Spatio-temporal kinematic analysis of shoot gravitropism in Arabidopsis thaliana

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Abstract Plant shoots can bend upward against gravity, a behavior known as shoot gravitropism. The conventional quantification of shoot bending has been restricted to measurements of shoot tip angle, which cannot fully describe the spatio-temporal bending process. Recently, however, advanced imaging analyses have been developed to quantitatively analyze the spatio-temporal changes in inclination angle and curvature of the shoot. We used one such method (KymoRod) to analyze the gravitropism of the Arabidopsis thaliana inflorescence stem, and successfully extracted characteristics that capture when and where bending occurs. Furthermore, we implemented an elastic spring theoretical model and successfully determined best fitted parameters that may explain typical bending behaviors of the inflorescence stem. Overall, we propose a data-model combined framework to quantitatively investigate shoot gravitropism in plants.

Key words: kinematics, mathematical model, proprioception, shoot gravitropism.

Introduction

Plants have a survival mechanism called shoot gravitropism, in which their shoots turn upward against gravity to effectively capture sunlight. In a broad sense, shoot gravitropism is thought to consist of a sensor and an actuator in plants; first, gravity is sensed by statocytes, then the signal is propagated to actuate the differential cell growth that causes upward bending. Previous studies on shoot gravitropism have mainly focused on its genetics and physiology, especially on the molecular mechanism of the gravitational sensor that triggers the whole process. Accordingly, genetic screening for mutants with abnormal shoot tip angles after bending has identified many important genes involved in shoot gravitropism in Arabidopsis thaliana (Morita and Tasaka 2004; Moulia and Fournier 2009). However, measurement of tip angle alone cannot fully describe the spatio-temporal bending process of a filament-shaped structure such as a shoot (Moulia and Fournier 2009). For example, it is possible that the tip angles of an S-shaped shoot and an I-shaped shoot could be the same if the tips are inclined in exactly the same direction. Furthermore, as bending occurs non-uniformly along the stem, spatio-temporal measurements may reveal significant biological events that occur after the initial response to gravitational sensing. Such measurements would require extraction of the spatio-temporal kinematics of every small segment of the shoot, for which some analytical tools have been proposed (Bastien et al. 2016; Basu et al. 2007).

In addition to such data-analytical approaches, theoretical approaches have also been used to mathematically characterize shoot gravitropism (Bastien et al. 2013, 2014; Chelakkott and Mahadevan 2017). In these studies, the filament structure (e.g., stem) is considered to be a continuous material in which elastic springs are connected, and the bending event can be described by the evolutional equation of length and curvature of the filament (Bastien et al. 2013, 2014). A major advantage of a theoretical approach is that mechanical parameters can be systematically changed to predict what happens with the filament-shaped material. Previous studies (Chelakkott and Mahadevan 2017) were able to characterize various types of bending processes by changing the dimensionless parameters that indicate the bending strength and the balance between growth, elasticity, and gravity (Chelakkott and Mahadevan 2017;...
Moula et al. 2019). Thus, the theoretical model might explain mechanical aspects of shoot gravitropism that cannot be observed in experiments. To reach such a novel mechanical understanding, however, it remains unclear how to reconcile theory and data.

In this report, we combined two different techniques—data-analytical and model-analytical—to study shoot gravitropism. First, we used the recently developed kinematic tool KymoRod (Bastien et al. 2016) to characterize the spatio-temporal inclination angle and bending curvature of the Arabidopsis inflorescence stem. Second, we reconstructed the elastic spring model which has a potential to explain actual bending events of stems. Overall, we emphasize that data-model combined approach is a powerful strategy for gaining a quantitative understanding of shoot gravitropism.

