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Anisotropic plant growth due to phototropism

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Abstract Phototropism—the directional curvature of organs in response to lateral differences in light intensity and/or quality—represents one of the most rapid and visually obvious reaction of plants to changes in their light environment. It is a topic of fundamental interest to understand the mechanics of plants during growth. We propose a generalization of the scalar Lockhart model (1965) to three dimensional deformation, solve the new equation in two particular cases and compare results with empirical data. We believe that carefully designed experiments linked to our model will provide (by determining the active transport coefficient) a new method for qualitative description of auxin redistribution during phototropism. The proposed method supplements very recent investigations concerning specific auxin-influx and -efflux carriers (LAX and PIN proteins).

Keywords Auxin redistribution · Dynamic growth rate · Phototropic response · Protein carriers

Mathematics Subject Classification (2000) 92B05

1 Introduction

The phenomenon of phototropism has been known ever since. Charles Darwin discovered in 1880 [1] that the phototropic stimulus is positioned at the tip of the plant. Darwin used grass seedlings for some of his experiments. He found

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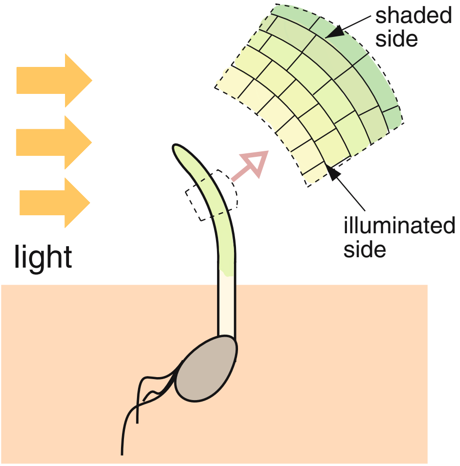


Fig. 1 Illustration of plant phototropism. Auxin transports actively due to sunlight from the illuminated to shaded side

that the tip of the seedling was necessary for phototropism but that the bending takes place in the region below the tip (Fig. 1). In the 1920s Fritz Went et al. [2] attempted to isolate the "diffusible substance" that was responsible for phototropism. The unknown substance that had diffused was named auxin.

The most recent research suggests that auxin is transported through plant tissues by specific cellular influx and efflux carrier proteins [3–5]. The regulated, differential distribution of auxin underlies many adaptation processes including organogenesis, meristem pattering and tropisms [6–10]. Some aspects concerning phytohormones, control of plant development in the context of modelling plant reactions to external signalling can also be found in [11,12].

In this paper we introduce a physical model suitable for the description of mechanisms emerging in plants exposed to the irradiation of light (we do not consider the biochemical aspect). We mainly focus our efforts on understanding the biomechanical aspect of the effect of incident unilateral light onto the growing seeds of maize *Zea mays* L. by considering phenomenon of phototropism throughout newly developed dynamic tensor equation of plant growth. Further theoretical search have resulted in two kinds of examplary solutions exactly reproducing the main experimental issues. The small number of model assumptions resulted in analytical solutions which precisely reflected experiments accompanying the theory. This in turn certifies that the physical model proposed in this article seems to be adequate for the quantitative description of lateral transport of auxin.

2 Materials and methods

The experiments were carried out with three days old maize plants (*Zea mays* L.) grown in tap water at 27°C. Seeds of maize were cultivated in darkness. Then individual seeds were transferred to an aerated solution containing standard micro- and macro-elements. At this time they were selected for straightness and length, and aligned in parallel by turning each seedling individually. They

