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Unifying model of shoot gravitropism reveals proprioception as a central feature of posture control in plants

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Gravitropism, the slow reorientation of plant growth in response to gravity, is a key determinant of the form and posture of land plants. Shoot gravitropism is triggered when statocysts sense the local angle of the growing organ relative to the gravitational field. Lateral transport of the hormone auxin to the lower side is then enhanced, resulting in differential gene expression and cell elongation causing the organ to bend. However, little is known about the dynamics, regulation, and diversity of the entire bending and straightening process. Here, we modeled the bending and straightening of a rod-like organ and compared it with the gravitropism kinematics of different organs from 11 angiosperms. We show that gravitropic straightening shares common traits across species, organs, and orders of magnitude. The minimal dynamic model accounting for these traits is not the widely cited gravisensing law but one that also takes into account the sensing of local curvature, what we describe here as a graviproprioceptive law. In our model, the entire dynamics of the bending/straightening response is described by a single dimensionless "bending number" *B* that reflects the ratio between graviceptive and proprioceptive sensitivities. The parameter *B* defines both the final shape of the organ at equilibrium and the timing of curving and straightening. *B* can be estimated from simple experiments, and the model can then explain most of the diversity observed in experiments. Proprioceptive sensing is thus as important as gravisensing in gravitropic control, and the *B* ratio can be measured as phenotype in genetic studies.

perception | signaling | movement | morphogenesis

Plant gravitropism is the growth movement of organs in response to gravity that ensures that most shoots grow up and most roots grow down (1–6). As for all tropisms, a directional stimulus is sensed (gravity in this case), and the curvature of the organ changes over time until a set-angle and a steady-state shape are reached (2, 7, 8). The change in shape is achieved by differential elongation for organs undergoing primary growth (e.g., coleoptiles) or by differential differentiation and shrinkage of reaction wood for organs undergoing secondary growth (e.g., tree trunks) (9). Tropisms are complex responses, as unlike other plant movements (e.g., fast movements) (5, 10) the motor activity generated is under continuous biological control (e.g., refs. 3, 11, 12).

The biomechanics of plant elongation growth has been analyzed in some detail (5, 13, 14), but less is known about the biological control of tropic movements and differential growth (3, 6). Many molecular and genetic processes that occur inside sensing and motor cells have been described (2, 15). For example, statocysts are cells that sense gravity through the complex motion of small intercellular bodies called statoliths (16). However, a huge number of sensing and motor cells act together to produce the growth movements of a multicellular organ. How are the movements of an organ controlled and coordinated biologically? This is a key question, as establishing the correct posture of aerial organs with respect to the rest of the plant has important physiological and ecological consequences (e.g., access to light or long-term mechanical stability) (4).

The gravitropic responses of some plants and even fungi have similar features (8). In essence, this has been described as a biphasic pattern of general curving followed by basipetal straightening (GC/BS) (4, 17). First, the organ curves up gravitropically, then a phase of decurving starts at the tip and propagates downward, so that the curvature finally becomes concentrated at the base of the growth zone and steady (7–9, 18–20). This decurving, which has also been described as autotropic (i.e., the tendency of plants to recover straightness in the absence of any external stimulus) (7, 21), may start before the tip reaches the vertical (4). It is striking that organs differing in size by up to four orders of magnitude (e.g., from an hypocotyl to the trunk of an adult tree) display similar traits, despite great differences in the timing of the tropic movement and the motor processes involved (3). However, there are also differences in the gravitropic responses. Depending on the species and the growth conditions, plants may or may not oscillate transiently about the stimulus axis or reach a proper alignment with the direction of the stimulus (e.g., ref. 8).

Currently, the phenotypic variability of the GC/BS biphasic pattern over a broad sample of species is, however, hard to estimate quantitatively, as most studies of gravitropism have only focused on measuring the tip angle (3). As we shall demonstrate, it is necessary to specify the local curvature C (or equivalently, the inclination angle A) over the entire growth zone (Fig. 1) and how it changes over time. If this is done, it is possible to build up a minimal dynamic model for tropic movements in space. This can be combined with dimensional analysis (as is used in fluid mechanics, for example) to characterize the size and time dependencies and set up dimensionless control parameters. This then makes it possible to compare experiments with predictions from the model quantitatively over a broad taxonomical sample of species with very different sizes and growth velocities and to reveal universal behaviors and controlling mechanisms.

The gravitropic responses of 12 genotypes from 11 plant species were studied, representing a broad taxonomical range of land angiosperms (*SI Appendix*, Fig. S4), major growth habits (herbs, shrubs, and trees), as well as different uses (agriculture, horticulture, and forestry but also major laboratory model plants for genetics and physiology). Different types of organs were

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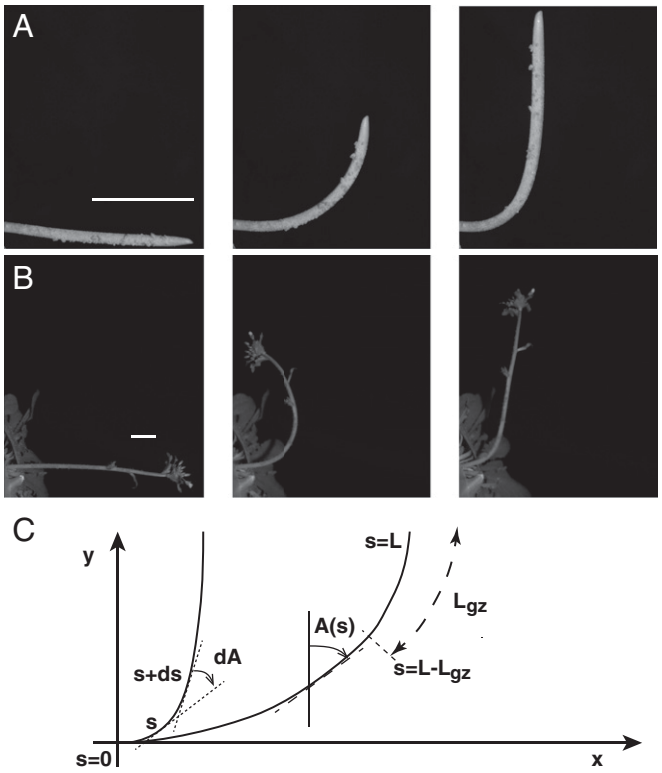

Fig. 1. Successive shapes formed by plant organs undergoing gravitropism and a geometrical description of these shapes. (*A*) Time-lapse photographs of the gravitropic response of a wheat coleoptile placed horizontally (Movie S1). (*B*) Time-lapse photographs of the gravitropic response of an *Arabidopsis* inflorescence placed horizontally (Movie S2). White bars, 1 cm. (*C*) Geometric description of organ shape. The median line of an organ of total length L is in a plane defined by coordinates x, y. The arc length s is defined along the median line, with $s = 0$ referring to the base and $s = L$ referring to the apex. In an elongating organ, only the part inside the growth zone of length L_{gz} from the apex is able to curve (with $L_{gz} = L$ at early stages and $L_{gz} < L$ later on), whereas the whole length is able to curve in organs undergoing secondary growth (i.e., $L_{gz} = L$). $A(s)$ is the local orientation of the organ with respect to the vertical and $C(s)$ the local curvature. The two curves shown have the same apical angle $A(L)$ but different shapes, so to specify the shape we need the form of $A(s)$ or $C(s)$ along the entire median. Due to the symmetry of the system around the vertical axis, the angle A is a zenith angle—that is, it is zero when the organ is vertical and upright. Thus, an orthotropic organ has a gravitropic set point angle of 0. For simplicity, clockwise angles are considered as positive.

studied: coleoptile, hypocotyl, epicotyl, herbaceous and woody vegetative stems, and inflorescence stems, representing the two types of tropic motors (differential elongation growth, reaction woods) and varying by two orders of magnitude in organ size and in the timing of the tropic movements. Organs were tilted horizontally and the gravitropic growth was recorded through time-lapse photography.

All of the plant organs studied first curved upwards before eventually reaching a near vertical steady-state form where the apical part was straight, as shown for two examples in Fig. 1 and in Movies S1 and S2. The images were used to generate color maps of the curvature of the organ in space (along the organ) and time, as shown for three examples in Fig. 2. Shortly after plants were placed horizontally, the dominant movement observed was a rapid up-curving (negatively gravitropic) along the entire organ. However, the apex soon started to straighten and the straightening gradually moved downward along the organ. Finally, the curvature tended to concentrate at the base of the growth zone, becoming fixed there. Such a typical GC/BS behavior was observed in all 12 cases studied, despite differences of around two orders of magnitude in organ sizes and convergence time, the time T_c taken for the organ to return to a steady state, ranging from several hours to several months.

Despite the common properties of the response, time lapse photography showed that plant organs acted differently when approaching the vertical. The apices of some plant organs never overshot the vertical (Fig. 1*A*), whereas others did so several times, exhibiting transient oscillations with the formation of C- or even S-shapes (Fig. 1*B*). Thus, a minimal dynamic model of gravitropism has to explain both the common biphasic GC/BS pattern and the diversity in transient oscillation and convergence time.

According to the literature, the current qualitative model of gravitropism in aerial shoots is based on the following hypotheses:

H1: Gravisensing is exclusively local; each element along the length of the organ is able to respond to its current state (22), since statocysts are found all along the growth zone (16). Gravisensing by the apex does not have a special influence (e.g., the final shapes of organs after decapitation are similar to intact controls) (1, 23).

H2: The local inclination angle A (Fig. 1) is sensed. This sensing follows a sine law (3, 6) (see below).

H3: In our reference frame, the so-called gravitropic set angle (GSA) (24) is equal to 0 (Fig. 1) so the motion tends to bring the organ upward toward the vertical (this corresponds to the botanical term "negative ortho-gravitropism," a most common feature in shoots).

H4: The action of the tropic motor is fully driven by the perception–regulation process and results in a change in the local curvature through differential growth and/or tissue differentiation. This response can only be expressed where differential growth and differentiation occurs, namely in the "growth zone" of length L_{gz} (3).

To form a mathematical model, we shall describe the shape of the organ in terms of its median—that is, its central axis (Fig. 1). We parameterize the median by the arc length s going from the base $s = 0$ to the apex $s = L$, and the angle $A(s,t)$ describes the local orientation of the median with respect to the vertical at time t. The corresponding local curvature $C(s,t)$ is the spatial rate of change of A along s and from differential geometry we know that:

$$C(s,t) = \partial A(s,t)/\partial s \text{ or } A(s,t) = A_0 + \int_0^s C(l,t)dl. \qquad [1]$$

The so-called "sine law" was first defined by Sachs in the 19th century and has been widely used since (see ref. 3 for a review). It can be expressed as a relationship between the change in the local curvature and the local angle as in:

$$\partial C(s,t)/\partial t = -\beta \sin A(s,t), \qquad [2]$$

where β is the apparent gravisensitivity. Note that Eq. **2** is unchanged when A changes to $-A$ and C changes to $-C$, as would be expected. This model is only valid in the growth zone, $s > (L - L_{gz})$, where L is the total organ length and L_{gz} is the length of the effective zone where active curving can be achieved. Outside this region, the curvature does not change with time.

In this model, changes in the overall length of the organ are not taken into account. This is quite reasonable in the case of woody organs, as they undergo curving through relatively small maturation strains in reaction woods, but it is less applicable to organs curving through differential elongation (3, 14). In expanding organs, each segment of the organ in the growth zone "flows" along the organ being pushed by the expansion growth of distal elements (3, 14) so Eq. **2** would remain valid only in

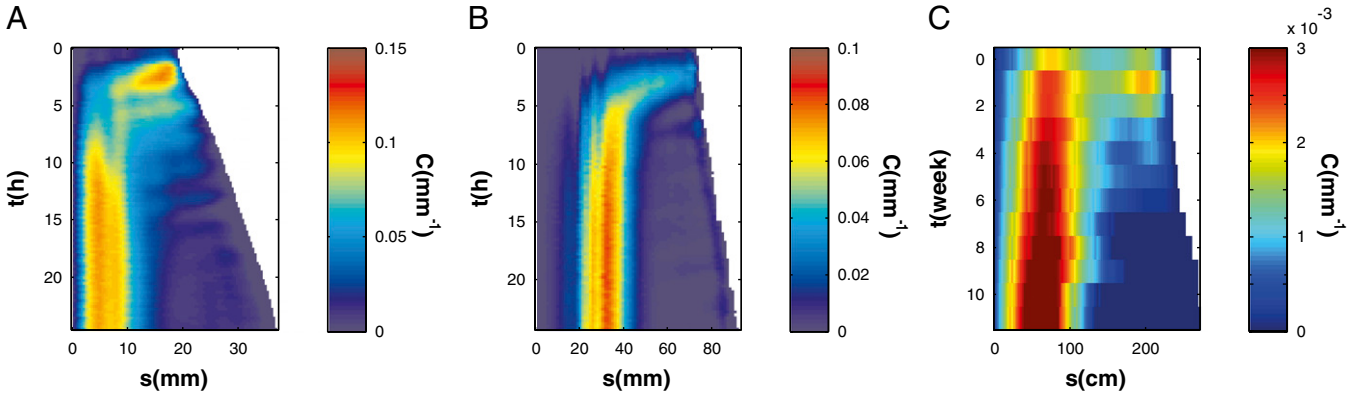

Fig. 2. Kinematics of the entire tropic movement of tilted plant organs shown as color maps plotting the curvature $C(s,t)$ with respect to time t and curvilinear abscissa s (the arc length along the median measured from the base to apex of the organ; Fig. 1). (*A*) Wheat coleoptile (*Triticum aestivum* cv. Recital). The yellow bar is 1 cm long. (*B*) *Arabidopsis* inflorescence (*A. thaliana* ecotype Col0). The yellow bar is 1 cm long. (*C*) Poplar trunk (Hybrid *Populus deltoides x nigra* cv I4551), reprocessed data from ref. 9.

a "comoving" context. To fully specify the changes in curvature, we would thus have to introduce local growth velocities into the model, replacing the derivative in Eq. **2** with the comoving derivative $DC(s,t)/Dt = \partial C(s,t)/\partial t + v(s,t)\partial C(s,t)/\partial s$, where $v(s,t)$ is the local growth velocity. However, in tropic movement, the growth velocities are generally small compared with tropic bending velocities (and the length of the organ that has left the growth zone during the straightening movement is also small) (14), so $DC(s,t)/Dt \approx \partial C(s,t)/\partial t$. The limits of this approximation will be discussed.