Materials and methods

Plant materials and growth conditions

Wild-type Arabidopsis thaliana (Columbia strain) was used for all analyses. The seeds were surface-sterilized in a solution containing 20% (v/v) sodium hypochlorite (nacalai tesque) and 0.1% (w/v) Triton-X (nacalai tesque), and sown on Murashige and Skoog (MS) medium with 0.6% gellan gum (Wako) containing 1% (w/v) sucrose (pH 5.7). The plates were incubated at 4°C in darkness for 2–3 days and transferred to a growth chamber under continuous light at 22°C in darkness for 2–3 days and transferred to a growth chamber at 22°C. After growth on plates for 14 days, the plants were transferred to soil, and cultured in a growth chamber at 22°C under a 16-h-light photoperiod for 16 days.

Induction of stem bending and time lapse imaging

For the stem bending test, we selected ~5 cm-long inflorescence stems in 30-day-old plants. The inflorescence stems were cut off, and incubated with liquid MS medium for 15 h under continuous light at 22°C. Subsequently, the stems were incubated for 1 h under dark conditions, and then all branches and leaves other than the flowers at the tip were removed. The stems were immediately placed in the horizontal direction into the imaging incubator. The insides of the imaging incubator were lined with light-blocking plastic plates and cheesecloth. The images of stems were taken with a digital camera (PowerShot SX60 HS, Canon) supplied with remote shutter release control (Canon RS-60E3/PENTAX CS-205, Rowa Japan) every 10 min for 6 h. The direction of gravity was detected by the index, in which the sinker was hung by the strings.

Image J and Matlab protocol

—Image J protocol

  - Crop using “Image/Crop”, and save using “File/save as/tiff format”
  - Copy using “Image/Duplicate”

— Matlab protocol

  · Make the image binary using “Image/Type/8 bit”
  · Remove background using “Image/Adjust/AutoThreshold”
  · Try all the threshold methods using ”Image/Adjust/AutoThreshold”, ”Try All”
  · Select one of all the trials and binarize the image with it
  · Select ”Wand (tracing) tool” and type the position of the stem in the image
  · Open ROI Manager using ”Analyze/tools/ROI Manager”
  · Add ROI of the stem for each image
  · Redraw the ROI to the original non-binary image
  · Remove the background using ”Edit/Clear Outside”
  — KymoRod protocol

  · start MATLAB
  · Install and select Kymorod in ”Application”
  · Select one JPEG image using ”Start new analysis”, and ”Choose image directly”
  · Select green using ”Color Image Channel”
  · Keep all Frames using ”Validate Selection”
  · Select ”Max Entropy” for the threshold method
  · ”Validate Threshold”
  · Select a smoothing factor of 20
  · Skeletonization with ”left” and ”update all the skeleton”
  · Curvature options remain default
  · ”Validate the Skeleton”
  · ”Compute Elongation”

Mathematical modeling

The mathematical model in this study is based on the previously reported mechanical model (Chelakkot and Mahadevan 2017). We assume that the centerline \([x(s,t), y(s,t)]\) of the shoot is determined by time \(t\) and the arc length \(s \in [0, L(t)]\). Here the total shoot length dependent on time is denoted by \(L(t)\) with \(L(0) = L_0\). The shape of the shoot is characterized by the angle \(\theta(s,t)\) between the local tangent and the vertical axis. The boundary condition of the basal end is \(\theta(0) = -\pi/2, x(0) = y(0) = 0\), and the apical end is free. We assume that the shoot grows uniformly at the growth zone, defined by \(L-L_0 \leq s \leq L\), as

\[
\frac{\partial d}{\partial t} = \dot{L}(s)d(s),
\]

where

\[
\dot{L}(s) = \begin{cases} L_0 & \text{if } s \in [L-L_0, L], \\ 0 & \text{otherwise}, \end{cases}
\]

and \(d\) is the length of an infinitesimal segment of the shoot. The dot notation is the time derivative of the index. The intrinsic curvature \(\kappa^*\) is renewed as follows:

\[
\frac{\partial \kappa^*}{L_0 \partial t} = -\beta \sin \theta - \gamma \kappa(\kappa^*),
\]

where \(\kappa\) is the current curvature, \(\beta\) the sensitivity of the curvature to the shoot angle (gravitational sensitivity), and
y the sensitivity of the current curvature ( proprioceptive sensitivity). As described in refs. (Bastien et al. 2014; Chelakkot and Mahadevan 2017), the equation (***) indicates that the total rate of change of intrinsic curvature inside the growth zone is given by the sum of the contributions of the gravitropism depending on the local orientation of the segment, and the straightening mechanism acting in response to an induced curvature.