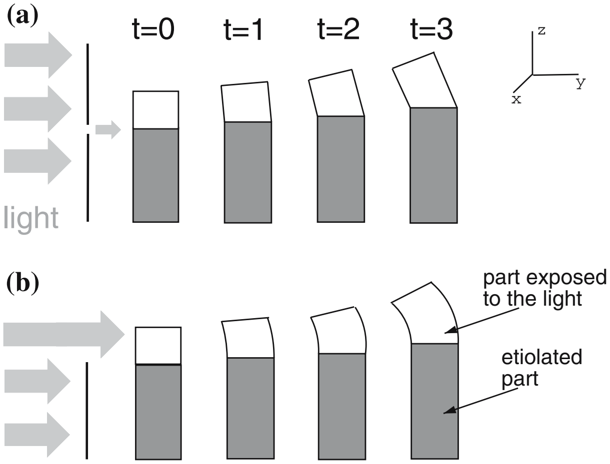


Fig. 2 Gedanken experiments: **a** the fragment of a coleoptile is exposed to the incident light through a narrow diaphragm, **b** the upper fragment of a coleoptile is exposed to the light incident over a shield

remained in the dark for another day and were, after further selection, used for the experiments.

We have performed two kinds of experiments where the seeds were exposed onto the continuous spectrum light source (corresponding to the sun light). In one of these a single coleoptile (which is in fact kind of multicellular cylindrical structure surrounding the primary leaf of germinating seed) was shielded in such a way that only its tiny fraction was brought to the light (see Fig. 2a). In the other one the upper half of a single coleoptile was irradiated with light and the lower part was etiolated (shaded), see Fig. 2b. In both experiments the coleoptile elongation and phototropic curvature was measured by the shadow-graph method (magnification 20 ×). Both experiments were carried out and repeated for five seedlings and the average bending has been estimated. The error (std. dev.) was of about 0.01 cm and 1° for the elongation and angle measurement, respectively.

3 Results

3.1 Derivation of tensor equation

Time-dependent Lockhart equation has been elaborated in the mid-1960s [12,13]. It describes elongation of a plant cell resulting from a dynamic balance between the water uptake and the cell wall yielding:

$$\frac{1}{V}\frac{\mathrm{d}V}{\mathrm{d}t} = \Phi\,(P - Y) \tag{1}$$

where P, Y and Φ stand for hydrostatic pressure, turgor threshold and cell wall yielding coefficient, respectively. The above equation describes global properties of a plant cell neglecting its local features (like spatial distortions). However, one may distinguish at least two kinds of geometrical anisotropies concerning plant cell growth. The "zeroth" kind anisotropy which appears in the most cases in plant cell growth where plants increase their volume mostly in one direction (elongation growth), see [15] for details. The "first" kind anisotropy, well known for a long time [1], consists in plant reaction to the influence of external factors like light and gravitational force designed as phototropism and gravitropism, respectively. (Tropism—plant movement reaction in which the direction of the response is dependent on the direction of the stimulus). Therefore Eq. (1) should, in principle, also account for the existing anisotropies of growth due to internal mechanical stresses. Hence, taking the above remarks into consideration, as "constitutive" differential equation, we propose the result of the following reasoning based on a model including plant cell anisotropic features, instead. We apply our model to a multicellular problem where we treat the plant tissue as a massive, homogeneous and viscoelastic structure and additionally, we consider an organ (e.g. coleoptile) where cells' elongation (not division) takes place exclusively and the Lockhart equation holds. We follow the line of the Lockhart equation re-analysis to multicellular plants [16].

Consider a displacement of a vector $\boldsymbol{\xi} = (\xi_1, \xi_2, \xi_3)$ within time interval $\Delta t = t' - t$. Then a point P from a given fraction of the cell volume V moves irreversibly (due to the internal stresses) to a new position P' (see Fig. 3): $P(x_1, x_2, x_3, t) \mapsto P'(x_1 + \xi_1, x_2 + \xi_2, x_3 + \xi_3, t')$. In Eq. (1) we deal with the relative change of the volume V treated as a global quantity in the course of time. In order to proceed to the local description we introduce vector $\boldsymbol{\xi}$ representing translation of the P point due to the change both the volume and the shape of the cell. Accordingly, we introduce instead of $\frac{1}{V}\frac{\mathrm{d}V}{\mathrm{d}t}$ the expression $\frac{\partial}{\partial t}\frac{\partial \xi_i}{\partial x_j}$. The quantity $\frac{\partial \dot{\xi}_i}{\partial x_j}$ (the dot denotes as usual the time-derivative) represents the change of coordinates of $\boldsymbol{\xi}$ vector in function of time and position of P. The elements $\frac{\partial \dot{\xi}_i}{\partial x_j}$ have been derived similarly to the Hooke's law in the elastostatic theory. The main difference consists in the fact that we deal with irreversible distortions (viscoelastic deformations) in a sense that we generalize

