Petal shapes of sympetalous flowers: the interplay between growth, geometry and elasticity

Martine Ben Amar¹,³, Martin Michael Müller² and Miguel Trejo¹

¹ Laboratoire de Physique Statistique, Ecole Normale Supérieure, UPMC Univ Paris 06, Université Paris Diderot, UMR CNRS 8550, 24, rue Lhomond, 75005 Paris, France
² Equipe BioPhysStat, ICPMB-FR CNRS 2843, Université de Lorraine, 1, boulevard Arago, 57070 Metz, France
E-mail: benamar@lps.ens.fr

New Journal of Physics 14 (2012) 085014 (16pp)
Received 27 April 2012
Published 17 August 2012
Online at http://www.njp.org/
doi:10.1088/1367-2630/14/8/085014

Abstract. The growth of a thin elastic sheet imposes constraints on its geometry such as its Gaussian curvature $K_G$. In this paper, we construct the shapes of sympetalous bell-shaped flowers with a constant Gaussian curvature. Minimizing the bending energies of both the petal and the veins, we are able to predict quantitatively the global shape of these flowers. We discuss two toy problems where the Gaussian curvature is either negative or positive. In the former case, the axisymmetric pseudosphere turns out to mimic the correct shape before edge curling; in the latter case, singularities of the mathematical surface coincide with strong veins. Using a variational minimization of the elastic energy, we find that the optimal number for the veins is either four, five or six, a number that is deceptively close to the statistics on real flowers in nature.
1. Introduction

The shapes adopted by living matter during its development have always fascinated scientists and artists [1, 2]. However, the link between the morphology of matter and the physical and biochemical processes related to its growth is a much more recent subject of study. In particular, growing slender biological tissues have received intensive attention because they constitute minimal systems in which, under certain assumptions, the common ideas of geometry and elasticity may be successfully combined to explain the shapes observed in nature. Some characteristic examples are the growth of flowers [3, 4], plant leaves [5–7] and certain types of unicellular green algae [8, 9].

Among slender biological objects, botany offers very beautiful examples owing to the huge variety and complexity of the generated colorful shapes. In this paper, we model the shape of sympetalous flowers that we can describe easily with the tools of differential geometry. We focus on two different cases: the surfinia, which is a kind of petunia, and the Angel’s trumpet (brugmansia) (see figure 1). These flowers generally have five petals that are fused in the case of the petunia variety and strongly linked together via veins in the case of brugmansia. Our aim is to show that some geometrical characteristics of the blooming flowers can be explained by the relaxation of growth-induced stresses which have built up in the bud. What happens inside the bud turns out to be a complex interplay between genetics and cellular biology in a confined space. Many studies have considered the petunia, a variety of high economical impact (for a review see [10]; for a careful analysis of cell division and expansion see [11]). The relaxation of stresses in a flower has been analyzed only recently for the blooming lily [12]: experimental measurements combined with a theoretical analysis show that differential growth and midrib constraints explain the blooming, at least in the case of the lily. In the same spirit, we want to
explain the final shape of the two above-mentioned sympetalous flowers quantitatively using a theoretical model together with measurements. Although the emergence of the determined geometric patterns is the result of a series of complex processes at the microscopic cellular level, the macroscopic structure of a soft tissue can sometimes be explained by the interplay between the tissue’s geometry and the stresses arising from anisotropic and non-uniform growth [8, 9]. In a continuum approach these slender tissues can be modeled as two-dimensional (2D) surfaces with an associated elastic energy. This energy contains a bending term accounting for out-plane deformations and a stretching term representing in-plane deformations [13]. The selected equilibrium shapes are then configurations that minimize the elastic energy.

Under certain assumptions that we will detail below, stretching is accommodated by adapting the Gaussian curvature $K_G$ of the surface, while the correct shape is selected by minimizing the bending energy. For some special cases of growth [8, 9, 14], the Gaussian curvature is zero almost everywhere but to get a handle on more general processes, we consider the case of constant and non-vanishing $K_G$. We show that, despite this simplistic hypothesis from a biological viewpoint, we obtain a real understanding of the complexity and richness of the morphology of living tissues. In particular, bell-shaped flowers such as the surfinia or the angel’s trumpet can be treated within this geometrical model. Even though the microscopic biological processes leading to these shapes are much more complicated, the simple problem considered here with imposed constant curvature sheds some light on the shape of such soft elastic tissues. Corresponding geometries being in fact ubiquitous in nature, we think that other organisms may also be treated within the presented framework.

2. Some basic facts of petal development

Flower development takes place in buds made of a calyx or simply the naked petals [15]. In this confined space, cell proliferation and differentiation intervene to simultaneously produce all the organs of the flower such as stamens and pistils, but also the structure of the petals involving the veins. Consider, for example, the petunia, which has already been studied by Jussieu around

Figure 1. Examples of sympetalous flowers. (a) A surfinia (Paris). (b) An Angel’s trumpet (brugmansia) (Morocco).
its petals are composed of the abaxial and the adaxial epidermis forming what is called a bilayer in the theory of soft elastic tissues. As a consequence, many simultaneous causes occurring during petal development inside the bud turn out to be responsible for elastic stresses: the confinement inside the bud, the role and nature of different cells leading to non-uniform growth, the juxtaposition of the two epidermal layers, but also the existence of veins.

