

# Growth, geometry, and mechanics of a blooming lily

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**Despite the common use of the blooming metaphor, its floral inspiration remains poorly understood. Here we study the physical process of blooming in the asiatic lily *Lilium casablanca*. Our observations show that the edges of the petals wrinkle as the flower opens, suggesting that differential growth drives the deployment of these laminar shell-like structures. We use a combination of surgical manipulations and quantitative measurements to confirm this hypothesis and provide a simple theory for this change in the shape of a doubly curved thin elastic shell subject to differential growth across its planform. Our experiments and theory overturn previous hypotheses that suggest that blooming is driven by differential growth of the inner layer of the petals and in the midrib by providing a qualitatively different paradigm that highlights the role of edge growth. This functional morphology suggests new biomimetic designs for deployable structures using boundary or edge actuation rather than the usual bulk or surface actuation.**

mechanics | curvature reversal

Plant and fungal movements, although limited by the absence of dedicated motile elements such as muscles, are nevertheless varied. They span a range of length and time scales, from the rapid movements in microscopic nematophagous fungi (1), to the slow opening and closing of leaf stomata. A striking example of rapid movements is seen in the Venus flytrap, which snaps in a fraction of a second as a result of an actively controlled release of turgor across the thickness of the leaf, switching its curvature (2). This and other examples of rapid movements in plants and fungi usually involve slender geometries and may be quantified in terms of the motion of water flow in a soft porous solid (3). Morphological transitions that guide cell, tissue, leaf, branch, root, and stem shape, on the other hand, are much slower and are driven by differential growth. Here we consider a ubiquitous example of plant movement driven by differential growth, the blooming of a flower, the inspiration for much art and poetry but surprisingly little science.

When a flower blossoms, its petals change curvature on a time scale of a few hours to days, consistent with the idea that these movements are growth driven. In flowers that bloom just once, differential cell proliferation is the dominant mode of growth, whereas in those that open and close repeatedly, cell elongation plays an important role (4). Frequently proposed explanations for petal movements posit a difference in growth rate between the abaxial and adaxial sides (surfaces) of a petal or an active role for the midribs (4, 5). However many flower petals have rippled edges, and this raises another qualitatively different possibility that we will explore here, namely that it is possible to change the shape of a lamina via excess growth of the margins relative to the center. This mechanism of differential planar growth has recently been shown to both explain the morphology of saddle and ripple shaped leaves and algal blades (6–10) and to engineer the shape soft thin sheets using differential swelling (11). Indeed, our approach quantifies and synthesizes the observations of von Goethe (12) who argued that flower petals are analogous to leaves physiologically.

## Observations and Experiments

We study the process of blooming in the common lily *Lilium casablanca* as its popularity and large size makes it easily available

and amenable to manipulation. Anatomically, a lily bud consists of 3 inner petals embraced by 3 outer sepals shown in Fig. 1 *A* and *B*. All petals/sepals are convex doubly curved surfaces (i.e., they are curved simultaneously in two orthogonal directions at all points along the mid surface), with their longitudinal curvature less than their lateral curvature. Both petal and sepals have midribs that are bilayer composite structures (Fig. 2*A*) with a soft leafy part (gray) that is contiguous with the petal/sepal and a stiff woody part (green) that is distinct from the lamina. Whereas the midrib of the outer sepals are featureless, those of the inner petals have grooves into which the margin of the outer sepals are tucked, as shown in Fig. 1*A*. This locking mechanism maintains the structural integrity of the bud while allowing for the rapid deployment of the petals once blooming starts.

