ON FLORAL SYMMETRIES

C.P. Bruter

Mathématiques, Université Paris 12

1. INTRODUCTION: KEPLER'S PROJECT

How does Nature fill up space? This question has implicitly been attacked by the Greeks, by the atomists, the philosophers of the Pythagorean school and by Plato, who in his *Timeus* fills the world with moving, regular solids.

In conjunction with the (yet embryonic) development of crystallography at the beginning of the sixteenth century, about 1609, J. Kepler writes an essay on the *The New Year's gift, or sexangular snow (Strena, seu de nive sexangula)*. Kepler does not only treat the form of the snow crystal, but also extends his reflection to the forms of the vegetal world, inquiring on the presence of pentamery and the symmetry of the sixth order. According to Kepler, following Platonic tradition, natural forces and geometry are responsible of the observed forms. The introduction of natural forces into the geometry is a problem which is not considered.

In his essay, Kepler explicitly deals with alveolus of the honey comb, pips of pomegranates, peas, and petals of flowers. The floral pentamery comes from the enfolding of the golden section ratio, the Fibonacci sequence (Kepler does not mention Fibonacci), and which appears in the construction of pentagones as in the dodecahedron and isocahedron. Kepler tries to apply these geometrical rules, derived from the physical world, in particularly in crystallography, to the plant kingdom.

A modern formulation of the Kepler's program could be the following. Given the numerous symmetries which are present in the kingdom, the theory of groups would be appropriate to study the filling up of the space by plants? If so, one could consider each leaf, and each flower - e.g. the flower of a *pyracantha* which before unfolding looks like a crystallographic egg - as the contraction of a spatial domain of crystallographic shape, the problem being then the search for tilings of R^3 by virtual crystals. This formulation is obviously incomplete: it does not take into account the phylogenetic, dynamic and environmental constraints.

Thus, without neglecting the importance of geometry, it is necessary to return to the observation, and to try to set up elements of explanation, a scheme of organization which matches better the biological reality.

2. FLORAL SYMMETRIES

2.0. Basic Hypotheses

The following hypotheses, although not original, deserve to be better understood qualitatively and quantitatively. They are based on observations.

H.1: Embryonic vegetal cells are influenced by light which tends to orient the cell divisions parallel to its direction.

H.2: The vegetal cells from a partial screen to the propagation of the light; the screen changes with the state of maturity of the cells.

H.3: Light changes the mechanical properties of the cells.

H.4: The vegetal cells 'memorise' the past morphological organizations, and incorporate them in an eventually new organization.

The last hypothesis is Larmarckian. For the moment, we are unable to test the hypothesis and to understand the way it could be encoded in the genes.

The other hypotheses seem to be easier to refine and to test.

2.1. Immediate Consequences

From these hypotheses a few consequences result.

C.1: the vegetal tip has a tendency to grow towards the light source.

C.2: The direction of growth changes during the day.

C.3: The cellular flow (number of cells, speed) in the neighbourhood of a point P in a section of the vegetal tip perpendicular to the light direction depends on this point.

This consequence is easy to quantify:

As the direction and the intensity of the light changes during the day the consequence of H1 is that the light induces some quasi symmetric effects, together with some phyllotaxic effect.

In the same sense, the nice and rigorous Coudert-Douady physical model has to be kept in mind, the luminous effect on the cells acting like an electrical source on a condenser (this is of course an hypothesis of analogical type).

C.4 The vegetal jet has a tendency to be organized in a phyllotaxic way around an axis of revolution.

C.5 There is a point π on this axis with a thin neighbourhood $N(\pi)$ as the cells which are located respectively above and under $n(\pi)$ do have different properties.

C.5 is a consequence of the hypotheses H.2 and H.3. H.3 deals with mechanical properties. They are obviously bound to other physiological, physical and chemical properties which may be hard to specify.

The following statement looks more like an hypothesis rather than a conclusion since we have no information on the elastic and dynamical properties of the cells.

H: A cellular cork thickens under $N(\pi(t))$ *proportionally* to the growth of the jet.

2.2. The Fundamental Symmetries

The fundamental symmetries are the symmetry of revolution (r-symmetry), and the symmetry of order 2.

2.2.1. The Symmetry of Revolution of the stem and the leaf in the one-leaf plant

The origin of this symmetry has been (partly) described in C4. More precisely, the r-symmetry may be understood as the effect of the light of the sun on a colony of primitive cells, aggregated in a disk. Acting for days and years, given the memory hypothesis H.4, and given the rotation of the earth around the sun, the phototropic reaction of the cells gives rise to this r-symmetry within the phyllotaxic organization.

r-symmetry is observed in the stem, and frequently the one of the vegetal tip, when observed at low magnification. It is the main symmetry of plants which, as the arum, show it in one leaf or one petal, as we shall explain.