Without any doubt one can thus claim that the petals inside the buds are highly stressed soft tissues originating from the growth process, which is controlled by genetics and biological processes at the cellular level. The opening of the bud typically takes a few hours only. It is a rapid process compared to the time scale of the plant and is probably stress-driven [12]. During this process petals continue to grow but only by cell expansion and not by cell proliferation.

Blooming flowers have inspired not only biological works and cross-disciplinary models such as [17], but also artists. One can find many videos on the Web where the blooming of different flower varieties is shown. They strongly suggest that the opening of a bud is like an act of liberation for the confined tissues which, by exploding the calyx, can reorganize themselves and relax the stresses. Our aim is to show that the final shape of flowers may appear as a way to relax the stresses by allowing further expansion and better spatial organization. The shape results from the minimization of the elastic energy, which has been stored during the growth process inside the bud, taking into account some constraints such as the attachment of the petals at the tube or the presence of veins.

3. Why growth fixes the Gaussian curvature

The length scale of a petal is about a centimeter, which is roughly a thousand times the scale of the cells. In this case, a mesoscopic viewpoint is valid that bridges the gap between the cellular level and the macroscopic scale of the petal. It simplifies the analysis and allows quantitative size predictions. Nevertheless, the theory of growing elastic soft tissue is rather recent compared with the age of elasticity theory. Already Galileo Galilei worked on the strength and fracture of beams, whereas it was Robert Hooke who discovered in 1660 the law of elasticity that now carries his name. In recent years, two complementary models have been developed to explain the shapes adopted by growing thin tissue. One model assumes that in-plane growth imposes length changes at every point of the surface, which can be anisotropic [18–21] and, closely related to it, metric variations imposed by the growth [9, 18, 22]. In general, a real surface cannot adjust with these imposed changes in the metric at any point and has to stretch. In this picture, growth acts as a source of curvature and can then be interpreted as a process where, at any time, the surface tries to fix the distance between two points at a given value. This implies that a so-called target metric exists [4, 18, 19, 22, 23], which fixes the Gaussian curvature $K_G$ due to the Theorema Egregium of Gauss (for a short introduction to Gaussian curvature, see appendix A.1).

The second model relies on a multiplicative decomposition of the deformation gradient [24]. This formalism turns out to be the most accurate theory for growth consistent with the requirements of the laws of elasticity. It mimics slow 3D growth, where the growth is represented by a tensor imposed by microscopic biological processes. This tensorial representation, common in 3D elasticity, allows us to introduce anisotropy and spatial inhomogeneities rather easily, especially for simple geometries such as spheres [25], cylinders [26–28] or horizontal layers [29, 30]. In the case of very slender and quasi-planar objects, a formulation derived from asymptotic analysis allows us to transform this formalism.
into a system of two coupled partial differential equations. Being an extension of the so-called Föppl–von Kármán equations of elasticity [7, 8, 13], the two equations describe the shape of the middle surface of the thin sample. The first equation concerns the deviation from the rest position induced by the growth and the second equation concerns the Airy potential or elastic potential. In this formulation growth acts as a source of two curvatures, Gaussian and mean curvature, which characterize the surface in 3D space. In general, the body tries to accommodate both curvatures to be in equilibrium but it is impossible for a surface to accommodate both curvatures exactly for an arbitrary choice of these curvatures. The imposed Gaussian curvature results from the stretching of the sample, whereas the imposed mean curvature is due to differential growth across the sample. Although generally weaker, this effect can be important for some cases such as the blooming of the lily [12]. It may contribute in the case of a bilayer and influences the bending of the tissue. However, the ratio of the bending energy versus the stretching energy is given by the square of the inverse of the thickness, showing that the stretching energy usually dominates for a well-behaved deformation field of the object. Consequently, the major contribution to the elastic energy of very thin tissues is due to the Gaussian curvature \( K_G \).

Both imposed curvatures can be calculated once the initial growth tensor is known, i.e. once the microscopic biological processes are well characterized. The last step turns out to be simply impossible. Moreover, such a theory has been proven for initially planar samples. We extend it to slender objects that are not planar initially. Our extension to arbitrary shells respects the requirements that the mathematical description of the surface is invariant when changing the coordinates. In a continuous and static or quasi-static approach we can claim that growth fixes preferred curvatures, the dominant one being the Gaussian curvature. One should, however, be aware that this curvature is only a preferred one from the viewpoint of elasticity since there exist other constraints we have to satisfy like the boundary conditions at the tube and at the veins which also perturb the shape of the flower.

4. Sympetalous flowers and Gaussian curvature

Sympetalous flowers roughly have the shape of a trumpet or bell with nice undulations at the border like petunias. We have decided to select flowers which respect as much as possible the condition that the Gaussian curvature is constant along the petal. We have found several candidates but here we focus on brugmansia and surfinia. Looking more closely at figure 1, one notices that brugmansia has very strong veins that exceed the border of the petals and look like reinforcing steel rods. One gets the impression that the petals of brugmansia are independent of each other and are strongly attached at the veins. Indeed, the curved surface reminds us of pieces of orange peel. In contrast, for the surfinia the nerves blend in with the petals. Since we assume that growth has induced a constant Gaussian curvature in both cases, we have to look more closely at surfaces with this property to model the shape of the flowers. Simple examples of such surfaces are the sphere, which has a constant positive \( K_G \), and the pseudosphere with constant negative \( K_G \) (for a short description of axisymmetric surfaces of constant Gaussian curvature, see appendix A.2). These two surfaces are ideal representations in the sense that they do not exhibit singularities, but we will see in the following that especially axisymmetric constant \( K_G \) surfaces are of particular interest for the flowers we consider here.