To obtain a more tractable model, which we shall solve analytically, we can use the approximation $\sin A \approx A + O(A^3)$ and approximate Eq. **2** by:

$$\partial C(s,t)/\partial t = -\beta A(s,t), \qquad [3]$$

where we note that the $A \to -A$ symmetry is retained. Because in our experiments $|A|$ did not exceed $\pi/2$ and because we are primarily interested in values near zero, this is a reasonable approximation (3). It should be noted that $A(s,t)$ and $C(s,t)$ are not independent, as any further variation in curvature modifies the apical orientation through the "lever-arm effect" expressed in Eq. **1**. In other words, the effect of changes in curvature on downstream orientation angles is amplified by the distance along the organ (3).

The solution of Eq. **3**, which we shall call the "A model," is:

$$A = A_0 J_0\left(2\sqrt{\beta t s}\right); \quad C = A_0\sqrt{\frac{\beta t}{s}}J_1\left(2\sqrt{\beta t s}\right), \qquad [4]$$

where J_n are Bessel functions of the first kind of order n. It has interesting properties. Firstly, the angle A does not depend on space s and time t individually, but only on the combination of $\sqrt{ts}$ and $\sqrt{t/s}$ and is thus an oscillatory function of $\sqrt{ts}$. However, the dynamics of the A model demonstrates that such a system cannot reach a vertical steady state when tilted and clamped at its base (Fig. 3*A* and Movie S3). Indeed, the only steady state in Eq. **3** is $A(s,t) = 0$, but this is forbidden by the basal clamping of the organ fixing $A(s=0,t) = \pi/2$ for all t. Oscillations therefore go on indefinitely, whereas their wavelengths decrease with time. Numerical simulations of Eqs. **3** or **2** displayed the same behavior (*SI Appendix* Fig. S2). This does not agree with any of the experimental results. The A model based on the sine law is therefore not a suitable dynamic model of the gravitropic straightening movement and has to be rejected. To account for the steady state attained after tilting, another hypothesis needs to be introduced:

H5: Each constituent element of the organ perceives its local deformation, the curvature, and responds in order to restore local straightness (7, 19). In animal physiology, this type of sensing is generally called "proprioception," a self-sensing of posture or orientation of body parts relative to the rest of the organism (25). This is not an unreasonable assumption as it is known experimentally that (*i*) plants can sense imposed bending (26, 27) and (*ii*) the curvature of the organ and subsequent mechanical loads have a direct effect on

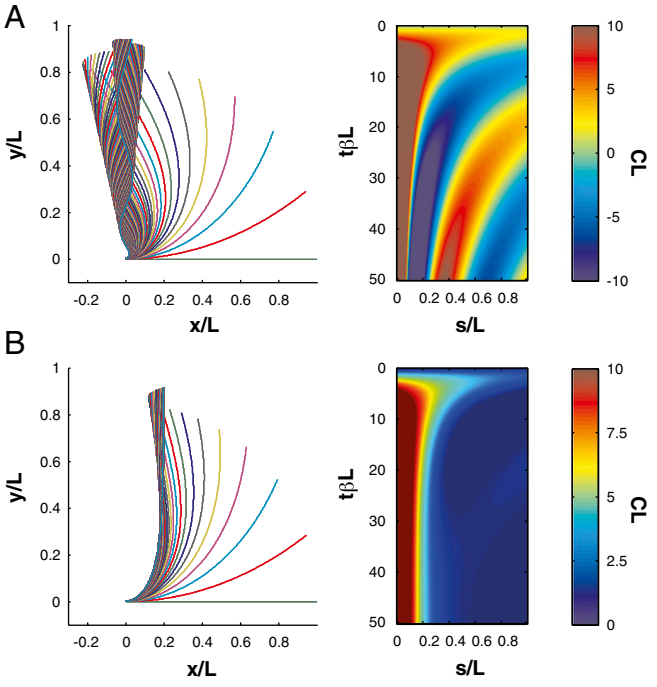

Fig. 3. Solutions of the dimensionless A and AC models. (*Left*) Time-lapse shapes along the movement. (*Right*) Color-coded space–time maps of curvature $C_{th}(s,t)$. (*A*) Graviceptive A model where the response only depends on the local angle. As the organ approaches the vertical, the basal part continues to curve. The organ overshoots the vertical, and the number of oscillations increases with time (Movie S3). (*B*) Graviproprioceptive AC model where the response also depends on the local angle and the local curvature. Here the curvature decreases before reaching the vertical. It does exhibit an S shape, but oscillations are dampened, and the organ converges to a solution where the curvature is focused near the base (Movies S4 and S5).

the orientation of microtubules that may then modify the rate of differential growth (28, 29).

This hypothesis yields a model called the "graviproprioceptive" model, or the "*AC* model":

$$\partial C(s,t)/\partial t = -\beta A(s,t) - \gamma C(s,t), \quad [5]$$

in the growth zone (i.e., for $s > L - L_{gz}$), and 0 elsewhere. Here the change in curvature is directly related to the local curvature itself via the parameter γ, the proprioceptive sensitivity. A more systematic derivation of the *A* and *AC* models from symmetry arguments and rod kinematics is given in *SI Appendix*. The solution of the *AC* model has the form:

$$\begin{aligned} A(s,t) &= A_0 e^{-\gamma t} \sum_{n=0}^{\infty} \left(\frac{\beta s}{\gamma^2 t}\right)^{-n/2} J_n\left(2\sqrt{\beta t s}\right) \\ &= A_0 e^{-\beta s/\gamma} - A_0 \sum_{n=1}^{\infty} (-1)^n \left(\frac{\beta s}{\gamma^2 t}\right)^{n/2} J_n(2\sqrt{\beta t s}), \end{aligned} \quad [6]$$

where it is seen that the dependence on $\sqrt{ts}$ and $\sqrt{t/s}$ is retained, but there is now an infinite sequence of Bessel functions. The first of the two expressions is appropriate for short times. The latter is appropriate for long times and shows that the oscillations are now dampened toward a final steady state, whose form is:

$$A_f(s) = A_0 e^{-\beta s/\gamma} = A_0 e^{-s/L_c}. \quad [7]$$

The dynamics of the *AC* model (Fig. 3*B* and Movies S4 and S5) is now qualitatively consistent with the experiments: the oscillations are dampened, and the organ converges to a steady state where the curvature is focused near the base through a typical GC/BS biphasic pattern.

The convergence length $L_c = \gamma/\beta$ is given by the decay length of the exponential toward the vertical, and it results from the balance between graviception and proprioception. The *AC* model thus gives a direct explanation of the common BS (autotropic) phase, where curvature starts to decrease before reaching the vertical (7, 20). For purely geometrical reasons (lever-arm effect, Eq. **1**), the apical angles decrease faster than the basal angles. Thus, curvature sensing first takes over gravisensing at the tip and decurving starts there. It then moves downward together with the decrease of *A* without any need for a systemic basipetal propagative signal. Another important scale is L_{gz}, the effective length of the growth zone where active curving can be achieved. The ratio $B_l = L_{gz}/L_c = \beta L_{gz}/\gamma$ is a dimensionless number that controls important aspects of the dynamics.

To assess whether the organ has time to converge to a steady state before the apex crosses the vertical, thereby avoiding overshooting, the time of convergence T_c can be compared with the time required for the apex to first reach the vertical, T_v. Using Eq. **5**, T_c can be approximated from the proprioceptive term that dominates when approaching convergence as $T_c = 1/\gamma$ and T_v can be approximated as $T_v = 1/(\beta L_{gz})$ from the graviceptive term dominating initial dynamics. This gives a "temporal" dimensionless number $B_t = T_c/T_v = \beta L_{gz}/\gamma$, which is actually identical to B_l. The fact that $B_t = B_l$ gives a direct link between convergence timing, transient modes, and steady-state form (i.e., a kind of form-movement equivalence). We call this number the "bending number" denoted by *B*.

To compare theory and experiments, *B*, L_{gz}, and L_c were measured morphometrically from initial and steady-state images as shown for *Arabidopsis* inflorescence in Fig. 4. Because L_{gz} is the length of the organ that has curved during the experiment, it can be directly estimated by comparing the two images. By definition, L_c can be measured directly on the image of the final shape as the characteristic length of the curved part (Fig. 4). The bending number *B* ranged from around 0.9–9.3 displaying broad intraspecific and interspecific variability over the experiments. Therefore, the *AC* model can be assessed from them.

The kinematic data from wheat, *Arabidopsis*, and poplar was analyzed in more detail to track the tropic movement after tilting (Fig. 1). The analytical solution $A_{ac}(s,t)$ for the *AC* model (Eq. **6**) was compared with the experimental angle space-time maps, given the bending number value. Angles were chosen instead of curvature here, as otherwise the determination of curvature would involve a derivative, producing more noise. The initial value of *B* for parameter estimation was estimated morphometrically. As the *AC* model does not account for elongation growth, we trimmed the data for wheat and *Arabidopsis* to the length of the growth zone at the beginning of the experiment, as shown in Fig. 5. Typical results from *Arabidopsis* inflorescences are shown in Fig. 5, and additional results from *Arabidopsis*, wheat, and poplar are provided in *SI Appendix*, Figs. S6, S7, and S8, respectively. The *AC* model was found to capture the common features of the angle space-time maps over the entire GC/BS process (compare Fig. 5 *A* and *B*). The (dimensionless) mean slope of comparison of the model vs. data (for the three species together) was 1.00 ± 0.15, the intercept was 0.07 ± 0.20, and the coefficient of determination was 0.92 ± 0.05, so the *AC* model captured around 90% of the total experimental variance in $A(s,t)$ and displayed no mean quantitative bias.

The form–movement equivalence predicted by the *AC* model was then directly assessed through a simple morphometric analysis of the tilting experiments on the 12 angiosperm genotypes. More precisely, we assessed whether the *AC* model predicted the discrete transitions between transient oscillatory modes around the vertical (e.g., Fig. 1 and *SI Appendix*, Fig. S5) with increasing values of the bending number *B*. At a given time *t*, the current mode is defined as the number of places below the apex where the tangent to the central line of the organ is vertical (*SI Appendix*, Fig. S5). If there is one vertical tangent more basal than the apex, then the organ overshoots the vertical once. This is mode 1, when a C shape is formed. If an S shape develops, then the transient mode will be mode 2, and a Σ shape is mode 3, and so on. The mode number *M* of the whole movement is then given by the maximal mode of all of the transitory shapes (e.g., in *SI Appendix*, Fig. S5, the mode of the movement of the inflorescence is $M = 1$ as a transient C shape is seen but not an S shape). In Fig. 6, the modes of 12 plant organ responses were plotted against the respective estimated bending numbers and compared with the predictions of the *AC* model.

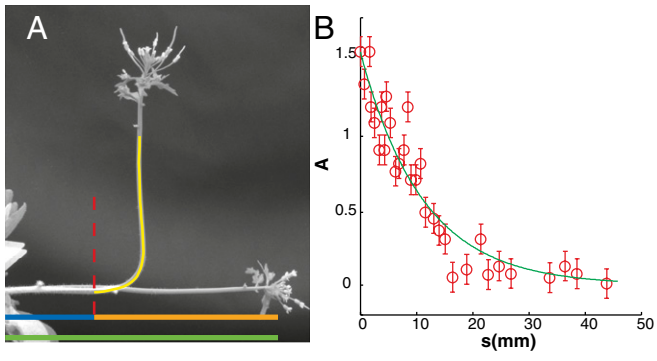

Fig. 4. Morphometric measurement of the bending number *B* from steady-state configurations of *Arabidopsis* inflorescences. (*A*) Estimation of the effective length L_{gz} by superimposing the first and last kinematics images. The red dotted lines indicate the zone where the organ started to curve. The effective length of the organ can then be defined as the distance from this point to the apex of the initial plant on the first image. (*B*) Estimation of the convergence length L_c by plotting the local inclination angle $A(s,t)$ along the organ beginning from the curved zone. To extract the convergence length L_c, the angle $A(s,t)$ is fitted with the exponential $A(s,t) = A_0 e^{-s/L_c}$, $n = 28$, $R^2 = 0.99$.