Based on the ref. (Chelakkot and Mahadevan 2017), three characteristic lengths exist: the characteristic sensitivity length $l_s=y/\beta$, characteristic length of growth $l_g$ (limit of growth zone), and characteristic length of relative effect of elasticity and gravity $l_g=(B(\rho g)^{1/3}$, where $B$ is the bending rigidity that is constant in this study, $\rho$ the linear mass density of the shoot, and $g$ the gravitational acceleration. The temporal change of the bending rigidity discussed in (Chelakkot and Mahadevan 2017) was not taken into account in this study because it was minor effect on the stationary state. Two critical dimensionless parameters for the shoot morphology are the growth-sensitivity parameter $S=l_s/l_g$ and growth-elasto-gravity parameter $\varepsilon=l_s/l_g$.

To obtain the shoot mechanical equilibrium, we solve the following momentum and balance equations:

$$\frac{\partial M}{\partial s} + V \sin \theta - H \cos \theta = 0, \quad \frac{\partial H}{\partial s} = 0, \quad \frac{\partial V}{\partial s} = -\rho g,$$

where $M(s,t)=B(x-k^*)$ be the internal moment (around z-axis) and $F(s,t)=(H(s,t), V(s,t))$ be the force acting on the cross section of the shoot at the arc-length $s$ and time $t$, with $H$ and $V$ being the horizontal and vertical force components, respectively (see more details on the equilibrium equation in Agostinelli et al. 2020; Chelakkot and Mahadevan 2017). To simulate the shoot morphology, we discretized the centerline into a set of vertices as $r_i=[x_i, y_i]$ with length $d_i$ and curvature $k_i=(\theta_i-\theta)/(r_{i+1}-r_i)$ at the index of the vertex $i$ ($i=1, 2, \ldots, N$). The position of the vertex $r_i(s,t)$ is updated based on the force and momentum balance equation (***)). To do it numerically, the damped Verlet method (Chelakkot and Mahadevan 2017) was used to solve the following equation corresponding to the equation (***)$; \Gamma \dot{r}(s, y)/\partial t=F_s$, where $\Gamma=1.05$ in this study. We note that the index $\Gamma$ is defined as the computational time to find the position of vertices under mechanical equilibrium. More precisely, we used the formula for vertex $i$:

$$\eta_i(t+\Delta t) = \left(2 - \frac{1}{\Gamma} \right) \eta_i(t) - \left(1 - \frac{1}{\Gamma^2} \right) \eta_i(t-\Delta t) \Gamma(t) \Delta t^2.$$

Using the stretching potential $U_s=(E/2)\sum_{i=1}^{N-1}(b_i-d_i)^2$, where $N_o$ is the number of vertices, $E$ is an elasticity parameter, $b_i=r_{i+1}-r_i$; $d_i$ is the equilibrium length of $b_i$; $U_b=(B/2)\sum_{i=1}^{N-1}(\phi_i-\phi^*)^2$ is the bending potential, where $B$ is the bending rigidity, $\phi_i=\cos^{-1}(b_i(b_i))$, $b_i=(r_{i+1}-r_i)/(r_{i+1}-r_i)$; and $\phi^*$ is the equilibrium angle between vectors $b_i$ and $b_{i+1}$ (see similar derivations of the stretching and bending potential in the ref. (Chirico and Langowski 1994). The force applied on vertex $i$ is given by

$$F_i = -V_i U_i - V_i U_b - \rho g d_i.$$

The index $g$ is the gravitational acceleration. The stretching force $F_s=\sum_i U_b$ can be obtained as follows: $F_s=\sum_i (d_i \partial V_i/\partial r_i)$, with Kronecher's delta $\delta_{ij}$

$$F_i^s = -E [(b_{i+1} - d_i r_{i+1}) - (b_i - d_i r_i)].$$

The bending force $F_b=\sum_i U_b$ can be obtained as follows:

$$F_b^s = \frac{\partial U_b}{\partial t} \frac{\partial t}{\partial r_i} = B \sum_{i=0}^{N-1} (\phi_i - \phi^*) \frac{\partial}{\partial t} |(r_{i+1}, r_i) |.$$

