motors were assumed to be located at the distal and central elongation zones (DEZ and CEZ, respectively).

$$\begin{aligned} \text{DGCR}(s, \beta) &= \sum_{i=0}^N M_i(s, \beta) \\ &= \sum_{i=0}^N A_i \sin(\beta) \exp\left(-\frac{s - s_{0,i}}{\sigma_i^2}\right), \end{aligned} \quad (18)$$

( $N$ , number of motors present). An extension of this expression to describe more than one sensor (i.e. more than one stimulation angle,  $\beta$ ), should be straightforward. When the root is initially stimulated by  $90^\circ$ , the stimulation angle and curvature angle of the whole organ are related by  $\beta = 90^\circ - \alpha_{\text{Tip}}$ .

Note that the model of the dependence of the motors on the stimulation angle is very simplistic. Signal transduction is not instantaneous in organs, so that information on the stimulation angle needs time to reach the sensitive tissue (refer to Swarup *et al.*, 2005 for the case of auxin). Moreover, it is still unclear if the Sine-Law is correct (e.g. Audus, 1964; Barlow *et al.*, 1993; Mullen *et al.*, 2000). However, as will become clear in the Results and Discussion, the fact that the reaction decreases in time is here more important than the actual law behind it.

### Results and Discussion

Using Eqns (5) and (18), two root gravitropism cases were simulated. The first assumes that one motor is responsible for curvature production and the second assumes two spatially separated motors (Wolverton *et al.*, 2002a). The parameters used in the simulation are presented in Table 1. These were chosen to resemble an *Arabidopsis thaliana* (L.) Heynh. root, and were based on the definition of the DEZ and the CEZ and on unpublished measurements of the gravitropism kinetics of *A. thaliana* roots (measurements conducted in the author's laboratory). The velocity distribution,  $v$ , was obtained by integration of a measured REGR distribution (the average over the first 3 h of a gravitropic reaction of an *A. thaliana* root; data set provided by K. A. Nagel, Forschungszentrum Jülich, D-52425, Germany). The REGR distribution and the gravitropism motors are shown in Fig. 3. As Eqn (5) is a conservation equation, it was solved

**Table 1** Simulation parameters of root gravitropism model

	Motor	$A$ ( $\text{mm}^{-1} \text{h}^{-1}$ )	$s_0$ (mm)	$\sigma^2$ ( $\text{mm}^2$ )
One motor	One	2.1	0.19	$2 \times 10^{-3}$
Two motors	One	1.05	0.19	$2 \times 10^{-3}$
	Two	1.05	0.3	$5 \times 10^{-3}$

