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INVITED SPECIAL PAPER

A GENERIC GEOMETRIC TRANSFORMATION THAT UNIFIES A WIDE RANGE OF NATURAL AND ABSTRACT SHAPES¹

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To study forms in plants and other living organisms, several mathematical tools are available, most of which are general tools that do not take into account valuable biological information. In this report I present a new geometrical approach for modeling and understanding various abstract, natural, and man-made shapes. Starting from the concept of the circle, I show that a large variety of shapes can be described by a single and simple geometrical equation, the Superformula. Modification of the parameters permits the generation of various natural polygons. For example, applying the equation to logarithmic or trigonometric functions modifies the metrics of these functions and all associated graphs. As a unifying framework, all these shapes are proven to be circles in their internal metrics, and the Superformula provides the precise mathematical relation between Euclidean measurements and the internal non-Euclidean metrics of shapes. Looking beyond Euclidean circles and Pythagorean measures reveals a novel and powerful way to study natural forms and phenomena.

Key words: modeling; Superformula.

Form in plants and other organisms has intrigued students of nature for a long time. The molecular processes underlying morphogenesis are being unraveled with increasing success. But the elucidation of biophysical processes and mathematical rules underlying morphogenesis and morphology is also a priority since these largely undeveloped processes and rules will provide the necessary links between gene action and form (Green, 1999).

Spherical, circular, and cylindrical forms and shapes are commonly observed in nature (D'Arcy Thompson, 1917; Wainwright, 1988). More complex forms in biology can also be analyzed in terms of circles and harmonics through elliptic Fourier analysis (Kuhl and Giardina, 1982; Kincaid and Schneider, 1983). This method has also been applied to plant leaves (McLellan, 1993). Other more recent approaches to describe natural forms and patterns include algorithms that can generate virtual plants (Prusinkiewicz and Lindenmayer, 1989; Prusinkiewicz, 1998). Dynamical modeling, such as patterning in shells (Meinhardt, 1998) or whorl morphogenesis in dasy-cladalean algae (Dumais and Harrison, 2000), also has been shown to be algorithmic.

With the advancement of computer technology, models are becoming increasingly sophisticated for imaging living organisms or their parts. Visualization methods for biological organisms or organs can be implemented using a range of different algorithms and methods. Geometric morphometrics has become a rapidly expanding field of research in biology (Jensen, 1990; Bookstein, 1996; Rohlf, 1996), but in plant leaves variability can be very large even within one species or genus. It should also be noted, however, that while algorithms can yield perfect virtual plants, it is impossible to find an algorithm that exactly describes a real plant (Van Oystaeyen et al., 1996).

In this paper I present a geometrical approach that permits

description of many abstract, naturally occurring and man-made geometrical shapes and forms with one surprisingly simple generic formula. I will show that many geometrical forms, both in nature and culture, can be interpreted as modified circles. In a most general way, I will refer to these shapes as Supershapes. They are not only useful for modeling, but also allow insight into why certain forms grow as they do.

MATERIALS AND METHODS

The circle and square, ellipse and rectangle are all members of the set of superellipses (Loria, 1910; Gridgeman, 1970) defined by:

$$|x/a|^n + |y/b|^n = 1 \tag{1}$$

The main disadvantage of superellipses is their limited symmetry. The use of polar coordinates $r = f(\phi)$ by substituting of $x = r \cdot \cos \phi$ and $y = r \cdot \sin \phi$, and the introduction of the argument $m/4$ of the angle ϕ introduces specific rotational symmetries. The exponent n can also differ. This leads to Eq. 2, for n_1 and $m \in \mathfrak{R}^+$ (positive real numbers) and for $a, b \in \mathfrak{R}^+_0$ (positive real numbers but not zero).

$$r(\phi) := \frac{1}{\left\{ \left[\left(\frac{1}{a} \cos \left(\phi \frac{m}{4} \right) \right)^{n_2} + \left(\frac{1}{b} \sin \left(\phi \frac{m}{4} \right) \right)^{n_3} \right]^{1/n_1} \right\}} \tag{2}$$

For $n_1 = n_2 = n_3 = 2$ and $m = 4$ in Eq. 2, an ellipse is obtained. A circle is obtained when additionally $a = b$, which can also be described by Eq. 1. But instead of dividing the plane in four sectors or quadrants only, as in Eq. 1, which is the major drawback of superellipses, the plane can now be divided into a number of sectors equal to m using Eq. 2. As with supercircles (Eq. 1), the absolute values cause a repetition of the graph of the first sector ($0 - 2\pi/m$) in subsequent sectors. Asymmetrical shapes can be generated by selecting different parameter values in different sectors (for example $n = 2$ in first and second quadrant, $n = 2.54$ in the third, and $n = 1.989$ in the fourth using Eq. 1).

