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The geometry of leaf morphogenesis: A theoretical proposition

MICHEL FERRE* and HERVE LE GUYADER**

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Abstract. Plant morphogenesis exhibits numerous bifurcations with particular angle values such as 41°, 53°, which, in lower plants, can be measured in the thallus, and, in higher plants, in the ribs of the leaves. An interpretation of these angles is attempted. Since they characterize the functioning of a morphogenetic field, a formalism was constructed suitable for the study of living systems. The mathematical tool devised here, named the Arithmetical Relator, combines Geometry and Arithmetic, and assumes that a general system results from the interaction between an internal cyclic structure and an environment to which this structure is adapted. The formalism described therefore takes into account partial self-reference and changes in the level of organization. Within this framework, the particular values of the ramification angles are extreme for slight shifts in the internal structure. A pattern of the relations between the genome, the cell and the organ is suggested.

Résumé. La morphogenèse végétale est le siège de nombreuses bifurcations. Celles-ci donnent naissance à des angles particuliers (41°, 53° ...) qui peuvent être mesurés au niveau du thalle des végétaux inférieurs et de la nervation foliaire des végétaux supérieurs. Une interprétation est recherchée: ces angles caractérisant le fonctionnement d'un champ morphogénétique, il a fallu bâtir un formalisme bien adapté au domaine du vivant en vue de cette étude. L'outil mathématique conçu, le "Relateur Arithmétique", alliant la géométrie et l'arithmétique, interprète un système comme le résultat de l'interaction entre une structure interne cyclique et un environnement auquel elle est adaptée. On peut alors rendre compte d'une auto-référence partielle et d'un changement de niveau d'organisation. Les valeurs particulières des angles de ramification sont extrêmales pour une petite variation de la structure interne du système. Une proposition concernant les relations entre génome, cellule et organe est donnée en conclusion.

* Ecole Nationale Supérieure de Techniques Avancées, Laboratoire de Mécanique et d'Energétique, 32 Bd. Victor, F-75015 Paris, France.
** Centre d'Etudes Nucléaires de Saclay, Département de Biologie, Bâtiment 28, F-91191 Gif-sur-Yvette Cedex, France.

1. Introduction

Morphogenesis is one of the most awkward problems raised by Theoretical Biology, because it involves numerous difficulties, of which one of the greatest is the resonance between different levels of organization. Its solution is essential for the understanding of living systems.

This article, in which the construction of a mathematical tool referred to as the Arithmetical Relator provides a biological interpretation of certain privileged ramification angles observed in plants, is intended as an illustration of this proposition originally formulated by Delattre (1980) as follows: "in the natural sciences, the real problem is to find the adequation between the theoretical language used, the observation to be accounted for, and the questions to be answered" ("dans les sciences de la nature, le véritable problème est de trouver l'adéquation entre le langage théorique utilisé, les observations dont on veut rendre compte et les questions auxquelles on souhaite répondre").

In practice, Biologists use one of the two following approaches:

1. the study of a particular subject which well illustrates the problem stated; this method proceeds from the particular to the general; or:
2. the initial construction of a formal system well adapted to the field under study and its subsequent application to concrete cases; this method proceeds from the general to the particular.

These seem to be two opposite approaches, but they are in fact complementary; consequently, we attempted to use both, by choosing the observations for which we wish to account (i.e. the ramification angles), the question we wish to answer (i.e. the significance of these angles in the morphogenetic process), and a suitable theoretical language.

In order to assess the advantages and drawbacks of this kind of approach, it seems of interest to compare the formalism of the Arithmetical Relator to the already well-known structural approaches such as the Catastrophe Theory or the Theory of Self-Reproducing Automata.

The Catastrophe Theory sets out to justify the existence of certain structures as resulting from a conflict between local dynamics interacting within a substrate. The main idea (Thom, 1972) is the fact that the understanding of a morphogenetic process does not require any knowledge of the spatial properties of the substrate, or of the acting forces involved in this process. In that case, the emergence of a structure would be due to "genericness" i.e. Nature always adopts the most straightforward local morphology compatible with local initial data. In this way, Thom uses the opposite approach to reductionism since, to describe a given morphology, he first constructs a pattern of differential systems on a control space, and then attempts to make the morphology observed coincide with a set of catastrophes provided by the pattern. The main criticism voiced against this kind of approach is that it allows quantitative prediction in Physics but not in Biology. Thom countered this criticism by stating that "what is important in a pattern is not its relevancy to experience but, on the contrary, its ontological significance, what it tells about how phenomena evolve and how it describes their underlying mechanisms" ("ce qui est important dans un modèle, ce n'est pas son accord avec l'expérience, mais au contraire, sa portée ontologique, ce qu'il affirme sur la manière dont les phénomènes se passent, ce qu'il décrit de leurs mécanismes sous-jacents"). In this respect, some of the basic principles of the Arithmetical Relator seem to be close to the Catastrophe Theory; as will be seen further on, certain ramification angles in plants in fact emerge from the formalism of the Arithmetical Relator, as phenotypic markers of a certain compatibility between internal structures and rhythms. As regards the problem investigated in this article (the numerical values of ramification angles in plants) we cannot make direct use of the Catastrophe Theory since we attempt to account for quantitative data. The compatibility described above between internal spaces (which we assume to be connected to the ontological significance of the Arithmetical Relator) has a role in the morphogenetic process, mainly due to its own logic. At this point, a connection emerges between the Arithmetical Relator and the Self-Reproducing Automata Theory. Von Neumann (1966) constructed this theory in answer to the following question: "what kind of logical organization is sufficient for an automaton to be able to reproduce itself?". On the basis of certain results in Physiology, several abstract machines have been built (such as kinematic and cellular automata) showing that copying is necessary for self-reproduction or, more generally, for reproduction without loss of complexity. However, while only pointing out the logical aspects of the process, von Neumann deliberately ignored the significance of the basic elements he used (these elements represented neither molecules nor cells) and was consequently unable to take into account the laws of Physics in general and of field effects in particular.

Is it essential for variables and parameters to have a precise significance for an approach to be valid? This question requires careful consideration. Whenever a mechanical pattern is chosen, an attempt is immediately made to provide it with adequation of the quantities used with known experimental entities such as molecules or cells. However, Biology is not only concerned with the description of structures but also

– and particularly – of the dynamics which work within them, so that the coincidence between the functional and physical structures (which constitute the subject of the description) is not obvious. That is why a logical process can be described independently from either the physical structure (as in von Neumann's approach) or the acting forces (as in Thom's approach).

In the formalism of the Arithmetical Relator, the concept of stability induces a notion of compatibility between underlying structures and its functioning is therefore relevant to the description of a logical process. However, the basis of this formalism includes some of the main principles encountered in the functioning of living systems. Further, the Arithmetical Relator involves the intellectual processes of Physics, by making use of mathematical entities relevant to Diophantine Algebra and Geometry. Thus, it allows calculus, and the numerical results can be experimentally confirmed. Nevertheless, the Arithmetical Relator cannot avoid the difficulties typical of structural approaches. The justification of the pattern is not easy (Le Guyader, 1979) and, here again, the interpretation of the variables and parameters in terms of Biochemistry, for example, does not emerge at once. The biological meaning of the compatibility process becomes clear only through a strong analogy. Although much epistemological work remains to be done in this respect, it seems to us that the ontological significance of the formalism of the Arithmetical Relator is already sufficient to incite Biologists to study some of the angular values which up till now have been neglected.

The correct statement of the problem naturally reveals the bases of a mathematical tool well-suited to it. What else but the cell is the raw material of Biology? "Cells are microscopic, to be sure, but they are not infinitesimal" (Erickson, 1976). Nevertheless, this crucial feature greatly restricts the research workers who would like to use the equations of fluid dynamics; Kuhn-Silk and Erickson (1979) had this problem in mind when they wrote: "it is more difficult to view a plant tissue as a continuum, since the fundamental units, the cells, of which it is composed, are larger in comparison to the usual units of measurement ... Because of this difference, we might anticipate that some of the power of fluid dynamical methods will be lost in application to plant tissues". Here again, the same difficulty arises both in space and time: in plants, time is measured by means of the plastochronic index, which is essentially a discrete quantity (Erickson, 1976; Lück et al., 1980). Given that discretization is evident from the starting point of the process, it seems natural to assume that variables and parameters are integers and therefore, relevant to Arithmetic.

The main measurements we want to take into account are angular values; to give them a biological interpretation in leaf morphogenesis, we need to construct a mathematical tool combining Geometry and Arithmetic. It should be pointed out that the existing topological patterns – in which Geometry is connected to Analysis – are based upon a space-time continuum from which the discrete emerges through singularities. It is not the aim of this article to privilege either of these approaches. However, although the combination of Geometry and Analysis has already been well studied (it constitutes the basis of the Catastrophe Theory), the combination of Geometry and Arithmetic is not so well understood at the present time (Moulin et al., 1971; Calvino et al., 1972; Le Guyader et al., 1979).

2. Logic and dynamics in biology

Biochemistry and Physiology clearly point out that a cell is a structure whose stability is maintained by inner dynamics known as the metabolism. A mathematical tool fit for the description of living systems must therefore include this salient feature, in a simple but fundamental manner.

2.1 *Quadratic forms and invariancy*

As regards external coherence, a formalism suitable for applications in Biology must take into account the knowledge acquired at the present time by Physics, which proposes a standard description of the real, i.e. the choice of measurable parameters, and the subsequent search for one or several quantities depending upon these parameters and keeping constant during the "natural" evolution of the physical phenomenon concerned. This is a typically Lagrangian approach. Whenever possible, Physicists like to give this constant quantity a quadratic form. Thus, when considered in the space of the parameters chosen, this quadratic form represents either a spinor norm (i.e. a number of elements, for instance particles, remains constant) or a vector norm (a length is constant).

In addition, a quadratic form, for instance $X^2 + XY + Y^2 = (-)_0$ in which the right-hand member is given by the coordinates (X_0, Y_0) of a particular point, may have two meanings:

- when considered as a simple non-metric relation between the parameters X and Y, it represents, in Cartesian axes, an ellipse whose ec-

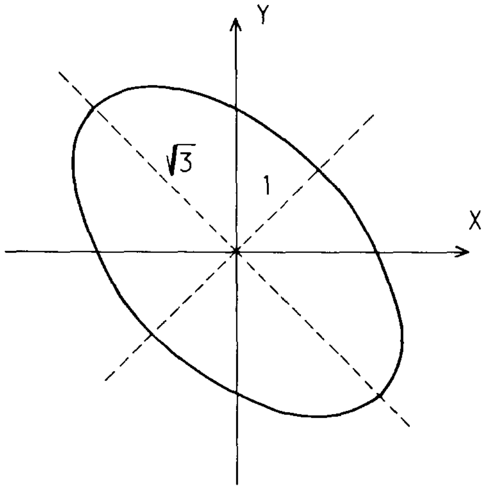


Figure 1. The relation $X^2 + XY + Y^2 = (-)_0$ regarded as a non-metric relation between the parameters X and Y, is the equation of an ellipse in Cartesian axes.

centricity is $\sqrt{2}/\sqrt{3}$ and whose major axis stands at 135° with the x-axis (Figure 1);

- considered as a metric relation, it represents the norm of a vector, (X, Y) being its components in a vector space which has $(\mathbf{e}_1, \mathbf{e}_2)$ as basic vectors. In this space, a scalar product – or inner product – $(\mathbf{e}_1 \cdot \mathbf{e}_2)$ is defined, in a real space, by:

$$(\mathbf{e}_1 \cdot \mathbf{e}_2) = \|\mathbf{e}_1\| \|\mathbf{e}_2\| \cos \Phi \tag{1}$$

where $\|\mathbf{e}_1\|$ and $\|\mathbf{e}_2\|$ measure (with the same unit) the lengths of the basic vectors, and Φ the angle they form.

With the following notation:

$$g_{ij} = (\mathbf{e}_i \cdot \mathbf{e}_j) = (\mathbf{e}_j \cdot \mathbf{e}_i) = g_{ji} \tag{2}$$

the example chosen shows that:

$$\begin{aligned} (\mathbf{e}_1 \cdot \mathbf{e}_2) &= (\mathbf{e}_2 \cdot \mathbf{e}_1) = g_{12} = g_{21} = 1/2 \\ (\mathbf{e}_1 \cdot \mathbf{e}_1) &= \|\mathbf{e}_1\|^2 = g_{11} = 1 \\ (\mathbf{e}_2 \cdot \mathbf{e}_2) &= \|\mathbf{e}_2\|^2 = g_{22} = 1 \end{aligned} \tag{3}$$

The expression of the norm of a vector $\mathbf{X} = X\mathbf{e}_1 + Y\mathbf{e}_2$ can be written as follows:

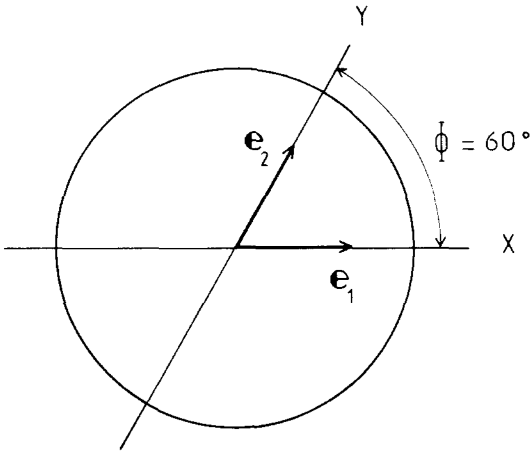


Figure 2. The relation $X^2 + XY + Y^2 = (-)_0$ regarded as a metric relation, is the equation of a circle.

$$\begin{aligned}(\mathbf{X} \,.\, \mathbf{X}) = \|\mathbf{X}\|^2 &= (X\mathbf{e}_1 + Y\mathbf{e}_2) \,.\, (X\mathbf{e}_1 + Y\mathbf{e}_2) \\ &= g_{11}\, X^2 + (g_{12} + g_{21})XY + g_{22}\, Y^2\end{aligned}$$

Then:

$$\|\mathbf{X}\|^2 = X^2 + XY + Y^2 = (-)_0 \tag{4}$$

When the right-hand member of the quadratic form is constant, this quadratic form represents, inside the basis ($\mathbf{e}_1$, $\mathbf{e}_2$) a circle (Figure 2) with a radius:

$$\|\mathbf{X}\| = \sqrt{\|\mathbf{X}\|^2}$$

In leaf morphogenesis, we attempted to follow the geometry of the organ, and it clearly appeared that in no case was the same number of elements, e.g. cells, maintained; consequently, we followed Physicist's example and adopted the second standpoint, which naturally immerses the pattern in a vector space structure (Vallet et al., 1978a).