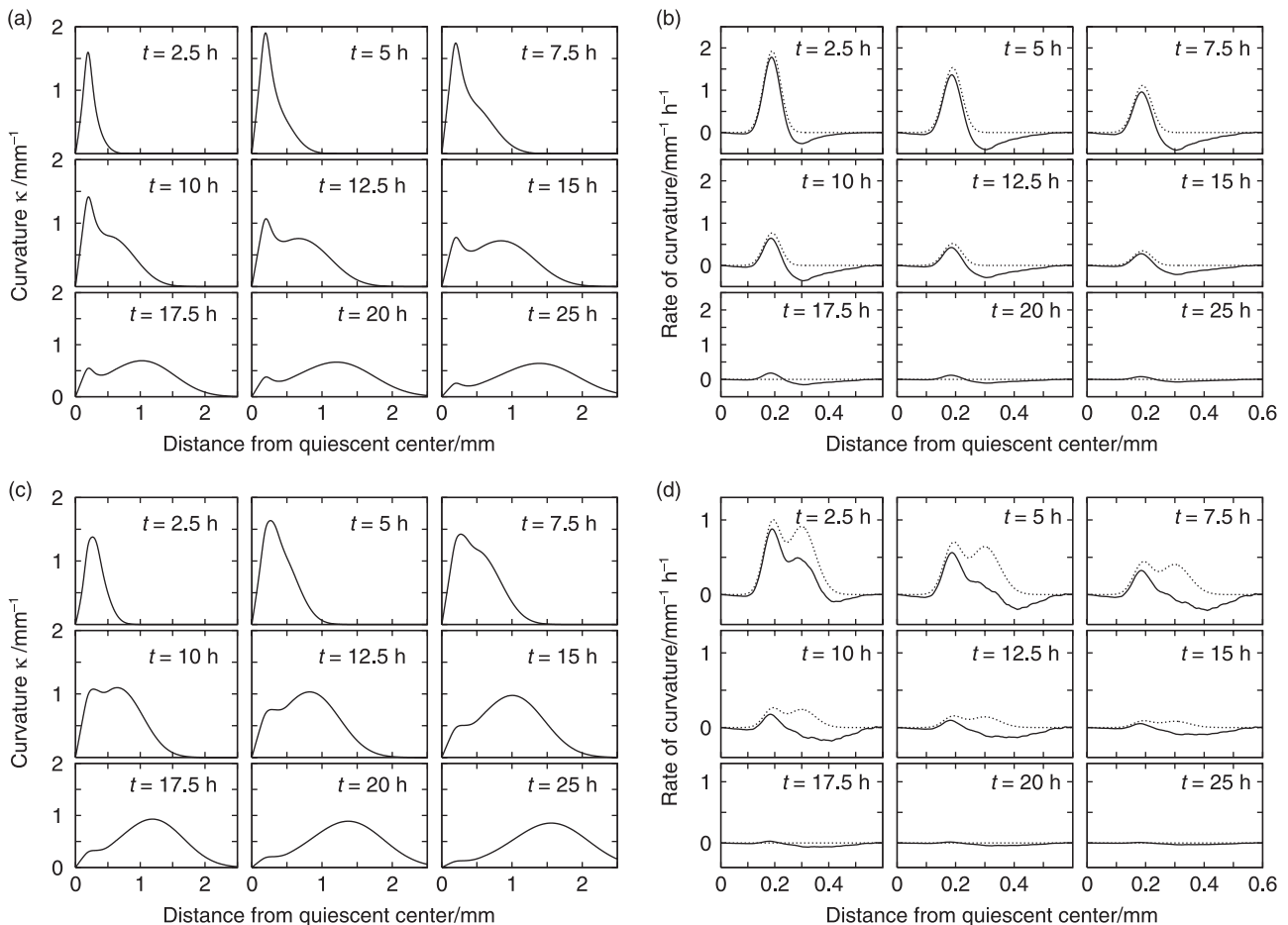
$A$ , amplitude;  $\sigma^2$ , extension of the motor;  $s_0$ , center position of the motor.

using the Conservative Lax Method, which has been shown to be stable for discretization widths (Potter, 1973). These widths were chosen here to meet this stability condition (time,  $10^{-3}$  h; space,  $3 \mu\text{m}$ ; fastest propagation velocity,  $< 80 \mu\text{m h}^{-1}$ ).

Figure 4(a,b) presents the simulation results under the assumption of one motor, while Fig 4(c,d) shows the results for two motors. Both cases showed a similar distribution of  $\kappa$ , composed initially of one peak located at the site of production, which reduced intensity in time and gave rise to a second broader peak (Fig. 4a,c). The second peak can be contributed to advection/convection of curvature (compare Eqn 2; Silk & Erickson, 1978; Silk, 1989), as becomes clear from the movement of its maximum. The first peak is caused by production and its distance to the quiescent center is thus constant. A change in the intensity of the first motor is essential for the existence of the second peak. If no change in intensity occurs, growth dilution (compare Eqn 4) would

ensure that beyond the curvature motors, the distribution of  $\kappa$  would fall monotonically without having a second maximum. Measurements of *Lepidium* and *Phleum* roots confirm the existence of a moving and a fixed peak (Selker & Sievers, 1987; Zieschang & Sievers, 1991). Wolverton *et al.* (2002a) interpreted those two peaks as two motors of gravitropism. However, the simulations presented here show that both cases, of one and two motors, exhibit this behaviour. Thus  $\kappa$  is insufficient to show the existence of two motors that are located so closely.