Clearly, most sympetalous flowers cannot be described by surfaces of constant Gaussian curvature even when we discard the final buckling at the ends of the petals. Some of them are
Figure 2. (a) The Gabon tulip tree (*Spathodea campanulata*), sympetalous flowers with obvious asymmetry and changes of Gaussian curvature. Photo by Pedro Acevedo-Rodriguez @ USDA-NRCS Plants database, courtesy of the Smithsonian Institution. (b) Montara manzanita (*Arctostaphylos montaraensis*): its shape seems to have an approximately constant positive Gaussian curvature surface everywhere, except for the tip, where the sign of curvature changes to avoid singularity. Copyright: Mark and Darice Dixon @ wildflowerswest.org.

not even symmetric, such as the flowers of the tulip trees (see figure 2(a)). Other flowers have a Gaussian curvature that changes sign, indicating a change in the spatial dependence of the growth process inside the bud [11, 12]. Focusing on this rather restrictive property seems to be too simple to reflect the complexity of flowers in nature. Nevertheless, the consequences of such a hypothesis from the viewpoint of elasticity with growth is far from trivial. It gives unexpected quantitative results that we will explain now.

5. Geometry and energy

As the mathematical representation of our surface, we use the vector function $X_s(u) \in \mathbb{R}^3$, where $u \in [0, 2\pi]$ and $s \in [0, s_f]$ are the local coordinates. To generate the surface, we consider a closed curve $X_0(u)$ that mimics the connection to the tube, whereas $X_{s_f}(u)$ corresponds to the free edge of the flower.

As explained previously and shown in [7, 8] for not too large elastic deformations, the growth of the tissue enforces a preferred Gaussian curvature. For simplicity, we consider the case of a constant preferred $K_G$ and call $S_0$ the corresponding surface. As long as the Gaussian curvature can be kept constant at every point, no stretching stresses will occur in the bulk of the surface and the only remaining elastic energy is the weak bending energy:

$$E_B = \int du \, ds \, \sqrt{g} \left( \frac{K}{2} - \kappa K_G \right).$$

(1)

Here $K$ is the mean curvature, $K_G$ the Gaussian curvature, $\kappa := \frac{h^3 Y_S}{12(1 - \nu^2)}$ is the bending rigidity and $\bar{\kappa} := -\frac{h^3 Y_S}{12(1 + \nu)}$ denotes the saddle-splay modulus. The coefficients $h$, $Y_S$ and $\nu$ are the thickness of the petal, its Young’s modulus and Poisson’s ratio, respectively. Due to the smallness of the bending moduli in $h^3$, $S_0$ can be considered as a quasi-stress-free configuration if $h$ is sufficiently small.

At the free edge ($s = s_f$), the elastic force and torque must cancel in equilibrium. This is generally not the case because of the bending term. Therefore, a boundary layer appears where
the petal breaks loose from the ideal mathematical surface re-inducing stretching stresses. The width $\Delta s$ of this layer has been estimated in [31] to scale as $\sqrt{h}$ for small $h$, so its elastic energy is negligible for the thicknesses considered.

On the other hand, we need to take into account the elastic energy of each vein, which is modeled as an isotropic, homogeneous elastic rod of circular cross section and fixed radius $r_0$. The elastic energy is given by $E_v = B/2 \int ds k^2$, where $k$ is the center line curvature of the rod and $B = \pi r_0^3 Y_v/4$ represents its bending modulus, with $Y_v$ denoting its Young’s modulus.

6. Axisymmetry

6.1. Geometrical construction of ideal surfaces

We need to find a way of easily constructing surfaces with a prescribed constant curvature. For simplicity, we first consider the axisymmetric case where the curve at the tube, $X_0(u)$, is a circle of radius $\rho_0$ in the horizontal $(x,y)$-plane. The surface tangent vectors $\partial_s X$ at $s = 0$ are not necessarily normal to this plane but can differ from the vertical $z$-direction by a constant radial tilt. We measure this tilt by an angle $\alpha$ from the horizontal plane. In this case

$$X_s(u) = (\rho(s) \cos u, \rho(s) \sin u, z(s))^T,$$

(2)

with the condition

$$(\partial_sz)^2 + (\partial_s\rho)^2 = 1,$$

(3)

if $s$ is the arclength. From classical textbooks of differential geometry, we know that the Gaussian curvature is given by [32]

$$K_G = \partial_s[(\partial_sz)^2]/(2\rho),$$

(4)

and for constant $K_G$ during growth, we obtain $(\partial_s\rho)^2 + K_G(\rho^2 - \rho_0^2) = \cos^2 \alpha$, and the following explicit solutions:

$$\rho(s) = \rho_0 \cos\left(\sqrt{K_G}s\right) + \frac{\cos \alpha}{\sqrt{K_G}} \sin\left(\sqrt{K_G}s\right),$$