2.2 *Inner dynamics: Reflections, symmetry and arithmetic*

This vector space, which is already a metric space, has to be provided with inner dynamics, which means that metabolism must animate this structure. Physics requires that both the quadratic form and its right-hand member keep constant. The simplest mathematical way of pre-

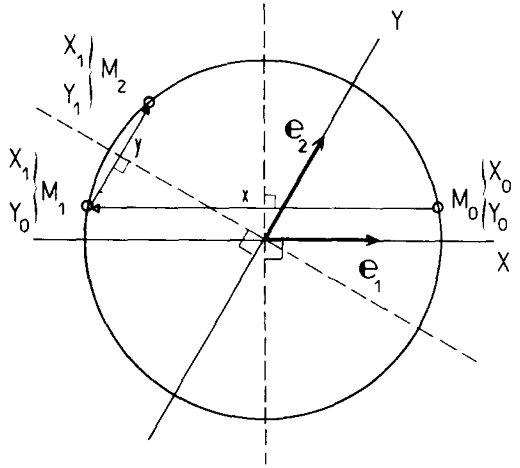


Figure 3. Second root process sequence in relation to $X(M_0 \rightarrow M_1)$ and $Y\ (M_1 \rightarrow M_2)$.

serving this feature seems to be the second root calculus upon a quadratic equation.

Thus, quadratic form

$$PX^2 + RXY + QY^2 = (-)_0 \tag{5}$$

may be regarded as a quadratic equation for either the X variable (Y keeping constant) or the Y variable (X keeping constant) (Verney et al., 1973; Apter et al., 1974a). The initial point $M_0(X_0, Y_0)$ changes successively into the points $M_1(X_1, Y_0)$ and $M_2(X_1, Y_1)$ with:

$$\begin{cases} X_1 = -X_0 - \dfrac{RY_0}{P} \\ Y_1 = -Y_0 - \dfrac{RX_1}{Q} \end{cases} \tag{6}$$

When the quadratic form is regarded as a metric relation, the second root calculus acquires a precise geometrical meaning: it is a symmetry with respect to the line which is orthogonal to the variable axis concerned (Figure 3).

More generally, when the space is more than two-dimensional, we consider, in a reflection with respect to the plane – or hyperplane – (Π), the vector **e**, which is perpendicular to the plane – or hyperplane (Figure 4).

The vector $\mathbf{M}_1$, issued from vector $\mathbf{M}_0$ through a reflection denoted $\mathfrak{X}_e$, is symmetrical to $\mathbf{M}_0$ with respect to the plane (Π), so that:

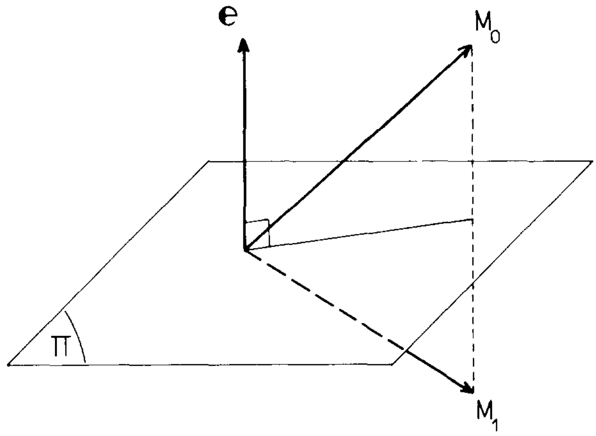


Figure 4. Reflection in relation to the vector **e**, expressed as: $\mathbf{M}_1 = \mathcal{X}_{\mathbf{e}}\mathbf{M}_0$.

$$\mathbf{M}_1 = \mathcal{X}_{\mathbf{e}}\mathbf{M}_0 = \mathbf{M}_0 - 2\,\frac{(\mathbf{e}\,.\,\mathbf{M}_0)}{|\mathbf{e}|^2}\,\mathbf{e} \tag{7}$$

This is a reflection as defined by Coxeter (1934) and, in the example above, we denote $\mathcal{X}_x$ (or more simply x) the reflection through which the point M_0 becomes the point M_1:

$$\begin{cases} M_1 = \mathcal{X}_x M_0 \\ M_2 = \mathcal{X}_y M_1 = \mathcal{X}_y \mathcal{X}_x M_0 \end{cases} \tag{8}$$

The initial point M_0 becomes the point M_2 through a rotation with the angle:

$$2\,\Phi = 2\,(\widehat{\mathbf{e}_1, \mathbf{e}_2})$$

Thus, in a simple mathematical way, an inner dynamics keeps a structure constant. However, Biochemists know that every step of a process is not always possible. It is therefore important that formalism should make the possibility of locking the dynamical process emerge naturally: in writing the quadratic form, we can only use relative integers for both coefficients and components. Thus, the quadratic form is connected with such a basis like $(\mathbf{e}_1, \mathbf{e}_2)$ as its coefficients (i.e. g_{11}, $2g_{12}$ and g_{22}) are integers: only the points with integer coordinates are taken into account. These points belong to the lattice defined upon the basic vectors $(\mathbf{e}_1, \mathbf{e}_2)$. Thus, the second root calculus (6) is only possible when the result is an integer. This is equivalent to saying that the reflection (7) is allowed when it transforms a point which belongs to the lattice into another point which belongs to the same lattice.

It is important to call the reader's attention to the fact that due to the use of reflections, the working of inner dynamics – and therefore, the set of points generated – is strongly related to the set of axes; thus "a vector space" is the equivalent of "a set of axes" and, therefore, changing the set of axes amounts to changing the connected vector space.

2.3 *Lattices and underlying cycles: The Basic Cyclic Relator*

There exist particular lattices which remain unchanged through a reflection with respect to either basic vectors. In a two-dimensional space, these lattices are defined by the following quadratic forms:

$$\text{elliptic forms}\left\{\begin{array}{l} X^2 + Y^2 \text{ generalized into } gX^2 + kY^2 \\ X^2 \pm XY + Y^2 \\ X^2 \pm 2XY + 2Y^2 \\ X^2 \pm 3XY + 3Y^2 \end{array}\right. \tag{9}$$

$$\text{hyperbolic form} \quad X^2 - Y^2 \text{ generalized into } gX^2 - kY^2 \tag{10}$$

The elliptic forms may be summarized by the following expression:

$$gX^2 + \epsilon gk\, XY + kY^2 \tag{11}$$

with:

$$\left\{\begin{array}{l} \epsilon = 0 \\ \qquad\qquad \text{or} \\ \epsilon = \pm 1 \quad \text{and} \quad g = 1,\ k = 1;\ 2 \text{ or } 3 \end{array}\right.$$

These quadratic forms present the noticeable property according to which the result of the second root calculus is always an integer whatever the initial point with integer coordinates (X_0, Y_0). The initial point is found again until a finite number of products denoted $\overrightarrow{(xy)}$ of the respective reflections $\mathfrak{X}_x$ and $\mathfrak{X}_y$ is reached (the arrow indicates the direction of reading). The particular relators so defined are named Basic Cyclic Relators (BCR). In two-dimensional space, there are four elliptic BCR (9) and each of them generates a group typified by the number G of reflections

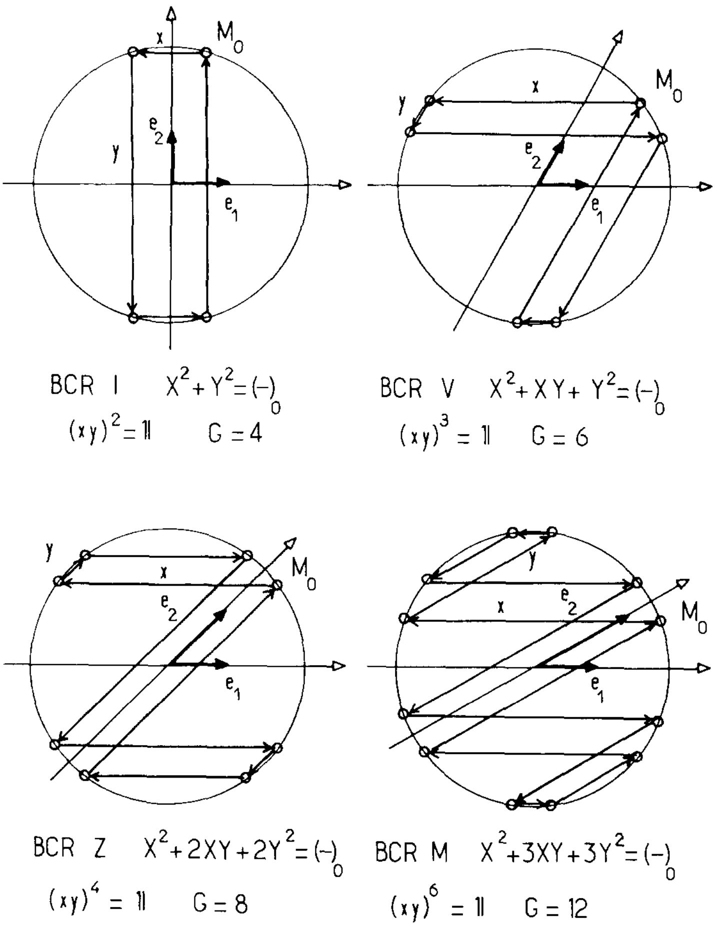


Figure 5. Cycles for the four two-dimensional Basic Cyclic Relators (BCR).

the cycle contains, depending upon the equivalence between the product (xy) and the rotation with an angle twice the angle of the lattice concerned. Figure 5 shows how these four BCR work and why the symbols I, V, Z and M are used to denote them (Apter et al., 1974b; Vallet et al., 1976; Ferré, 1983).

There are 10 families of BCR in three-dimensional space, and 36 families in four-dimensional space (Vallet et al., 1978a). Thus, the definition of an inner dynamics (i.e. reflections) which keeps a structure (i.e. a lattice) invariable, naturally leads to the notion of a cyclic process, a basic notion in both Physics (thermodynamics, oscillators, etc.) and Biology (cyclic metabolisms, inner clocks, etc.)

Generally, a lattice (a two-dimensional lattice, for instance) is not a BCR. A sequence of reflections ($xyxy$. . .) necessarily leads to a point outside the lattice, when a step is reached which depends upon both the lattice and the initial point, and the process is then locked.

Nevertheless, it may start again when a third dimension $\mathbf{e}_\nu$, named "environment", is added to the two-dimensional lattice ($\mathbf{e}_1^0$, $\mathbf{e}_2^0$). When the "call to environment" actually unlocks the process, we say that the Relator is "stabilized upon its BCR", or that it is "adapted" to its environment.

3. The adaptation system-environment: The Arithmetical Relator

As long as the process of reflection of the internal variables (X, Y) continues, the relator constitutes a "closed system". When its internal process locks, the system must "open"; to do so, it must call on the environment to unlock this process. The possibility of opening seems to be necessary for a system to take account of changes in the level of organization, and even of resonance linking different levels of organization. Therefore, the unlocking process must be controlled by the internal process itself, and both processes must be based on the same mathematical operation.

3.1 *Stabilization and definition of the Relator*

In order to understand both the geometrical and algebraic working of the Arithmetical Relator, it is necessary to construct it step by step, as follows: an environment is superimposed on a BCR; we shall take here the simple but not restrictive example in which the BCR is two-dimensional, in relation to the basic vectors ($\mathbf{e}_1^0$, $\mathbf{e}_2^0$) – and the environment is one-dimensional in relation to the basic vector $\mathbf{e}_\nu$. The resulting three-dimensional space (Figure 6) is termed the "primary space" ($\mathbf{e}_1^0$, $\mathbf{e}_2^0$, $\mathbf{e}_\nu$) and has the following metric coefficients:

$$\gamma_{ij} = (\mathbf{e}_i \,.\, \mathbf{e}_j) = (\mathbf{e}_j \,.\, \mathbf{e}_i) = \gamma_{ji} \text{ where } i \text{ and } j = 1, 2 \text{ or } \nu$$

This environment $\mathbf{e}_\nu$ transforms the BCR by keeping unchanged one of its basic vectors (for instance $\mathbf{e}_1^0$) and changing the other one $\mathbf{e}_2^0$ into the transformed vector $\mathbf{e}_2$ through a reflection with respect to the vector $\mathbf{e}_\nu$, so that:

$$\mathbf{e}_2 = \mathcal{X}_\nu\, \mathbf{e}_2^0 = \mathbf{e}_2^0 - 2\,\frac{\gamma_{2\nu}}{\gamma_{\nu\nu}}\,\mathbf{e}_\nu \qquad (12)$$

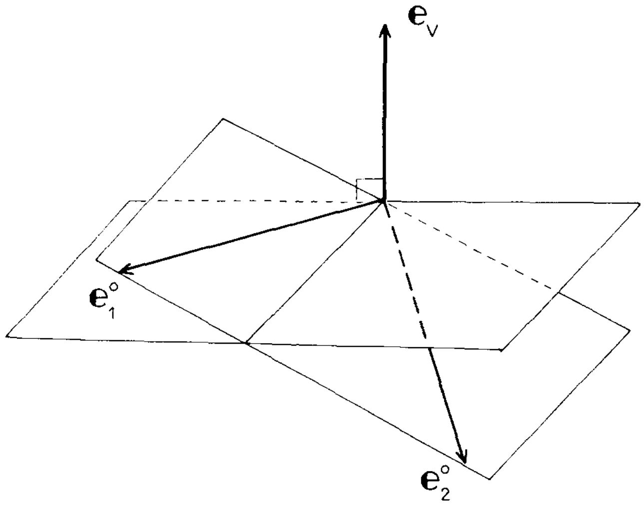


Figure 6. Construction of the Relator: the underlying BCR ($\mathbf{e}_1^0$, $\mathbf{e}_2^0$) and the environment $\mathbf{e}_v$.