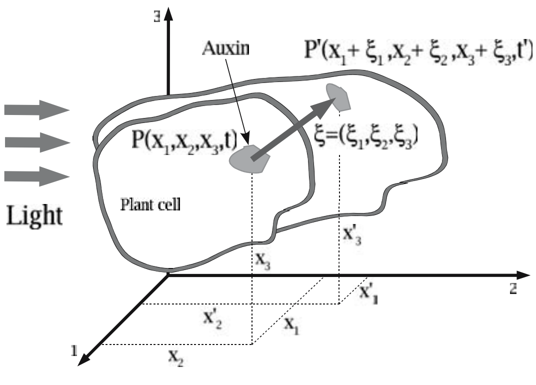


Fig. 3 Illustration of anisotropic deformation of a plant cell. Area P moves irreversibly to position P' causing deformation of the cell shape due to internal stresses

the Lockhart equation. In general, $\forall_{i\in\{1,2,3\}}\ \xi_i$ explicitly depends both on time t (cell magnifies) and the coordinates x_1, x_2, x_3 (here: due to the auxin action cell bends toward the unilateral influence of light). Such approach we will justify in the further part of this article where we derive the special (global) Lockhart equation as a limiting case of the general (tensor) equation.

Similarly, we perform on the right-hand side of Eq. (1) the following generalization: the magnitude $P - Y$ we replace with $(P - Y)^{ij}$ (which denote elements of a matrix) and subsequently for all $i, j \in \{1, 2, 3\}$

$$\frac{\partial \dot{\xi}_i}{\partial x_j} = \Phi(P - Y)^{ij}. \tag{2}$$

From the physical point of view Eq. (2) represents coupling between the dynamic deformation field (l.h.s.) and the stress field (r.h.s.). It may be rewritten in tensor form in the following way: as we define the growth rate as $\mathbb{G}_R^{ij} : = \frac{\partial \dot{\xi}_i}{\partial x_j}$ and $(\mathbb{P} - \mathbb{Y})^{ij} : = (P - Y)^{ij}$ we get

$$\mathbb{G}_R = \Phi(\mathbb{P} - \mathbb{Y}) \tag{3}$$

where Φ in general depends on position and time $\Phi = \Phi(x_1, x_2, x_3, t)$. We would like to make a remark here. In elastostatic theory not $\frac{\partial}{\partial t}\frac{\partial \xi_i}{\partial x_j}$ but $\varepsilon^{ij} : = \frac{\partial \xi_i}{\partial x_j}$ constitute elements of deformation matrix used for description of anisotropic changes in the bulk's shape. Certainly, both matrices are dependent: $\mathbb{G}_R^{ij} = \frac{\partial}{\partial t}\varepsilon^{ij}$. Hence the quantity of the l.h.s. of Eq. (3) has local and especially dynamical properties (as its elements are time-derivatives of the deformation matrix). Therefore we may label $\mathbb{G}_R$ the dynamical growth tensor. Yet the r.h.s. of Eq. (3) which is normally the product of scalar quantities can be expressed as product of a scalar $\Phi(x_1, x_2, x_3, t)$ (which may depend not only on time and location, but also on many other parameters like temperature, air composition, pH, etc.) and tensor $\mathbb{P} - \mathbb{Y}$ which is responsible for the internal stress (in excess of turgor threshold). We adopt Cartesian coordinates (and align the growing shoot along z-direction), see also Fig. 2. Taking as granted such interpretation $\mathbb{P} - \mathbb{Y}$ must obey:

1. Pascal's law which states that pressure applied to a confined fluid at any point is transmitted undiminished throughout the fluid. Thus the stress tensor reads $\mathbb{P}$ and according to the Pascal's principle $P_{xx} = P_{yy} = P_{zz} = P > 0$ where P denotes hydrostatic pressure like in the original Lockhart equation. For the same argument as above the turgor threshold tensor $\mathbb{Y} = \mathrm{diag}(Y, Y, Y)$.
2. Symmetry: because $\varepsilon^{ij} = \frac{\partial \xi_i}{\partial x_j}$ in general is not a proper deformation tensor in the physical sense, it may contain not only pure deformations but also rigid rotations (cell may rotate or be shifted as a whole), in particular it is not a symmetric one. Then the symmetrized form of ε is the proper deformation tensor and consequently not $\mathbb{P} - \mathbb{Y}$ is the stress tensor but its symmetrized form $(\mathbb{P} - \mathbb{Y}) = \frac{1}{2}((\mathbb{P} - \mathbb{Y}) + (\mathbb{P} - \mathbb{Y})^T)$.

3. $(P-Y)^{ij}$ elements represent the following properties: the diagonal elements $(P-Y)^{ii}$ are normal stresses (perpendicular to the corresponding surfaces) while the off-diagonal elements $(P-Y)^{ij}$ for $i \neq j$ are the tangential stresses, which act onto the surface perpendicular to the x_i and parallel to the direction x_j. The diagonal elements $(P-Y)^{ii}$ reflect isotropic pressure inside vacuole. For the case of the whole plant tissue $(P-Y)^{ii} = (P_A + \sigma - Y)^{ii}$ should be estimated as the sum of apoplasm hydrostatic pressure in excess of turgor threshold $P_A - Y$ and the tension σ in the cell wall (P_A is the suction component while σ is proportional to the turgor, see [16]). Such estimation is related to the phenomenon of turgor recovery in absence of water uptake or loss. Since the shape of a plant cell is almost entirely determined by its wall the off-diagonal elements reflect tangential stresses in plasmalemma and cell wall itself or in the apoplasm for the whole plant tissue case. In this sense, in a single cell generalization of the Lockhart equation we impose the boundary conditions.
4. Following the elastostatic theory we know that half of a sum of deformation matrix' elements $\frac{\partial \xi_1}{\partial x_2}$ and $\frac{\partial \xi_2}{\partial x_1}$ constitutes γ_3 deviation angle from x_2x_3 plane, similarly $\frac{1}{2}(\frac{\partial \xi_1}{\partial x_3} + \frac{\partial \xi_3}{\partial x_1})$ gives γ_2 angle of deviation from x_1x_2 plane and eventually $\frac{1}{2}(\frac{\partial \xi_2}{\partial x_3} + \frac{\partial \xi_3}{\partial x_2}) = \gamma_1$ angle of deviation from x_1x_3 plane.

3.2 Illustrative solutions

Equation (3) is the general equation. In order to find some of its special solutions we make the following simplifying assumptions: (a) Zeroth time approximation for variables: $\Phi, P, Y, D = \mathrm{const}(t)$ (D stands for auxin active transport coefficient); (b) Initial conditions $\forall_{i=x,y,z},\ \xi_i(x,y,z,t=0) = 0$; (c) Cell wall yielding coefficient Φ obeys $\Phi|_x = \Phi|_y = 0$, $\Phi|_z = \Phi$ (we denote $\Phi|_x\colon = \Phi(x, y = \mathrm{const}, z = \mathrm{const})$) which expresses the fact that wall yielding and growth (not bending) takes place exclusively in the vertical z direction (the "zeroth" kind anisotropy); (d) Boundary conditions: Φ, P and Y are confined to the cell interior; (e) Auxin is a phytohormone which acts, among others, as a substance accelerating plant cell growth. Auxin influenced by unilateral action of light transports actively into and through shaded side of plant cell and, accordingly, it causes its inhomogeneous growth (see Fig. 1). This phenomenon is strictly bounded — as we know from elastostatic theory - with additional non-zero tangential stresses. The analysis of $\mathbb{P} - \mathbb{Y}$ tensor elements has led us to conviction that only yz and zy of the $\mathbb{P} - \mathbb{Y}$ matrix should remain non-zero in order to observe the bending toward the light source as in Fig. 2 (the other elements would give additional bending that in the considered cases does not appear). These non-zero values must be coupled to the auxin inhomogeneous distribution which depends linearly on z direction.

