Università di Pisa

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Technical Report : TR-97-01

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January 13, 1997

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From String Rewriting to Logical Metabolic Systems

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Keywords and Phrases: String rewriting system, Grammar, Formal Language, Formal System, L-systems, Artificial Life, DNA Computing, Metabolic Systems.

1 Introduction

In recent years many formalisms have emerged that are based on the notion of formal grammar or, more generally, of string rewriting. In fact, the grammatical paradigm seems a very natural way to provide new computational models for expressing phenomena such as parallelism, cooperation, distribution [7]. Furthermore, after Lindenmayer introduced L-systems [23], string rewriting has become a formal tool in the description of developmental phenomena of biological organisms, and more recently, grammatical models have been elaborated in research on 'artificial life' for the simulation of aspects of life such as: birth, growth, death, reproduction, evolution, proliferation, stagnancy and pollution [29]. Important possibilities of interaction between formal languages and biology arise from molecular biology models of DNA and their applications in solving combinatorial problems and in suggesting new patterns of string rewriting, inspired by genetic elaboration of cellular information [1, 18, 19, 20, 2, 21]. In this case the term 'biological mathematics', versus mathematical biology [21], indicates the reverse side of interaction between two disciplines. Other approaches, closer to the more general algebraic notion of term rewriting systems [4, 16], introduced computational models inspired by a chemical metaphor [3, 6, 28].

In this paper we focus on the notion of *metabolism* and the way it can be expressed in symbolic terms. We claim that an adequate formalization of this concept could help to unify several approaches based on the string rewriting mechanism and could suggest new perspectives in the search for more powerful and general methods in the symbolic description of symbolic dynamical systems [15, 17] where evolution obeys some internal laws of structural recombination.

2 The conceptual development of symbolic systems

Taxonomy was the first step in developing biology, therefore in the spirit of biological mathematics it might to be appropriate to start with a brief analysis and classification of the main kinds of symbolic systems. Without being exhaustive, we point out some very general features that are crucial in the determination of some fundamental *phyla* of grammatical models and related formalisms.

Among the early historical formal systems, were logistic and deductive calculi (in Frege-Hilbert style or in natural deduction, sequent, Gentzen style or in analytic, confutative style) [39]. Strongly related to them, there are Curry, Lorentzen and Church's formal calculi [12, 25, 38], which tried to individuate the inductive structure of any hypothetic-deductive process. Post's systems were the first attempt to put the matter in terms of string rewriting; in fact his original intention [33] was to provide the symbolic form of any axiomatic system. All these systems, logistic, formal or Post were strongly based on the notion of formal, free or bound, variables. This means that some of their elements, called (formal) variables, are implicitly or explicitly equipped with a set of functions, called assignments, from variables to some values, with respect to which symbolic expressions have to be evaluated or instantiated (if bound variables are also considered, some additional rules have to be included).

Chomsky grammars [5] are a sort of simplified form of Post system, where no variables occur (non terminal symbols, already introduced in extended Post systems, play a completely different role) and the basic rewriting mechanism is substring pattern matching and substring replacement. Originally motivated by studies in structural linguistics, they can be considered as a cornerstone in the conceptual path, from which the classic formal language theory stems out with its fundamental concepts and results: automata, operations on languages, classes of languages, closure properties, normal forms and decidable and undecidable results [37, 36]. Some biological content can also be traced in classic formal language theory, if we consider the original context of Kleene's theorem [22].

L-systems with their main variants: OL, (E)OL, (E)DOL, (E)TOL, (E)IL [34, 35, 36], introduced new technical perspectives (parallel rewriting mechanisms) and developmental aspects. In the basic notion of L-system, as in Post systems, non terminal symbols play a role that is not as crucial as in Chomsky grammars.

Contextual grammars were introduced by Marcus (M-systems would be a more appropriate terminology) in order to express a closer formalization of the basic generative mechanism of natural languages [27, 30], where non terminal symbols are completely avoided.