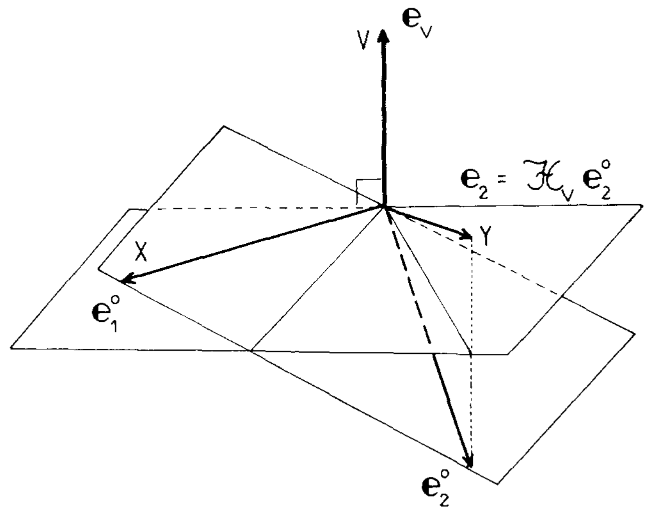


Figure 7. Construction of the Relator: the environment ($\mathbf{e}_v$) mirror effect on the underlying BCR ($\mathbf{e}_1^0$, $\mathbf{e}_2^0$) preserves $\mathbf{e}_1^0$ and changes $\mathbf{e}_2^0$ into $\mathbf{e}_2 = \mathcal{H}_v \mathbf{e}_2^0$. This relator works in the set of axes ($\mathbf{e}_1^0$, $\mathbf{e}_2$, $\mathbf{e}_v$) with the variables (X, Y, V).

This transformation, called the "mirror effect" describes the action of the environment upon a partition of the internal variables (Figure 7) (Ferré, 1981, 1983). Thus, the primary space ($\mathbf{e}_1^0$, $\mathbf{e}_2^0$, $\mathbf{e}_v$) becomes the "working space" ($\mathbf{e}_1^0$, $\mathbf{e}_2$, $\mathbf{e}_v$), whose metric coefficients are deduced from (12)

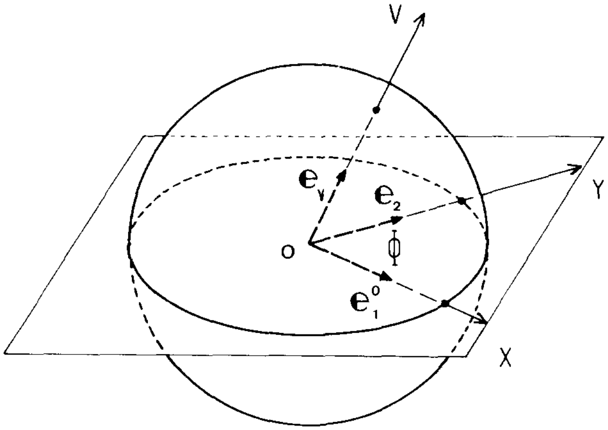


Figure 8. A three-variable homogeneous quadratic form like $F(X, Y, V) = m =$ const is represented as a sphere with radius $\sqrt{m}$ in a set of oblique axes.

$$\begin{cases} g_{11} = \gamma_{11} \\ g_{22} = \gamma_{22} \\ g_{vv} = \gamma_{vv} \end{cases} \qquad \begin{cases} g_{12} = \gamma_{12} - 2\dfrac{\gamma_{1v}\,\gamma_{2v}}{\gamma_{vv}} \\ g_{1v} = \gamma_{1v} \\ g_{2v} = -\gamma_{2v} \end{cases} \tag{13}$$

Any vector $\mathbf{X}$ with the components (X, Y, V) in this space, is such that:

$$\mathbf{X} = X\,\mathbf{e}_1^0 + Y\,\mathbf{e}_2 + V\,\mathbf{e}_v$$

and its scalar square can be written as follows:

$$\begin{aligned}(\mathbf{X} \,.\, \mathbf{X}) = \|\mathbf{X}\|^2 = & \left[\gamma_{11}\,X^2 + 2\gamma_{12}\,XY + \gamma_{22}\,Y^2\right] \\ & + \gamma_{vv}\left(2\frac{\gamma_{1v}}{\gamma_{vv}}X + V\right)\left(-2\frac{\gamma_{2v}}{\gamma_{vv}}Y + V\right)\end{aligned} \tag{14}$$

When $\|\mathbf{X}\|^2$ remains constant, equation (14) represents, in the working space $(\mathbf{e}_1^0, \mathbf{e}_2, \mathbf{e}_v)$, the equation of a sphere with a radius of $\|\mathbf{X}\|$ (Figure 8). In the first term of the quadratic form (14), the metric coefficients are connected to a subspace which is now a truly underlying subspace; when it is a BCR (as in the example chosen here), and if P denotes the factor which is common to the coefficients γ_{11}, $2\gamma_{12}$ and γ_{22}, this term may be written, in accordance with the expression (11):

$$P(gX^2 + \epsilon gkXY + kY^2) \tag{15}$$

The second term of the quadratic form (14) renders the BCR/environment coupling. We shall now assume that the environment possesses maximum stability, i.e. it is represented by a BCR to which no mirror effect is applied. In the example chosen here, the environment is one-dimensional and the second root process for the variable V – i.e. the reflection $\mathfrak{X}_v$ – must never lock according to the integer criterion. Through this reflection, the variable V becomes V^*, so that:

$$V^* = -V - 2\frac{\gamma_{1v}}{\gamma_{vv}}X + 2\frac{\gamma_{2v}}{\gamma_{vv}}Y \tag{16}$$

When the coefficients of the quadratic form are integers and prime numbers, division by integer $\gamma_{vv} = D$ in the equation (16) occurs whatever the values of X and Y, if the following conditions are met:

$$\begin{cases} \gamma_{1v} = DA' \\ \gamma_{2v} = -DB' \end{cases}$$

where A' and B' are integers.

The quadratic form becomes:

$$\|\mathbf{X}\|^2 = P(gX^2 + \epsilon gkXY + kY^2) + D(A'X + V)(B'Y + V) \tag{17}$$

On completion of the reflections $\mathfrak{X}_x$ and $\mathfrak{X}_y$, the variables X and Y take the following values:

$$\begin{cases} X^* = -X - \dfrac{DA'(B'Y + V)}{gP} \\ Y^* = -Y - \dfrac{DB'(A'X + V)}{kP} \end{cases} \tag{18}$$

To rid the process of any divisibility condition due to the coefficients g and k, it is assumed that:

$$\begin{cases} A' = gA \\ B' = kB \end{cases} \qquad \text{where } A \text{ and } B \text{ are integers}$$

Finally, the expression of the quadratic form (14) becomes:

$$\|\mathbf{X}\|^2 = P(gX^2 + \epsilon gkXY + kY^2) + D(gAX + V)(kBY + V) = (-)_0 \tag{19}$$

Note that the "environment" distorts the underlying structure of the BCR, and its angle Φ_0 becomes the angle Φ, so that, according to (19):

$$\cos \Phi = \cos \Phi_0 + \frac{DAB\sqrt{gk}}{2P} \qquad (20)$$

The environment may be regarded as a modelization of the operation of observing an inner structure (i.e. the BCR ($\mathbf{e}_1^0$, $\mathbf{e}_2^0$)), since a distorted image (i.e. the internal space ($\mathbf{e}_1^0$, $\mathbf{e}_2$)) results from such observation. From this point of view, the mirror effect process acts as a "stimulus" (in the sense indicated by von Neumann) through which the environment "questions" the underlying BCR which might represent some functional entity (cell metabolism, for example) and a distorted image (the response stimulus) emerges from this interrogation. This distorted observation is today well established in Physics. According to von Neumann, it is becoming evident in Biology through the problem of self-reproduction, which requires a copy of the system to be reproduced, precisely because of the distorted image obtained through a form of stimulation like direct questioning of this system.

When the underlying BCR has more than two dimensions, the mirror effect may act on a chosen partition of BCR variables so as to obtain the desired structure in quadratic form. The use of a multidimensional environment subspace allows the dovetailing of several partitions, i.e. several structures. By this means, the mirror effect induces strong nonlinearity in the structure of the Arithmetical Relator.

3.2 *Structure of the working space and elementary cells*

With the mirror effect, the base vector $\mathbf{e}_2^0$ can obviously be kept unchanged and $\mathbf{e}_1^0$ be transformed into $\mathbf{e}_1$, so that:

$$\mathbf{e}_1 = \mathcal{X}_v \, \mathbf{e}_1^0 = \mathbf{e}_1^0 - 2\,\frac{\gamma_{1v}}{\gamma_{vv}}\,\mathbf{e}_v \qquad (21)$$

This leads to the same quadratic form, but reveals a second underlying BCR with basic vectors ($\mathbf{e}_1$, $\mathbf{e}_2$) derived from the first BCR ($\mathbf{e}_1^0$, $\mathbf{e}_2^0$) through a reflection $\mathcal{X}_v$ (Figure 9). The equations of these two subspaces inside the working space ($\mathbf{e}_1^0$, $\mathbf{e}_2$, $\mathbf{e}_v$) are precisely the two coupling terms present in the quadratic form (19), that is:

$$gAX + V = 0 \quad \text{and} \quad kBY + V = 0 \qquad (22)$$

These terms also appear in the expressions of the variables X and Y after the respective reflections $\mathcal{X}_y$ and $\mathcal{X}_x$, as follows:

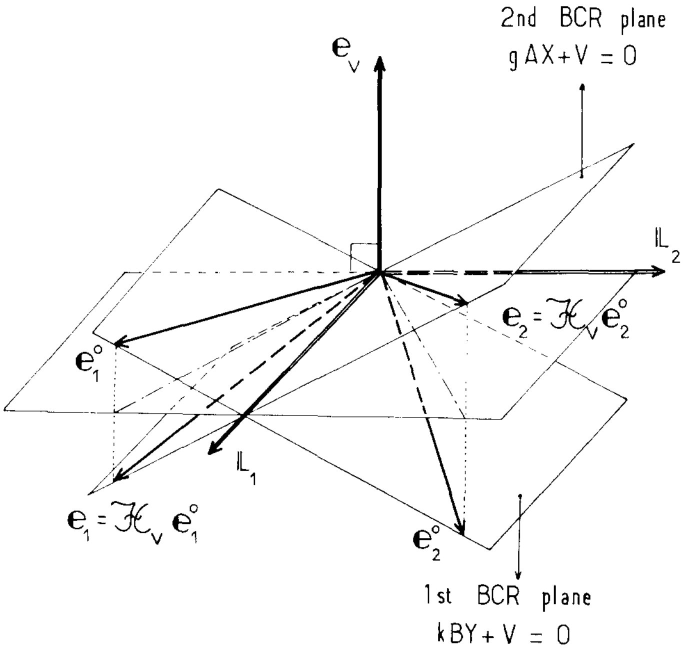


Figure 9. Structure of the working space: the two BCR planes ($\mathbf{e}_1^0$, $\mathbf{e}_2^0$) and ($\mathbf{e}_1$, $\mathbf{e}_2$) and the set of principal axes ($\mathbf{L}_1$, $\mathbf{L}_2$, $\mathbf{e}_v$).

$$\begin{cases} Y^* = -Y - \dfrac{DB\,(gAX + V)}{P} \\ X^* = -X - \dfrac{DA\,(kBY + V)}{P} \end{cases} \tag{23}$$

When the coefficients D, P, A and B are prime numbers, these two reflections are respectively possible under the following two conditions:

$$gAX + V \equiv 0 \text{ (modulo } P) \tag{24}$$

$$kBY + V \equiv 0 \text{ (modulo } P) \tag{25}$$

This means that the remainder after division by P is zero.

These conditions give the working space ($\mathbf{e}_1^0$, $\mathbf{e}_2$, $\mathbf{e}_v$) a foliated structure by means of two sets of parallel planes whose lattices are BCR.

It follows that the combination of the BCR cycle and mirror effect allows geometrical description of the functioning of the Arithmetical Relator.

The mirror effect has the following very important property, which is valid whatever the configuration:

the product of three reflections respectively oriented by the vectors $\mathbf{e}_\nu$, $\mathbf{e}_i$ and $\mathbf{e}_\nu$, is equivalent to one reflection oriented by the vector derived from the vector $\mathbf{e}_i$ through a reflection oriented by the vector $\mathbf{e}_\nu$.

This property is expressed by the following relation:

$$\mathcal{X}_{\mathbf{e}_\nu}\ \mathcal{X}_{\mathbf{e}_i}\ \mathcal{X}_{\mathbf{e}_\nu} \equiv \mathcal{X}_{(\mathcal{X}_{e_\nu}\ \mathbf{e}_i)} \tag{26}$$

For instance:

$$\mathcal{X}_\nu\ \mathcal{X}_{\mathbf{e}_2}\ \mathcal{X}_\nu \equiv \mathcal{X}_{\mathcal{X}_\nu\ \mathbf{e}_2} \equiv \mathcal{X}_{\mathbf{e}_2^0}$$

or, more concisely:

$$VyV \equiv \overset{0}{y} \tag{27}$$

When the BCR is of the (I) type, the cycle (Figure 5) is equivalent to the sequence:

$$\overset{0}{x}\,\overset{0}{y}\,\overset{0}{x}\,\overset{0}{y} \equiv \mathbb{1} \tag{28}$$

Therefore, to obtain a cyclic sequence for the relator, the reflection $\overset{0}{y}$ is replaced by (VyV). Cycle (28) for BCR becomes, for the Relator:

$$\overset{0}{x}\ VyV\ \overset{0}{x}\ VyV \equiv \mathbb{1} \tag{29}$$

Since a reflection is involutive, a sequence equivalent to reflection V is inferred from (29), so that:

$$\overset{0}{x}\ VyV\ \overset{0}{x}\ Vy \equiv V \tag{30}$$

In the environment subspace (here one-dimensional), the cycle is obtained with the sequence:

$$VV \equiv \mathbb{1}$$

from which, in accordance to (30) the cycle for the relator is inferred (i.e. the cycle of reflections in the working space ($\mathbf{e}_1^0$, $\mathbf{e}_2$, $\mathbf{e}_\nu$) with X, Y and V as variables):

$$x\ VyV\ x\ VyV\ x\ VyV\ x\ Vy \equiv \mathbb{1} \tag{31}$$

The upper index ^{0} indicates that the corresponding reflection $\overset{0}{x}$ operates in the BCR; since the mirror effect preserves the x-axis $\mathbf{e}_1^0$, this index can be cancelled. Note that a cycle is obtained in the environment subspace and that it implies two cycles in the internal space ($\mathbf{e}_1^0$, $\mathbf{e}_2$) or BCR space ($\mathbf{e}_1^0$, $\mathbf{e}_2^0$).