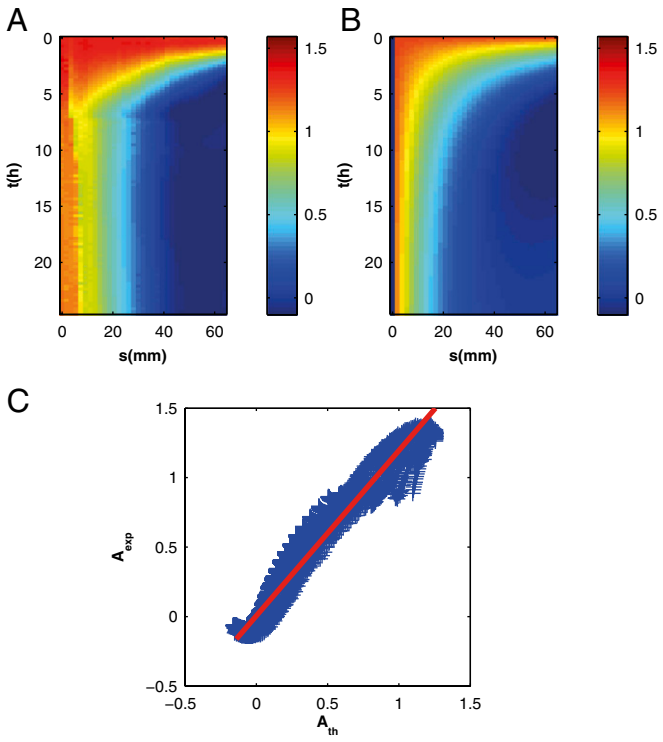

Fig. 5. Quantitative comparison between experimental (exp) and predicted (th) angle space–time maps of $A(s,t)$ for an *Arabidopsis* inflorescence for the whole gravitropic response. (*A*) Experimental angle space–time map of $A_{exp}(S,t)$ trimmed for $s \leq L(t=0)$, as the *AC* model does not consider changes in length. (*B*) Angle space–time map predicted by the *AC* model $A_{ac}(s,t)$. (*C*) Quantitative validation plot of experimental $A_{exp}(s,t)$ vs. theoretical $A_{th}(s,t)$. Orthogonal linear fit slope, 1.13; intercept, 0.17; $R^2 = 0.94$.

The prediction displays stepwise increases in modes at bending numbers corresponding to 2.8 for the transition from mode 0 to mode 1 and 3.9 for the transition from mode 1 to mode 2. No plant in the experiments displayed mode transitions for smaller bending numbers than was predicted by the *AC* model. Many individual plant responses were found near the transition from mode 0 to mode 1—that is, between the mode in which they cannot reach the vertical and the mode where they overshoot the vertical and oscillate. The transition from mode 2 to mode 3 only occurs for very large bending numbers ($B > 10$) and was never seen in any of the experiments. In two-thirds of the plants, the prediction of the oscillations by the *AC* model was correct. However, about one-third of the plants oscillated less than predicted. To some extent, this may be due to inaccuracies in the estimation of bending numbers, but second-order mechanisms (possibly related to elongation growth) are likely to be involved, ones that add to the common gravipriproprioceptive core described by the *AC* model.

Nevertheless, the fact that the *AC* model accounts for the common GC/BS pattern with no quantitative bias and captures the transitions between three different modes over one order of magnitude of bending numbers and a broad taxonomical range is an indication of its robustness. All this strongly suggests that hypothesis 5 and its mathematical description by the *AC* model captures the universal core of the control over gravitropic dynamics. The longstanding sine law for gravitropism (3) should thus be replaced by the gravipriproprioceptive dynamic *AC* model, which highlights the equal importance of curvature- and gravisensing. Doing so has already yielded three major insights.

i) The *AC* model can achieve distinct steady-state tip angles for the same vertical GSA. In particular, plants with $B < 2.8$ cannot reach their GSA (as specified in the gravitropic term of the *AC* model) even in the absence of biomechanical and physiological limits in their motor bending capacity (3, 10, 12). Therefore, the GSA cannot be measured directly from experiments and can only be assessed by *AC* model–assisted phenotyping.

ii) The fact that most plants display very few oscillations before converging to the steady state despite destabilization through lever-arm effects does not actually require the propagation of long-distance biological signals and complex regulation. The value of the dimensionless bending number simply has to be selected in the proper range—that is, graviceptive and proprioceptive sensitivities have to be tuned together as a function of organ size possibly pointing to molecular mechanisms yet to be discovered.

iii) The *AC* model can account for the behavior of actively elongating organs despite neglecting the effects of mean elongation growth. Subapical elongation growth may have destabilizing effects by spreading curvature, convecting, and fixing it outside the growth zone in mature tissues (14). Our result means that the values for the time of convergence to the steady-state T_c were small enough compared with the characteristic times for elongation growth in all of the species studied. As T_c depends mostly on the proprioceptive sensitivity, possibly there is natural selection for this trait as a function of the relative elongation rate (and organ slenderness) and for fine physiological tuning.

Proprioceptive sensing is thus as important as gravisensing for gravitropism. The study of molecular sensing mechanisms (2, 15) can thus now be extended to the cross-talk between gravi- and propriosensing as a function of organ size. Candidate mechanisms for the proprioception of the curvature may involve mechanical strain- or stress-sensing (27, 30) triggering microtubules reorientation (28, 29). Ethylene seems to be involved (17) but not the lateral transport of auxin (21). Whatever the detailed mechanisms involved, putative models of molecular networks controlling gravipriproprioceptive sensing (31) should be consistent with the *AC* model and with the existence of a dimensionless control parameter, the bending number. Moreover, the bending number B is a real quantitative genetic trait (32, 33). It controls the whole dynamics of tropic movement and encapsulates both the geometry

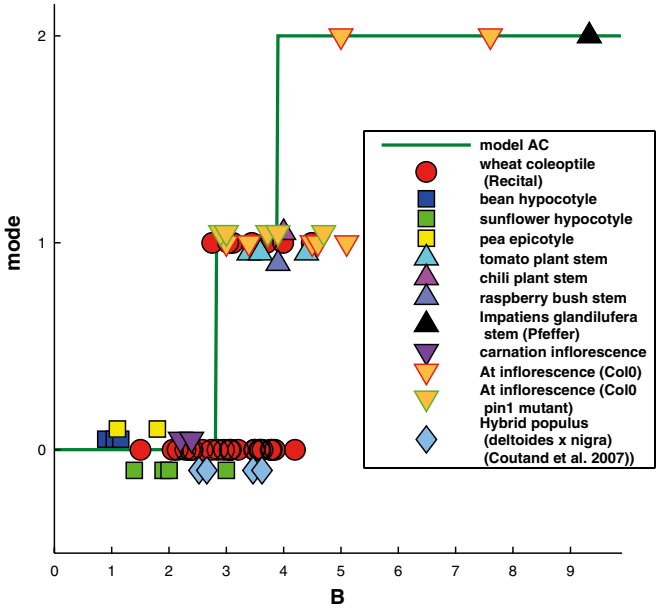

Fig. 6. Mode number M plotted against bending number $B = L_{gz}/L_c$ for individual plants ($N = 67$). The green line shows the same plot for the *AC* model.

and the perception–regulation functions involved (34). The simple measurement of B is now possible and this may be used for the high-throughput phenotyping of mutants or variants in many species. From a more general perspective, it would now be interesting to explore how plants manage to control gravitropism despite the destabilizing effects of elongation growth. Areas to investigate are whether there is physiological tuning of B during growth and whether there is natural selection for proprioceptive sensitivity as a function of the relative elongation rate and organ slenderness. For this, it will be necessary to combine noninvasive kinematics methods to monitor elongation growth at the same time as curvature (e.g., refs. 32, 33) with a more general model that explicitly includes the expansion and convection of cells during growth (3, 14). Finally, this approach can also be used to study the gravitropism of other plant organs and other growth movements like phototropism or nutation, which will show whether this theory of active movement is universal.

Materials and Methods

Experiments were conducted in growth cabinets for etiolated wheat coleoptiles (*Triticum aestivum* cv. Recital) or controlled temperature greenhouses for the nine other types of plant organs—bean hypocotyl (*Phaseolus vulgaris*), sunflower hypocotyl (*Helianthus annuus*), pea epicotyl (*Pisum sativum*), tomato stem (*Solanum lycopersicum*), chili stem (*Capsicum annuum*), raspberry cane (*Rubus ideaus*), carnation inflorescence (*Dianthus caryophyllus*), and *Arabidopsis thaliana* inflorescences from a wild-type (ecotype Col0) and its *pin1* mutant [a mutant of the PIN1 auxin efflux carier displaying reduced auxin longitudinal transport (11) (see *SI Appendix*, sections S2.1 and S2.4 for more details)]. Plants were grown until a given developmental stage of the organ of interest (e.g., until the beginning of inflorescence flowering for *Arabidopsis* in Fig. 4). They were then tilted and clamped horizontally $A(s = 0, t) = \phi/2$ for all t under constant environmental conditions in the dark (to avoid interactions with phototropism). Number of replicates were 30 for wheat, 15 for *Arabidopsis*, and 5 for all the other species. Published data were also reprocessed from similar experiments on *Impatiens glandilufera* stems by Pfeffer (35) and on poplar trunks (*Populus deltoides x nigra* cv I4551) by Coutand et al. (9). More precisely, two types of experiments were conducted, as explained in *SI Appendix*, section S2.2 and S2.5: (*i*) detailed kinematics experiments on two model species (*Arabidopsis* and wheat), based on time-lapse photography and quantitative analysis of curving-decurving kinematics (*SI Appendix*, sections S2.2 to S2.4) and (*ii*) simplified morphometric experiments on all the genotypes, to estimate the bending number (through $B_l = L_{gz}/L_c$) and the (transient) global mode M, defined as the maximum number of places below the apex where the tangent to the central line of the organ is vertical (*SI Appendix*, Fig. S5 and section S2.5). Quantitative assessment of the *AC* model was conducted by fitting Eq. **6** to the datasets from the detailed kinematics experiments (including also poplar; see *SI Appendix*, section S2.6), whereas a qualitative assessment on mode transitions and space-time equivalence was conducted on the dataset from the morphometric experiment (including also *Impatiens*; see *SI Appendix*, section S2.5).

ACKNOWLEDGMENTS. We thank Dr. C. Coutand for providing the poplar data, S. Ploquin and Dr. C. Girousse for help with the wheat experiments, Drs. A. Peaucelle and H. Hofte for help with the *Arabidopsis* experiments, and Emondo (Boston) for editing the English.

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Supporting Information

Bastien et al. 10.1073/pnas.1214301109

Movie S1. Gravitropic movement of a wheat coleoptile, after an initial tilting at 90° from the vertical. Note that this wheat coleoptile never overshot the vertical during the straightening process. Other coleoptiles in the experiment did not even reach the vertical even at their tip (not shown in the movie).

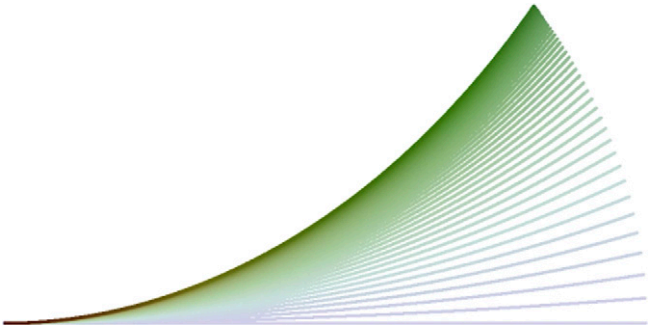
Movie S1

Movie S2. Gravitropic movement of an inflorescence of *A. thaliana* after an initial tilting at 90° from the vertical. The inflorescence of *A. thaliana* exhibited a transient C shape during the straightening process and overshot the vertical.

Movie S2

Movie S3. Solution of the *A* model. The color (from blue to red) codes for the absolute value of the curvature C(s,t). The simulated organ never reaches a steady state and oscillation increases along the organ.

Movie S3



Movie S4. Solution of the *AC* model, $B = 1$. The color (from blue to red) codes for the absolute value of the curvature C(s,t). The simulated organ reaches a steady state but does not reach the vertical.

Movie S4

Movie S5. Solution of the *AC* Model, $B = 10$. The color (from blue to red) codes for the absolute value of the curvature C(s,t). The simulated organ reaches a steady state after exhibiting a transient S-shaped mode during the process.