To follow the bud of the Lily *Lilium casablanca*, we place it with its stem immersed in water in an environment of uniform humidity and temperature, under continuous fluorescent lighting and then film it with time lapse video to record the blooming process at intervals of 1 min. The blooming process takes four and a half days until the lily opens fully over which time we ensure that the ambient conditions are kept constant (Movie S1). Fig. 1*C* shows a typical opening sequence of a lily. During the first 4 days, the young green bud (10 cm long and 2.5 cm wide) absorbs about 0.2 L of water, increasing in length by 10% and in diameter by 20% and turns white. Although the bud is closed at the end of this stage, it is ready to burst forth quite literally; evidence for this can be seen by peeling back the outer sepals that show that the inner petals have wrinkled edges, as shown in Fig. 2*C*. It is worth pointing out that the inner petals wrinkle before blooming whereas the outer sepals wrinkle at the end of blooming. At the end of the fourth day (Fig. 1*C* and Movie S1) these growth-induced stresses in the bud reach a critical value large enough to overcome the petal-sepal lock. This causes the flower to bloom rapidly as the petals/sepals reverse curvature and bend outward. Simultaneously, wrinkles of typical wavelength (approximately 1.5 cm) develop along the edges of these laminae. To quantify the growth of these tissues, we paint equidistant black dots (1-cm apart) along both the periphery, the center, and along the midribs of both the petal and sepal in their closed state and track them over time. This allows us to measure the total in-plane relative growth strain of the tissue along the long axis of the petal over the period associated with blooming. We find that there is a growth strain 10% of the midrib in both petals and sepals is relatively uniform. However, the marginal growth strain in the sepal in the longitudinal direction is more than 20% basally and increases to nearly 50% distally (Fig. 3*A*). This lateral strain gradient in a lamina of finite width can give rise to global saddle-shaped structures as well as rippled edges (10) and is consistent with our observations of wrinkling of the petal edges in the prestressed bud and in the fully bloomed lily. In addition to

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observations (5). However, this cannot and does not lead to the reversal of curvature in the petals and is thus responsible only for a small contribution to the final conformation of the flower. Taken together these observations, combined with the edge rippling of petals that is observed both in the bud and bloomed states clearly shows that edge growth is both necessary and sufficient for blooming, and hereuntofore we will focus on understanding how this is brought about.

### Mathematical Model of Blooming

At a mesoscopic scale, because both cell elongation and cell proliferation lead to differential growth and strain, we see that the mechanical basis for the margin-driven deployment of a doubly curved petal stems from the coupling between bending and stretching in thin curved shells. A minimal theory that couples growth to the shape of a thin lamina of nonuniform thickness takes the form of the Föppl-von Kármán equations (13) generalized to account for differential growth, both in the plane and across the thickness (10), as well as a nonzero natural curvature of the shallow shell. These may be written as

$$\Delta \left( \frac{\Delta \Phi}{t} \right) - (1 + \nu) \left[ \frac{1}{t}, \Phi \right] + \frac{E}{2} ([w, w] - [w_0, w_0]) + E \lambda_g = 0 \quad [1]$$

$$\Delta(D\Delta(w - w_0)) - (1 - \nu)[D, w - w_0] - [\Phi, w] + \Omega_g = 0, \quad [2]$$

where  $\partial_{xy}P = \partial^2 P / \partial x \partial y$ ,  $\Delta P = \partial_{xx}P + \partial_{yy}P$ ,  $[P, Q] = \partial_{xx}P \partial_{yy}Q - 2\partial_{xy}P \partial_{xy}Q + \partial_{xx}Q \partial_{yy}P$ ,  $t(x, y)$  is the spatially inhomogeneous thickness,  $\nu$  is Poisson's ratio,  $E$  is Young's modulus,  $D = Et^3 / 12(1 - \nu^2)$  is the bending stiffness of the shell that is assumed to be made of a linear isotropic material,  $\Phi$  is the Airy stress potential,  $w_0(x, y)$  is the initial transverse coordinate, and  $w(x, y)$  is the current coordinate. The in-plane differential growth tensor is

$$\lambda_g = \partial_{yy}\epsilon_{xx}^g + \partial_{xx}\epsilon_{yy}^g - 2\partial_{xy}\epsilon_{xy}^g, \quad [3]$$

while the differential growth gradient across the thickness leads to a transverse curvature growth tensor

$$\Omega_g = \partial_{xx}[D(\kappa_{xx}^g + \nu\kappa_{yy}^g)] + \partial_{yy}[D(\kappa_{yy}^g + \nu\kappa_{xx}^g)] + 2(1 - \nu)\partial_{xy}(D\kappa_{xy}^g), \quad [4]$$