Using the relation

$$\frac{\partial}{\partial t} |(r_{i+1} - r_i))(I - r_i \cdot r_i)/b_i,$$

$$F_i^b = -B(A_i - A_{i-1} + B_i - B_{i-1}),$$

where $A_i=\phi_i-\phi^*(r_{i+1} - r_i \cos (\phi_i)/b_i \sin (\phi_i)); B_i=\phi_i-\phi^*(r_{i+1} - r_i \cos (\phi_i)/b_i \sin (\phi_i));$ For the numerical simulation, singular points (0 denominator) in $A_i$ and $B_i$ are avoided by

$$\phi_i - \phi^* < \frac{10^{-6}}{\sin (\phi_i)}.$$

The evolution of the growth equation (*) and curvature equation (**) are performed by

$$d_i(t+\Delta t) = d_i(t) + \dot{\Delta}t, \quad k_i(t+\Delta t) = k_i(t) + \dot{\Delta}t(-\beta \sin \theta_i - \gamma k_i).$$

**Results and discussion**

**KymoRod provides a quantitative spatio-temporal description of bending**

To quantify the spatio-temporal kinematics of shoot bending during shoot gravitropism, we first overviewed the recently developed analytic tool KymoRod (Bastien et al. 2016). In our study, we obtained the data used for KymoRod analysis in five main steps. (1) We acquired raw time lapse data of the bending motion of the *A. thaliana* inflorescence stem. For this step, we cut 5-cm segments from the inflorescence stems of wild-type plants and removed the leaves to make filament-shaped images of the stem. (2) We used ImageJ to binarize the raw images to exclude the image background. (3) The contour of the object was detected. (4) This contour was used to estimate the centerline. (5) Finally, the inclination angle and curvature of the centerline were extracted (Figure 1A, for details, see Material and methods). The inclination angles can be plotted on the stem (Figure 1B,
left) or on a color map as a function of time (\(t\), hereafter in minutes) and curvilinear coordinate (\(s\), hereafter in millimeters), where the curvilinear coordinate is defined as the distance along the stem from the bottom edge (Figure 1B, right). As the inclination angle (\(\theta\)) is defined as the angle from the vertical axis (see Figure 1B, left), we represented the stem direction as horizontal from left to right by orange, vertical by green, and horizontal from right to left by blue in this study. Likewise, the curvature data (\(\kappa\)) can be plotted on the stem (Figure 1C, left), or on a color map as a function of time and curvilinear coordinate (Figure 1C, right). By coloring downward convex curvature blue and upward convex curvature red, it can be seen that the blue region has an upward bend and the red region has a downward bend, although there are only a few such reddish regions in this example (Figure 1C).

We note that inclination angle and curvature are both necessary for understanding the spatio-temporal change in stem shape. Considering the stem as a function \(y=f(x)\) of the Cartesian coordinate system \((x(s), y(s))\), the inclination angle \(\theta(s, t)\) and the curvature \(\kappa(s, t)\) are included in the first and second space derivatives, respectively, indicating that the inclination angle corresponds to the direction of the stem segment, whereas the curvature corresponds to the degree of bending of the stem segment. The inclination angle may range between 0 and \(\pi/2\) during bending, so we quantified the curvilinear coordinate with the test cases \(\theta=\pi/6\), \(\pi/4\), and \(\pi/3\) as the landmarks of changing directions (plots in Figure 1B, right). We observed that the temporal relocation curves of all three angles within the stem were not qualitatively different. We next quantified the curvilinear coordinate with \(\kappa=-0.04\), \(-0.06\), and minimum (min) as the landmarks of bending (plots in Figure 1C, right). As was observed for the inclination angle, the temporal relocation of curvature within the stem was similar among the three conditions. Together, these data strongly suggest that once an Arabidopsis stem starts to bend in response to gravity, the bending will occur spatially continuously within stem tissues.