Movie S5

Other Supporting Information Files

SI Appendix (PDF)

A unifying model of shoot gravitropism reveals proprioception as a central feature of posture control in plants - supplementary information-

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1- Construction of the mathematical model

1.1 General equation. The plant organs considered in this study are slender structures. During tropic movements cells do not undergo shear growth and torsion can be neglected (3). Therefore the organ can be considered mechanically as an (actively) flexing rod (3). Its successive shapes can thus be fully described by the local orientation $A(s,t)$ and the local curvature $C(s,t)$ fields. Note that curvature C is an objective quantity defining the local shape of the organ irrespective of its local inclination A. The mechanism that produces the movement, like differential growth, modifies the local curvature of the organ. The equation that drives the system should thus determine the temporal variation in the local curvature

$$\frac{\partial C(s,t)}{\partial t} = \phi, \qquad [1]$$

where ϕ is a function of the geometry, the biomechanics of bending and the perception-regulation process, s is the curvilinear abscissa from the base to the apex and t is the time elapsed since the plant was tilted horizontally. It is postulated that the perception-regulation process driving the dynamics of the movement is of the first order, i.e. that the biomechanical motors are not limiting the movement as is often the case (3). In addition, the perception involved in gravitropism is local (see the argument for Hypothesis H1 in the main text). The perception of a segment at position s should be a function of the local angle and curvature $A(s,t)$ and $C(s,t)$, and this local perception then results in a local response. Equation [1] can thus be rewritten

$$\frac{\partial C(s,t)}{\partial t} = \phi(A, C). \qquad [2]$$

Assuming that both the tilting angle $A(s,t)$ and the curvature $C(s,t)$ are small, the function ϕ can be expanded as polynomials of $A(s,t)$ and $C(s,t)$ near the vertical (straight) configurations of the organ.

$$\begin{aligned}\frac{\partial C(s,t)}{\partial t} &= \alpha + \beta_1 A + \beta_2 A^2 + ... + \gamma_1 C + \gamma_2 C^2 + ... + \\ &\quad + \delta_1 AC + \delta_2 A^2 C + \delta_3 A C^2 + ... \end{aligned} \qquad [3]$$

When the organ is nearly straight and vertical, there is no gravitropic response. So $A = 0$, $C = 0$ is a stable solution of the equation. Furthermore, as the behavior of the organ is independent of rotation around the vertical axis, the transformation $A \to -A$, $C \to -C$ should leave the system unchanged. This implies that all even-order terms in [3] disappear, yielding

$$\begin{aligned}\frac{\partial C(s,t)}{\partial t} &= \beta_1 A + \beta_3 A^3 + ... + \gamma_1 C + \gamma_3 C^3 + ... \\ &\quad + \delta_2 A^2 C + \delta_3 A C^2 + ... \end{aligned} \qquad [4]$$

This is the most general equation describing gravitropism of an elongated aerial organ.

For simplicity, we will first assume that the β and γ coefficients do not depend on position s or time t, i.e. that the sensitivities to angle and curvature are both time-independent and homogeneous. These assumptions have experimental support. Time-independence of the straightening response is envisageable in that tropic responses are fast in terms of the entire developmental timecourse of the organ (S1). Spatial homogeneity of the sensing capacity throughout the growth zone is supported by observations of the even distribution of statocytes or the response to high magnetic fields (22).

1.2 Test of two response functions: sine law (the A model) and exponential law. We may now compare two phenomenological ϕ functions that have been proposed in the literature, the sine law and the exponential law, to the general equation [4].

The sine law was defined by Sachs in the 19th century (see (3) for a review). Here then equation [2] can be rewritten as

$$\frac{\partial C(s,t)}{\partial t} = \alpha \sin A(s,t) \qquad [5]$$

where α is a parameter. Expanding $sin(A)$ as a power series (valid for any A) yields

$$\sin A = A - \frac{A^3}{3!} + \frac{A^5}{5!} + O(A^7) \qquad [6]$$

Since there are no even-order terms, the equation satisfies the symmetry condition mentioned above and the sine law is thus a special instance of equation [4]. In this work, we have used the approximation $\sin A \approx A$, for equation [5] giving

$$\partial C(s,t)/\partial t = -\beta A(s,t) \qquad [7]$$

Equation [7] is a mathematical specification of the hypothesis that the rate of local change in local curvature C is controlled only by a graviceptive term depending on the local inclination angle A. We have thus called this model the graviceptive model, or the *A* model (see also equation [3] in the main text).

We may now consider the exponential law postulated in the complete model of the tropic reaction in (20). This law is described by the following function

$$\frac{\partial C(s,t)}{\partial t} = \alpha\, e^{\frac{A-\pi/2}{A_1}} = \alpha\, e^{\frac{A}{A_1}} e^{-\frac{\pi}{2A_1}} \qquad [8]$$

The effect of this function becomes very small when A is less than $\pi/2 - A_1$ and thus only affects the start of the reaction. The power series of e^{A/A_1} is given by

$$e^{A/A_1} = 1 + \frac{A}{A_1} + \frac{1}{2}\left(\frac{A}{A_1}\right)^2 + \frac{1}{3!}\left(\frac{A}{A_1}\right)^3 + \frac{1}{4!}\left(\frac{A}{A_1}\right)^4 + ... \qquad [9]$$

Here even terms appear so this function violates the symmetries of the system and is therefore not a suitable model. This illustrates the importance of considering the symmetry of the problem when modeling especially when the exponential function is used.

1.3 First-order equation. Near $A(s,t) = 0$ and $C(s,t) = 0$, equation [4] can be linearized. This first order expression is in fact a second order approximation since we have seen previously that all the even terms disappear and the first cross-product terms A^2C and C^2A are third-order. The generalized equation of gravitropism at the second order is thus given by

$$\frac{\partial C(s,t)}{\partial t} = -\beta A - \gamma C \qquad [10]$$

For an initially straight organ clamped at the base and tilted with an initial angle A_0 from the vertical, the boundary conditions are then given by

$$A(0,t) = A(s,0) = A_0 \qquad [11]$$
$$C(s,0) = 0 \qquad [12]$$

Equation [10] is a mathematical specification of the hypothesis that the rate of change in local curvature C is controlled by a graviceptive term depending on local inclination angle A and a proprioceptive term depending on the sensing of local curvature by each organ segment C (while respecting the symmetry of the problem, and using a second order approximation). This new model has been therefore called the graviproprioceptive model, or the *AC* model (see also equation [5] in the main text).

1.4 Steady state and the dimensionless number B_l. The steady state of the equation [10] is given by

$$\frac{\partial C(s,t)}{\partial t} = 0 \qquad [13]$$
$$-\beta A(s,t) - \gamma C(s,t) = 0 \qquad [14]$$
$$C(s,t) = \partial_s A(s,t) \qquad [15]$$

As $A(s,t) = 0$ is forbidden by the boundary condition if $A_0 \neq 0$, there is only one steady solution

$$-\beta A(s,t) - \gamma \frac{\partial A(s,t)}{\partial t} = 0 \qquad [16]$$
$$A(s,t) = A_0 e^{-\frac{\beta s}{\gamma}} \qquad [17]$$

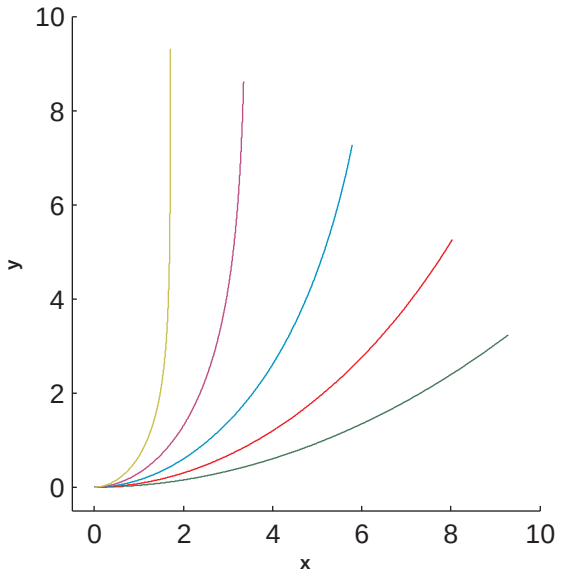

Fig. 1. Final shape of the *AC* model for different values of B_l with $L_{gz} = 10$. From the lower line (green) to the upper one (yellow) the values of B_l are respectively 0.5, 1, 2, 4 and 8.

Equation [17] thus defines the steady-state shape of the organ. Along the organ at steady state, the angle $A(s)$ decreases from A_0 to A_0/e ($\sim 0.37A_0$) over a length L_c given by

$$L_C = \frac{\gamma}{\beta} \qquad [18]$$

L_c is called the convergence length. It is then possible to designate a dimensionless number B_l by expressing L_c relatively to a characteristic effective length for bending L_{gz} (the length of the growth zone where active curving can be achieved):

$$B_l = \frac{\beta L_{gz}}{\gamma} \qquad [19]$$

Each value of B_l corresponds to one and only one specific shape (Figure 1). When B_l is a small number the apex of the organ cannot reach the vertical despite the fact that the graviceptive setpoint angle is $A = 0$, because the convergence length is too large compared to the length of the organ.

1.5 Timing of the movement and dimensionless number B_t. It is insightful to compare the time for the apex to reach the vertical to the time for the organ to converge to its final shape. Indeed when the organ reaches the vertical some time before convergence occurs, the organ may exhibit transient spatial oscillations.

A straightforward (under)estimation of the time for the apex to reach the vertical can be obtained by ignoring the proprioceptive process and further assuming that the angle A stays at its maximal value of A_0.

$$\frac{\partial C(s,t)}{\partial t} \approx -\beta A_0 \qquad [20]$$

with the solution

$$A(s,t) = A_0 - \int_{L_{gz}}^{s} ds \beta A_0 t \qquad [21]$$

i.e.,

$$A(0,t) = A_0 - \int_{L_{gz}}^{0} ds \beta A_0 t = A_0(1 - \beta L_{gz} t) \qquad [22]$$

Thus the time T_v to bring the apex to the vertical orientation ($A = 0$) is

$$T_v = \frac{1}{\beta L_{gz}} \qquad [23]$$

Likewise, when the gravi-proprioceptive term dominates, the convergence time T_c to the final shape is given by the characteristic time required by the organ to reach the steady state

$$T_c = \frac{1}{\gamma} \qquad [24]$$

It is now possible to define a dimensionless number for the movement as the ratio of the convergence time T_c and the vertical time T_v

$$B_t = \frac{\beta L_{gz}}{\gamma} \qquad [25]$$

By comparing equation [19] and equation [25] we see

$$B_l = B_t = B \qquad [26]$$

This "bending number" will quantify the number of transient overshoots that occur when the organ approaches the steady state as discussed in the main text.

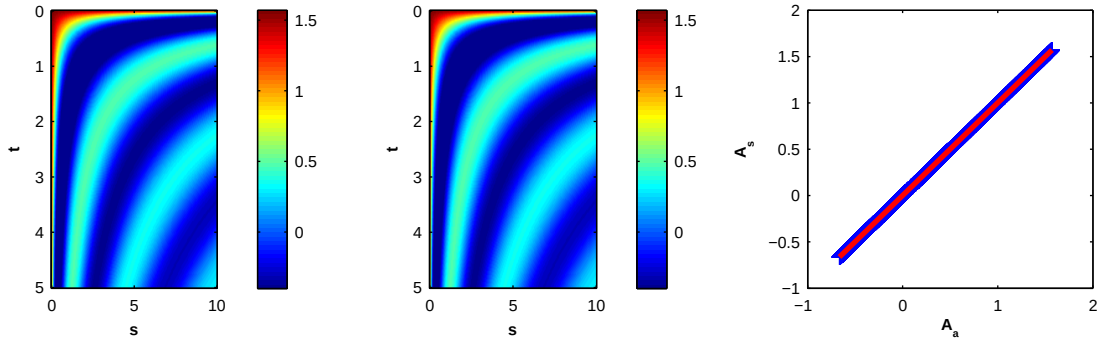

Fig. 2. Quantitative comparison between the analytical solution $A_a(s,t)$ (left panel) for the angle and the numerical solution $A_s(s,t)$ (middle panel) for the *A* model with $\beta = 1$ and $L_{gz} = 10$. Quantitative validation plot $A_a(s,t)$ vs $A_s(s,t)$ (right panel) with orthogonal linear fit (slope 1.0, intercept 0.0, R2 = 1.0).

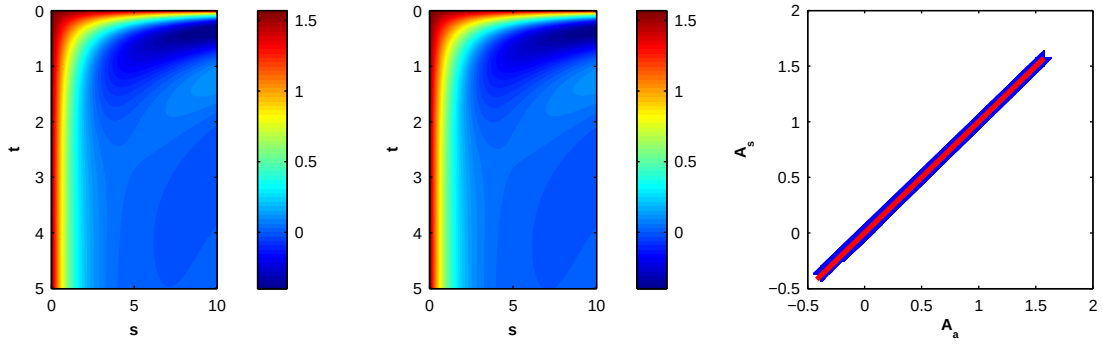

Fig. 3. Quantitative comparison between the analytical solution $A_a(s,t)$ (left panel) of the angle and the numerical solution $A_s(s,t)$ (middle panel) for the *AC* model with $B = 10$ and $L_{gz} = 10$. The quantitative validation plot $A_a(s,t)$ vs $A_s(s,t)$ (right panel) with orthogonal linear fit (slope 1.0, intercept 0.0, R2 = 1.0)

1.6 Analytical Solution and Numerical Simulations. The *A* model corresponds to the case, where the proprioceptive term is removed, and only the angle perception is kept:

$$\frac{\partial C(s,t)}{\partial t} = -\beta A \qquad [27]$$

With the initial condition $A(s, t = 0) = A_0$ this has the solution

$$A(s,t) = A_0\sqrt{\frac{\beta t}{s}}J_0\left(2\sqrt{\beta t s}\right) \qquad [28]$$

as can be seen by directly inserting it into the equation and performing the differentiations (S2) using

$$C(s,t) = \frac{\partial A(s,t)}{\partial s} \qquad [29]$$

This analytical solution A(s, t) of the *A* model [28] was compared to the angle space maps obtained through numerical simulations of Equation [27], for many sets of values for the two parameters. A typical example is shown in Figure S3. Again, no discrepancies were found between the analytical solution and the numerical experiments, so Equation 28 is correct and can be used to investigate the behavior of the *A* model and assess it against experimental data.