Eq. 2 modifies the metrics of functions and all associated graphs. The situation just described above can be considered as a modification of a constant function $R = 1$ (deformation of the unit circle), but other functions $f(\phi)$ can be used as well. When combined with other functions, the Superformula will modify the metrics of these functions and all associated graphs (Eq. 3).

¹ Manuscript received 22 January 2002; revision accepted 22 October 2002. This work is dedicated to my fathers. My sincerest thanks go to Tom Gerats and Bert Beirinckx for remarks, support, and encouragement.
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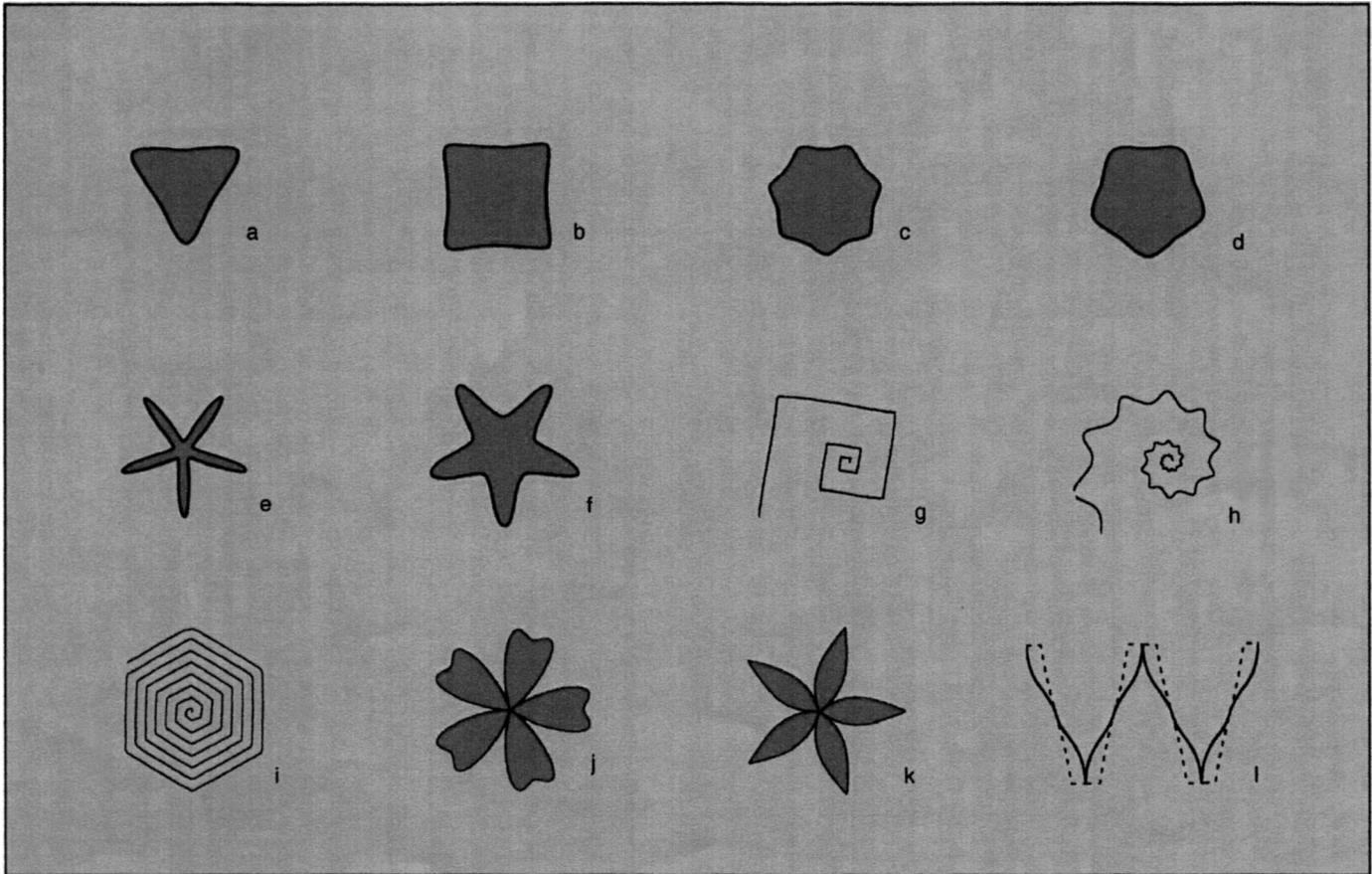