which is the equivalent pressure induced by transverse growth gradients. Eq. 1 quantifies the incompatibility of the in-plane strain due to (i) the difference in the Gauss curvature  $[w, w]$  of the shell (an intrinsic invariant of the surface) from its natural value  $[w_0, w_0]$  and (ii) the additional contribution from in-plane differential growth. Eq. 2 describes the force balance in the out-of-plane direction due to the in-plane stresses in the curved shell and the growth curvature tensor associated with transverse gradients in the growth. In light of our experimentally measured growth strains shown in Fig. 3A we retain only the term  $\partial_{yy}\epsilon_{xx}^g$ , ignoring all other components of the in-plane growth strain tensor and the transverse growth curvature tensor entirely, given that our experiments eliminate the role of the midrib as the primary driver of blooming.

To complete the formulation of the problem, we prescribe the boundary conditions that the edge  $\Gamma$  of the shallow elliptical shell is free of torques and forces, so that (13),

$$D\{\partial_{nn} + \nu(\partial_{ss} + \partial_s\psi\partial_n)\}(w - w_0)|_{\Gamma} = 0 \quad [5]$$

$$\begin{aligned} & \{D[\partial_n\Delta + (1 - \nu)\partial_s(\partial_{ns} - \partial_s\psi\partial_s)] + \partial_n D[\partial_{nn} + \nu(\partial_{ss} + \partial_s\psi\partial_n)] \\ & + 2(1 - \nu)\partial_s D[\partial_{ns} - \partial_s\psi\partial_s]\}(w - w_0)|_{\Gamma} = 0, \end{aligned} \quad [6]$$

where  $n$  is the unit normal and  $s$  is the arc length along the boundary curve  $\Gamma$  of the elliptical shell which has a curvature  $\partial_s\psi$ .

The nonlinear system of partial differential Eqs. 1–6 has no analytic solutions for general forms of the thickness and/or growth strain tensor, and so one must resort to approximate methods of solution. We use a combination of numerical method that allows us to explore the parameter regimes of the problem, and also show that a simple exact solution for a class of thicknesses and growth strains captures the essence of the mechanisms at play.

### Analysis

**Numerical Simulations.** We follow (14) and use a discrete approximation to an elastic shell in terms of equilateral-triangular elements, with the elastic energy density  $F = F_s + F_b$  as the sum of the stretching energy  $F_s = \frac{\sqrt{3}S}{4} \sum_{ij}(r_{ij} - a_0)^2$ , where  $r_{ij}$  is the current spring length and  $a_0$  is the rest spring length and the bending energy  $F_b = \frac{B}{\sqrt{3}} \sum_{\alpha\beta}(\vec{n}_\alpha - \vec{n}_\beta)^2$ , where  $\vec{n}_\alpha$  and  $\vec{n}_\beta$  are the unit normal vectors of the two facets, and  $S$  and  $B$  are the 2D Young's modulus and bending stiffness respectively. In the continuum limit as  $a_0 \rightarrow 0$ , the total discrete energy density  $F_s + F_b$  converges to the continuum elastic energy density of a shell

$$F = \frac{1}{2} \iint \left( \frac{Eh^3}{12(1 - \nu^2)} F_b + \frac{Eh}{1 - \nu^2} F_s \right) dx dy, \quad [7]$$

where the bending energy density  $F_b = (\partial_{xx}w^e + \partial_{yy}w^e)^2 + 2(1 - \nu)[(\partial_{xy}w^e)^2 - \partial_{xx}w^e \partial_{yy}w^e]$  with  $\partial_{ij}w^e = \partial_{ij}(w - w_0) - \kappa_{ij}^g$  and the stretching energy density  $F_s = (\epsilon_{xx}^e + \epsilon_{yy}^e)^2 + 2(1 - \nu)(\epsilon_{xy}^e - \epsilon_{xx}^e \epsilon_{yy}^e)$  with  $\epsilon_{ij}^e = \epsilon_{ij} - \epsilon_{ij}^g$ . The Euler-Lagrange equations associated with the functional in Eq. 7 yield Eqs. 1 and 2.