The rate of change of curvature  $d\kappa/dt$ , which could erroneously be interpreted as a measure of curvature production (compare Eqns 4 and 5), fails also to show a clear separation of both motors (Fig. 4b,d). If the distribution of  $\kappa$  is determined with a low resolution, which has been the case as a result of technical reasons (e.g. Selker & Sievers, 1987; Zieschang & Sievers, 1991), the existence of one or two motors cannot be



**Fig. 4** Simulated curvature and rate of curvature along a root axis. (a) Distribution of curvature,  $\kappa$ , along a root axis, under the assumption of one gravitropism motor located at the distal elongation zone (DEZ). (b) Distribution of rate of change of curvature,  $d\kappa/dt$  (solid line) and differential growth curvature rate (DGCR) (dashed line). One motor located at the DEZ is assumed to be responsible for curvature. (c) Distribution of  $\kappa$ , under the assumption of two gravitropism motors located at the DEZ and at the central elongation zone (CEZ). (d) Distribution of  $d\kappa/dt$  and DGCR. Two motors located at the DEZ and CEZ are assumed to produce curvature.

definitively determined using  $d\kappa/dt$  (Fig. 4b,d). Both cases show, as a result of growth dilution, a similar  $d\kappa/dt$  pattern. In the case of two motors, the second motor appears to be strongly reduced, so that the pattern may be interpreted as a slightly wider motor (Fig. 4d). Curvature production may, in general, be underestimated around the elongation maximum, if  $d\kappa/dt$  is assumed to be a measure of production.

In contrast to  $\kappa$  and  $d\kappa/dt$ , the DGCR shows clearly either one or two motors (Fig. 4b,d). The theoretical results are confirmed here; the DGCR measures the production of curvature and emphasizes the two motors independently of growth dilution. A hint for the specific function of the two motors is also found here. The model shows that the first motor, located where growth dilution is small, has a key role in curvature initiation, while the second, located where growth dilution is maximal, is crucial in maintaining curvature (Fig. 4d). Note that the model presented here is not able to differ between one motor with a large spatial extension and two spatially separated motors. This question can only be answered experimentally, through investigation if these cell groups are either controlled by two different sensors (Wolverton *et al.*, 2002a,b), or regulated through different phytohormones (Aloni *et al.*, 2004). Nonetheless, the model shows that a better measure of curvature production (DGCR) is essential to elucidate this.

The DGCR was defined as the slope of the tropic speed distribution  $\omega(s) = d\alpha/dt(s)$  (Eqn 6), and is thus analogous to the REGR, defined as the slope of the velocity distribution  $v(s)$ . Such an analogy between translational and rotational movement is well known in physics (e.g. Halliday & Resnick, 1988). The DGCR can be interpreted as follows. A rigid body can only move by means of a translation and/or a rotation. Because it is rigid, any volume element of it rotates with the same angular velocity. In nonrigid bodies, such as graviresponding roots and hypocotyls, the angular velocity changes in space, reflecting deformation. In cylindrical organs, the tropic speed,  $\omega$ , and variations of it in space, reflect curvature, the production of which is quantified by the DGCR. The DGCR represents the amount of curvature angle produced per unit length and unit time. (The DGCR can be expressed either in radians or in degrees per unit length and unit time. Radians should be used when a comparison to  $d\kappa/dt$  is sought.) Curvature angle kinetics of root segments have been used intuitively to characterize the gravitropic reaction of roots (Mullen *et al.*, 1998b; 2000; Wolverton *et al.*, 2002a,b). However, these do not allow a quantitative determination of curvature production, although this is essential to understand the control and signal pathways behind differential growth. This gap is filled by the DGCR and should thus serve as a helpful tool for future measurements.

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