After solving Eq. (3) we assign its two particular solutions to the related experiments performed with the use of a diaphragm or semi-plane screen to obtain point or semi-plane light source. Although the presented model is founded on the Lockhart equation elaborated for plant cells it may be extended to whole plant organs, like for example, coleoptiles as it has been done in our experiments. In theory it can be accomplished by replacing the cell wall yielding coefficient Φ with an effective one Φ_{eff} for the apoplasm. Given Eq. (3) and the presented assumptions we discuss its example solutions as illustrated in Fig. 2a, b. Here we make an additional assumption: Auxin diffusion through a plant cell as a result of the action of light takes place in a positive y direction. Thus $P_{xy} = P_{xz} = P_{yx} = P_{zx} = 0$ and $P_{yz} = P_{zy} = Dz$ where D is a coefficient bounded with nonequilibrium auxin transport by the protein carriers, $[D] = \text{Pa/mm}$. We assume symmetry of the stress tensor as we do not take into account plant cell (or in fact coleoptiles as in the authors' performed experiments) rigid rotations. We put $D > 0$ (positive phototropism).

Taking into account all these remarks we end up with the following explicit tensor equation for the dynamic growth rate

$$\mathbb{G}_R = \begin{pmatrix} 0 & 0 & 0 \\ 0 & 0 & \Phi Dz \\ 0 & \Phi Dz & \Phi(P-Y) \end{pmatrix} \tag{4}$$

by virtue of point (c). Accordingly, accepting the zeroth time approximation for Φ, P, Y and D after integration we obtain the set of six independent equations for the deformation matrix elements: $\frac{\partial \xi_x}{\partial x} = \frac{\partial \xi_x}{\partial y} = \frac{\partial \xi_x}{\partial z} = \frac{\partial \xi_y}{\partial y} = 0$, $\frac{\partial \xi_y}{\partial z} = \frac{\partial \xi_z}{\partial y} = \Phi Dzt$ and $\frac{\partial \xi_z}{\partial z} = \Phi(P-Y)t$. From the above equations we have $\gamma = \Phi Dz\, t$. Depending on the actual type of experiment the coefficient $D = d\frac{1}{z}$ ((a) point-like case) or $D = \text{const.}$ ((b) semi-plane case). We eventually obtain the following solutions for the $\boldsymbol{\xi}$ vector

$$\begin{cases} \xi_y(z,t)\Big|_z = \Phi D\, zt \Longleftrightarrow \xi_z(y,t)\Big|_y = \Phi D\, yt \\ \xi_z(z,t)\Big|_z = \Phi(P-Y)\, zt \end{cases} \tag{5}$$

or

$$\begin{cases} \xi_y(z,t)\Big|_z = \frac{1}{2}\Phi D\, z^2 t \Longleftrightarrow \xi_z(y,t)\Big|_y = \Phi D\, yzt \\ \xi_z(z,t)\Big|_z = \Phi(P-Y)\, zt \end{cases} \tag{6}$$

for the point-like and semi-plane cases, respectively. The remaining deformations in both cases vanish: $\xi_x = 0$, $\xi_z|_x = 0$, $\xi_y|_y = 0$, $\xi_y|_x = 0$. In Eqs. (5) and (6) the solutions depend explicitly on time. Hence we receive two kinds of solutions: (a) linear (γ =const(z)) and (b) non-linear ($\gamma \propto z$) bending. For the "diaphragm case" we may draw the following conclusion. By assuming the existence of non-zero tangential stress (strictly bounded with the light action onto the auxin redistribution) constant in a narrow range exposed to the light we have obtained $\gamma = \Phi Dt$ angle and consequently the linear bending. (In spite of the fact that we have generally assumed the existence of the vertical gradient of auxin distribution we notice that in the point-like case in the lighted tiny fragment of the coleoptile D can be considered as almost constant at a short distance and vanishing in its close vicinity like $1/z$.) We may determine this angle in experiment. As we can check in Fig. 4 ("diaphragm case") γ after $t = 2$h is constant and equal to 5°.