The analytical solution of the graviproprioceptive equation [10] with boundary conditions [11] and [12] are

$$A(s,t) = A_0 e^{-\gamma t}\sum_{n=0}^{\infty}\gamma^{n/2}\left(\frac{\beta s}{\gamma t}\right)^{-n/2}J_n\left(2\sqrt{\beta t s}\right) \qquad [30]$$

which can also be verified by direct differentiation, although more cumbersome (S2). This analytical solution A(s, t) of the *AC* model [30] was compared to the angle space map obtained through numerical simulations of Equation [10] for many sets of values for the two parameters. A typical example is shown in Figure S2. No discrepancies were found between the analytical solution and the numerical experiments, so Equation [30] is correct and can be used to investigate the behavior of the *AC* model and assess it against experimental data. The detailed mathematical derivation of the analytical solutions is available on ArXiv (S2).

2- Experiments

2.1 - Plant Materials and tilting experiments. Experiments were conducted in growth cabinets for etiolated wheat coleoptiles (*Triticum aestivum* cv. Recital) or controlled temperature greenhouses for the nine other types of plant organs - bean hypocotyl (*Phaseolus vulgaris*), sunflower hypocotyl (*Helianthus annuus*), pea epicotyl (*Pisum sativum*), tomato stem (*Solanum lycopersicum*), chili stem (*Capsicum annuum*), raspberry cane (*Rubus ideaus*), carnation inflorescence (*Dianthus caryophyllus*), and *Arabidopsis thaliana* inflorescences from a wild type (ecotype Col0) and its *pin1* mutant (a mutant of the PIN1 auxin efflux carier displaying reduced auxin longitudinal transport (11)). Plants were grown until a given developmental stage of the organ of interest (e.g until the beginning of inflorescence flowering for Arabidopsis in Figure 4). They were then tilted and clamped horizontally $A(s = 0, t) = \pi/2$ for all t under constant environmental conditions in the dark (to avoid interactions with phototropism). Number of replicates were 30 for wheat, 15 for *Arabidopsis* and 5 for all the other species. Published data were also reprocessed from similar experiments on *Impatiens glandilufera* stems by Pfeffer (35) and on poplar trunks (*Populus deltoides x nigra* cv I4551) by Coutand et al. (9).

2.2 - Detailed kinematics experiments. Time lapse photography was performed using a flash light, where the light was filtered to retain only green light, which did not stimulate any phototropic response. After initial tilting of the organ, the tropic movement was followed until a clear steady-state shape was achieved. One typical experiment on *Arabidopsis thaliana* is presented in Figure S5.A.

2.3 - Kinematics of Curving-Decurving. The central line of the organ was extracted from the pictures at successive times t and curvature C and curvilinear abscissa s at successive points along the central line were computed using a method described in refs (3,9). Space-time plots with color coding indicating the magnitude of the angle or the curvature were then generated to illustrate the pattern of the gravitropic movement.

2.4 Plant Material: phylogenetics of species studied. Eleven species were chosen from a broad taxonomical range of land angiosperms including monocots and dicots, see Figure S4. Different types of organs were studied: coleoptile, hypoctyl, epicotyl, inflorescence stems, or stems of vegetative shoots. The plants studied represent many of the growth habits of angiosperms, e.g. herbaceous plants, biennial shrubs and trees.

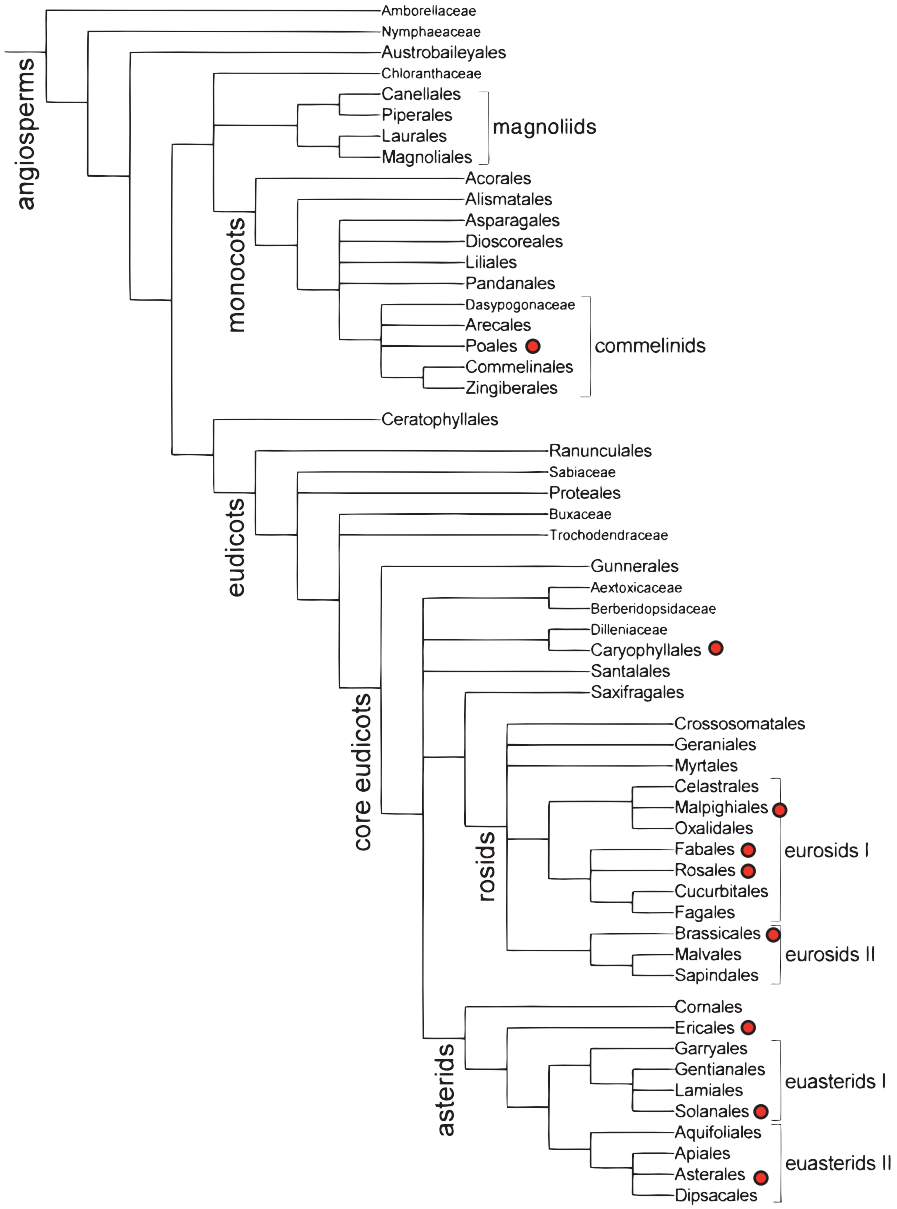

Fig. 4. Phylogenetic distribution of the species under study (modified from The Angiosperm Phylogeny (S3)). Families of the studied species are marked by a red dot.

2.5 Morphometric experiment and Characterization of transient oscillatory modes. Estimates of the bending number (through $B_l = L_{gz}/L_c$) and of the (transient) global mode M (Figure S5.B) were obtained. To estimate the length L_{gz} (the length of the organ along which active curving can take place), the first image of the kinematics just after tilting the organ was compared to the last one when the organ has reached a steady state (Figure 4). The distance between the apex and the most basal point with non-zero curvature on the last image gives the total length that was able to curve at the start of the experiment.This gives an approximation of the length of the growth zone L_{gz}.To get the convergence length L_c on the image of the steady state shape, the local orientation angle is taken from the point where the organ started to curve (Figure 4). Then the plot of $A(s)$ is fitted with an exponential function, $A_0 e^{-s/L_c}$. This fit gives a direct estimate of the convergence length to the vertical L_c. The measurement of the modes are illustrated in Figure S5.B. At a given time t the current mode is defined as the number of places below the apex where the tangent to the central line of the organ is vertical (Figure S5.B). In the example (Figure S5.A) the inflorescence of Arabidopsis displayed transient J then C shape and finally, just before convergence, an S shape. (Figure S5.B). Transient oscillatory modes were characterized by the mode number M defined as the maximal number of places in which the tangent to the central line of the organ is vertical simultaneously during the straightening mouvement. This transient state is the most curved state. In our experiments, only modes 0, 1 and 2 were observed. The value of mode M for (Figure S5.A) tilting experiment is thus M= 2.

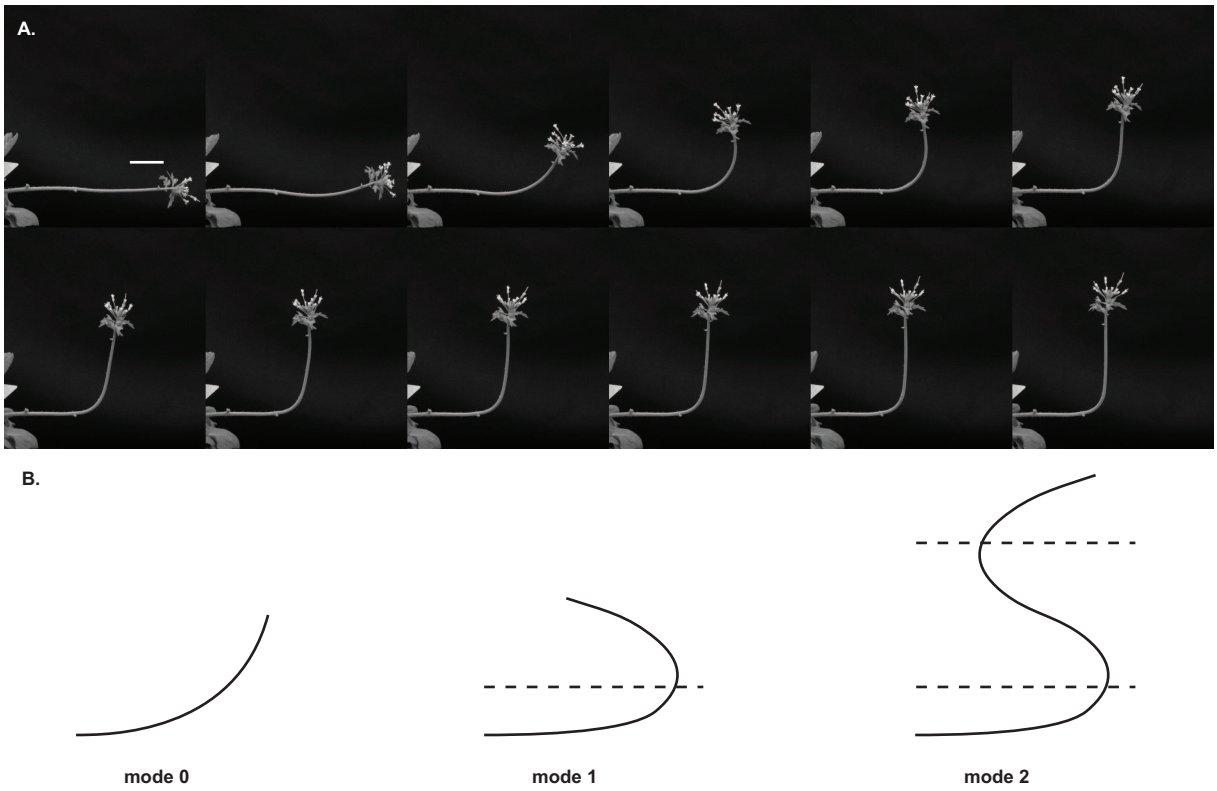

Fig. 5. A.Timelapse photographs of a tilting experiment on the inflorescence of *Arabidopsis thaliana* taken at 2- hour intervals. The apical part overshoots the vertical once 8 hours after tilting (4th image, C-shape). The white bar is 1 cm long. B.Quantification of the transient modes of the gravitropic movement. Mode M is the maximal number of places in which the tangent to central line of the organ crosses the vertical simultaneously. The curved line represents the gravitropic organ and the dashed lines represent different modes. No dashed line, mode 0 or J-shape; one dashed line, mode 1 or C shape; 2 dashed lines, mode 2 or S shape.