**Characterization of when and where the shoot bends**

To further characterize stem bending behavior, we analyzed five independent bending events in the wild type. Using the techniques described above, we could determine how the inclination angle and curvature are distributed in space and in time (Figure 2A, C). The corresponding positions with \(\theta=\pi/4\) and those with \(\kappa=\text{min}\) are shown in Figure 2B, D. We note that reliable

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**Figure 1.** (A) Procedures for KymoRod analysis. From the raw image data, the outline and centerline of the stem and flowers are extracted, and the inclination angle and curvature of the stem are quantified based on these data. (B) Visualization of the spatio-temporal inclination angle of the stem (left panel), and color plot of the inclination angle as a function of time and curvilinear coordinate (right panel). The angles \(\pi/6\), \(\pi/4\), and \(\pi/3\) measured from the bottom edge of the stem were plotted. (C) Visualization of the spatio-temporal curvature of the stem (left panel), and color plot of the curvature as a function of time and curvilinear coordinate (right panel). The curvatures \(-0.04\), \(-0.06\), and minimum (min) measured from the bottom edge of the stem were plotted.
inclination angles and curvatures could not be obtained near the stem tip (i.e., about 5–10 mm from the tip) in these five examples, because the flowers at the stem tip made the contour extraction difficult. Thus, we omitted the data from this region for further analysis. In contrast to methods relying on tip angle alone, our method can describe the spatio-temporal change in shape of entire stem segments. For example, the relocation of $s (\theta = \pi/4)$
can follow different shaped trajectories (e.g., samples 2 and 3 in Figure 2B), and the relocation of s (κ= min) can produce discontinuous plots (e.g., samples 2 and 3 in Figure 2D). In addition, we established that bending occurs at a specific position from the stem tip in Figure 2B, D. Based on these qualitative observations, we defined the eight parameters shown in Table 1 for evaluating when and where the stem bends, as illustrated in Figure 2E, F.

Based on our analyses of the five bending events, the stems started to bend after 40−70 min (see tstart and κstart) and the values for sstart and κstart indicate that there is a drastic change at s/L0 = 0.40−0.65, or roughly estimated as s=18−31 mm from the stem tip. Thus, there should be a sudden increase in the differential growth between upper and lower cells at the position s=18−31 mm from the stem tip, suggesting that the bending does not occur gradually starting at the stem tip but rather occurs suddenly at the specific position. Moreover, the stationary direction-changing positions sκmin and the stationary bending positions sL0/4 had value ranges around s/L0 = 0.15−0.40, that is, s=31−44 mm from the stem tip. These results indicate that the position of greatest bending shifts gradually toward the base of the stem over time until it reaches the stationary bending position. Furthermore, the slopes α′ and β′, which indicate the rate of the gradual shift in bending position, are estimated to be −1,200−0 excluding outliers, with the estimated speed 600/L0=11.6 min/1 mm.

Among the five bending events, the color diagrams of angle and curvature were qualitatively similar but quantitatively different (Figure 2B, D), meaning that the angle and curvature contain different information. For example, the values of slopes α′ and β′ were not very consistent with each other in samples 2, 3, and 5 (Figure 2E, F), suggesting that the direction and degree of stem segment bending might be influenced by different factors. Also, because of the spatio-temporal noise of measurement error and statistical error, s (κ= min) has a spatial fluctuation over time, making the calculation of slope β′ more sensitive to noise than that of α′.