The first half-sequence cannot start unless

$$kBY + V \equiv 0 \text{ (modulo } P)$$

and the second half-sequence cannot start unless

$$g\,AX + V \equiv 0 \text{ (modulo } P)$$

According to Figure 5, the sequences equivalent to reflection V can be written, for each type of two-dimensional BCR:

$$\begin{aligned}
&(I) \quad V \equiv x\,VyV\,x\,Vy \\
&(V) \quad V \equiv x\,VyV\,x\,VyV\,x\,Vy \\
&(Z) \quad V \equiv x\,VyV\,x\,VyV\,x\,VyV\,x\,Vy \\
&(M) \quad V \equiv x\,VyV\,x\,VyV\,x\,VyV\,x\,VyV\,x\,VyV\,x\,Vy
\end{aligned} \tag{32}$$

The functioning of the Relator (or the natural system of which this Relator is a model) in the working space ($\mathbf{e}_1^0$, $\mathbf{e}_2$, $\mathbf{e}_v$) depends upon the regulated interaction between the reflections in the environment subspace and those in the BCR subspace: the latter emerges as a true underlying structure. It is then possible, in accordance with sequences (32) equivalent to reflection V, to built up the "elementary cells" from which are inferred the "natural sequences" constructed by the Relator.

3.3 *Structure of working space and partial self-reference*

The two BCR planes, defined by (22), intersect along a line supporting a vector denoted $\mathbf{L}_1$, which remains unchanged throughout the reflection $\mathcal{X}_v$ and is therefore perpendicular to the vector $\mathbf{e}_v$ (Figure 9). On the basis of a vector $\mathbf{L}_2$ perpendicular to vectors $\mathbf{L}_1$ and $\mathbf{e}_v$, we can build up a set of axes ($\mathbf{L}_1$, $\mathbf{L}_2$, $\mathbf{e}_v$) orthogonal to one another whatever the BCR. This set constitutes the "principal axes" whose corresponding unit vectors are in fact the eigenvectors of the subspace of the working space ($\mathbf{e}_1^0$, $\mathbf{e}_2$, $\mathbf{e}_v$) which is orthogonal to $\mathbf{e}_v$, in relation to a metric connected in this subspace to the BCR (Ferré, 1983). To illustrate the fundamental part played by this frame in the construction of the working space, one has to consider, in Figure 10, the importance of the vector $\mathbf{e}$, which is orthogonal to the first BCR plane. This vector is the axis of the rotation equivalent to the product of the reflections ($\mathcal{X}_{\mathbf{e}_1^0}\,\mathcal{X}_{\mathbf{e}_2^0}$) and therefore determines the BCR cycle from which the elementary cell is inferred. As the Relator is designed for applications to biological systems, only transformations which take into account the stability of the structure

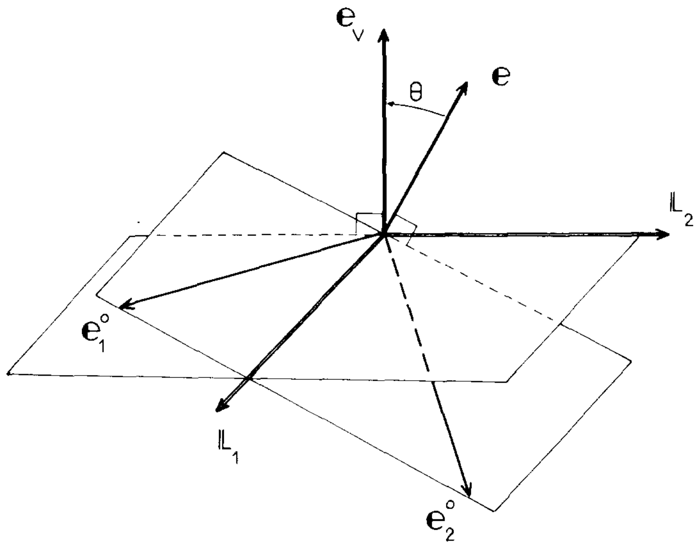


Figure 10. Definition of vector **e**, orthogonal to the underlying BCR.

can be considered. The configuration of the working space immediately reveals one of these transformations; it consists of a rotation of the BCR plane ($\mathbf{e}_1^0$, $\mathbf{e}_2^0$) in relation to the axis **e**. If Φ_0 denotes the angle of the BCR lattice, let

$$\begin{cases} D_c = 4 \sin^2 \Phi_0 = 4 \left(1 - \epsilon^2 \frac{gk}{4}\right) \\ P_0 = g A^2 + \epsilon gkAB + kB^2 \end{cases} \tag{33}$$

The cosine of the angle Θ between the vectors **e** and $\mathbf{e}_v$ is such that

$$cos^2 \Theta = 1 - \frac{DP_0}{D_c P} \tag{34}$$

Note that when

$$P = LP_0 \tag{35}$$

(where L is an integer coefficient which is necessary for homogeneity) the orientation of the BCR plane in relation to the environment axis $\mathbf{e}_v$ becomes independent of the coupling coefficients A and B.

The quadratic form (19) is then written

$$\begin{aligned} &L(gA^2 + \epsilon gkAB + kB^2)(gX^2 + \epsilon gkXY + kY^2) \\ &\quad + D(gAX + V)(kBY + V) = (-)_0 \end{aligned} \tag{36}$$

This expression is perfectly symmetrical in relation to both sets (A, B) and (X, Y). Such a Relator may work with either (X, Y) variables (A and B are kept constant) or (A, B) variables (X and Y are kept constant); in that case the Relator is said to be "bi-quadratic". this feature is of great importance for applications in Physics and Biology, since it shows that the Relator's formalism can take account of multiplicative domains; moreover, when (X, Y) are the main variables, a biquadratic Relator can transform itself into its own internal metric by means of a momentary bifurcation to the variables (A, B).

The configuration in Figure 9 is independent of both the variables (X, Y) and the coefficients (A, B). The bifurcation from one type of functioning to the other conforms this geometry. The components of vectors $\mathbf{L}_1$ and $\mathbf{L}_2$ in the primary set of axes ($\mathbf{e}_1^0$, $\mathbf{e}_2^0$, $\mathbf{e}_v$) are remarkably simple as follows:

$$\begin{cases} \mathbf{L}_1 = kB\,\mathbf{e}_1^0 + gA\,\mathbf{e}_2^0 & (37) \\ \mathbf{L}_2 = -\left(A + \epsilon k\frac{B}{2}\right)\mathbf{e}_1^0 + \left(B + \epsilon g\frac{A}{2}\right)\mathbf{e}_2^0 + \frac{1}{2}P_0\,\mathbf{e}_v & (38) \end{cases}$$

and their respective norms

$$\begin{cases} \|\mathbf{L}_1\|^2 = gkP_0P \quad \text{and} & (39) \\ \|\mathbf{L}_2\|^2 = P_0P\left(1 - \epsilon^2\frac{gk}{4}\right)\left(1 - \frac{DP_0}{D_cP}\right) & (40) \end{cases}$$

are kept constant in relation to P_0 and P.

Thus, the frame ($\mathbf{L}_1$, $\mathbf{L}_2$, $\mathbf{e}_v$) acts as an "objective" frame in which all the relators based on the same type of BCR can be positioned. Each of them has a different set of coupling coefficients (A, B) such that:

$$gA^2 + \epsilon gkAB + kB^2 = P_0$$

remains constant.

With respect to these vectors,

- the parameter P_0 represents a quantity typical of the underlying BCR
- except for the parameter D (D is the norm of the environment vector), the coefficients A and B describe the coupling between the underlying BCR and the environment.

Consequently, the metric connected to the underlying cycle provides partial information concerning its own coupling with the environment. When both the objective frame and parameter P are given, the only possibilities open to the underlying BCR for adaptation to a given environment are provided by the solutions to the following Diophantine equation:

$$gA^2 + \epsilon gk\, AB + kB^2 = P$$

This equation reveals a partial self-reference.

There is in fact only one free parameter: the norm D of the environment vector, whose value must be kept below the critical value D_c defined in (33), if an elliptic metric is desired.

3.4 *Elementary cells and natural sequences: Internal diversification*

The question of natural sequences has dealt with elsewhere from a general point of view (Luminet, 1980). In this article, it is sufficient to illustrate the notion of natural sequence with a simple example, for instance the case of a Relator stabilized on a BCR(I):

$$P(X^2 + Y^2) + D(AX + V)(BY + V) = (-)_0 \qquad (41)$$

This Relator starts to work under the following initial conditions:

$$X_0 = x_0 P^K \qquad Y_0 = y_0 P^K \qquad V_0 = v_0 P^K \qquad (42)$$

where x_0, y_0, v_0 and K are integers.

- when $K = 0$, the reflection $\mathfrak{X}_v$ is the only possible operation and the cycle is simply written

  $$VV = \mathbb{1}$$

- when $K = 1$, both the reflections $\mathfrak{X}_x$ and $\mathfrak{X}_y$ are allowed by the divisibility conditions emerging in (23); therefore the successive second root processes can generate the sequence (31) which is equivalent to a cycle in the working space.
- when $K = 2$, the sequence (30) equivalent to reflection V, replaces each reflection V in the cycle (31).

Thus, the parameter K emerges as a complexity factor. When it increases, it generates dovetailing by replacing reflection V by its equivalent sequence. Nevertheless, this process seems too regular to be able to account for complex exchanges between a system and its environment. It disregards the natural tendency of any living system to diversify its inner states to a maximum, i.e. in the case of the relator, to execute the reflections $\mathfrak{X}_x$ and $\mathfrak{X}_y$ in relation to the internal variables as often as possible before executing the unlocking reflection $\mathfrak{X}_v$. This trend can be allowed for if the following rules are observed when working the Relator:

- reflection $\mathfrak{X}_x$ (or $\mathfrak{X}_y$) must be executed whenever possible, whatever the previous reflection; therefore reflection $\mathfrak{X}_v$ will only occur when necessary, in accordance with the alternation of the internal reflections $\mathfrak{X}_x$ and $\mathfrak{X}_y$;
- certain divisibilities, different from those allowed by the factor K intervening in the initial conditions, may be created by congruences. Such congruences are of two types:
  1. congruences between initial conditions, named (α) congruences; for instance in (42), if we set

     $$K = 0 \qquad \text{but} \qquad By_0 + v_0 \equiv 0 \text{ (modulo } P)$$

     the first reflection $\mathfrak{X}_x$ is allowed, and the first reflection $\mathfrak{X}_v$ in cycle $VV \equiv \mathbb{1}$ is replaced by its equivalent sequence (30). The cycle is then written:

     $$x\ VyV\ x\ VyV \equiv \mathbb{1}$$

     The second reflection in cycle $VV \equiv \mathbb{1}$ is allowed by the symmetrical congruence

     $$Ax_0 + v_0 \equiv 0 \text{ (modulo } P)$$

  2. congruences between the coefficients of the quadratic form (for example as in biquadratic assumption), named (γ) congruences; such a congruence implies that, in the working space of the Relator there is an angle ψ, commensurable with 2π, so that:

     $$\psi = 2\pi \frac{p}{q} \qquad \text{with } p \text{ and } q \text{ as integers}$$

     When the rotation of angle ψ is equivalent to a sequence of reflections related to the axes of the working space, it can be naturally performed by the Relator and a cycle is obtained by repeating this sequence q times.

When one or several congruences are taken into account, the Relator performs more complex sequences (i.e. more complex exchanges with its environment); nevertheless, the Relator remains able to execute the simple sequences derived from the mirror effect and the elementary cells.

In connection with this notion of natural sequences three important features must be stressed:

- the construction presented in 3.1 shows that the definition of an arithmetical relator requires three elements:

  1. a quadratic form whose coefficients and variables are relative integers;
  2. a process of reflections modelizing the inner dynamics, and
  3. one point, given by its integer coordinates which determine the initial conditions for the sequence of reflections, as well as the value of the right-hand member of the expression (19).

However, it is important to notice that, since the natural sequences performed are related to congruences between the initial conditions or between the metric coefficients, a relator remains undefined as long as the numerical values of these parameters are not given. This feature makes the formalism of the arithmetical relator comparable to the theory of Undefined Finite Automata.

- when K increases, the number of reflections in a natural sequence also increases quickly and this sequence may become too long to allow computation; however, the process of dovetailing can be reversed in order to define the reduced sequences (built up from a few reflections) which allow quick computation of the internal state of the Relator after completion of the natural sequence concerned (Nottale, 1981).
- for a given value of the parameter K, the congruences provide the relator's functioning with additional divisibilities allowing internal diversification. In a wider sense, this point of view makes it possible to assume that total self-reference might concern systems whose inner dynamics or metabolism continue to function whatever the environment, i.e. "closed systems"; this is why partial self-reference is preferred, since the formalism of the Arithmetical Relator is designed to fit "open" systems.

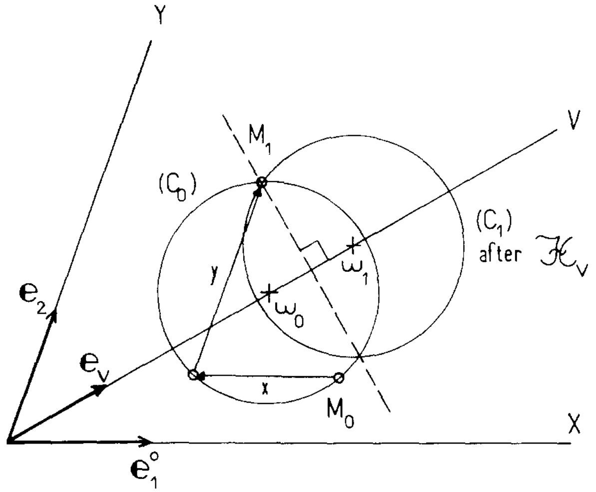


Figure 11. A degenerated Relator: the environment axis $\mathbf{e}_v$ belongs to the BCR $(\mathbf{e}_1^0, \mathbf{e}_2^0)$. When the sequence (xyV) functions in the direction of the arrow,

- point M_0 becomes M_1 through $(\overrightarrow{xy})$, and
- the circle (C_0) becomes the circle (C_1) through $\vec{V}$.