2.6 Quantitative Assessment and Statistical Fit.. The analytical expression for the angle A_{ac} of the *AC* model [10] was fitted to the experimental angle-space mapping numerically through a non linear optimization algorithm combining steepest gradient with random sampling of the parameter space (to avoid local minima), using the bending number estimated from the morphometric method as a starting value. The comparison between the measured angle dynamics $A_{exp}(s,t)$ and that predicted by the *AC* model $A_{ac}(s,t)$ was based on orthogonal functional linear regression, since the model prediction can also display random errors through the estimation of B (S4).

3. Detailed kinematics experiments and quantitative assessment of the AC model.

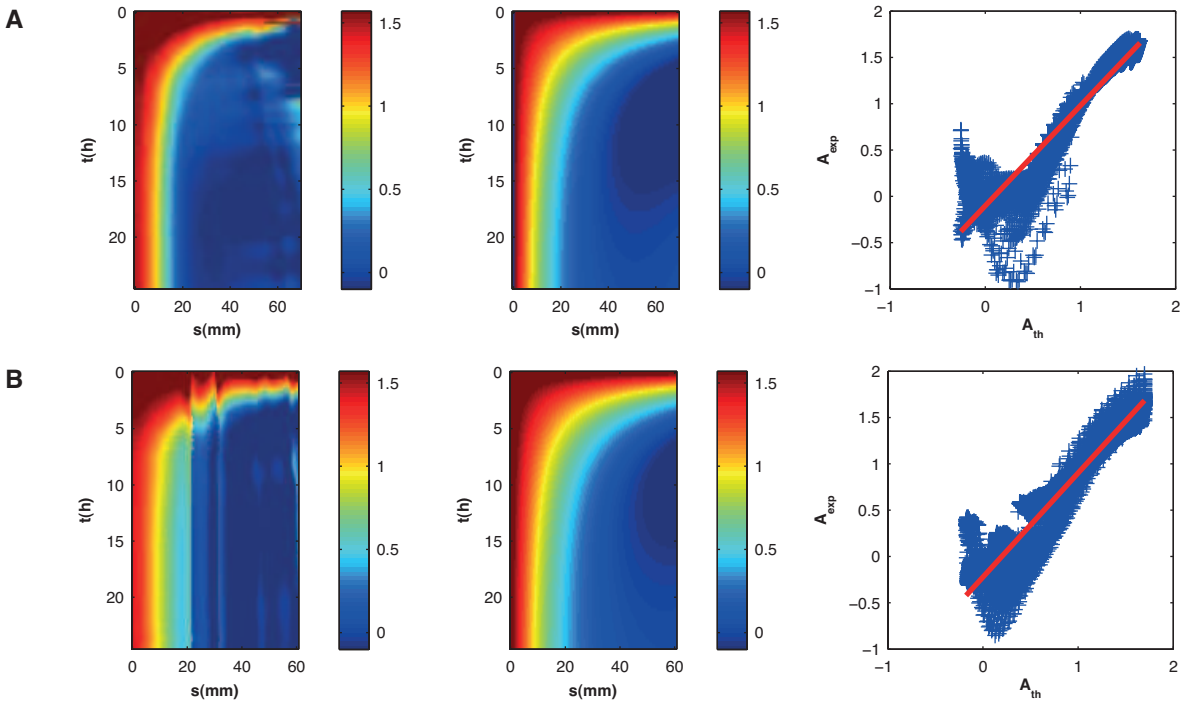

Fig. 6. Quantitative comparison between experimental (exp) and predicted angle spacetime map of A(s, t) in *Arabidopsis thaliana* inflorescence for the entire gravitropic response of two different individuals A and B. Experimental angle space-time map of $A_{exp}(s,t)$ (left panels), the angle space-time map predicted by the AC model $A_{th}(s,t)$ (middle panels) and quantitative validation plot of $A_{exp}(s,t)$ vs $A_{th}(s,t)$ (right panels). A. Orthogonal linear fit slope 1.14, intercept -0.067, R2 = 0.90. B. Orthogonal linear fit slope 1.17, intercept 0.017, R2 = 0.95.

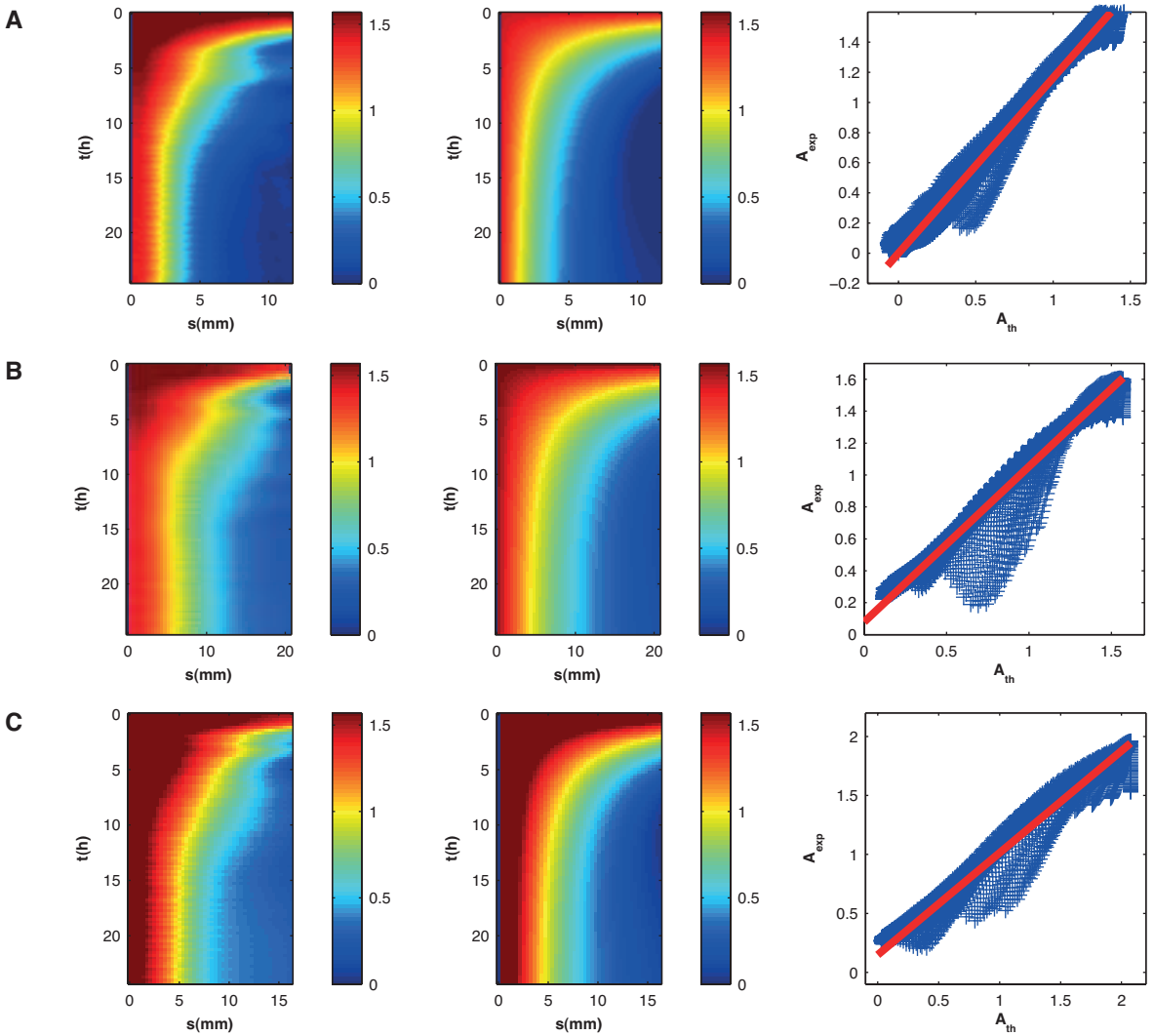

Fig. 7. Quantitative comparison between experimental (exp)and predicted (th) angle spacetime map of A(s, t) in wheat coleoptile for the entire gravitropic reponse of three different individuals A, B and C. Experimental angle spacetime map of $A_{exp}(s,t)$ (right panels), angle spacetime map predicted by the AC model $A_{th}(s,t)$ (middle panels) and quantitative validation plot $A_{exp}(s,t)$ vs $A_{th}(s,t)$ (right panels). A. Orthogonal linear fit slope 1.16, intercept 0.0003, R2 = 0.97. B. Orthogonal linear fit slope 0.97, intercept 0.078, R2 = 0.96. C. Orthogonal linear fit slope 0.88, intercept 0.15, R2 = 0.96.

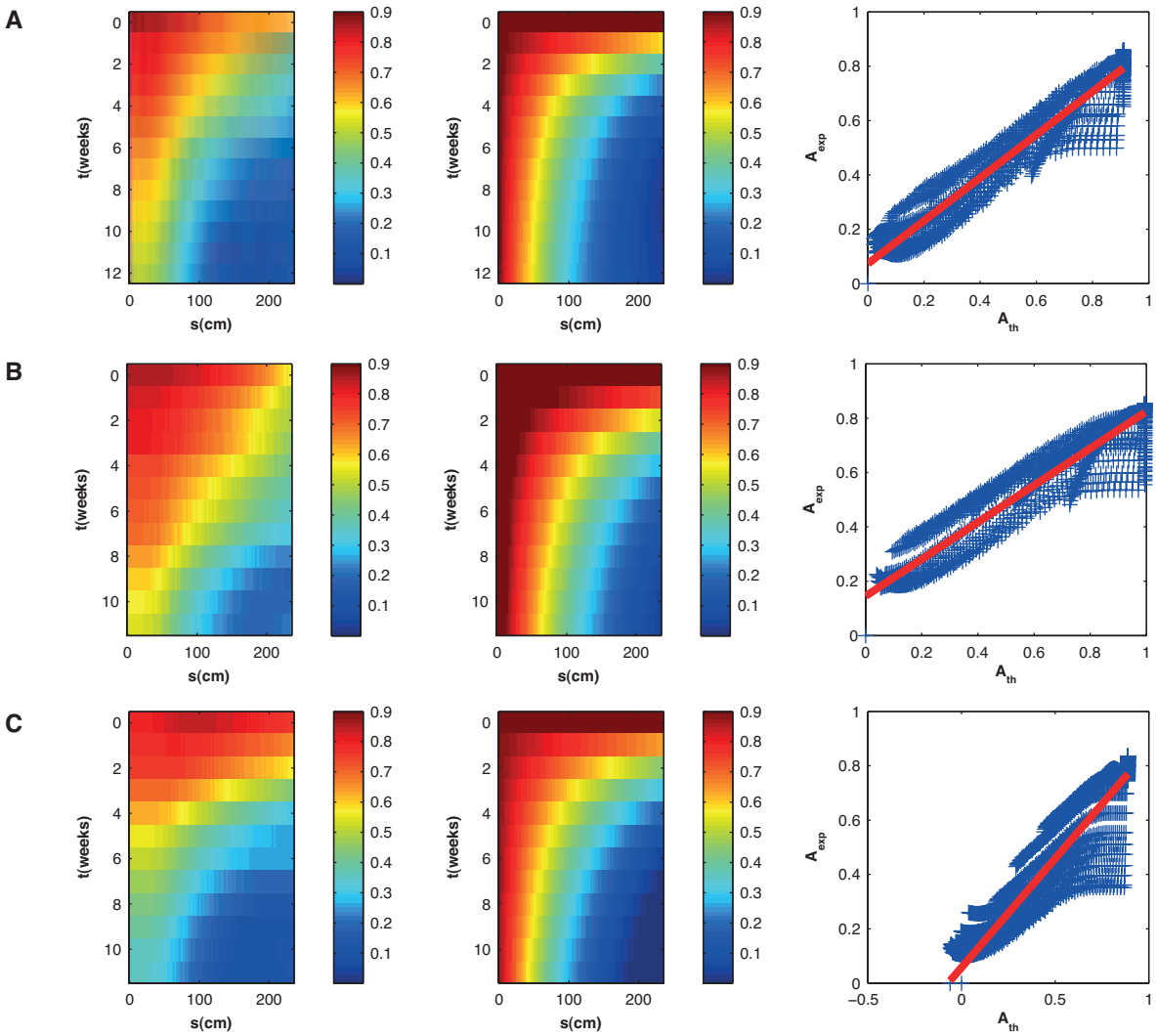

Fig. 8. Quantitative comparison between experimental (exp)and predicted (th) angle spacetime map of A(s, t) in poplar trunk for the whole straightening dynamics of three individuals A, B and C. Experimental angle spacetime map of $A_{exp}(s,t)$ (left panels), angle spacetime map predicted by the ACmodel $A_{th}(s,t)$ (middle panels) and quantitative validation plot $A_{exp}(s,t)$ vs $A_{th}(s,t)$ (right panels). A. Orthogonal linear fit slope 0.90, Intercept 0.037, R2=0.91, B. Orthogonal linear fit slope 0.88, Intercept 0.10, R2=0.86 and C. Orthogonal linear fit slope 0.80, Intercept 0.058, R2=0.80.