In the "semi-plane case" $\gamma = \Phi D z t$, what implies from Eq. (6), and γ angle increases linearly with time and, in contrary to the previous example, depends on z coordinate. This causes a gentle bending of a probed coleoptile which is expressed by a curvature toward the light source (see Fig. 2b). We assign this solution to an experiment where the upper half of a coleoptile is exposed to the light and the lower part is etiolated. We also notice that since in Eq. (6) quadratic solution appears ($\xi_y \sim z^2$) then the bending of a coleoptile toward the light source has parabolic character. We may formulate this result in a following way. Auxin greater concentration in the apical part of the coleoptile (which is equivalent to the assumption that tangential stress linearly depends on z coordinate) causes stronger (parabolic) bending of plant toward the light source. Thus bending angle γ depends on the height, $\gamma = \Phi D z t$, and—as one can compare in Fig. 4 ("semi-plane case")—agrees with the empirical data for which $\gamma(z) \simeq 46.7z$ deg (after $t = 4$ h) with determination coefficient $R = 0.996$.

3.3 Back from local to global equation

Accepting Eq. (3) as a starting point the Lockhart equation may be easily obtained (as a limiting case) if one uses the foregoing assumptions (corresponding to the original Lockhart model): (1) The variables Φ, P and Y do not depend on x, y and z coordinates; (2) All off-diagonal elements of the stress tensor vanish (there are no tangential stresses which would cause cell bending). Thus in the stress tensor only diagonal $(\mathbb{P} - \mathbb{Y})^{xx} = (\mathbb{P} - \mathbb{Y})^{yy} = (\mathbb{P} - \mathbb{Y})^{zz}$ elements remain non-zero according to the Pascal's principle; (3) $\Phi(x, y, z, t)$ has the following properties: $\Phi|_x = \Phi|_y = 0$ and $\Phi|_z = \Phi$ because of the "zeroth" kind anisotropy. Hence, from Eq. (3) we receive a system of nine equations among which only one is non-trivial

$$\frac{\partial \dot{\xi}_z}{\partial z} = \Phi(P - Y). \tag{7}$$

The remaining derivatives are equal to zero.

In order to proceed from local to global properties we evaluate the following integral: $\int_0^z \frac{\partial \dot{\xi}_z}{\partial z} \mathrm{d}z' = \frac{\partial}{\partial t} \int_0^z \frac{\partial \xi_z}{\partial z} \mathrm{d}z' = \frac{\mathrm{d}z}{\mathrm{d}t}$ which represents the total change of the length z in time t. Similarly, we integrate the r.h.s. of Eq. (7) and divide both sides by $z = \int_0^z \mathrm{d}z'$ to obtain

$$\frac{1}{z}\frac{\mathrm{d}z}{\mathrm{d}t} = \frac{1}{z}\Phi(P - Y)\int_0^z \mathrm{d}z'$$

by virtue of the assumption (1). Thus we receive

$$\frac{1}{z}\frac{\mathrm{d}z}{\mathrm{d}t} = \Phi(P - Y)\Big/\frac{xy}{xy}$$

$$\frac{1}{xyz}\frac{\mathrm{d}(xyz)}{\mathrm{d}t} = \Phi(P - Y)$$

arriving back ($xyz = V$) to the Lockhart Eq. (1) which has been obtained from the more general tensor equation of growth.