Fig. 1. Natural supershapes generated by Eq. 2. The numbers between brackets refer to (m; n₁; n₂ = n₃). The value of a = b is 1 except for Fig. 1e where a = b = 10. (a) *Nuphar luteum* petiole (3; 4.5; 10); (b) *Scrophularia nodosa* stem (4; 12; 15); (c) *Equisetum* stem (7; 10; 6); (d) Raspberry (5; 4; 4); (e) Starfish 1 (5; 2; 7); (f) Starfish 2 (5; 2; 13). (g–h) spirals (r = e^{0.2φ}) modified by Eq. 2. Values of m and n are (g) m = 4; n₁ = 100; (h) m = 10; n₁ = 5. (i) Spiral of Archimedes (r = φ) modified by Eq. 2 with (m = 6, n₁ = 250; n₂ = n₃ = 100). (j–k) Modified Rose curves [cos (m.φ)] with m = 2.5 inscribed in polygons with values of m; n₁; n₂ = n₃, (j) 2.5; 1/1.3; 2.7, (k) 2.5; 5; 5. (l) Super- and subcosines: cosine functions (cos φ) inscribed in polygons with values of (m; n₁; n₂ = n₃) = (4; 1; 1), supercosines, solid line and (4; 25; 25), subcosines, dashed line.

$$r = f(\phi) \frac{1}{\sqrt{\left(\frac{1}{a} \cos\left(\frac{m}{4}\phi\right)\right)^{n_2} + \left(\frac{1}{b} \sin\left(\frac{m}{4}\phi\right)\right)^{n_3}}} \quad (3)$$

This generic equation generates a large class of super- and subshapes (Fig. 1), including the super- and subcircles as special cases. I therefore propose the name Superformula for Eq. 3 based on the notion of supercircles, superellipses, and superquadratics.

Eqs. 2 and 3 can also be generalized in more than two dimensions extending to three- or higher dimensional spaces. Alternatively, two-dimensional shapes can also be described in a multidimensional parameter space \mathfrak{R}^6 with the various parameters (a, b, n₁, n₂, n₃, m).

Eq. 2 is a conversion formula between the internal metrics of shapes and our classical Euclidean plane (or space). Given a shape, the parameters of the formula can be obtained by performing a limited number of measurements. For symmetrical shapes (a = b and n₁ = n₂ = n₃ as in Table 1, columns 2 and 4), two measurements are sufficient, one at 0° or 2π/m (distance R from origin or centroid to shape) and one at π/m (distance S from origin or centroid to shape) using Eq. 4, which is obtained by solving Eq. 2 for n (with a = b and n₁ = n₂ = n₃ for specific angles). Angles other than k.2π/m or k.π/m can be used, but R and S generally are minimum and maximum distances.

$$\frac{1}{\ln\left(\frac{R}{S}\right) \frac{1}{\ln(2)} + \frac{1}{2}} := n \quad (4)$$

If the values of the parameters differ (Table 1, columns 3, 5, and 6), extra measurements will generate more equations that need to be solved. The parameters can then be found using methods such as maximum likelihood estimates and nonlinear optimization algorithms, which are beyond the scope of this paper.

RESULTS

Integer and non-integer rotational symmetries—The variable m (Eq. 2) can define zerogons (m = 0), monogons (m = 1), and diagons (m = 2), as well as triangles, squares, and polygons with higher rotational symmetries. The argument m allows the orthogonal axes to fold in or out like a fan and determines the number of points fixed on the unit circle (or ellipse for a ≠ b) and their spacing. These points will always remain fixed.