3.5 *Partial self-reference and propagation effect*

Although cyclic processes are of great importance in both Physics and Biology, they nevertheless exhibit numerous propagation phenomena, and the formalism of the Arithmetical Relator must allow for this feature. On the biquadratic assumption $P = LP_0$, with $L = 1$, when the norm D of the environment vector has the critical value D_c, the quadratic form degenerates since the BCR subspace includes the environment, but the mirror effect remains valid for stabilization (Ferré, 1983). The square of a vector $\mathbf{X}$ such as

$$\mathbf{X} = X\mathbf{e}_1^0 + Y\mathbf{e}_2 + V\mathbf{e}_v$$

is a degenerated quadratic form whose right member, which is kept constant during the functioning of the Relator represents the square radius of a circle (C_0).

Figure 11 shows that the center of this circle remains upon the line supporting vector $\mathbf{e}_v$, on which it is set by its coordinate V. During a sequence of products (xy), the point with the coordinates (X, Y) remains on the circle (C_0), whereas the reflection $\mathcal{K}_v$ keeps this point fixed and transform the circle (C_0) into the circle (C_1). The latter circle is symmetrical with respect to the line which is perpendicular to the axis $\mathbf{e}_v$ and

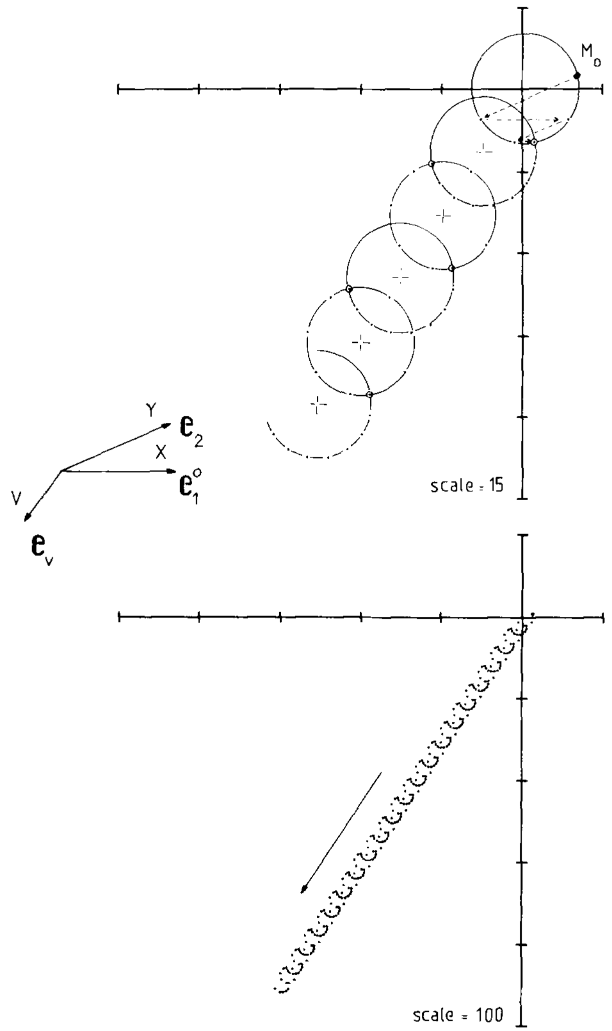


Figure 12. Example of propagation by a degenerated Relator:

$$P(X^2 + Y^2) + D(AX + V)(BY + V) = (-)_0$$
$$\{P, A, B, D\} = \{13, 2, 3, 4\} \qquad \{x_0, y_0, v_0\} = \{1, 1, 0\} \qquad K = 4$$

is drawn just before the above $\mathcal{X}_v$ operation, starting from the point representing the internal state of the Relator at that time.

Therefore, except in the case of particular initial conditions, the behavior of the Relator becomes non-cyclic and, in the internal space $(\mathbf{e}_1^0, \mathbf{e}_2)$, displays a propagation effect along the axis $\mathbf{e}_v$ (Figure 12), with a rate of displacement which increases with the frequency of the calls to the environment (Vallet et al., 1978b).

The propagation effect is consistent with the significance of the environment axis defined in 3.1 as the orientation of the observation of an inner structure assumed to be represented by a BCR. This consistency is clear when the Arithmetical Relator is applied to the description to polarized light (Ferré, 1983). In this application, the environment axis follows the direction of the illumination by polarized light of any anisotropic medium which distorts the initial polarized light. This distorsion is deduced from an energy measurement and typifies the anisotropic medium.

3.6 *Consistency with biological reality*

Due to the simple construction of the Relator formalism, there is no doubt about its self-consistency. But how far is it relevant to Biology? There are striking analogies between the working of the Arithmetical Relator and the description of living systems proposed by experimenters, for instance:

- the Relator emerges as a model of the interaction between a cyclic underlying structure and the environment to which it is adapted;
- the working space is structured by means of lattices and sets of parallel planes defined in (24) and (25);
- during operation, the point representing the state of the Relator migrates from a plane belonging to one set to a plane belonging to the other set, in accordance with (23). Thus, this structure exhibits inner dynamics which resemble a metabolism that may either be extremely stable, due to the simple dovetailing of elementary cells, or more complex because of (α) and (γ) congruences.
- the metric of the underlying structure provides partial information concerning the possibilities of adaptation to a given environment;
- the construction of the Relator may follow the procedure described below:

  let an environment (referred to above as $\mathbf{e}_\nu$) and a system (referred to above as the internal space ($\mathbf{e}_1^0$, $\mathbf{e}_2$)) be typified by the quantities D and P. The system will find its own position in the objective frame by partial self-reference, according to a solution of the Diophantine equation (39) for the set of variables (A, B):

$$gA^2 + \epsilon gkAB + kB^2 = P$$

The system will then fit the environment by means of the mirror effect, which enables it to find the underlying structure – above referred to as the BCR space $(\mathbf{e}_1^0, \mathbf{e}_2^0)$ – capable of driving its sequences, if the angle Φ of the given initial lattice fulfils the relation (20).

From this standpoint, the minimum but not the trivial values for the quantity P are, according to the BCR quadratic forms (9):

$$\left|\begin{array}{llllllll} \mathrm{BCR}\ (I) & P_0 & = 1^2 & & + & 1^2 & = 2 \\ \mathrm{BCR}\ (V) & P_0 & = 1^2 & + \quad 1.1 & + & 1^2 & = 3 \\ \mathrm{BCR}\ (Z) & P_0 & = 1^2 & + \ 2.1.1 & + & 2.1^2 & = 5 \\ \mathrm{BCR}\ (M) & P_0 & = 1^2 & + \ 3.1.1 & + & 3.1^2 & = 7 \end{array}\right. \qquad (43)$$

4. Application to plant morphogenesis: Collating the frameworks and ramifications

The angles formed by plants during morphogenesis are not necessarily the conventional values of trigonometry (i.e. 30°, 45°, 60° etc.). For example, in *Sphacelaria cirrhosa* Agardh. seaweed, the angle between the principal axis and one of its ramifications exhibits a constant average value of (41° ± 1.5°) significantly different from 45° (Ducreux, 1977). This value is also encountered as a rib-stem angle in the leaves of certain Dicotyledons. Recent studies have shown that the leaf morphogenesis and the venation are directly related; thus, Jeune (1972) stated that "the polar axis of the first divisions in the lamina seems to be oriented in a direction parallel to the lateral ribs... We indeed observe a close relationship between the orientation of the mitoses and that of the secondary order ribs" (Jeune, 1978) ("l'axe polaire des premières divisions du limbe est, semble-t-il, orienté parallèlement aux nervures latérales... On constate en effet une relation assez étroite entre l'orientation des mitoses et celle des nervures d'ordre 2"). Consequently the venation angles are directly related to the geometry of leaf embryogenesis in Dicotyledons. The same idea was subsequently formulated by Stewart and Dermen (1975).

Any model from which a theoretical interpretation of such angles can be deduced must take account, even in an approximate way, of the various processes controlling the growth of the plant organism. Ducreux (1977) showed that the ramification angle in Sphacelaria is due to the morphogenetic action of the apex cell of the main stem axis. Thus, as Brière (1982) also showed in moss, the architecture of a thallus depends upon the interaction of at least two levels of organization: the cell level and the organism level. What happens in higher plants? Cusset's short historical account of the theory of leaf morphogenesis in Dicotyledons (1983) is very instructive: in a primary type of pattern such as that described by Lignier (1887) and Avery (1933), the cell is the basic unit, and the leaf is built up step by step; Cusset also refers to a second type of pattern in which, on the contrary, the leaf is considered as a whole (Trécul, 1853) and goes on to quote Hagemann (1970), who almost denies the notion of cell; according to this author, the lamina builds up the cells, and the organ determines their position. Again according to Cusset, the oscillation between these extreme standpoints has recently been tempered by taking into account, not only the morphological criteria, but also the functional criteria obtained by observing the orientations of the metaphase plates (Fuchs, 1968; Maksymowytch, 1973). This makes it possible to propose patterns connecting structure and function with each other. Jeune (1978, 1981) assumed that lobes or leaflets could arise through a rhythmical process from two generating centers located in the lower part or in the apex of the leaf. The function of these centers might be to provide the "positional information" defined by Wolpert (1971) as follows: "a suggested solution to the pattern problem is that the cells are assignated positional information which effectively gives them their position in a coordinate system, and this positional information is used to determine the cell's molecular or cytodifferentiation".

These generating centers, which have a fixed position, display a constant rhythm of initiation, and generate continuous elements (lobes or leaflets). Jeune, therefore, writes (1975) that they play a "fundamental role in determining the form of the leaf, the orientation of the mitoses which are distributed throughout the entire lamina and affect neighbouring rows of cells at certain precise points and in growth centers whose emergence and functioning conform to quantifiable laws" (Jeune, 1975) ("... rôle fondamental pour la détermination de la forme de la feuille, des orientations de mitoses réparties sur l'ensemble du limbe et affectant, à des niveaux précis, des files cellulaires voisines, en des foyers de croissance dont l'apparition et le fonctionnement répondent à des lois quantifiables"). The form of the leaf is therefore a product of the connection and the equilibrium between the working of the generating centers, the intensity of the intercalary growth, and the determinism of the orientations of the mitoses. From the standpoint of Theoretical Biology, leaf morphogenesis seems to be a subject particularly well suited to the study of the relations between structure and function, and between the cell and the organ. Furthermore, given the "undoubted analogy between the emergence of the lateral lobes at the base of the young leaf and the emergence of the leaves at the top of the stem" (Jeune, 1975) ("l'analogie certaine entre l'apparition des lobes latéraux à la base de l'ébauche et celle des feuilles vers le sommet de la tige''), a subject as precise as the study of the venation angles certainly forms part of the more general problem of plant morphogenesis.

The above considerations involve different types of theoretical problems: for instance, we should not trust our primary intuition since ''the simpler the form of the leaf, the more complex its growth'' (Jeune, 1978) (''le développement de la feuille est d'autant plus complexe que la forme est plus entière''). This is strikingly exemplified in the Chestnut tree (*Castanea sativa* Miller). This feature is also illustrated by the difficulties encountered in computer programming as regards the positioning of the ''operational cells'' generated by a particular programme (Simon et al., 1980) since such positioning necessarily involves tearing and overlapping. In addition, it is essential to be aware of what underlies the notion of ''positional information''. According to Wolpert (1971) ''the crucial feature is that the positional value provides the cell with its position within the system and that this value is used together with the cell's genome to specify its molecular differentiation. This implies that three levels interact with each other: the organ, the cell, and the genome. This corresponds to the problem formulated by Buis (1983): ''as the elementary act of growth takes place at the cell level, it would be desirable to understand the link between this fundamental level and the level of the organized cell population which constitutes the organ'' (''l'acte de croissance élémentaire s'effectuant à l'échelle de la cellule, il conviendrait que l'on fasse le joint entre ce niveau fondamental et celui de la population cellulaire organisée qui est l'organe''). Buis is in fact referring here to the interaction which occurs between the different levels of organization.

During leaf morphogenesis, the fundamental processes, particularly mitosis, are directly related to the structural evolution of the leaf, as shown by the venation angles and form of the lamina. However primitive in form, the organism remains a living thing throughout all the stages of its genesis – and this is the main difference between Biology and Technology –. The compatibility between structure and function, which preserves the organism's stability despite numerous breaks in its symmetry such as those occurring in bifurcation, persists from the very beginning of embryogenesis.

4.1 *Compatibilities between structure and function: The conjugation of the Relators*

The transformation of the Relator through rotation of the BCR plane on itself is only one particular aspect of the more general problem of the bifurcation of a biquadratic Relator from a functioning with (X, Y)

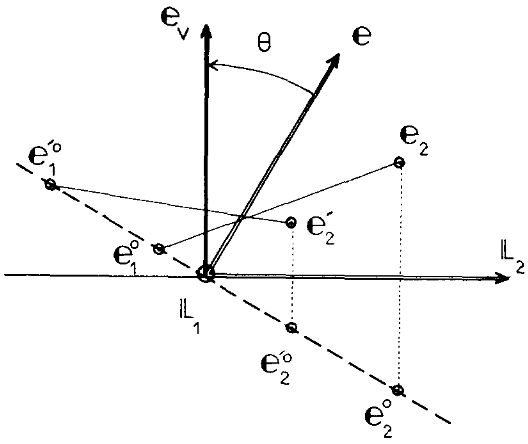


Figure 13. Definition, in the set of principal axes, of the conjugation of the working space of a Relator as a transformation through a rotation of the BCR plane ($\mathbf{e}_1^0$, $\mathbf{e}_2^0$) about the orthogonal vector $\mathbf{e}$. The figure is drawn in the front plane parallel to the plane ($\mathbf{L}_2$, $\mathbf{e}_\nu$).

as variables to functioning with (A, B) as variables, given that during this rotation, the quantity

$$P_0 = gA^2 + \epsilon gkAB + kB^2$$

remains constant.