(5)

$$z_g(s) = \frac{A}{\sqrt{K_G}} \varepsilon\left(\arcsin\left[C\sqrt{K_G}\rho(s)\right] B\right),$$

(6)

where $\varepsilon(s,k)$ denotes the elliptic integral of the second kind [33] and $A$, $B$ and $C$ are non-dimensional functions of $\alpha$ and $\rho_0^2 K_G$. Thus, the explicit solution for $z(\rho)$ that satisfies the initial conditions $z(\rho_0) = 0$ and $z'(\rho_0) = \tan(\alpha)$ is given by $z(\rho) = z_g(\rho) - z_g(\rho_0)$.

In the following, all lengths and curvatures will be scaled with $\sqrt{|K_G|}$, i.e. $\tilde{s} := s\sqrt{|K_G|}$, $\tilde{K}_\perp := K_\perp/\sqrt{|K_G|}$, etc. For a homogeneous elastic membrane the only degrees of freedom are the sign of $K_G$ and the initial conditions $\rho_\th$ and $\alpha$. From [32], we know that these surfaces with constant Gaussian curvature may exhibit shape singularities that we need to consider carefully. That is why we must distinguish these surfaces depending on the sign of $K_G$.

6.2. Surfaces with negative Gaussian curvature

First we consider the negative $K_G$ case, which gives surfaces called pseudospherical surfaces. Singularities arise because the hyperbolic plane cannot be immersed completely into $\mathbb{R}^3$ [34]. Typically, these singularities are cuspidal edges that themselves can exhibit series of cusps (the so-called swallowtail points). The pseudosphere represented in the inset of figure 3 has a circular...
Figure 3. Total bending energy $\tilde{E}_T$ for $m = -1/2$, $b = 300$, $\alpha = \pi/2$, $y = 3$, $n = 5$, $\tilde{h} = 0.009$, $\tilde{r}_0 \simeq 6\tilde{h}$ and different values of $\tilde{\rho}_0$. For these parameters, $\tilde{E}_V/\tilde{E}_T \approx 10\%$ in the linear regime (i.e. for small $\tilde{\sigma}_f$). Inset: axisymmetric pseudosphere with five veins.

cusp due to the imposed axisymmetry. It is located at a distance $\tilde{\rho}_c$ from the center of the tube given by

$$\tilde{\rho}_c := \tilde{\rho}(\tilde{\sigma}_c) = \sqrt{\tilde{\rho}_0^2 + \sin^2 \alpha}$$

with

$$\tilde{\sigma}_c = \text{arccosh} \left( \frac{\tilde{\rho}_0 \sqrt{\tilde{\rho}_0^2 + \sin^2 \alpha} - \cos \alpha}{\tilde{\rho}_0^2 - \cos^2 \alpha} \right).$$

At this cusp, the curvature in the azimuthal direction $\tilde{K}_\parallel = -\partial_z/(\rho/|\mathbf{K}_G|)$ vanishes and the other $\tilde{K}_\perp = -\partial_{\rho}(\partial_z)/|\mathbf{K}_G|$ diverges, with the surface converging towards the horizontal plane. The physical elastic surface cannot follow the mathematical one anymore since close to this singularity the bending energy of the surface diverges, contrary to our main hypothesis of the weakness of this energy. The real tissue will respond by relinquishing axisymmetry and the petal will again deviate from the ideal mathematical surface. The constraint on the value of the Gaussian curvature will be given up locally and stretching will then play a role as well appearing before the singularity is reached. This could explain why the flowers do not remain pseudospherical and axisymmetric but exhibit curly patterns at the edge, giving rise to the beauty and diversity of nature. A study of these shapes would go beyond the scope of this paper but can be achieved by using numerical tools such as a bead–spring model [4].

6.3. The role of the veins

Consider now that this axisymmetric surface contains $n$ veins whose center lines coincide with meridian curves on the surface (curves of constant $u$). If the growth process stops at $\tilde{\sigma}_f$ before the singularity is reached, the bending energies $\tilde{E}_B := E_B/\kappa$ and $\tilde{E}_V := E_V/\kappa$ can be exactly calculated as a function of $\tilde{\sigma}_f$, $\tilde{\rho}_0$, $n$ and $\alpha$. When $\alpha = \pi/2$ the total bending energy
\( \ddot{E}_T = \ddot{E}_b + \ddot{E}_V \) can be expressed as

\[
\ddot{E}_T = \pi \tilde{\rho}_c^2 \left[ \frac{\arctan (\sinh \tilde{s}_f)}{\tilde{\rho}_0} + \text{arctanh} (\tilde{\rho}_0 \sinh \tilde{s}_f) \right] - \frac{1}{2} n b \tilde{s}_f + \frac{1}{2} n b \tilde{\rho}_c \text{arctanh} (\tilde{\rho}_c \tanh \tilde{s}_f) - \pi (4 + 2m) \tilde{\rho}_0 \sinh \tilde{s}_f,
\]