When the plant is growing, according to the hypothesis H, close to the apex a kind of central cap is shaped, which affects a slow down, and then a blocking, of the rising of the flow of cells, and, like a piece of wood transversal to the direction of a liquid flow, forces the flow of cells to spread out perpendicularly to the direction of the axis of revolution.

A priori, the flow may run from one or several points close to the apex. Let us suppose there is a point around which the mechanical properties of the vegetal tissue becomes weaker due to differentiation of the cells under the light conditions. The cellular flow is going to run across this weak point, may be also by the effect of the light pressure caused by the first cells. In this way a change in the direction of the cell multiplications is induced. May be the flow is incurved by the simple effect of gravity acting on the first cells and such that it comes in a plane perpendicular to the gravity axis and then it can expand along this plane, *keeping mnemonic trace of the previous r-symmetry.*

As a consequence, the trace of the axis of revolution in the plane on which the leaf expands yields the axis of symmetry of the leaf - for the C.2 reason, the symmetry is not rigorous.

The original symmetry of revolution around the axis of the stem tends to be preserved through parallel transport orthogonal to this axis, so that the unique leaf, which is primitively created, is itself a tiling of the plane which catches light. Of course, this tiling is partial, it cannot cover the whole plane for obvious physical reasons.

So far, we got in touch with the reasons for the existence of the symmetry of a leaf.

A plant can have one leaf. It can also have several leaves, the generation of each leaf being in some sense the repetition of the generation of the first leaf, according to a phyl-lotaxic rhythm bound to the process of evolution of the cap $N(\pi(t))$. Very soon after the flow of cells expands in the orthogonal direction to the stem axis, the apex of the cap differentiates again and a new sequence begins with the growth of the stem until a new cap completely forms and a new leaf appears. In some cases, the process more or less stops when a covering of the 2-disk orthogonal to the light direction is achieved by the leaves. The order of the covering deserves to be systematically studied - it is of course of order 1 in case of a one-leaf plant. Usually, this covering is under the influence of the phyllotaxic transformation giving rise to the well-known spirals (they are figured in projection in the subsequent drawings).

2.2.2. The symmetry of order 2; the symmetry of order 3.

In the above case, leaves appear separately; one may ask whether this aerial foliar system is the most primitive one. We shall make this hypothesis.

We look at another well-known process, where the leaves appear in pairs. A pair of leaves, B, is two leaves being symmetrically positioned. Many plants, e.g., mint, have a

foliar system composed of pairs of leaves, the pairs being placed orthogonally to each other. In some cases, one pair is composed of leaves placed in mirror symmetry, while the following pair has a center of symmetry.

In these cases, we can use the common language of differential geometry. Then the simplest covering of the 2-disk is achieved by repetition of the data of simple atlas composed from 2 pairs of charts. These charts represent two orthogonally placed, successive pairs of leaves. The charts divide the disk into four parts: one chart represents one pair of leaves.

The physiological and biochemical features of this process are not easy to grasp. We shall give here two complementary ways of understanding the process.

I. We shall first suppose that there is a biological underlying process that can be partly described by a mathematical formulation. As the formation of leaves results form a process of bifurcation, we shall look at the simplest way in which a mathematical system can bifurcate. The use of simplicity is a reasonable suggestion approaching the general process of unfolding. This is the way the Taylor formula works.

Let θ be the angle of the direction of the axis of a leaf with the vertical line, and u a vector of parameters (physiological, biochemical, etc., parameters). The bifurcation process is directed by some function $f(\theta,u)$ invariant by some group of symmetries. As we have seen before, the group of symmetries of the stalk $(SO(2)))$, breaks into the group of symmetries of the one-leaved plant which is $Z/2$. The simplest bifurcation set with $Z/2$ symmetries is the so-called fork:

The branches BB' and BB" are stable, while the branch BC is usually unstable, but other processes can stabilize this branch. Thus, the simplest bifurcation process is compatible with various usual systems of leaves, the basic ones being the two following:

In these cases, B (resp. T) has to be considered a unique chart, though composed of two (respectively three) leaves. According to the previous section, the basic atlas of charts covering the 2-disk is made of two orthogonal B, or two orthogonal triads T. Of course, the symmetries of the corresponding flowers are a direct consequence of the symmetries of the charts of leaves, according to Goethe's theory (Goethe, 1975).