### Table 1. Eight parameters that describe when and where the stem bends

| Quantity | Explanation | Range of values |
|----------|-------------|-----------------|
| start | The first time when any position reaches θ=π/4 | 60−70 |
| start | The curvilinear coordinate of the position that first reaches θ=π/4 | 0.40−0.65 |
| start | The curvilinear coordinate of the position s (θ=π/4) at t=300 min | 0.20−0.40 |
| κ′ | The slope of (s/L0, t) with 5 time points from time s=0 | −300−1,200 |
| κ start | The first time when any position reaches κ<ν | 40−70 |
| κ min | The curvilinear coordinate of the position that first reaches κ<κc | 0.55−0.65 |
| κ L0/4 | The curvilinear coordinate of the position s (κ= min) at t=300 min | 0.15−0.40 |
| β′ | The slope of (s, t) with 5 time points from time s=0 | −1,200−0 |

An elastic spring model reconstructs bending events qualitatively similar to observed events

Next, we implemented a theoretical model and sought a best fitted parameter set based on the previous work (Chelakkot and Mahadevan 2017). In this model the stem is described by vertices that are connected with elastic springs, which are subject to three mechanical forces: stretching force, bending force, and gravity (Figure 3A). The elastic springs reach a mechanical equilibrium with all the applied forces at each step. During each step, the parameters (the length of stem segment d and the intrinsic curvature of the stem κ*) are evolved with two equations: (1) dκ/dt=L(s)d and (2) dκ/Ls=−β sin θ−κ. Here, the parameter L(s) is the elongation rate of the stem, β gravitational sensitivity, γ proprioceptive sensitivity, and κ the current curvature (see also Materials and methods). The important dimensionless parameters are the bending strength S=l/l and the balance between growth, elasticity, and gravity ε=l/L. With these parameters, different types of bending events can be described as shown in the stationary state in Figure 3C.

We fit two representative quantities in this study: the elongation ratio er=(l−l0−l0 min)/l0−l0 min and the minimum curvature at 300 min κ300 min. In practice, we calculated the deviation between the model parameter set (er_model, κ κ300 min_model) and the data quantities (er_data, κ κ300 min data) by changing the parameters (S, ε). As a result, the extracted values were within the parameter range: S∈[0.04, 0.4], ε∈[0.04, 0.4], as shown by dotted lines in Figure 3C. These values were based on the fitting of the restricted parameters (er, κ κ300 min), but the actual bending behaviors were well extracted (Figure 3D−F). The stationary bending positions produced by the model are exactly the same as those observed in the five bending events, although the entire shoots are not perfectly fitted. This implies that the fitting of the two-parameter set (S, ε) might be a key process to explain the stationary bending position.

To gain a better understanding of the ability of the theoretical model, we calculated the same eight quantities as shown in Figure 3G. We note that a few characteristic features are consistent with the data, e.g. tstart and...
However, other quantities were not consistent between the model and the data. The discrepancies for $s_{\theta=\pi/4}^{\text{start}}$ and $s_{\kappa=\text{min}}^{\text{start}}$ might be caused by the high temporal resolution of the theoretical model, which results in the precise detection of the bending position even if the curvature is suddenly changed (see samples 1 and 4). The same explanation may apply to the slopes $\alpha'$ and $\beta'$ by definition of $s_{\theta=\pi/4}^{\text{start}}$ and $s_{\kappa=\text{min}}^{\text{start}}$. Therefore, to improve the
predictive performance of the model, we may have to consider more precise characteristics that describe the bending with higher temporal precision. Moreover, to improve the model, it may be possible to include the temporal delay in gravitational sensing (Agostinelli et al. 2020).

To summarize, we successfully established a system for analyzing shoot gravitropism using a data-model combined approach. The important advantage of this novel approach is the ability to check the correspondence between the model and the data quantitatively. If a perfect match between data and model can be achieved, the next step for understanding shoot gravitropism would be a mechanical description in the mathematical model with stretching force, bending force, and gravity. This interdisciplinary approach is expected to provide a much more comprehensive understanding of the relationship between biological events and mechanical events during shoot gravitropism.

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