The value of the angle of the internal lattice ($\mathbf{e}_1^0$, $\mathbf{e}_2 = \mathcal{X}_\nu \mathbf{e}_2^0$) is a function of the position of the underlying BCR lattice during its rotation around the vector $\mathbf{e}$. This construction is shown in Figure 13 where, for greater simplicity, we only represent a front plane parallel to vectors $\mathbf{L}_2$ and $\mathbf{e}_\nu$, together with its intercepts with the characteristic axes and planes.

What are the bases of structural consistency? It certainly needs an objective framework which makes it possible to position the two systems of variables (X, Y) and (A, B) in relation to each other; the framework ($\mathbf{L}_1$, $\mathbf{L}_2$, $\mathbf{e}_\nu$) seems naturally suitable as it is independent from both (X, Y) and (A, B) in the case of a biquadratic Relator. Moreover, the angle Θ, which stands between the vectors $\mathbf{e}$ and $\mathbf{e}_\nu$ must obviously be kept constant, as was done in the above formulation.

As to the question of functional consistency, two elements which belong to the same organism must have consistent metabolisms. In the case of the Relator, the "metabolism" is connected with the cycles generated by the process of reflection, and tightly related to both the underlying BCR lattice ($\mathbf{e}_1^0$, $\mathbf{e}_2^0$) and the internal lattice ($\mathbf{e}_1^0$, $\mathbf{e}_2$) of the Relator. Functional stability emerges when transformations which preserve both lattices are found within the objective frame.

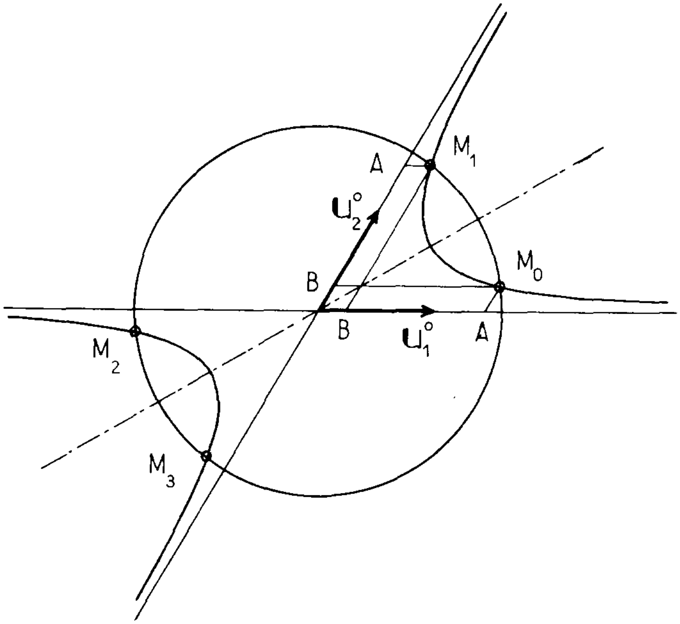


Figure 14. Conjugation in a lattice ($\mathbf{u}_1^0$, $\mathbf{u}_2^0$) with (A, B) as variables, identical to the BCR lattice ($\mathbf{e}_1^0$, $\mathbf{e}_2^0$).

The value investigated is the value of the angle of rotation through which the internal lattice ($\mathbf{e}_1^0$, $\mathbf{e}_2$) returns to the initial value of its angle Φ. Thus, both the initial and final internal lattices display maximal consistency with each other, because their axes are superimposable. Now, it follows from equation (20) that the quantity $AB\sqrt{gk}$ retains the same value before and after the rotation of BCR. In the case of a biquadratic Relator, the transformation thus defined is therefore connected with the solutions to the following Diophantine equations:

$$\begin{cases} gA^2 + \epsilon gkAB + kB^2 = \text{const.} \\ AB\sqrt{gk} = \text{const.} \end{cases} \qquad (44)$$

In the underlying BCR lattice ($\mathbf{u}_1^0$, $\mathbf{u}_2^0$), equations (44) represent the intersection between a circle and a hyperbola whose axes coincide with the bisectors of axes $\mathbf{u}_1^0$ and $\mathbf{u}_2^0$ (Figure 14). The intersection points are themselves symmetrical in relation to these bisectors. Therefore, the solutions to equations (44) are provided by the points common to both the given lattice and the lattice symmetrical to it in relation to the bisector of the axes of the first lattice. When the lattice is isotropic (i.e. its basic vectors have the same length) the symmetry of the geometrical figure is preserved and any point (A, B) which belongs to the lattice has a symmetrical point (B, A). When the lattice is anisotropic (i.e. its basic vectors have different lengths) it no more longer coincides with the lattice symmetrical to it in relation to the bisector of its axes; moreover, since the underlying lattice considered here is a BCR, there is no point common to both symmetrical lattices. When this symmetry is cancelled by the anisotropy of the underlying metric, it can be set up again through a permutation of the unities of the axes. In that case, in a BCR space with (A, B) as variables, the transformation sought will connect the point M with the coordinates (A, B) in the space $(\mathbf{u}_1^0, \mathbf{u}_2^0)$, to the point M' with the coordinates (B, A) in the space $(\mathbf{U}_1^0, \mathbf{U}_2^0)$ issued from the previous space through permutation of the lengths of the basic vectors, according no

$$M = \begin{bmatrix} A \\ B \end{bmatrix} \text{ in } (\mathbf{u}_1^0, \mathbf{u}_2^0) \Rightarrow M' = \begin{bmatrix} B \\ A \end{bmatrix} \text{ in } (\mathbf{U}_1^0, \mathbf{U}_2^0)$$

$$(\mathbf{U}_1^0, \mathbf{U}_2^0) = (\mathbf{u}_1^0, \mathbf{u}_2^0) \begin{bmatrix} \sqrt{\frac{k}{g}} & 0 \\ 0 & \sqrt{\frac{g}{k}} \end{bmatrix} \tag{45}$$

Thus, both the underlying BCR and internal lattices are preserved.

When the Relator is non-biquadratic, the transformation through rotation of the BCR plane around the orthogonal vector $\mathbf{e}$ is such that the angle Θ remains constant. Therefore $\cos \Theta$ = const. and, according to equation (34):

$$P_0 = gA^2 + \epsilon gk\, AB + kB^2 = \text{const.}$$

Thus, the transformation of a non-biquadratic Relator involves exactly the same problem as that of a biquadratic Relator. When the mathematically feasible transformations are considered, partial self-reference follows naturally.

We would stress that the conjugation is defined with (A, B) as variables in an underlying BCR metric; a functional partial self-reference thus emerges in addition to the structural partial self-reference mentioned above. This constitutes a very close analogy with structural and metabolic compatibilities which exist between cells and tissues: in the present case, these compatibilities reside in an underlying structure.

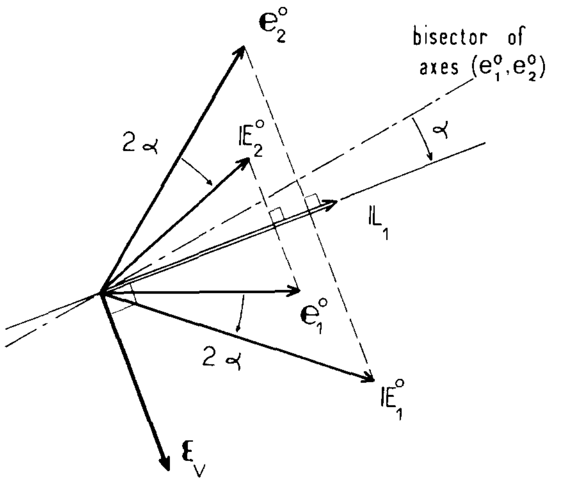


Figure 15. Conjugation in the BCR plane: the axes $(\mathbf{e}_2^0, \mathbf{e}_1^0)$ respectively become the axes $(\mathbf{E}_1^0, \mathbf{E}_2^0)$ through the reflection $\mathcal{X}_{\mathbf{E}_v}$ where the vector $\mathbf{E}_v$ is orthogonal to the principal axis $\mathbf{L}_1$.

4.2 *Conjugation within the objective framework*

As the conjugation has now been defined with (A, B) as variables, we can proceed to study its representation with (X, Y) as variables in the objective frame $(\mathbf{L}_1, \mathbf{L}_2, \mathbf{e}_v)$.

Let $(\mathbf{e}_1^0, \mathbf{e}_2^0)$ be the basic vectors of the initial given BCR; the latter rotates around the vector $\mathbf{e}$, which is orthogonal to the plane of the BCR, and the angle of this rotation, denoted 2α, is such that the angle of the internal lattice $(\mathbf{e}_1^0, \mathbf{e}_2)$ is preserved. After both rotation and permutation of the lengths of the basic vectors, we obtain the framework $(\mathbf{E}_1^0, \mathbf{E}_2^0)$ (Figure 15), and we can show that:

- the angle of rotation 2α is twice the angle between the principal axis $\mathbf{L}_1$, and the interior bisector (or the exterior bisector depending on the sign of the product AB) of axes $(\mathbf{e}_1^0, \mathbf{e}_2^0)$ in the BCR plane;
- the basic vectors $(\mathbf{E}_1^0, \mathbf{E}_2^0)$ of the conjugate BCR are derived from the respective basic vectors $(\mathbf{e}_2^0, \mathbf{e}_1^0)$ of the initial BCR, through a symmetry related to the support of the vector $\mathbf{L}_1$.

This symmetry leads to an interesting geometrical interpretation: let ε_v be a vector whose norm equals the critical value D_c – defined in (33) – and whose support is the projection onto the BCR plane of the support of the environment vector $\mathbf{e}_v$; let $(\varepsilon_1^0, \varepsilon_2^0)$ be two vectors respectively collinear with the vectors $(\mathbf{e}_1^0, \mathbf{e}_2^0)$, and let the biquadratic assumption be, such that

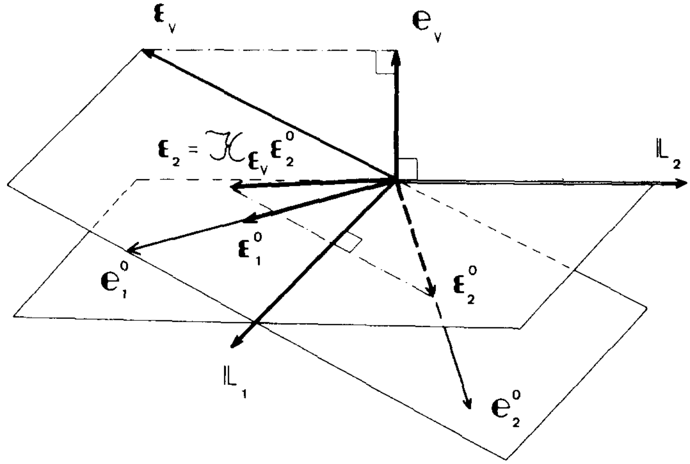


Figure 16. Definition of the associated degenerated Relator based on BCR (ε_1^0, ε_2^0) and environment ε_v: the mirror effect preserves ε_1^0 and changes ε_2^0 into $\varepsilon_2 = \mathcal{X}_{\varepsilon_v} \varepsilon_2^0$.

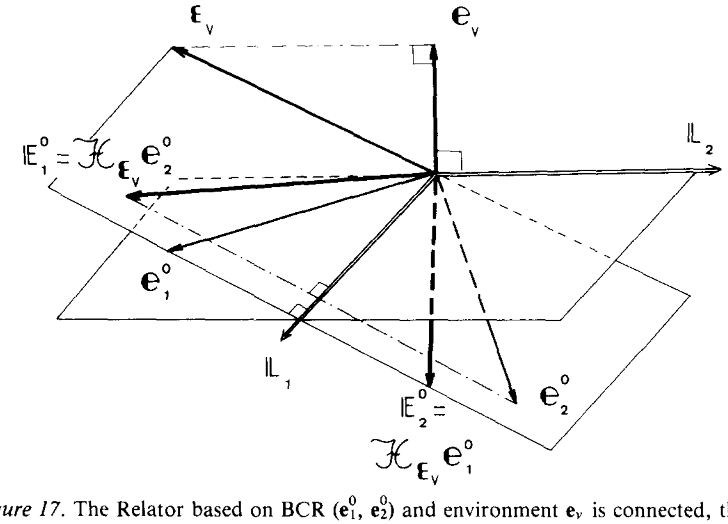


Figure 17. The Relator based on BCR ($\mathbf{e}_1^0$, $\mathbf{e}_2^0$) and environment $\mathbf{e}_v$ is connected, through the conjugation, to the Relator based on the same environment and the BCR ($\mathbf{E}_1^0$, $\mathbf{E}_2^0$) $\equiv$ $\mathcal{X}_{\varepsilon_v}$ ($\mathbf{e}_2^0$, $\mathbf{e}_1^0$).

$$\|\varepsilon_1^0\|^2 = gP_0 \qquad \|\varepsilon_2^0\|^2 = kP_0 \qquad (\varepsilon_1^0 \,.\, \varepsilon_2^0) = \frac{1}{2}\,\epsilon gkP_0 \tag{46}$$

We can then build a degenerated relator – denoted R_0 – based on the BCR (ε_1^0, ε_2^0) and the environment ε_v. After adaptation using the mirror effect, the internal space is defined by the vectors (ε_1^0, $\varepsilon_2 = \mathcal{X}_{\varepsilon_v} \varepsilon_2^0$); as they are respectively collinear with $\mathbf{e}_1^0$ and $\mathbf{E}_1^0$, they form the angle 2α at which the BCR rotates on itself (Figures 16 an 17).

Given that the vector ε_v is perpendicular to the vector $\mathbf{L}_1$, the above symmetry can be regarded as a reflection $\mathcal{X}_{\varepsilon_v}$. This is why the conjugation of any relator R is induced by the process of the call to environment of a degenerated Relator R^*, which may be taken to be connected with R, since it is built upon the same BCR axes (but with different basic vectors).