where \( m := \tilde{\kappa}/\kappa \) and \( b := B \sqrt{|K_G|}/\kappa \) (see figure 3). For a thin shell, \( m \) is given by \( v - 1 \), where \( v \approx 1/2 \) for incompressible living elastic tissues [13]. For a homogeneous elastic rod, \( b \) is a function of \( v, h, r_0 \) and the ratio \( y := Y_V/Y_S \). The parameter \( b \) can be estimated using very simple geometric arguments and the mechanical data available for typical flowers [35, 36]. Very unfortunately, these biomechanical data and geometrical measurements are rather sparse in the botanic literature. For \( \alpha \neq \pi/2 \), the expression for \( \ddot{E}_T \) is more complicated but remains linear in \( s \) for small \( \tilde{s}_f \). In this regime \( \ddot{E}_T \approx \tilde{C}(\tilde{\rho}_0, \alpha, m, n, h, y)\tilde{s}_f \), where \( C \) is a complicated function of the parameters. The energy minimization selects an optimal initial radius \( \tilde{\rho}_0^{\text{min}} \) which is a function of \( \alpha, m, n, h \) and \( y \). Accordingly, the variational elastic method gives us a relation between geometric quantities measured from the primordium, which can be experimentally checked if the Gaussian curvature is known.

### 6.4. Test of our model

We apply our strategy to a variety of petunia—the surfinia—which resembles a pseudosphere with five principal veins (see again figure 1(a)). In the literature, we found only one paper with experimental measurements on buds and petals but unfortunately with partial data. It concerns a variety of Petunia called *Petunia integrifolia* [36]. We bought a commercial plant of surfinia and made the measurements ourselves. All flowers of the plant (approximately 20) have a Gaussian curvature of approximately \( K_G = -1 \text{ cm}^{-2} \). This justifies our claim that the surfinia is a good candidate for our model. To compare our theory with nature, we have also measured geometric quantities such as the radius at the primordium \( \rho_0 \), the radius at the curling zone \( \rho_c \), the height at the curling zone \( z_c \) and the angle \( \alpha \) of each flower. We found that

\[
\rho_0 \simeq 0.09 \text{ cm}, \quad \rho_c \simeq 1.1 \text{ cm}, \quad z_c \simeq 2.75 \text{ cm} \quad \text{and} \quad \alpha \simeq \pi/2,
\]

with a rather good constancy from one flower to the other. Additionally, we have measured the length \( s_c \) and the radius \( r_0 \) of the veins. We obtain

\[
s_c \simeq 3.4 \text{ cm}, \quad r_0 \simeq 6h \simeq 0.054 \text{ cm},
\]

in agreement with a naive geometric estimation at the primordium. Taking into account a published estimation for the ratio between Young’s moduli [35]: \( y = 3 \), choosing \( \alpha = \pi/2 \), we calculate the following geometrical parameters for the petal:

\[
\tilde{\rho}_0^{\text{min}} = 0.1 \text{ cm}, \quad \rho_c = 1.0 \text{ cm} \quad \text{and} \quad z_c = 2.8 \text{ cm},
\]

and for the veins: \( s_c = 3.1 \text{ cm}. \rho_c \) is calculated using equation (7), \( z_c \) with equations (6) and (8), in rather good agreement with our measurements on these flowers (see equations (10) and (11)).

### 6.5. Stability of axisymmetric shapes

If axisymmetry is relaxed for these surfaces with constant negative curvature, the surface can, nevertheless, have a constant Gaussian curvature at every point. However, the shape of the
surface has to be determined numerically since no analytical solutions are known. We have shown for this case [37] that the surface \( \bf X_s(u) \) satisfies the equation

\[
\partial_u \partial_s \bf X = (n \cdot \partial_u \partial_s \bf X)^{-1} \left[ (n \cdot \partial_u \partial_s \bf X)^2 - g K_G \right] n,
\]

where \( n \) is the normal vector of the surface and \( g \) its metric determinant\(^4\).

If we allow small deformations from the initial circle of radius \( \tilde{\rho}_0 \), the new initial curve can be expanded into \( n \) modes \( \bf X_n^0(u, \epsilon) = \rho_n^0(\epsilon)[1 + \epsilon \cos(nu)][\cos u, \sin u, 0]^T \). We keep the total arc length of this curve fixed at \( \tilde{L}_0 = 2\pi \tilde{\rho}_0 \), which implies that \( \tilde{\rho}_n^0(\epsilon) = \tilde{\rho}_0/[1 + (1 + n^2)\epsilon^2/2] \).

Since the curvature of the curve has to be positive for all \( u \) to satisfy the constraint on \( K_G \), there is a maximum \( \epsilon_n^{\text{max}} \) that decreases with increasing \( n \). The bending energy of the surface without veins can be calculated numerically and compared with the axisymmetric case. One finds that it increases with \( \epsilon^2 \) for a fixed \( n \) and \( \tilde{s}_f \) if \( \alpha = \pi/2 \). Consequently, the axisymmetric shape is preferred.

7. A piecewise surface

For constant positive \( K_G \), a good axisymmetric candidate for representing bell-shaped flowers is the spindle surface [32] but it contracts into a singular point during its growth. Nature has found two ways to solve this problem: (i) by interrupting the flower growth as for Montara Manzanita (\textit{A. montaraensis}) (http://plants.usda.gov/), whose Gaussian curvature can be estimated to be roughly constant and positive (see figure 2(b)) or (ii) by dividing the petal into pieces attached with veins (see figure 1(b)), each piece keeping approximately a constant positive curvature \( K_G \).