It must be noticed that a mixing of B and T may occur. The following morphology is currently observed:

Such a morphology might occur because the process of stabilization of the branch BC of the fork appears at the apex, but not at the following steps where it is absorbed by the already present stalk.

The processes causing the bifurcation are largely unknown. The following observation might give a hint to understand how, in some cases, this process might have taken place: it is a well known observation that leaves of some rather primitive plants are affected by a process of splitting, a dehiscence process:

The hypothesis can be made that a rather fast phylogenetic process has been recapitulated inside an ontogenic process. According to this hypothesis, the process of splitting might have induced the simultaneous formation of triads of leaves.

II. Let us return to the description of generation of the one-leaf plant. At the apex is a process of differentiation whereby the cells become highly plastic, then bend in the direction of the sun: the $Z/2$ symmetry (with respect of the south direction) of its apparent movement induces the corresponding symmetry of the leaf.

The group of cells at the apex is like a kind of viscous liquid, submitted to internal tensions, affected by light, and which tends to flatten as a film. According to solutions of

the Plateau problem (Taylor, 1976), symmetries of order 2, 3 and even 5 can appear, corresponding to observed symmetries of leaves and flowers. This explanation is similar to the one I introduced (Bruter, 1982) when discussing the pentamery in the animal kingdom.

Though the leaf is diffeomorphic to the thickened 2-disk ($D^2 \times I$), the gradient of development is not isotropic: given the effect of light, the natural tendency would be null in north direction, increasing from east to south, decreasing from south to west. This gradient induces a frequently non-euclidean metric on the surface of the leaf, so that the symmetries of order 3 and 5 in particular are slightly deformed, giving rise to a central (southern) part call it the of the leaf or leaf larger than all the others, while, in the case of the five-order symmetry, the first two collateral (the south-eastern and south-wester) leaves or parts of the leaf are larger than the eastern and western ones.

2.2.3. The Symmetry of Order 5

The fact that such a symmetry does not allow any tiling is usually seen as a geometrical argument against the spontaneous appearance of the symmetry of order 5. Many leaves and flowers have this symmetry.

However, careful observation revealed that most of them have a *false* or pseudo five-order symmetry. Flowers with false five-order symmetry, e.g. pansies, have two kinds of petals: the largest ones are arranged in a triad T, while two smaller ones form a B-pair. The difference of size between the T- and the B-leaves can be very apparent or, on the contrary, very small.

This fact does not exclude the possibility of a spontaneous, intrinsic five-order symmetry in some flowers. This must be further investigated. For instance gentians seem to have such a symmetry; but the organization of the foliar system is contrary to the presence of such a perfect symmetry.

As it seems that there are apparently (and at least) two kinds of such symmetries, we have to look for two kinds of explanation. With regard to the intrinsic five-order symmetry, the analogy with a film organization *à la Plateau* might be a reasonable way of explanation.

The more common pseudo-five-order symmetry would result from a *process of projection* of a secondary B-pair on a primary triad T, in order to achieve a complete covering of the 2-disk, that either the triad or the pair are unable to fulfil. This process of projection describes formally a fast process of suppression of the part of the stem which keeps the triad apart form the pair. Pansies are an example where this process is not completely achieved. Contrary, when such a process is fulfilled the 5 petals unfold simultaneously, so that the 2-disk is bound to be divided in equal subdomains, giving rise to a perfect five-order symmetry.

3. CRITICAL CONCLUSIONS

No doubt many readers will be unhappy about these considerations: the hypotheses are numerous and most 'proves' are incomplete. We have controversial suggestions rather than experimental data organized in an unchallengeable theory. But, the scope of this considerations was to try to introduce new ideas to tackle the difficult problem of foliar and floral symmetries. Some ideas might be useful and realistic, particularly the topological considerations belonging to a modern version of the Plato-Kepler programme.

REFERENCES

Bruter, C.P. (1990). On some morphological principles in botany arising from mathematical considerations. Acta biotheoretica 38: 171-180.

Bruter, C.P. Quelques hypothèses inspirées par les observations du Docteur Couly. Actes du deuxième Séminaire de l'Ecole de Biologie Théorique du CNRS, Publ. Univ. Rouen, 355-359.

Goethe, J.W. (1975). La métamorphose des plantes. Paris, Ed. Triades.

Taylor, J.E. (1976). The structure of singularities in soap-bubble-like and soap-film-like minimal surfaces. Annals of Math. 103: 489-539.