The values of n₂ and n₃ determine whether the shape is inscribed or circumscribed in the unit circle. For n₂ = n₃ < 2 the shape is inscribed (subpolygons), while for n₂ = n₃ > 2 the shape will circumscribe the circle (superpolygons). A circle is defined either as a zero- or zero-angle for any value of n₁, given m = 0, or for any rotational symmetry m given that n_{2,3} = 2. The value of n₁ will further determine the shape.

TABLE 1. Examples of various abstract shapes. Modification of parameters of Eq. 2 for positive integer rotational symmetries m from 0 to 8 for $R = 1$.

Rotational symmetry m	$n_1 = n_2 = n_3 = 1$	$n_1 = 1000$	$n_1 = n_2 = n_3 = 1/2$	$n_1 = 30$	$n_1 = 80$	n_i as column 3	
		$n_2 = n_3$		$n_2 = n_3 = 15$	$n_2 \neq n_3$	$a = 2$	
0			2				
1			500				
2			500				
3			1980				
4			1000				
5			620				
6			390				
7			320				
8			250				

Corners can be sharpened or flattened and the sides can be straight or bent (convex or concave) as shown in Table 1.

Subpolygons are inscribed in the circle (Table 1, columns 2 and 4) and rotated by π/m relative to superpolygons, circumscribing the circle (Table 1, columns 3 and 5). Interestingly, when subpolygons transform into superpolygons (and vice versa), corners transform into sides, and sides into corners, because of the fixed points on the unit circle. Equal shapes are generated that close after one rotation ($0 - 2\pi$) by selecting zero or a positive integer for m . Exactly the same shape is generated for every subsequent rotation by 2π .

This changes when further changes of Eq. 2 are applied, such as when the ratio n_2/n_3 varies (Table 1, column 6) or when the values of a and b differ (Table 1, column 7). Also, when m is positive but not an integer, the shape generated does not close after one rotation. If m is a rational number, the shape will close after a number of rotations equal to the denominator of m . The numerator of m determines the number of angles e.g., for $m = 5/2$ the shape will close with five angles after only two rotations and will then have $5/2$ or 2.5 angles in one rotation (Fig. 2). This shape will then be repeated every 4π .

There will be no repeating pattern using irrational numbers. The notion of dihedral symmetry as defined for regular polygons (Weyl, 1952; denoted by D_n and defined for an integer in Eqs. 2 and 3) can thus be extended to include cyclic C_n and

dihedral D_n symmetries for any real number in the plane with m rational or irrational.

Because all these shapes are described by the same equation, numerical calculations such as area and polar moment of inertia I_p for this large class of forms can be done by integration of one single equation. This permits calculations for optimization of area or moment of inertia. For example, when a circle develops into a supercircle a moderate increase of area rapidly leads to a large increase of I_p .

A very important consequence is that the area is constant for a given shape, defined by the exponents n , irrespective of the value of m . The areas of shapes shown in Table 1, columns 2, 4, and 5, e.g., are constant for $m > 0$. Because a symmetry is generally defined in geometry as a transformation that leaves a certain quantity (here, area) invariant, the symmetry here is the value of m (for $m > 0$).

Examples of natural shapes—A wide range and remarkable variety of forms throughout the different kingdoms can be modeled with the Superformula (Gielis, 1999, 2001). In Fig. 1, examples are shown of natural supershapes or superpolygons, such as triangular shapes in the petiole of *Nuphar luteum* and in marine diatoms like *Pseudotriceratium*, *Sheshukovia*, *Triceratium*, and *Trigonium* (Fig. 1a). Other diatoms