The main question concerns the optimal number of pieces\(^5\).

We introduce \( n \) ridges connecting \( n \) identical surface pieces (see figure 4), the initial curve of each piece being given by a circular arc of radius \( \tilde{\rho}_0 \). Then, each arc is connected to two

---

\(^4\) An equivalent equation specialized to Gaussian normal coordinates can be found in [38].

\(^5\) A similar problem of self-assembly has been studied experimentally [39] and analytically [40] using initially planar pieces of an elastic sheet with various boundaries. The main conclusion of the theoretical work is that the elastic energy focuses on the edges and depends strongly on the initial planar shape. Being similar from the viewpoint of the principles, our initial configuration is geometrically very different and can thus strongly modify the conclusions.
Figure 5. The elastic energy \( E/(Y_S h) \) of a surface with veins of radius \( \tilde{r}_0 = 0.02 \) as a function of \( n \) for \( \alpha = \pi/2 \) and \( \tilde{s}_t = 0.27 \). The initial length of the curve is set to \( \tilde{L}_0 = 1.5 \). The different curves represent different values of the thickness \( \tilde{h} \): \( \tilde{h}_1 = 0.012, \tilde{h}_2 = 0.027, \tilde{h}_3 = 0.032, \tilde{h}_4 = 0.037, \tilde{h}_5 = 0.042 \) and \( \tilde{h}_6 = 0.052 \). For realistic measures of mechanical parameters (\( m = -1/2, Y_S = 1 \) MPa, \( Y_V = 3 \) MPa and \( \tilde{h} \approx 2\tilde{r}_0 \)), the energy is minimal for \( n = 4, 5 \) or 6.

neighbor at joints that are a distance \( \tilde{R}_0 \) away from the center. If we assume that the length \( \tilde{L}_0 \) of the entire curve is independent of \( n \), \( \tilde{R}_0 \) is given by \( \tilde{R}_0 \sin [\tilde{L}_0/(2\tilde{\rho}_0 n)]/\sin (\pi/n) \).

The shape of one piece can be found by cutting out a section of an axisymmetric surface of positive \( K_G \) with two planes that meet at an angle of \( 2\pi/n \) (see again figure 4). We observe that at some value of \( \tilde{s}_t \), which increases with \( n \), the surface leaves the ridges and bulges inwards. At this point the real surface cannot fulfill the constraint on \( K_G \) anymore and has to stretch.

However, the selection of the number \( n \) of veins will happen at the beginning of the growth process. We consider again the elastic energy to find optimal values. The pure bending term diverges at the joints. To regularize the surface we thus suppose that \( n \) veins of a given radius \( \tilde{r}_0 \) exist at each ridge (see figure 4). They are wrapped by the surface in such a way that the surface does not have a kink at the contact lines. Note that this regularization violates the restriction of constant positive \( K_G \) and stretching has to be taken into account as well. If the wrapping is interpreted as an elastic relaxation from the original reference configuration with sharp ridges, the energy of the ridges reduces to [18]

\[
E_{\text{ridges}} = \int_0^{\tilde{s}_t} \int_{u_c(s)}^{\pi/n} 2n\sqrt{G(n)} \left[ h_1^2 A^{abcd}(g_{ab} - G_{ab})(g_{cd} - G_{cd}) + h^3 \frac{1}{24} A^{abcd} k_{ab} k_{cd} \right] du \, ds, \tag{14}
\]

where \( g_{ab} \) and \( k_{ab} \) are the metric and the extrinsic curvature tensor of the final surface, whereas \( G_{ab} \) is the metric of the reference state and \( G \) its determinant. A combination of its products defines the elastic tensor \( A^{abcd} \) [18].
The total elastic energy $E$ is thus given as the sum of $E_{\text{ridges}}$ and the bending energy of the free surface. We minimize this energy as a function of $n$ for different values of $h$. The remaining geometric and elastic parameters involved in the calculation have been chosen in agreement with the mechanical data obtained for typical flowers [35]. Our results are depicted in figure 5 in which the minimal energy is obtained when $n = 4, 5$ or $6$. These selected symmetries are corroborated in nature where most of the flowers exhibit a number of petals in this range ($\sim 64\%$) [41]. In this way, when the living tissue is constrained to grow with constant and positive $K_G$, the possible singularities are replaced by a discrete number of veins connecting isometric spherical surfaces. We note that although figure 5 allows us to elucidate the minimal value of $n$, the curves are not very sharp around it. Proceeding as for the axisymmetric case assuming that veins are well described by elastic rods, a simple estimation of their energy gives us $E_V/Y_s h \simeq 0.001n$ (i.e. $\sim 40\%$ of the total energy for $n = 5$ and $\tilde{h} = 0.042$). Thus, the total elastic energy will obviously display a sharper minimum.