Minimizing the discrete energy given above as a function of the relative in-plane growth strain, characterized in terms of the variations in the rest length  $a$ , allows us to simulate the deployment of the petal/sepals. Scaling all lengths by the thickness of the petal ( $h = 1$  mm), we generate an elliptical shallow shell of semimajor axis  $a = 25$  (longitudinal axis  $x$ ) and semiminor axis  $b = 10$  (lateral axis  $y$ ) with natural curvatures  $\kappa_x = 0.04$  and  $\kappa_y = 0.02$ . To mimic the differential growth gradients in the petal, we increase the rest length of the springs using the form  $\epsilon_{xx}^g = (y/b)^4 + e^{-(b-y)}$ ; the first term generates the global saddle shape whereas the second is responsible for edge rippling, simulating the behavior of outer sepals. To minimize the discrete analog of Eq. 7, we use a damped molecular dynamics method (15) with a series of incremental growth strains of 0.01% followed by 100,000 steps with time step  $\Delta t = 0.1$  until equilibrium is reached. The results are shown in Fig. 3B, and as a movie (Movie S2), and clearly show both the blooming process as well as the subsequent wrinkling of the edge. Variations in lateral growth gradients can lead to a reversal of the sequence of the event such that edge rippling precedes global curvature change.

Whereas our numerical simulations allow us to probe the effect of strong edge-localized lateral growth gradients in an elliptical doubly curved elastic shell and are consistent with experimental observations, they do not expose the underlying simplicity of the mechanisms involved. This can be seen using an analytic theory, which we turn to next.

**Simplified Theory.** We focus on the consequence of minimal quadratic gradient in the growth strain that yields an exactly solvable theory of blooming, analogous to that thermally induced buckling in shells (13). It is sufficient to consider a single petal, modeled as a shallow elliptical shell of semimajor axis  $a$  (longitudinal axis  $x$ ) and semiminor axis  $b$  (lateral axis  $y$ ) with a naturally convex shape, as shown in Fig. 4A. We describe its transverse coordinate using  $w_0 = -\frac{1}{2}(\kappa_x x^2 + \kappa_y y^2)$  with  $\kappa_x > 0$  and  $\kappa_y > 0$  the

spontaneous principal curvatures. For convenience, we define a dimensionless parameter  $m = \kappa_{x0}/\kappa_{y0}$  to characterize the shape of the natural curved petals; for most petals  $m \in [0,1]$ , so that they are weakly curved longitudinally and strongly curved laterally. Following our observations and measurement on lily petals and sepals, we assume that the dominant contribution to the growth is given by  $\epsilon_{xx}^g = g(y/b)^2$  with  $g > 0$  denoting the maximum value at the edge, and  $\epsilon_{yy}^g = \epsilon_{xy}^g = 0$ . The current transverse coordinate takes the form of  $w = -\frac{1}{2}(\kappa_x x^2 + \kappa_y y^2)$  with  $\kappa_x$  and  $\kappa_y$  the principal curvatures of the deformed shape. Finally, we assume that a petal may be modeled as a shell with a lenticular cross-sections (i.e., a thickness  $t = t_0(1 - \frac{x^2}{a^2} - \frac{y^2}{b^2})$ ) where  $t_0$  is the maximum thickness of the shell at its center, so that its bending rigidity is

$$D = D_0 \left(1 - \frac{x^2}{a^2} - \frac{y^2}{b^2}\right)^3, \quad [8]$$

where  $D_0 = Et_0^3/12(1 - \nu^2)$ . Then, if the Airy stress potential

$$\Phi = \beta D(x,y) \quad [9]$$

with  $\beta$  an unknown constant that describes the in-plane elastic response, we find that along the boundary  $\Gamma$  of the elliptical shell

$$D|_{\Gamma} = \partial_n D|_{\Gamma} = \Phi|_{\Gamma} = \partial_n \Phi|_{\Gamma} = 0 \quad [10]$$

vanish identically so that the boundary conditions Eqs. 5 and 6 are also satisfied identically. The assumption of a lenticular cross-section with a thickness that varies quadratically (at least) is tantamount to stating that the forces and torques on the edges vanish faster than either the in-plane stress or the curvature, so that the edges are automatically free of forces and torques (13).