When one of the basic vectors of the BCR (for instance $\mathbf{e}_1^0$) is perpendicular to $\mathbf{e}_v$, and therefore coincides with $\mathbf{L}_1$ (as when $A = 0$), the symmetry-permutation product of the conjugation becomes a 90° rotation on the axes of BCR, i.e. a multiplication by the complex number i ($i^2 = -1$). This warrants the use of the word "conjugation" to define the transformation.

For Biologists, this method of operation is of great interest because, in relation to the vector ε_v, the reflection resembles a process which modifies the working space of the Relator while preserving the quadratic form. This constitutes a coupling of structure and function, whose expression is one of the most difficult problems in Physiology and Biochemistry.

4.3 *Different ways of collating the frameworks*

The initial and conjugate working spaces may be positioned in relation to each other in three different ways, according to the process to be treated preferentially; this operation is termed the "collating" of the frameworks.

- The definition of the conjugation does the collating with respect to the principal axes; both Relators are in the same principal axes while their respective internal spaces ($\mathbf{e}_1^0$, $\mathbf{e}_2 = \mathcal{X}_v\, \mathbf{e}_2^0$) and ($\mathbf{E}_1^0$, $\mathbf{E}_2 = \mathcal{X}_v\, \mathbf{E}_2^0$) are different. This is shown in Figure 18, representing a frontal plane parallel to the vectors ($\mathbf{L}_2$, $\mathbf{e}_v$). The representative points which, in the principal axes, belong to both Relators are such that we can assume this configuration to lead to applications in Quantum Mechanics. However, comparison of the two Relators with (X, Y) as variables requires the planes ($\mathbf{e}_1^0$, $\mathbf{e}_2$) and ($\mathbf{E}_1^0$, $\mathbf{E}_2$) to coincide. This coincidence may be obtained in two different ways:
  - if the directions of the environment vectors are the same, the above planes will coincide but the axes ($\mathbf{e}_1^0$, $\mathbf{e}_2$) and ($\mathbf{E}_1^0$, $\mathbf{E}_2$) will be different (Figure 19). This configuration leads to the notion of dual Relator (Nottale, 1982) and to applications in Thermodynamics and Macrophysics.
  - if the axes ($\mathbf{e}_1^0$, $\mathbf{e}_2$) and ($\mathbf{E}_1^0$, $\mathbf{E}_2$) are made to coincide (Figure 20),

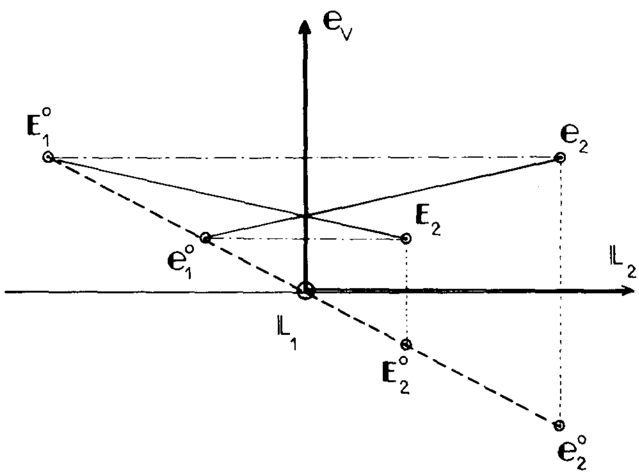


Figure 18. The collation, in the set of principal axes, of both the initial working space ($\mathbf{e}_1^0$, $\mathbf{e}_2$, $\mathbf{e}_v$) and conjugate working space ($\mathbf{E}_1^0$, $\mathbf{E}_2$, $\mathbf{e}_v$).

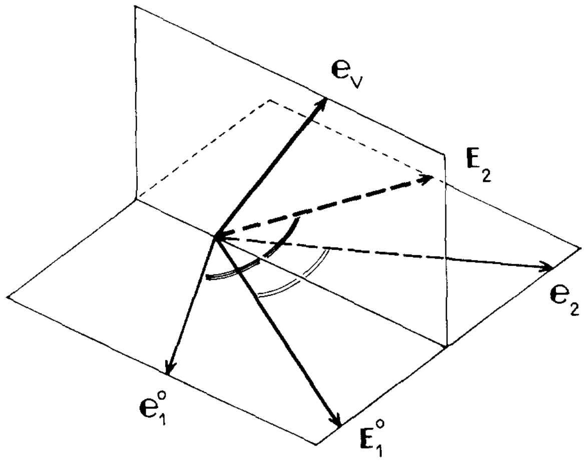


Figure 19. The collation, in relation to the same environment axis, of the two internal conjugate spaces ($\mathbf{e}_1^0$, $\mathbf{e}_2$) and ($\mathbf{E}_1^0$, $\mathbf{E}_2$).

the environment axes, denoted $\mathbf{e}_v$ and $\mathbf{E}_v$, will be different; this configuration shows diversification of the environmental axis, and therefore, leads to the emergence of angular values typical of ramifications.

This set of three configurations allows a new interpretation of the connection between the three main fields encountered in the study of Nature – Microphysics ($m\varphi$), Macrophysics ($M\varphi$)) and Biology (Bio).

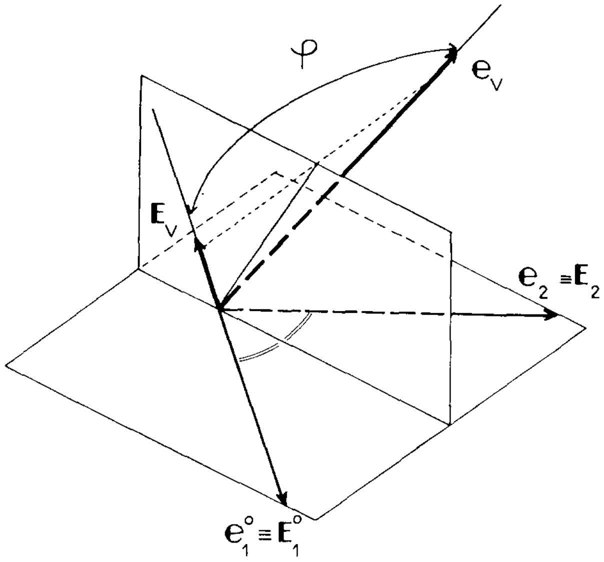


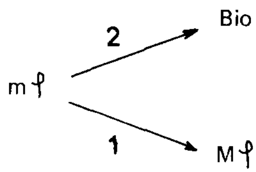
Figure 20. The axes of the two internal conjugate spaces brought into coincidence, leading to differentiation of the environment axis onto $\mathbf{e}_v$ and $\mathbf{E}_v$.

According to modern cosmology, the conventional scheme leads to the following sequence:

$$m\varphi \rightarrow M\varphi \rightarrow \text{Bio}$$

While most Physicists seem to believe that Macrophysics is derived from Microphysics, the derivation of Biology from Macrophysics has not yet been proved. This idea is essentially based on the well-known fact that processes in living systems obey the laws of Physics, which amounts to saying that an organism is consistent with its physical environment.

The logic of the Arithmetical Relator permits the following scheme:



The first arrow concerns collation to a common environment: the system tends towards homogeneity and unity. The second arrow represents the collation corresponding to the coincidence between the supports of the basic vectors of both internal spaces; this gives rise to a diversification of the environment which tends towards heterogeneity, multiplicity and the obvious possibility of changing the level of organization.

Thus, it seems possible to understand why it is so difficult to extent to Biology the formalisms suitable for Physics.

4.4 *The ramification angles on the biquadratic assumption*

It was shown in a previous section (3.5) that an environmental axis can be compared to a direction of propagation. Botanical experiments show that the ribs of a leaf represent the prime directions in the growth of lamina. Therefore it seems natural to use the third of the above forms of collation as a pattern for bifurcations in leaf venation. When the internal axes are made to coincide, both lattices themselves coincide, if they are isotropic. In that case the structures and the internal rhythms of both conjugate relators display maximal consistency with each other. The conjugate environmental axes $\mathbf{e}_\nu$ and $\mathbf{E}_\nu$ include an angle φ which depends on the dimensionless coefficient

$$\tau = \frac{B}{A}\sqrt{\frac{k}{g}} \tag{47}$$

which is closely related to the rotation of BCR. As regards stability, it is important to know the extreme values of the angle φ as a function of the parameter τ responsible for the ramification. The cosine of this angle φ is expressed as

$$\cos\varphi = 1 - \frac{D}{4}\,\frac{(1-\tau)^2}{(1+\epsilon\tau\sqrt{gk}+\tau^2)\,(1-\frac{1}{2}\epsilon\sqrt{gk}) - \frac{1}{2}D\tau} \tag{48}$$

Whatever the BCR, this cosine is extreme for the values (Figure 21):

$$\tau = \pm 1 \qquad \text{and} \qquad \tau \to \pm\infty$$

When $\tau = +1$, the angle φ equals zero; the axes $\mathbf{e}_\nu$ and $\mathbf{E}_\nu$ are in coincidence and there is no ramification. The other extreme values ($\tau = -1$ and $\tau \to \pm\infty$) are of much greater interest to plant morphogenesis.

Table 1 shows the numerical results given by the isotropic BCR (*I*) and (*V*). A bifurcation – i.e. a break in symmetry – is a harzardous step in plant ontogenesis. Now the angular values calculated above allow maximum stability of the compatibilities of the underlying structures. Angular values like 41° 25′ or 53° 08′ which might not, at first

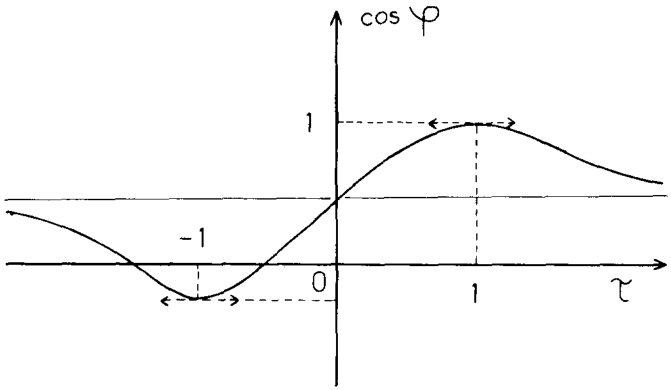


Figure 21. When the cosine of the ramification angle varies as a function of the non-dimensional parameter $\tau = B\sqrt{k}/A\sqrt{g}$ the three following extrema result:

$\tau = +1 \qquad \tau = -1 \qquad$ and $\qquad \tau \to \pm\infty$

Table 1. Extreme values of the ramification angles for the isotropic BCR (*I*) and (*V*) as a function of the parameter *D*, the norm $\|e_v\|^2$ of the environment vector.

BCR (I)

$\tau \to \infty \qquad \cos\varphi \to 1 - \frac{D}{4}$ | $\tau = -1 \qquad \cos\varphi = \frac{4-D}{4+D}$

	cos φ	φ	cos φ	φ
D=1	3/4	41°25′	3/5	53°08′
D=2	1/2	60°	1/3	70°32′
D=3	1/4	75°31′	1/7	81°47′
D=4	0	90°	0	90°

BCR (V) $\varepsilon = +1$

$\tau \to \infty \qquad \cos\varphi \to 1 - \frac{D}{2}$ | $\tau = -1 \qquad \cos\varphi = \frac{1-D}{1+D}$

	cos φ	φ	cos φ	φ
D=1	1/2	60°	0	90°
D=2	0	90°	− 1/3	109°28′
D=3	− 1/2	120°	− 1/2	120°

BCR (V) $\varepsilon = -1$

$\tau \to \infty \qquad \cos\varphi \to 1 - \frac{D}{6}$ | $\tau = -1 \qquad \cos\varphi = \frac{9-D}{9+D}$

	cos φ	φ	cos φ	φ
D=1	5/6	33°33′	4/5	36°52′
D=2	2/3	48°11′	7/11	50°29′
D=3	1/2	60°	1/2	60°

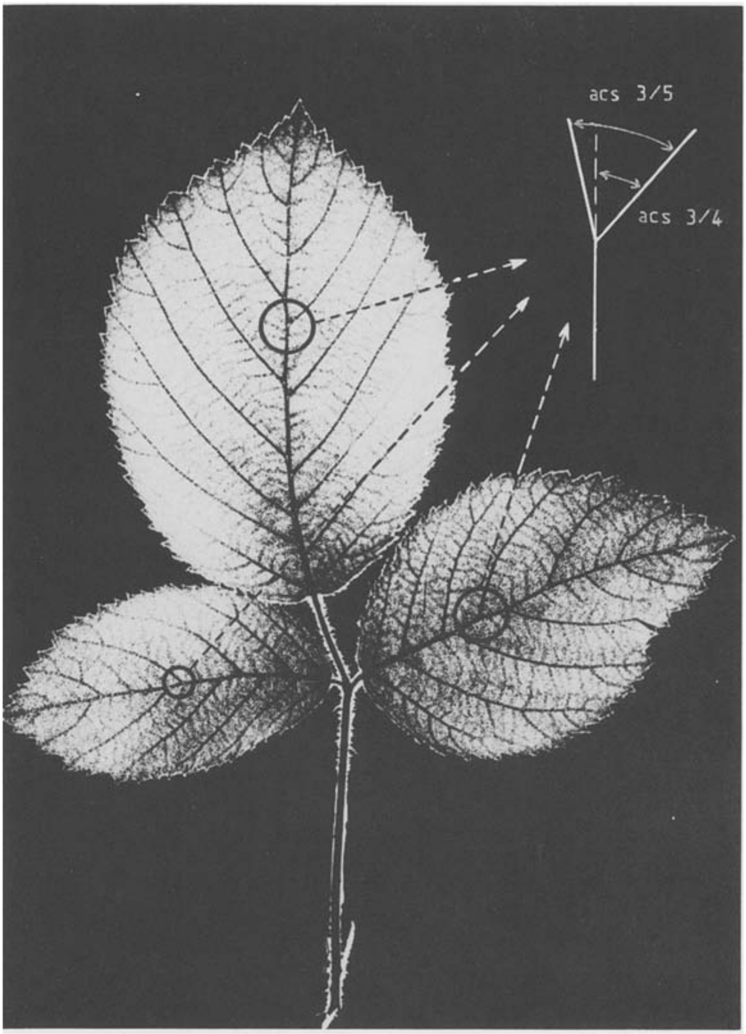


Plate 1. Bramble leaf (venation angle near acs 3/4 = 41° 25′).

sight, seem very important thus acquire considerable biological significance. Such values are found either in leaf venation or in twig bifurcations, provided they are measured at the level of description, i.e. at organ and not at cell level.