8. Conclusions

Using very simple ideas involving geometry and elasticity, we have explained some essential features concerning the morphology and the selection of symmetries during the growth of living soft tissues. In particular, we have compared our models with the shape of certain flowers. We supposed that the growth process imposes a constant Gaussian curvature on the tissue. This hypothesis allows us to understand the global shapes adopted by sympetalous bell-shaped flowers, even if nature modifies slightly their Gaussian curvature during the growth process. In the case of $K_G = -1$, the preferred shape is axisymmetric with respect to its isometric perturbations. As soon as singularities are reached, stretching and bending will play a role, causing undulations of the final shape. If the surface has $K_G = +1$ it exhibits ridges where the stretching is concentrated. We state that nature can relax these stresses by veins, as suggested in other contexts [42]. In this case the selected symmetries are corroborated in nature where most flowers exhibit four, five or six veins. This is in line with other interpretations which rest on microscopic processes such as phyllotactic processes originating in the bud.

Acknowledgments

This work was partially supported by the National Science Foundation under grant no. NSF PHY05-51164. MT acknowledges financial support from CONICYT.

Appendix. Gaussian curvature

A.1. Definition

At each regular point $P$ of a smooth surface one can define the Gaussian curvature $K_G$ as the product of the two principal curvatures (see figure A.1). These are the inverse of the two principal radii of curvature. The two principal radii can be obtained geometrically by looking at the intersection of the surface with a normal plane. At the point $P$ one can define one normal direction but an infinity of normal planes obtained by a rotation around the normal. Once we
**Figure A.1.** The Gaussian curvature is defined as the product of the two principal curvatures at each point of a surface, i.e. \( |K_G| = \frac{1}{R_1} \cdot \frac{1}{R_2} \) with \( K_G < 0 \) in this figure.

**Figure A.2.** Spherical surfaces. (a) The sphere is the classical surface of positive constant Gaussian curvature. (b) The spindle surface also has a constant and positive \( K_G \) but it also exhibits two cuspidal singularities at the vertical axis. (c) The bulge surface has two circular singularities at a given distance from the center axis.

perform the rotation, the curve of intersection between the surface and the normal plane has a radius of curvature which varies, the two extremal values defining the principal radii. The sign of the radius of curvature depends on whether the curve bends away from or towards the normal. The sign of the Gaussian curvature is thus positive when the surface is convex or concave in \( P \) and negative if the surface looks like a saddle locally.
A.2. Axisymmetric surfaces of constant Gaussian curvature

A well-known example of an axisymmetric surface of constant positive Gaussian curvature is the sphere. What is less known is that one can find other types of axisymmetric surfaces with constant $K_G > 0$ [32]: the spindle surface looks like a rugby ball with a singularity at the vertical axis, whereas the bulge surface contains circular singularities at a distance away from the axis (see figure A.2).

A similar picture is found for axisymmetric surfaces of constant negative Gaussian curvature: the equivalent of the sphere is the pseudosphere: it has a point-like singularity on the vertical axis at minus infinity and a second circular singularity at a finite distance away from the vertical axis. The equivalent of the spindle surface is a pseudospherical surface with the point-like singularity at one point of the vertical axis. Finally, one can also find a pseudospherical surface which never reaches the vertical axis similar to the bulge surface (see figure A.3).

References

[1] Wentworth Thompson D 1992 *On Growth and Form* (Mineola, NY: Dover)
[2] Da Vinci L 1970 *The Notebooks of Leonardo Da Vinci* ed J P Richter (Mineola, NY: Dover)
[3] Rolland-Lagan A G, Bangham J A and Coen E 2003 Growth dynamics underlying petal shape and asymmetry *Nature* **422** 161
[4] Marder M and Papanicolaou N 2006 Geometry and elasticity of strips and flowers *J. Stat. Phys. A* **125** 1069
[5] Nechaev S and Voituriez R 2001 On the plant leaf’s boundary, ‘jupe à godets’ and conformal embeddings *J. Phys. A: Math. Gen.* **34** 11069
[6] Marder M 2003 The shape of the edge of a leaf *Found. Phys.* **33** 1743
[7] Dervaux J, Ciarletta P and Ben Amar M 2009 Morphogenesis of thin hyperelastic plates: a constitutive theory of biological growth in the Föppl–von Kármán limit *J. Mech. Phys. Solids* **57** 458
[8] Dervaux J and Ben Amar M 2008 Morphogenesis of growing soft tissues *Phys. Rev. Lett.* **101** 068101
[9] Müller M M, Ben Amar M and Guven J 2008 Conical defects in growing sheets *Phys. Rev. Lett.* **101** 156104
[10] Rijpkema A, Gerats T and Vandenbussche M 2006 Genetics of floral development in *Petunia* *Adv. Bot. Res.* **44** 237

New Journal of Physics **14** (2012) 085014 (http://www.njp.org/)
[11] Reale L, Porceddu A, Lanfaloni L, Moretti C, Zenoni S, Pezzotti M, Romano B and Ferranti F 2002 Patterns of cell division and expansion in developing petals of *Petunia hybrida* Sex. Plant Reprod. **15** 123

[12] Liang H and Mahadevan L 2011 Growth, geometry, and mechanics of a blooming lily *Proc. Natl Acad. Sci. USA* **108** 5516

[13] Landau L D and Lifshitz E M 1986 *Theory of Elasticity* (Oxford: Heinemann)