1. **Silk WK, Erickson RO (1978) Kinematics of hypocotyl curvature. *Am J Bot* 65(3):310-319.**

2. **Bastien R, Moulia B, Douady S, Bohr T (2012) Analytical Solution of the Proprio-Graviceptive equation for shoot gravitropism of plants arXiv:1210.3480 [q-bio.TO]**

3. **The Angiosperm Phylogeny Group (2003) An update of the angiosperm phylogeny group classification for the orders and families of flowering plants: Apg ii. *Botanical Journal of the Linnean Society* 141(4):399-436.**

4. **Dagnelie, P (2006) *Statistique théorique et appliquée. Tome 2. Inférence statistique à une et à deux dimensions* (2nd ed). De Boeck et Larcier, Brussels, Belgium. French**

Analytical Solution of the Proprio-Graviceptive equation for shoot gravitropism of plants.

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We derive the analytical solutions to the second order generalised gravi-proprioceptive equation given in our recent paper [1]. These equations show how plants adjust to the surrounding gravitation field and highlight the fact that the plant must be able to not only sense its local posture with respect to the gravitational field, but also to sense its own local curvature. In [1] we obtained explicit analytical solutions of these equations in terms of (sums of) Bessel functions, and in the present paper we derive these solutions.

arXiv:1210.3480v1 [q-bio.TO] 12 Oct 2012

Gravitropism is a slow movement by which plants reorient their growth in response to gravity. In a recent paper [1], we have studied the gravitropic response of a broad range of plants by placing them horizontally in a dark room and monitoring how they curve upwards in response to gravity. It was shown that the minimal dynamical model accounting for these observations is not the usual gravisensing law, where the plant simply senses the local tilt angle, but what we have called a *gravi-proprioceptive* law, where one takes into account that the plant can, in addition, sense its own local curvature. In that paper, exact solutions for the linearized versions of both the graviceptive and the gravi-proprioceptive law were given and compared to experiment. We here give the derivation of these solutions

The plant is described as a slender rod with arc length s going from $s = 0$ at the base to $s = L$ at the tip. The local tilt angle $A(s,t)$ describes the orientation with respect to the vertical gravitational field, such that $A = 0$ is vertical. The generalized (gravi-proprioceptive) law of gravitropism describes how the local curvature $C(s,t))$ changes in response to the local tilt angle *and* the local curvature itself as

$$\frac{\partial C(s,t)}{\partial t} = -\beta A(s,t) - \gamma C(s,t), \tag{1}$$

where the curvature and the tilt angle are related by

$$C(s,t) = \frac{\partial A(s,t)}{\partial s}, \tag{2}$$

and where the coefficient β controls the graviceptive term (sensing of tilt angle) and the coefficient γ controls the gravi-proprioceptive term (sensing the curvature).

The subject of the present paper is to solve this equation with the experimentally relevant boundary and initial condition. Thus we assume that the plant is initially straight with an angle, say A_i from the vertical. Since (1) is *linear* in A, we can, without loss of generality, take $A_i = 1$. The solution with a different A_i will simply be obtained by multiplying our solution by A_i.Thus we assume the initial conditions

$$A(s, t = 0) = 1 \tag{3}$$

and

$$C(s, t = 0) = \frac{\partial A(s, t = 0)}{\partial s} = 0 \tag{4}$$

for all $0 < s < L$. Further we assume that the plant is *clamped* in the sense that tilt angle at the base remains equal to $A_i = 1$ for all future times. Thus the boundary condition is

$$A(s = 0, t) = 1 \tag{5}$$

for all $t \geq 0$

I. THE GRAVICEPTIVE MODEL

We first consider the purely graviceptive model, i.e., (1) with $\gamma = 0$:

$$\frac{\partial C(s,t)}{\partial t} = -\beta A(s,t) \tag{6}$$

To solve this equation, we first set $\beta = 1$ with out loss of generality simply by using the scaled time βt. Now, using that

$$C(s,t) = \frac{\partial A(s,t)}{\partial s} \tag{7}$$

we can write (6) as

$$\frac{\partial^2 A(s,t)}{\partial s \partial t} = \partial^2_{st} A = -A \tag{8}$$

where we use the short hand notation $\partial/\partial x = \partial_x$. Note that C satisfies the same equation.

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A. Solution by separation

We shall now try to find separated solutions of (8). From our numerical work it seems that the solutions depend on $\sqrt{s}$ and $\sqrt{t}$ and since both s and t are assumed positive, we can introduce the new independent variables (ξ, η) as

$$\xi = (s\,t)^{1/2} \quad \text{and} \quad \eta = \left(\frac{t}{s}\right)^{1/2} \tag{9}$$

or

$$s = \frac{\xi}{\eta} \quad \text{and} \quad t = \xi\eta \tag{10}$$

and obtain

$$\partial_s = (\partial_s\xi)\,\partial_\xi + (\partial_s\eta)\,\partial_\eta = \frac{1}{2}\eta\,\partial_\xi - \frac{1}{2}\eta^2\xi^{-1}\,\partial_\eta \tag{11}$$

$$\partial_t = (\partial_t\xi)\,\partial_\xi + (\partial_t\eta)\,\partial_\eta = \frac{1}{2}\eta^{-1}\,\partial_\xi + \frac{1}{2}\xi^{-1}\,\partial_\eta \tag{12}$$

Using this, we find

$$\partial^2_{st} = \frac{1}{4\xi^2}\left(\xi^2\partial^2_{\xi\xi} + \xi\partial_\xi - \eta\partial_\eta + \eta^2\partial^2_{\eta\eta}\right) \tag{13}$$

Note that the $\partial^2_{\xi\eta}$ cancel and that the invariance of (6) on exchanging s and t implies an invariance when $\eta \to \eta^{-1}$. In these variables, (8) for an arbitrary function Ψ can be written

$$\left(\xi^2\partial^2_{\xi\xi} + \xi\partial_\xi - \eta\partial_\eta + \eta^2\partial^2_{\eta\eta} + 4\xi^2\right)\Psi(\xi,\eta) = 0 \tag{14}$$

If we now assume that the solution can be written in the separated form

$$\Psi(\xi,\eta) = f(\eta)g(\xi) \tag{15}$$

we get the two eigenvalue equations

$$\xi^2 g''(\xi) + \xi\,g'(\xi) + 4\xi^2 g(\xi) = \lambda\,g(\xi) \tag{16}$$

$$\eta^2 f''(\eta) - \eta f'(\eta) = -\lambda\,f(\eta) \tag{17}$$

Substituting $y = \log\eta$ gives (17) the form

$$f''(y) - 2f'(y) + \lambda\,f(y) = 0 \tag{18}$$

with solutions

$$f(y) = e^{p\,y} = \eta^p \tag{19}$$

with

$$p^2 - 2p + \lambda = 0 \tag{20}$$

or

$$p = \left(1 \pm \sqrt{1-\lambda}\right)\Big) \tag{21}$$

and then (16) becomes

$$\xi^2 g''(\xi) + \xi\,g'(\xi) + \left(4\xi^2 - p(2-p)\right)g(\xi) = 0 \tag{22}$$

If we finally substitute $x = 2\xi$, this becomes

$$x^2 g''(x) + x\,g'(x) + \left(x^2 - p(2-p)\right)g(x) = 0 \tag{23}$$

which is recognised as Bessel's equation of order n, where $n^2 = p(2-p)$. For n to be a real number we must restrict p to lie in the interval $p \in [0,2]$. In this interval we can write the full solution as

$$\Psi_n(s,t) = K\left(\frac{t}{s}\right)^{p/2} J_n(2\sqrt{s\,t}) \tag{24}$$

If n is to be an integer we must choose $p = 0$, 1 or 2 giving $n = 0$, 1 and 0, respectively. To find a solution for A, we must satisfy the boundary condition $A(s \to 0, t) = A(s, t \to 0) = 1$ and since

$$\left(\frac{t}{s}\right)^{p/2} J_n(2\sqrt{st}) \to s^{(n-p)/2}t^{(n+p)/2} \tag{25}$$

for small $s\,t$, we must choose $n = p = 0$, i.e.,

$$A(\xi,\eta) = J_0(2\xi) \tag{26}$$

or, returning to the variables s and t and re-inserting β,

$$A(s,t) = J_0(2\sqrt{\beta s\,t}) \tag{27}$$

We can also find the curvature

$$C(s,t) = \partial_s A(s,t) = \sqrt{\frac{\beta t}{s}}J_1\left(2\sqrt{\beta t s}\right) \tag{28}$$

which, since C also satisfies (8), also has the form (24). For small s, the s-dependence cancels since $J_1(x) \approx x/2$ for small x, and we get

$$C(s,t) \to \beta t \tag{29}$$

for small s or t and thus $C(s, t \to 0) = 0$ as we demanded.

B. Solution by Laplace transformation

We could have solved (8) more directly Laplace transforming is (in s), which gives

$$p\partial_t\hat{A} - \partial_t A(s=0,t) = -\beta\hat{A}, \tag{30}$$

where

$$\hat{A}(p,t) = \int_0^\infty A(s,t)e^{-ps}ds \tag{31}$$

is the Laplace transform of $A(s,t)$. From the boundary condition (5) we get $\partial_t A(s=0,t) = 0$ and

$$\partial_t\hat{A} = -\frac{\beta}{p}\hat{A}, \tag{32}$$

which has to be solved with the initial condition $A(s, t = 0) = 1 \Rightarrow A(p, \hat{t} = 0) = 1/p$ with the solution

$$\hat{A} = \frac{1}{p}e^{-\frac{\beta t}{p}}$$

We see that $\hat{A}(p,t)$ is analytic in the complex p-plane except at the isolated (essential) singularity $p=0$. The inverse Laplace transform $A(s,t)$ can simply be found as the residue (see e.g. [2] Theorem 8.2.1)

$$A(s,t) = \frac{1}{2\pi i}\oint_{C(0,\epsilon)} \frac{e^{sp-\frac{\beta t}{p}}}{p} dp = J_0(2\sqrt{\beta s t}) \tag{33}$$

where the last equality is a special case of the well-known identity derived e.g. in [3]:

$$F_n(s,t) = \frac{1}{2\pi i}\oint_{\Omega(0,\epsilon)} \frac{e^{ps-\frac{t}{p}}}{p^{n+1}} dp = \left(\frac{s}{t}\right)^{n/2} J_n(2\sqrt{st}\,) \tag{34}$$

valid for any $n > -1$.

II. THE PROPRIO-GRAVICEPTIVE MODEL

We now consider the generalised equation of gravitropism

$$\partial_t C(s,t) = -\beta A(s,t) - \gamma C(s,t) \tag{35}$$

and with scaled time $T = \gamma t$ and $S = (\beta/\gamma)s$ we obtain

$$\partial^2_{ST} A = -A - \partial_S A \tag{36}$$

In the following we drop the capitals and our equation becomes

$$\partial^2_{st} A = -A - \partial_s A \tag{37}$$

again with the initial conditions (3) and (4) and the clamped boundary condition (5).

Note that (37) has that stationary (asymptotic) solution

$$A_0(s) = e^{-s} \tag{38}$$

satisfying the boundary conditions 3 and 4. One might try the substitution $A(s,t) = B(s,t)e^{-t}$, since the equation for B would simply be (6). However, the boundary condition (5) would be $B(s=0,t) = e^t$ which is time dependent and complicates matters.

The Laplace transform is

$$\hat{A}(p,t) = \int_0^\infty A(s,t)e^{-ps} ds \tag{39}$$

and the Laplace transform of 37 (with $\gamma = \beta = 1$) gives

$$p\partial_t \hat{A} - \partial_t A(s=0,t) = -\hat{A} - (p\hat{A} - A(s=0,t)) \tag{40}$$

From the boundary condition, we know that $A(s=0,t)$ is constant in time and thus $\partial_t A(s=0,t) = 0$. Also $A(s=0,t) = 1$ so we obtain

$$p\partial_t \hat{A} = -\hat{A} - p\hat{A} + 1 \tag{41}$$

or

$$\partial_t \hat{A} + \frac{1+p}{p}\hat{A} = \frac{1}{p} \tag{42}$$

with the solution

$$\begin{aligned}\hat{A} &= \frac{1}{1+p} + \frac{1}{p(1+p)} e^{-\frac{1+p}{p}t} \\ &= \frac{1}{1+p} + \left(\frac{1}{p} - \frac{1}{1+p}\right) e^{-t}e^{-\frac{t}{p}} \\ &= \frac{1}{p}e^{-t}e^{-\frac{t}{p}} + \frac{1}{1+p}\left(1 - e^{-t}e^{-\frac{t}{p}}\right),\end{aligned} \tag{43}$$

where $\hat{A}(p, t=0) = 1/p$ in accordance with the boundary condition. It correctly approaches the stationary state since

$$\hat{A}(p,t) \to \frac{1}{1+p} = \hat{A}_0 \tag{44}$$

for $t \to \infty$ when $p > 0$ and $\hat{A}(p,t)$ is analytic in the complex p-plane except at the isolated singularities $p = 0$ and $p = -1$.