As regards leaf venation, examples of such angles are shown in Plates 1, 2 and 3. An angle value near acs 3/4 (41° 25′) is found in the Bramble (*Rubus* sp.) (Plate 1), and Lime-tree (*Tilia sylvestris* L.) (Plate 2). In the leaf of the latter, even order three ribs exhibit this angle ramification value. A ramification angle of 60° is observed in the leaf of the Cherry-

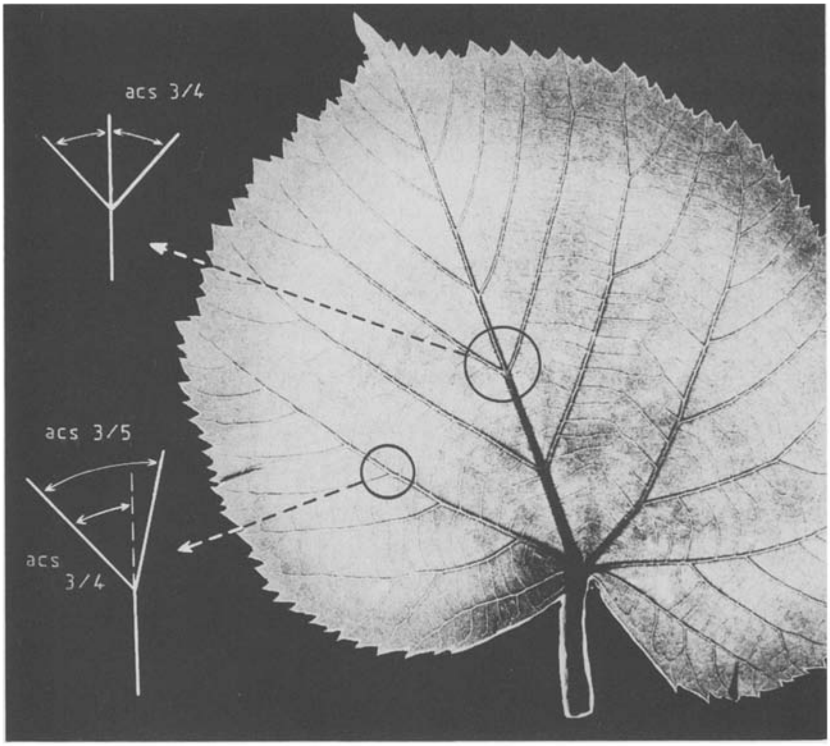


Plate 2. Lime-tree leaf (venation angle near acs 3/4 = 41° 25′).

tree (*Prunus cerasus* L.) (Plate 3). There seems to be no relation between geometry and plant classification, as shown by the two Rosaceae mentioned above.

As regards twig ramifications, some of the angle values calculated here have been observed between stems and twigs. The original feature of these angles lies in the fact that just beyond the ramification point, the plant morphology acquires an asymmetrical *Y* structure, leading to the simultaneous appearance of both the angle values related to a particular value of the norm *D* of the environment axis. For example, in an Umbellifera (Plate 4), the angles measured are close to the values obtained for BCR (*I*) when $D = 1$, i.e. both angle values acs 3/4 (41° 25′) and acs 3/5 (53° 8′). The twigs of the Hazel-tree (*Corylus avellana* L.) have an angle value corresponding to $D = 2$, i.e. to acs 1/2 (60°) and acs 1/3 (70° 32′).

Numerous other examples of such values have been found, not only in plants, but also in wing venation of certain insects such as the Cicada and detailed descriptions of these examples will be published later.

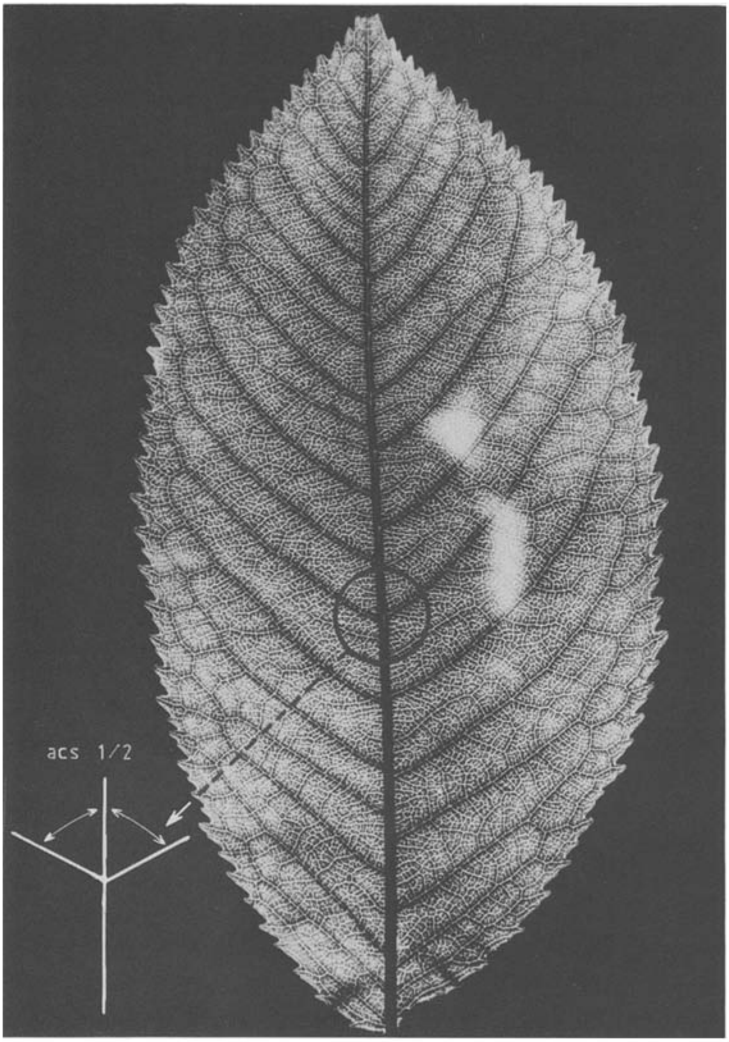


Plate 3. Cherry-tree leaf (venation angle near acs 1/2 = 60°).

The angle values just defined seem of special interest to morphologists, although it should be pointed out that some plants do not conform to this pattern and it is important to find out why. The present work should be helpful to Botanists studying plant architecture, particularly that of trees such as Oldeman (1974) and Hallé (1979). These authors in fact describe morphological patterns which "are noticeably independent of the size of plants, their ecology and even their genetics, since the same architecture may appear in plant families as different, for exam-

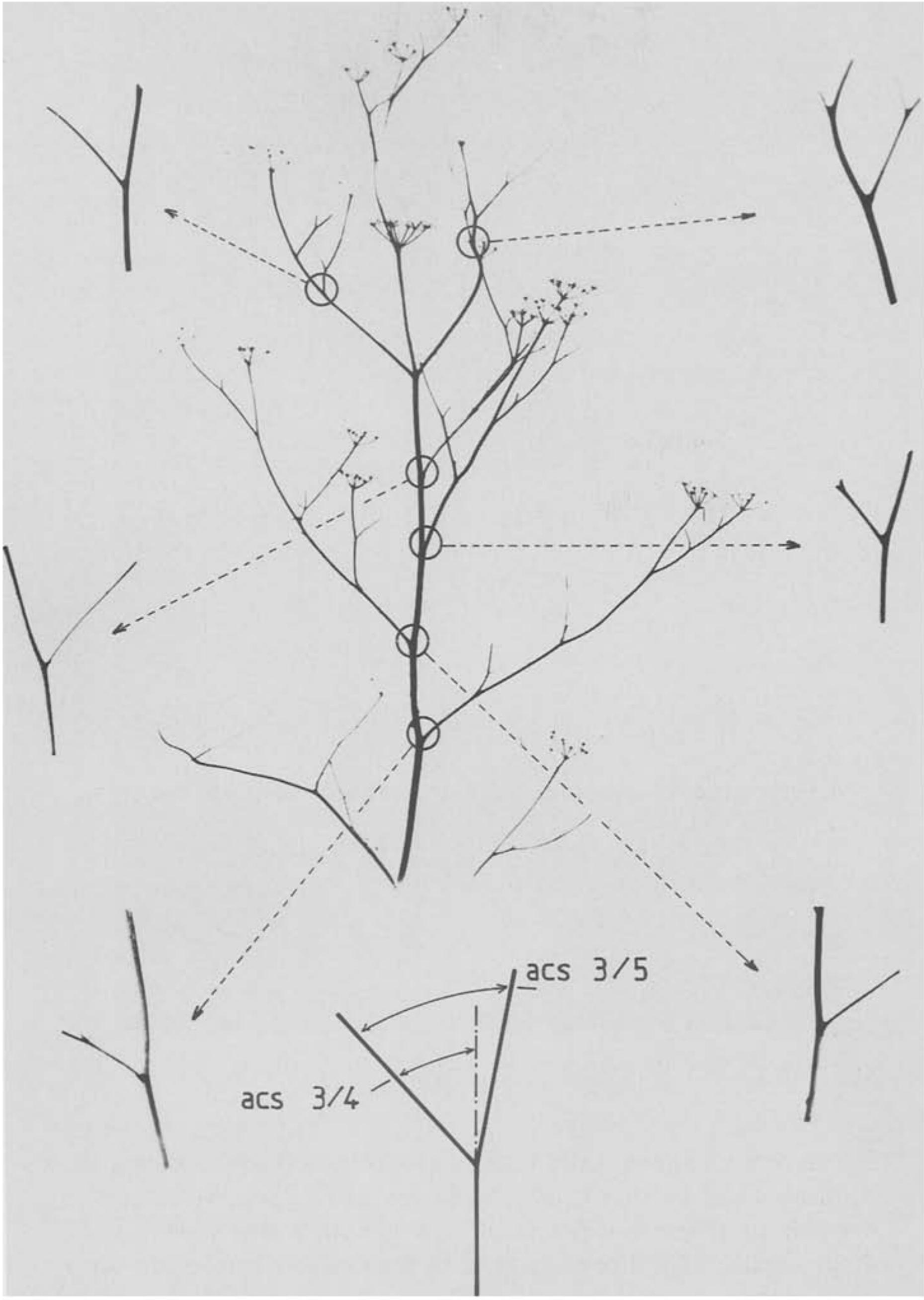


Plate 4. The ramification angles in an Umbellifera, close to acs 3/4 = 41° 25′ and acs 3/5 = 53° 08′.

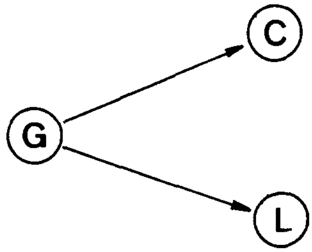
ple, as a Pine-tree and an Oak, or a Nutmeg-tree and a Yew-tree" (Hallé, 1979) ("...manifestent une remarquable indépendance vis-à-vis de la dimension des plantes, vis-à-vis de leur écologie, et même vis-à-vis de la génétique, puisqu'une même architecture peut apparaître dans des groupes végétaux aussi peu apparentés que peuvent l'être, par exemple, un Pin et un Chêne, ou un Muscadier et un If"). At different levels of organization, a few basic structures can be defined, allowing the "restoration of a conception of the plant as a whole".

5. Conclusion

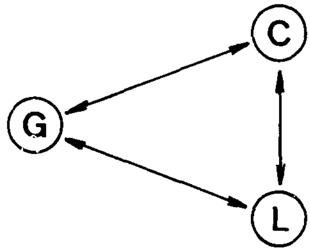
The discovery of a biological significance of the ramification angles in Dicotyledons allows visualization of both the structure and functioning of the Arithmetical Relator. This mathematical tool was constructed with a view to its application in Biology and is probably suitable for careful study of the logic of living systems (Le Guyader, 1981). Its most original features include the following:

- the ability to drive a system adapted to its environment by means of an underlying cyclic structure;
- the natural emergence of both a structural and functional partial self-reference;
- the emergence of a geometrical "metabolism" related to the organization of space, and
- an approach to the complex problem of positioning the working spaces in relation to each other.

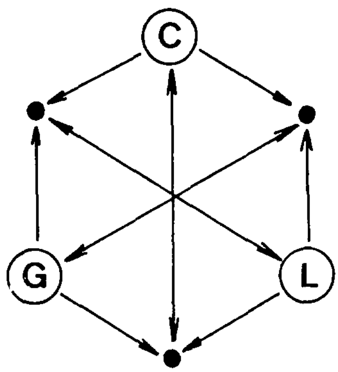
It obviously follows that the interpretation of venation and bifurcation angles leads to the type of morphogenetic study inherent in the "pattern problem" formulated by Wolpert. Given the fact that ribs correspond to the prime directions of growth, the venation angle will be the result of the interaction between three different levels of organization: the genome G, the cell C and the leaf L. The structure of the relator enables the genome to be connected to the underlying BCR, the cell with the stabilized Relator with (X, Y) as variables, and the leaf with a relator whose internal axes coincide with the environment axes shown by the third collation. Therefore, the logic of the relator seems to provide a satisfactory answer to the question of the geometry of leaf morphogenesis for which, according to Cusset (1983), thirteen theories have been proposed. Except for the theories in which either the cell or the leaf is the only prime notion, most of them fit one of the following frames:



Cusset (1983) and Jeune (1981) proposed a complete equilibrium between the three poles:



The Arithmetical Relator may allow another interpretation of this ternary diagram; in fact, it seems that 3 must be parted into (2 + 1) rather than into (1 + 1 + 1). We should also consider the interaction between one of the poles and a combination of the two others, according to the diagram below:



It seems to us that this diagram can be applied to problems concerning living systems relating to changes in the level of organization, such as cell differentiation of organogenesis, in Plant or Animal life.

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