[14] Stoop N, Wittel F K, Ben Amar M, Müller M M and Herrmann H J 2010 Self-contact and instabilities in the anisotropic growth of elastic membranes *Phys. Rev. Lett.* **105** 068101

[15] Reid M S 2005 Flower development: from bud to bloom *Proc. 8th IS Postharvest Phys. Ornamentals, Acta Hort* **669** 105

[16] Jussieu A 1803 Sur le *Pétonia*, genre nouveau de la famille des plantes solanées *Ann. Muséum Natl d'Histoire Naturelle* **2** 214

[17] Barrio R A, Hernández-Machado A, Varea C, Romero-Aris J R and Álvarez-Buylla E 2010 Flower development as an interplay between dynamical physical fields and genetic networks *PLoS One* **5** e13523

[18] Efrati E, Sharon E and Kupferman R 2009 Elastic theory of unconstrained non-Euclidean plates *J. Mech. Phys. Solids* **57** 762

[19] Sharon E and Efrati E 2010 The mechanics of non-Euclidean plates *Soft Matter* **6** 5693

[20] Dias M A, Hanna J A and Santangelo C D 2011 Programmed buckling by controlled lateral swelling in a thin elastic sheet *Phys. Rev. E* **84** 036603

[21] Kim J, Hanna J A, Byun M, Santangelo C D and Hayward R C 2012 Designing responsive buckled surfaces by halftone gel lithography *Science* **335** 1201

[22] Guven J and Müller M M 2008 How paper folds: bending with local constraints *J. Phys. A: Math. Theor.* **41** 055203

[23] Klein Y, Efrati E and Sharon E 2007 Shaping of elastic sheets by prescription of non-Euclidean metrics *Science* **315** 1116

[24] Rodriguez E K, Hoger A and McCulloch A D 1993 Stress-dependent finite growth in soft elastic tissues *J. Biomech.* **27** 455–67

[25] Ben Amar M and Goriely A 2005 Growth and instability in elastic tissues *J. Mech. Phys. Solids* **53** 2284

[26] Ciarletta P and Ben Amar M 2012 Growth instabilities and folding in tubular organs: a variational method in nonlinear elasticity *Int. J. Nonlinear Mech.* **47** 248

[27] Ciarletta P and Ben Amar M 2012 Pattern formation in fiber-reinforced tubular tissues: folding and segmentation during epithelial growth *J. Mech. Phys. Solids* **60** 525

[28] Ciarletta P and Ben Amar M 2012 Surface instabilities of soft cylinders: competition between elastic growth and capillarity *Soft Matter* **8** 1760

[29] Ben Amar M and Ciarletta P 2010 Swelling instability of surface-attached gels as a model of soft-tissue growth under geometric constraints *J. Mech. Phys. Solids* **58** 935

[30] Ciarletta P and Amar M 2012 Papillary networks in the dermal–epidermal junction of skin: a biomechanical model, Special Issue: ‘Recent Advances on the Biomechanics of Growth and Remodeling’ *Mech. Res. Commun.* **42** 68

[31] Efrati E, Sharon E and Kupferman R 2009 Buckling transition and boundary layer in non-Euclidean plates *Phys. Rev. E* **80** 016602

[32] Struik D J 1988 *Lectures on Classical Differential Geometry* (Mineola, NY: Dover)

[33] Struik D J 1988 *Lectures on Classical Differential Geometry* (Mineola, NY: Dover)

[34] Abramowitz M and Stegun I A (ed) 1970 *Handbook of Mathematical Functions* (New York: Dover)

[35] Hilbert D 1901 Über Flächen von konstanter Gausscher Krümmung *Trans. Am. Math. Soc.* **2** 87

[36] Kobayashi H, Daimaruya M and Fujita H 2003 Unfolding of morning glory flower as a deployable structure *Solid Mech. Appl.* **106** 207

[37] Ando T, Ishikawa N, Watanabe H, Kokubun H, Yanagisawa Y, Hashimoto G, Marchesi E and Suarez E 2005 A morphological study of the *Petunia integrifolia* complex (Solanaceae) *Ann. Bot.* **96** 887

**New Journal of Physics** **14** (2012) 085014 (http://www.njp.org/)
[37] Trejo M, Ben Amar M and Müller M M 2009 Hamiltonian formulation of surfaces with constant Gaussian curvature *J. Phys. A: Math. Theor.* **42** 425204

[38] Santangelo C D 2009 Buckling thin disks and ribbons with non-Euclidean metrics *Europhys. Lett.* **86** 34003

[39] Boncheva M, Andreev M A, Mahadevan L, Winkelman A, Reichman D R, Prentiss M G, Whitesides S and Whitesides G M 2005 Magnetic self-assembly of three-dimensional surfaces from planar sheets *Proc. Natl Acad. Sci. USA* **102** 3924

[40] Alben S and Brenner M P 2007 Self-assembly of flat sheets into closed surfaces *Phys. Rev. E* **75** 056113

[41] Nishiyama Y 2004 Why is a flower five-petaled? *J. Sci. Educ. Tech.* **13** 107

[42] Couder Y, Pauchard L, Allain C, Adda-Bedia M and Douady S 2002 The leaf venation as formed in a tensorial field *Eur. Phys. J. B* **28** 135