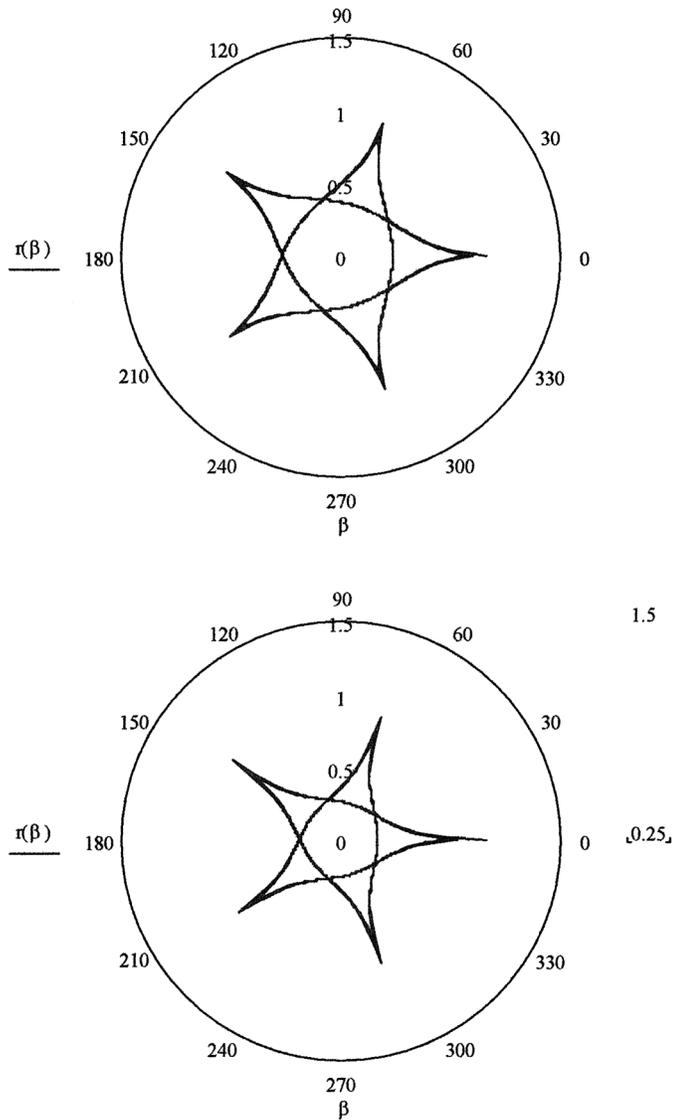


Fig. 2. Polygons of non-integer symmetry; rose sepals and carambola fruits ($m = 5/2$). Top, $n = 0.5$. Bottom, $n = 0.4$.

like *Stictodiscus* are quadrangular or pentagonal or can have different symmetries (Round et al., 1991).

Supercircular stems (referred to as tetragonal or square, Fig. 1b) occur in a wide variety of plants such as *Silphium perfoliatum* (Asteraceae), *Verbena bonariensis*, in Lamiaceae, *Tibouchina* (Melastomataceae), *Scrophularia nodosa* (Scrophulariaceae), *Galium* species (Rubiaceae), *Buddleja davidii* (Buddlejaceae), *Chimonobambusa quadrangularis* (Poaceae; McGowan, 1889), and in young stems and branches of *Tectona grandis* (Verbenaceae), as well as in succulents such as *Euphorbia* sp. (Euphorbiaceae), *Cissus quadrangula*, and *C. cactiformis* (Vitaceae) and species of *Orbea*, *Stapelia*, *Frerea*, and *Huernia* (Asclepiadaceae).

Clematis montana (Ranunculaceae) and *Impatiens glandulifera* (Balsaminaceae) stems have hexagonal symmetry. Vegetative stems of horsetails, *Equisetum*, can be heptagonal (Fig. 1c), while the thicker fertile stems can have symmetries of up to 14. Stems of raspberries (*Rubus sulcatus* and *R. phylllostachys*) and cacti like *Stenocereus thurberi*, *S. gummosus*, and

Lophocereus schottii (Molina-Freaner et al., 1998) are hexagonal or pentagonal (Fig. 1d).

Supercircular forms are also frequently observed at the anatomical level, such as in square or rectangular tracheids in pinewood. In bamboo culms, longitudinal sections have long and short parenchyma cells resembling piles of superelliptical building blocks (Liese, 1998; Takenouchi, 1931).

Cells in genera of brown algae belonging to Dictyotaceae (Dictyotales: Phaeophyta) like *Zonaria*, *Exallosorus*, *Homoostrichus*, and *Lobophora* can easily be characterized by the rectangular shape of their cells. Other examples of polygonal arrangements at the microscopic level are found in developing flower primordia of actinomorphic flowers. Trimerous, pentagonal, and quadrangular flowers can be found in different genera.