The above assumption of a quadratic form for the lenticular cross-section, the original and the current displacement field and the growth strain allows us to reduce Eqs. 1 and 2 to a set of three nonlinear algebraic equations (13)

$$\bar{\kappa}_x \bar{\kappa}_y - \bar{\kappa}_{x0} \bar{\kappa}_{y0} = -\beta - \beta_g \quad [11]$$

$$(1 + \nu - \beta)(\bar{\kappa}_x + \bar{\kappa}_y) = (1 + \nu)(\bar{\kappa}_{x0} + \bar{\kappa}_{y0}) \quad [12]$$

$$(1 - \nu + \beta)(\bar{\kappa}_x - \bar{\kappa}_y) = (1 - \nu)(\bar{\kappa}_{x0} - \bar{\kappa}_{y0}), \quad [13]$$

with three dimensionless unknowns  $\beta$ ,  $\bar{\kappa}_x$ , and  $\bar{\kappa}_y$ . Here,  $\beta_g = 2g/\bar{b}^2$  is a measure of growth strain,  $\beta$  is a measure of the elastic in-plane strain as characterized by (9),  $\bar{\kappa}_{x0} = \kappa_{x0}L$ ,  $\bar{\kappa}_{y0} = \kappa_{y0}L$ ,  $\bar{\kappa}_x = \kappa_x L$ ,  $\bar{\kappa}_y = \kappa_y L$ , and  $\bar{b} = b/L$ , with the intrinsic length  $L = \frac{ab}{t_0} \left(\frac{1-\nu^2}{4+2\nu+5(a^2/b^2+b^2/a^2)}\right)^{1/2} \equiv \lambda^{1/2} ab/t_0$ . It is useful to introduce a parameter  $\alpha = \bar{\kappa}_{x0} \bar{\kappa}_{y0} = m \bar{\kappa}_{y0}^2$ , a rescaled natural Gauss curvature that measures the bend-stretch coupling, so that there is a critical growth strain  $\beta_g^* = \beta_g^*(\bar{\kappa}_{x0}, \bar{\kappa}_{y0})$  that demarcates the stretch-dominated regime from the bend-dominated regime.

To see how a petal changes its geometry during blooming, we first explore the case of naturally curved spherical shell with  $\bar{\kappa}_{x0} = \bar{\kappa}_{y0} = \bar{\kappa}_0 > 0$  (or  $m = 1$ ), so that Eqs. 11–13 read

$$\bar{\kappa}_x \bar{\kappa}_y - \bar{\kappa}_0^2 = -\beta - \beta_g \quad [14]$$

$$(1 + \nu - \beta)(\bar{\kappa}_x + \bar{\kappa}_y) = 2(1 + \nu)\bar{\kappa}_0 \quad [15]$$

$$(1 - \nu + \beta)(\bar{\kappa}_x - \bar{\kappa}_y) = 0. \quad [16]$$

The above equations have two solution regimes depending on the magnitude of the differential growth  $\beta_g$  relative to a critical value

$\beta_g^*(\kappa_0, \kappa_0) = (1 - \nu) + \frac{1}{4}(1 - \nu)(3 + \nu)\bar{\kappa}_0^2$  as for thermally induced buckling (13).

(i) *Before buckling*:  $0 < \beta_g < \beta_g^*$ . From Eq. 16, we see that if  $1 - \nu + \beta \neq 0$ , then  $\bar{\kappa}_x = \bar{\kappa}_y$ , and the first two Eqs. 14 and 15 yield the cubic

$$(\bar{\kappa}_x - \bar{\kappa}_0)\{\bar{\kappa}_x(\bar{\kappa}_x + \bar{\kappa}_0) + 1 + \nu\} + \beta_g \bar{\kappa}_x = 0, \quad [17]$$

with only one real root for  $\bar{\kappa}_x$ , and furthermore

$$\beta = (1 + \nu) \left(1 - \frac{\bar{\kappa}_0}{\bar{\kappa}_x}\right). \quad [18]$$

Thus we see that as the growth strain  $\beta_g$  increases from zero, the shell unbends slowly but remains spherical, while the in-plane strain  $\beta$  decreases monotonically as shown in Fig. 4C.