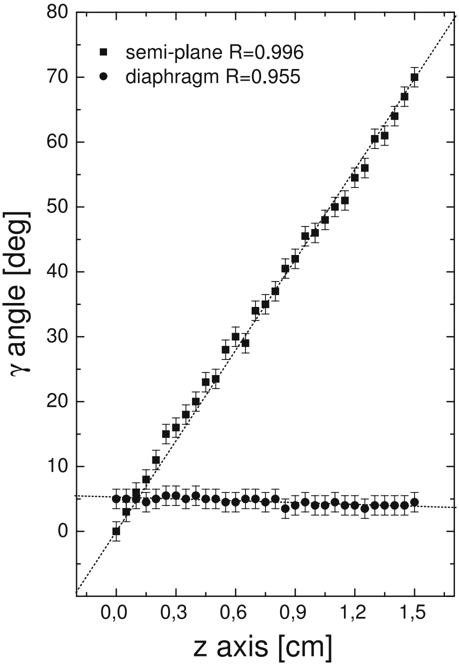
4 Discussion

In this paper we have introduced a generalization of the classic Lockhart equations of turgor driven cell expansion in plants. Then we apply newly developed equations to explain phototropism, the unilateral growth of plant shoots towards light. The Lockhart equation looks at cell elongation as the result of a dynamic balance between water uptake (driven by salt concentration gradient) and cell wall expansion. We rewrite the equations in tensor form, to capture also changes in cell shape, not only its length. Even though it is well known that phototropy results from unequal growth rates at either sides of the shoot the mathematical treatment formalizes the insight. It looks as though that the model does not help distinguish the current controversy of the mechanism of differential auxin distribution. Nevertheless, it may either involve auxin redistribution as in the lateral transport of auxin (point–light case) or impaired basipetal transport on the shaded side leading to local accumulation (semi-plane case).

We have also found solutions of Eq. (3) in two particular cases. In one of these ((a) point-light case) the calculated bending angle γ does not depend on zth coordinate. In the other ((b) semi-plane case) γ linearly depends on z. These theoretical results have been next probed in two experiments. In one of these the coleoptile was shielded in such a way that its tiny fraction was brought to the light (Fig. 2a) while in the other the upper half of the coleoptile was irradiated with light and the lower part was etiolated (Fig. 2b). The outcome of these experiments was as previously expected. Indeed, both curves as presented in Fig. 4 have exactly reproduced theoretical results. The experimental data in both cases are interpolated by linear function *via* Levenberg–Marquadt algorithm and the exactness of the fits is confirmed by very high determination coefficients (see the legend in Fig. 4). One of these lines, however, is parallel to the z axis (γ does not depend on z and is approximately equal to 5°) while the other one increases with z (γ linearly depends on z). Both results are in accordance with the theoretical predictions, Eqs. (5) and (6), respectively.

To sum up, in this article we have developed tensor description of time evolution of plant cell in the presence of light illumination causing auxin redistribution. Even though we have considered a single cell model only it is evident, in a certain approximation, that the whole system of bound and specialized cells (tissue) would evolve in a similar way providing that we replace a

Fig. 4 Actual experiments: the bending angle (in degrees), corresponding to the phototropic curvature, versus z axis for both cases considered in this paper. In the diaphragm experiment the γ angle was measured after $t = 2$h while in the semi-plane one – after $t = 4$h. R stands for the determination coefficient. The error bars indicate the estimated error (1°) for the angle measurement and 0.01 cm for the length



cell wall yielding coefficient Φ with an effective one ($\Phi \mapsto \Phi_{\mathrm{eff}}$, for the stem). Such approach is fully justified providing that the turgor recovery is relatively small ($P > Y$), see [16]. We have considered, in our opinion, the two most interesting example solutions of Eq. (3) and, accordingly, suitable experiments have been designed. A one-to-one correspondence between our model calculations and the authors' performed experiments have been acquired.

Auxin distribution and activity in growing plant tissue has also been measured using fluorescent protein markers and microscopy [3–5]. Hence we propose a complementary method based on our model: It seems possible to describe quantitatively the process of auxin redistribution coupled to the value of the coefficient D (via the measured γ angle at least in case of phototropic response due to incident light for living plants). In our study, we relate the introduced coefficient D to the intracellular movement of auxin transport proteins (AUX1 and [LAX] family for auxin influx while [PIN] family for auxin efflux). The asymmetric positioning of the latter in the cell determines the non-zero tangential tensions in $\mathbb{P} - \mathbb{Y}$ tensor and nonvanishing D coefficient. The connection between light perception and protein relocation as well as the signalling of auxin lateral distribution together with theoretically derived γ angle dependence of active transport D coefficient looks apparently to be cleared up. Charles Darwin's observations made in the Nineteenth Century seem to have gained a new physical insight.

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