Thus the inverse Laplace transform $A(s,t)$ is simply the sum of the residues [2] of the function

$$\begin{aligned}A(s,t) = \sum_{\text{singularities p}^*} \frac{1}{2\pi i}\oint_{\Omega(p^*,\epsilon)} e^{ps}\left(\frac{1}{p}e^{-t}e^{-\frac{t}{p}}\right. \\ \left. + \frac{1}{1+p}\left(1 - e^{-t}e^{-\frac{t}{p}}\right)\right)\end{aligned} \tag{45}$$

at each of its singularities in the complex p-plane. The pole at $p = -1$ is a simple pole, but the residue is zero since the numerator $1 - e^{-t}e^{-\frac{t}{p}}$ is zero for $p = -1$. We therefore only need the residue at $p = 0$, which is an essential singularity. Thus we have to evaluate the contour integral of $e^{ps}\hat{A}(p,t)$ over a closed curve $\Omega(0,\epsilon)$ encircling the origin. The contribution of the term $e^{ps}/(1+p)$ vanishes, since it has no pole at $p = 0$, and we can write

$$A(s,t) = A_1(s,t) + A_2(s,t), \tag{46}$$

where

$$A_1(s,t) = \frac{e^{-t}}{2\pi i}\oint_{\Omega(0,\epsilon)} \frac{e^{sp-\frac{t}{p}}}{p} dp \tag{47}$$

and

$$A_2(s,t) = -\frac{e^{-t}}{2\pi i}\oint_{\Omega(0,\epsilon)} \frac{e^{sp-\frac{t}{p}}}{1+p} dp, \tag{48}$$

where first term is given by (33)

$$A_1(s,t) = e^{-t} J_0(2\sqrt{st}\,). \tag{49}$$

Near the origin (more precisely, as long as $\mid p \mid < 1$) we can expand

$$\frac{1}{1+p} = 1 - p + p^2 \ldots = \sum_{n=0}^{\infty} (-p)^n \tag{50}$$

so that

$$A_2(s,t) = -\frac{e^{-t}}{2\pi i}\sum_{n=0}^{\infty} \quad \oint_{\Omega(0,\epsilon)} e^{sp-\frac{t}{p}}(-p)^n dp$$
$$= e^{-t}\sum_{n=0}^{\infty} T_n(s,t), \qquad (51)$$

where

$$T_n(s,t) = -\frac{1}{2\pi i}\oint_{\Omega(0,\epsilon)} e^{sp-\frac{t}{p}}(-p)^n dp. \qquad (52)$$

We define $z = -1/p$ and thus $dp = dz/z^2$, whereby

$$T_n(s,t) = \frac{1}{2\pi i}\oint_{\Omega(0,\epsilon)} e^{tz-\frac{s}{z}} z^{-(n+2)} dz$$
$$= \left(\frac{t}{s}\right)^{\frac{n+1}{2}} J_{n+1}(2\sqrt{st}\,) \qquad (53)$$

for any $n > 0$. Note the sign change since the contour Ω is now traversed in the *clockwise* direction. Thus we can write

$$A_2(s,t) = e^{-t}\sum_{m=0}^{\infty}\left(\frac{t}{s}\right)^{\frac{m+1}{2}} J_{m+1}(2\sqrt{st}\,)$$
$$= e^{-t}\sum_{n=1}^{\infty}\left(\frac{t}{s}\right)^{\frac{n}{2}} J_n(2\sqrt{st}\,) \qquad (54)$$

and the full solution is

$$A(s,t) = e^{-t}\sum_{m=0}^{\infty}\left(\frac{t}{s}\right)^{\frac{n}{2}} J_n(2\sqrt{st}\,)$$
$$= e^{-s} - \sum_{n=1}^{\infty}(-1)^n\left(\frac{s}{t}\right)^{n/2} J_n(2\sqrt{st}\,) \qquad (55)$$

which, going back to the original variables using $t \to \gamma t$ and $s \to (\beta/\gamma)s$ gives

$$A(s,t) = e^{-\gamma t}\sum_{m=0}^{\infty}\left(\frac{\gamma^2 t}{\beta s}\right)^{\frac{n}{2}} J_n(2\sqrt{\beta st}\,)$$
$$= e^{-\beta s/\gamma} - \sum_{n=1}^{\infty}(-1)^n\left(\frac{\beta s}{\gamma^2 t}\right)^{n/2} J_n(2\sqrt{\beta st}\,) \qquad (56)$$

If the initial angle is A_i, we get the same solution, but with the factor A_i multiplying the solution (56).

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Beyond the sine law of plant gravitropism

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The great German plant physiologist Wilhelm Pfeffer rightly claimed that "no plant is entirely without the power of movement" (1). If this fact remains underappreciated, it is perhaps because plant movements typically unfold over minutes, hours, or days, and thus exceed the attention span of all but the most dedicated observer. Among the large array of plant movements, the tropisms—that is, those movements that are directed toward or away from an external stimulus such as gravity or light—are the most fascinating because they highlight beautifully the sentient nature of plants and the goal-directedness of their growth habit. The pervasiveness of plant tropisms is revealed when one stops to consider the unlikeliness that seeds lodged haphazardly within the crevices of a rugged terrain should sprout stems that reliably find their way up. Were it not for the ability of the young plants to sense light and gravity, forests would be impenetrable tangles of stems and branches growing in all directions. Their prevalence in the plant kingdom explains why tropisms have been an active area of research since the beginning of the 19th century. By the end of the 19th century, the field had reached such a level of development and popularity that eminent biologists, including Charles Darwin and Pfeffer, could devote entire books to the topic (1, 2). Given this long and illustrious tradition of research, one might expect today's biologists to have extracted all useful information from standard observational research of plant tropisms. A paper published in PNAS should convince the readers that much can still be learned from careful, quantitative observation of biological processes. In a systematic study of shoot gravitropism in 11 taxa, Bastien et al. (3) at once establish the universal response to gravity as a process of initial stem curving followed by apical straightening and debunk the idea that current models of gravitropism offer a plausible explanation for the process.

The standard model of gravitropism can be traced back to Julius Sachs, who stated that the component of gravity acting at right angle to a plant axis (a stem or root) determines the strength of the stimulus (4). Accordingly, the gravitropic response should be proportional to the sine of the angle between the organ axis and the vertical; thus, a stem placed horizontally would show the strongest response, which would then gradually decline as the stem approaches the vertical. Since its formulation, Sachs' sine law has been validated repeatedly, sometimes with minor modifications (5, 6). It was also noted that the sedimentation of statoliths within gravisensing cells would lead to some form of sinusoidal dependence on angle (7, 8). Thus, the sine law, despite its simplicity, offered a good fit of overall plant response to gravity and even enjoyed some level of mechanistic justification in the sedimentation pattern of statoliths.

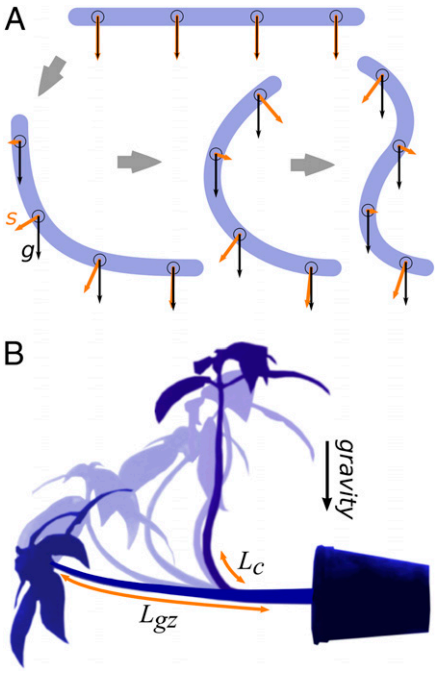

Fig. 1. Shoot gravitropism beyond the sine law. (*A*) Diagrams of a stem responding to gravity according to the sine law. Sensing and curving are distributed over the entire length of the stem. The orange arrows indicate the component of the gravity vector (*g*) that serves as the effective bending stimulus (*s*). The stem repeatedly overshoots the vertical because the basal part of the stem is still receiving a strong stimulus and is therefore actively curving even as the apical part approaches the vertical. (*B*) The gravitropic response of *Impatiens glandulifera* sketched from Pfeffer's original photographs. This plant is a prime example of a gravitropic response with a large bending number ($B \sim 9$). It overshoots the vertical twice, thus forming first a "C" and then a "S" shape, but ultimately converges on a stable configuration whereby a large section of the stem is straight. The first two time points of the response highlight the development of curvature over the extensive growth zone (L_{gz}), whereas the last time point shows the curvature converging ultimately to a much shorter length scale (L_c). The rapid convergence to an erect configuration is indicative of the stabilizing effect of autotropic straightening in gravitropic responses.

The shortcomings of the sine law surface when one attempts to build a regulatory model out of it. To develop such a model, one must ask where gravity is sensed and how the sensing elements respond to a gravitropic stimulus. In the case of the root, gravity sensing is limited to the columella cells of the root cap (9, 10). The signal is then transmitted to the elongation zone via a redistribution of auxin flow (11, 12). The stem, however, shows a notable difference from the root. Experimental evidence indicates that the entire stem senses gravity and can responds to it locally (13, 14) whereas the apex itself appears to play no particular role, since decapitated plants respond normally to gravity (15). As Bastien et al. (3) clearly show, a stem whose distributed gravisensing elements react to gravistimulation according to the sine law would zigzag about the vertical repeatedly without ever reaching a stable configuration. This response arises because the basal elements of the stem keep responding to gravity and, therefore, keep curving upward long after the apical region of the stem has reached the vertical. As a result of the sustained curving of the basal elements, the stem apex overshoots its target repeatedly (Fig. 1*A*). Moreover, the apical straightening that is an integral part of the gravitropic response of stems is never fully achieved in a model based on the sine law. It thus appears that a crucial element is missing from the standard model of gravitropism.

The solution put forward by Bastien et al. (3) implicates a form of plant proprioception called autotropism. Autotropism is the Newton's first law of plant tropisms; that is, in the absence of external stimuli, plant organs maintain straight growth. Thus, elongating stem segments that are not receiving a gravitropic stimulus telling them to bend would naturally straighten under their internal autotropic response. Autotropism was already known to Pfeffer and his contemporaries (1), and the counteracting role it plays with gravitropic curving has also been included in models (16, 17). Despite these precursors, the model put forward by Bastien et al. (3)

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distinguishes itself by its simplicity and elegance—it is, in fact, the minimal model compatible with the two opposing "forces" of gravitropic bending and autotropic straightening.

Unlike models based solely on Sachs' sine law, the gravitropic/autotropic model put forward by the authors explains why the universal gravitropic response in plant stems proceeds from an initial overall bending of the stem followed by basipetal straightening (3, 18). As shown in their paper (3), a stem placed horizontally will rapidly converge to a steady-state solution where the stem angle (A) decreases exponentially over the length (L_{gz}) of the growth zone:

$$A(s) = \frac{\pi}{2}\exp(s/L_c) \text{ for } 0 \le s \le L_{gz}$$

In this equation, L_c is the length scale over which the stem angle changes when the plant has completed its response to gravity. L_c is set by the relative strength of the gravitropic (bending) and the autotropic (straightening) responses. If the gravitropic response dominates, L_c is small, indicating that the stem angle changes over a short distance, thus imposing a high local curvature. In contrast, a large L_c indicates a dominant autotropic reaction, which prevents the development of strong curvature at any point along the stem.

The major breakthrough of this work is the conclusion that the two lengths L_{gz} and L_c govern the entire gravitropic response of a plant. The authors define a nondimensional bending number B as L_{gz}/L_c. This ratio captures explicitly the spatial aspect of the gravitropic response (i.e., it is the ratio of two important lengths in the system), but it also, implicitly, captures a temporal feature of the gravitropic response because the length of the growth zone (L_{gz}) is the initial distance over which the curvature is observed, and L_c is the final distance over which the stem will be curved when the gravitropic response has been completed (Fig. 1*B*). It is the implicit temporal component of the bending number that makes it a useful metric of gravitropic responses in plants. For a plant to show an effective rectifying response to gravity, it will need a zone of curvature production (i.e., growth zone) at least as long as the intrinsic length scale (L_c) set by the internal balance of gravitropic and autotropic reactions. In other words, bending numbers are typically greater than 1. For B values close to 1, the length of the growth zone is comparable to the length over which curvature will be present when the gravitropic response has been completed. Therefore, the stem approaches the vertical smoothly without overshooting. For large B values, the length of the growth zone greatly exceeds the region of final curvature. As a result, curvature will initially develop over a large region of the stem before converging to a smaller region. In the convergence process, the stem will zigzag around the vertical, forming first a "C" shape and possibly a "S" shape. The largest B value recorded so far, approximately 9, is for the *Impatiens* plant studied by Pfeffer himself (Fig. 1*B*). An infinite B is obtained if the gravitropic curving overpowers the autotropic straightening. In this case, we recover the sine law model and the plant never really settles into a steady-state vertical position.

Future research will have to include autotropic straightening as an integral part of shoot gravitropism.

The beauty of the bending number resides in the fact that it can be measured directly from images taken early and late in the response of gravitropically stimulated plants (Fig. 1*B*). Simple length measurements performed on these two endpoints can tell us everything that has occurred in the intervening time. Overall, the study of Bastien et al. (3) offers an exquisite example of the power of quantitative observations even in the context of a century-old problem such as gravitropism. Future research will have to include autotropic straightening as an integral part of shoot gravitropism.

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