(ii) *After buckling*:  $\beta_g \geq \beta_g^*(\bar{\kappa}_0, \bar{\kappa}_0) > 0$ . Now the curvatures are unequal after buckling (i.e.,  $\bar{\kappa}_x \neq \bar{\kappa}_y$ ), so that third of Eq. 16 requires  $\beta = \nu - 1$ . Then we may solve for the curvatures from Eqs. 14 and 15 to get

$$\bar{\kappa}_x = \frac{1 + \nu}{2} \bar{\kappa}_0 - (\beta_g - \beta_g^*)^{1/2} \quad [19]$$

$$\bar{\kappa}_y = \frac{1 + \nu}{2} \bar{\kappa}_0 + (\beta_g - \beta_g^*)^{1/2}; \quad [20]$$

i.e., there is a pitchfork bifurcation in the solution and the shell suddenly unbends anisotropically with the petal bending outward longitudinally while curving inward laterally. Fig. 4B shows three typical configurations of a shell with an elliptical planform cut from a spherical cap as it opens. We pause to observe that when  $\beta_g > \beta_g^*$ , the stretching strain  $\beta = \nu - 1$  becomes constant, indicating the exchange of stability from a stretch-dominated regime to a bend-dominated regime of the shell occurs via pitchfork bifurcation as shown in Fig. 4D. Any further in-plane growth is converted directly to bending deformations, so that the shell becomes a perfectly efficient bending actuator beyond the bifurcation. The subsequent increase in longitudinal curvature is consistent with earlier observations (5), as well as our own.

More generally, when a petal is not spherically curved,  $0 < \bar{\kappa}_{x0} < \bar{\kappa}_{y0}$  (or  $m < 1$ ), the in-plane response characterized by  $\beta$  must be found by solving a quintic defined by Eqs. 11–13

$$(1 + \nu - \beta)^2 [4(1 - \nu + \beta)^2 (\bar{\kappa}_{x0} \bar{\kappa}_{y0} - \beta - \beta_0) + (1 - \nu)^2 (\bar{\kappa}_{x0} - \bar{\kappa}_{y0})^2] - (1 - \nu + \beta)^2 (1 + \nu)^2 (\bar{\kappa}_{x0} + \bar{\kappa}_{y0})^2 = 0, \quad [21]$$

using, for example, the polynomial root solver *FindRoot* in *Mathematica* (Fig. 4D). Again the shape of the petal as a function of the growth strain (i.e.,  $\bar{\kappa}_x$  and  $\bar{\kappa}_y$ ) is obtained from Eqs. 12 and 13 as shown in Fig. 4D. We see that for nonspherical petals when  $m < 1$ , the pitchfork bifurcation is unfolded so that there is no sudden transition and the petal opens smoothly. However, there is still a critical value of the growth strain  $\beta_g^*(\bar{\kappa}_{x0}, \bar{\kappa}_{y0})$  that separates the stretch-dominated and bend-dominated regimes. In terms of the total elastic energy of the petal (see Eq. 7) and its discrete analog, the critical point  $\beta_g^*$  is found when  $\partial_{\beta_g} \partial_{\beta_g} F_s$  reaches a maximum, which  $\partial_{\beta_g} \partial_{\beta_g} F_s$  signifies a switch from stretch-dominated deformations to bend-dominated deformations just as for a spherical curved shell with  $m = 1$ , as shown in Fig. 4E. Indeed, this transition may be quantified in terms of the stretch-bend geometric coupling parameter  $\alpha = \bar{\kappa}_{x0} \bar{\kappa}_{y0} = m \bar{\kappa}_{y0}^2 \sim \Delta_{x0} \Delta_{y0} / t_0^2$  where  $\Delta_{x0} = \lambda^{1/2} a^2 \kappa_{x0}$  and  $\Delta_{y0} = \lambda^{1/2} b^2 \kappa_{y0}$  are the longitudinal and lateral rise respectively (16). In Fig. 4E, we see that when  $\alpha \ll 1$ , the critical scaled growth strain  $\beta_g^*$  is small, whereas when  $\alpha > 1$ , the critical growth strain  $\beta^*$  is large (i.e., a weakly curved



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