Examples of non-integer value rotational symmetries are found in plant phyllotaxy (Fig. 2). Angles of 2.5 with $m = 5/2$ have five angles in two rotations as is observed in sepals of rose (Fig. 2) and cross sections of *Averrhoa carambola* (star fruit; Fig. 2). The angles are spaced 144° apart, and the shape closes after two rotations only. Angles of $5/1$ (pentagonal shapes with $m = 5/1$ both integer and rational) have five angles in one rotation of 360° , spaced 72° apart. So while pentagrams and natural $5/2$ angles superficially share the same rotational symmetry, D_5 with pentagons (Weyl, 1952), their generic symmetry is non-integer. It is interesting to note that with Eq. 2 small deviations are possible, such as $5/2.1$ angles, resulting in five angles in slightly more than two rotations. The number of rotational symmetry m defines the precise spacing of the angles.

Starfish, shells, flowers, and generalized Fourier series—

Similar forms can be observed in animals. When the inward folding of the sides of pentagons is more pronounced, shapes of starfish are obtained (Fig. 1e and 1f). After the initial larval stage with bilateral and left/right symmetry, starfish (Asteroidea) develop into an adult stage with radial symmetry (Lowe and Wray, 1997). Radial symmetry is a prominent feature of various other echinoderms.

Logarithmic spirals occur widely in nature, for example, in phyllotaxy of plants (Jean, 1994) and in shells of molluscs, with *Nautilus* as the classical example (D'Arcy Thompson, 1917). Other excellent examples can readily be observed in various other shells such as *Architectonica perspectiva* (Architectonicidae) and snails such as the famous manus green papuina (*Papustyla pulcherrima*).

But unlike *Nautilus* and various snails, many shells are not simple logarithmic spirals as seen in the varices and combs of shells of trapezium horse conch (*Pleuroploca trapezium*, Fig. 1h), *Cymbiola imperialis*, *Strombus* species, and murexes. Here the logarithmic spiral is inscribed in a polygon, defined by Eq. 2. Another example is a square logarithmic spiral (Fig. 1g) and the spiral of Archimedes inscribed in a hexagon (Fig. 1i). Inscribed in a triangle, the logarithmic spiral models triangular coiling as observed in various ammonoids. Triangular coiling has occurred at least three times during the evolution of the ammonoids, in genera such as *Solicyclenia*, *Kamptoclymenia*, *Trigonoshumardites*, and *Trigonogastrioceras*. Other genera have quadrangular or triangular coiling in early stages of development (Becker, 2000).

Trigonometric functions also can be modified by Eqs. 2 and 3 as shown both in polar coordinate graphs (Fig. 1j-k) and in the wave representation (Fig. 1l). The relation between shapes

of flowers and trigonometric functions like sine and cosine was first postulated by the monk Grandus in the 17th century (D'Arcy Thompson, 1917). This relation is not surprising because in polar coordinates, cosine and sine functions define circles with their center on the shape itself.

Inscribing flowers in superpolygons allows one to model various flowers with radial symmetry and shows how petals are efficiently packed in a limited area (Fig. 1j–k). Indeed, when the area of the petals of *Geranium* is compared to the area of the underlying superpolygons, the area used is over 90%. “Square” arrangements of leaves can be seen in sepals of various species of *Hydrangea* and in leaflets of the water fern, *Marsilea quadrifolia* (Marsilaceae).

Figure 11 also indicates how a generalized Fourier series can be defined, in which any component of the Fourier series can be moderated by Eq. 2. Thus, all shapes in Table 1, Figs. 1, 2, 3a–f, and 4 can be described in a single, constant generalized Fourier component moderated by Eq. 2. Likewise, the super- and subcosines of Fig. 2k–l can be described in one cosine Fourier component. As a direct consequence, each of these shapes is described by a finite series, instead of being an approximation by an infinite series of trigonometric terms as in a classical Fourier series.

Increasing the degrees of freedom—In general, one could think of the basic Superformula as a transformation to fold or unfold a system of orthogonal coordinate axes like a fan. This creates a basic symmetry and metrics in which distances can further be deformed by local or global transformations. Such additional transformations increase the plasticity of basic supershapes. The degrees of freedom of supershapes defined by Eq. 2 can be enhanced by various techniques such as parameterization of the equation or by using probabilities.

Combining Eq. 2 and Pattern Theory (Grenander, 1993) captures variation in nature in a probabilistic way. In this powerful combination, shapes defined by Eqs. 2 and 3 will serve as deformable templates I_0 . These shapes can also be used in a geometric morphometrics study to compare natural shapes based on the outlines. Since such models preserve the symmetry that is readily observed by any student of nature, a knowledge-based approach to pattern recognition of natural shapes is realized.

Equation 2 offers great opportunities in computer applications to describe plants and natural shapes in three dimensions, either as an extension of superquadrics or as generalized cylinders. The use of superquadrics is based on the spherical product of two two-dimensional supershapes (Barr, 1981). Superquadrics have also found wide application in computer environments (Jacklic et al., 2000) to model hearts and human bodies.

The major drawback of superquadrics and superellipses is their limited symmetry. Extending the notion of superquadrics by Eq. 2 greatly enhances the potential to describe natural forms, especially since symmetries are taken into account. If for example, 20 sections are taken from a succulent stem and each section described by (R, m, n_1, n_2, n_3) , the whole stem is characterized uniquely by a maximum of 100 numbers.

The use of superquadrics has further been extended by the possibility of local and global deformations. This extension allows modeling of natural and man-made shapes to any degree of precision, but such deformations require larger sets of parameters. Global deformations affect the whole superquadric

and includes deformations such as tapering, bending, or any hierarchical combination thereof.

Local deformations can be implemented in different ways (Jacklic et al., 2000). Increasing the degrees of freedom of the superquadrics has been possible by parameterization, including the use of Bezier curves as functions in the exponent of superquadric equations (Zhou and Kambhamettu, 1999) and by blending multiple models (DeCarlo and Metaxas, 1998). Other ways to increase the degrees of freedom have included hyperquadrics (Hanson, 1988) and ratioquadrics (Blanc and Schlick, 1996). Implementing Bezier curves as exponent function in Eq. 2 also allows the modeling of highly asymmetrical shapes.

DISCUSSION

Generalizing the equation of the ellipse (Eq. 1) into Eq. 2 allows us to understand the mathematical simplicity and beauty of many natural forms differing only in parameter values. Equations 2 and 3 allow for a great reduction of complexity of shapes and provides new insights into symmetry, including non-integer symmetries. Here only two-dimensional shapes are treated, but Eqs. 2 and 3 can be extended in other dimensions as well.

Given the extraordinary correspondence to natural shapes, we can postulate that Eqs. 2 and 3 unveil a very basic geometry of nature, in which coordinate axes in any dimension can fold or unfold like fans, while at the same time distances are still based on the same spacing of numbers on coordinate axes as in the classical orthogonal system, through XY-coordinates and trigonometric functions.

Equation 1 not only deforms the unit circle into various sub- and supercircles, but the reverse is also true: superellipses are all circles (Hersh, 1998) with a metric defined by Eq. 1. More generally all the shapes and graphs defined by the Superformula are circles with a metric defined by Eq. 2 (Gielis, 2001), which provides the analytical link between internal metrics of forms and our classical Euclidean distance measures.

The Superformula inherently allows for small modifications of parameters (e.g., gradually changing the form of stem sections along a stem) and can become a powerful tool in the study of nature. It allows for every individual shape to have its own defined parameters, e.g., to discriminate individual diatoms or subsequent sections of stems of cacti.

For each of these shapes, area and other associated characteristics can easily be calculated by integration. For a given set of exponents in Eq. 1, the area remains invariant to changes in the symmetry m . It is anticipated that in the future, physics-based models (finite elements) can be implemented to study the distribution of forces in plants and organs. The shapes can also be understood as “atomic” shapes, for which more complex forms can be built with certain combinations.

Considering that the mathematics behind the Superformula are easily understood and given the wide range of applications, both in technology (Gielis, 1999) and science, I believe that the Superformula has the potential to transform the way we look at symmetry and shape in a profound manner.

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