Grammar systems [7, 29, 14] and regulated rewriting system [13], develop grammatical approaches where simple components are integrated in order to reduce, by means of cooperative, distributed or regulated behaviors, the expressive power of monolithic complex systems in terms of simpler parts.

Ecogrammars [8, 10], in the mainstream of OL systems, introduce in the developmental perspective an action/reaction pattern in order to cope with the environment in the framework of a multi-agent symbolic rewriting paradigm.

H-systems and related splicing based systems [1, 18, 19, 20, 24, 2, 9, 21] introduce further string rewriting mechanisms; conceptually, they can be compared to L-systems and contextual grammars, as they are concerned with the basic generative mechanism rather than the way of structuring generative components.

All the systems considered exploit different cooperative, parallel and distributed strategies. Furthermore, current studies are trying to combine heterogeneous string rewriting systems in order to put together different aspects of expressive power [11].

However, all these theories are essentially about generative power. In fact, these systems have a principal derivation relation such that, applying its transitive (or transitive and reflexive) closure to some initial words, a language can be generated that constitutes the most important evaluation parameter.

Perhaps for historical reasons, some interesting and useful aspects of early logistic, formal and Post systems are almost completely absent in the developments considered above: variables and implicit or explicit typing mechanisms. Other aspects, of chemical and biochemical reactions, such as, stratification, aggregative levels, locality, osmosis, permeability, and encapsulation are diffucult to express using only strings. Moreover, the analysis of symbolic systems representing a biochemical solution cannot be limited to their generative aspects, but entails adopting the more general perspective of discrete dynamical systems [15, 17], where also termination properties, determinism, stability, periodicity, interactivity between different parts (synergy or antagonism, resonance) are considered. In order to make this discussion more precise, let us look at metabolic processes in more detail.

3 The general structure of metabolic processes

In a developmental system the generative mechanism is used to model the different stages of a growing process. In this perspective, the language generated by an L-system is the formal counterpart of the history of a development, where all the instantaneous configurations, put together, constitute the generated language as a diachronic structure. A metabolic process is rather different. In fact it is a synchronic structure since what is transformed at any step is not only a string, but a set of strings, that is a language, where global information is spread over all its elements and where intrinsic notions of classification, aggregation and localization are assumed. Any metabolic passage is based on a structural recombination of some constituents of the global structure (some elements are destroyed and others are constructed according to a consuming/producing pattern). In a *closed metabolic system* at any time the atomic constituents are the same. However, if an environment is also assumed to exist which adds new things (reagents, energy, food), then the size of the system can grow, and a natural generative process can be associated with it.

More specifically, consider different molecules, for example: HHO, COO, ATP, nucleotides, which can be represented by words of a suitable alphabet (in this context HHO is the chemical type of a water molecule). Some of them are combined into bigger units called (macro) molecules or are grouped into solutions separated by membranes where they are continuously floating in a casual way. There are essentially four types of possible reactions: i) new units are created or modified by combining or recombining smaller units; ii) some smaller units are obtained by destroying a bigger one; iii) two or more units react and disappear producing other units; iv) some elements leave the membrane where they are and reach another membrane. At any moment the system is completely specified by how many basic elements of each type are present, how they are grouped into membranes or molecules, and which chemical types these molecules have. At any step some transformations can hold in a membrane if some *catalysts* or *enzymes* are present, and more generally if some conditions are verified that involve elements in the membrane (locality principle). For example, consider a membrane where some level of its structure includes two other membranes S and S'. A possible metabolic transformation can then be described by the following schema: if no element of type A is in the membrane S, and in the membrane S' there are elements of a type B, then a molecule of type AC in S can migrate from S to S' and can combine with two elements B thus producing a new molecule of type ACBB in S'.

A Chomsky grammar can be considered as a particular case of a metabolic system where a production $\alpha \rightarrow \beta$ transforms a language L into a language L' according to the following rule: *if for some strings φ and ψ the string $\varphi\alpha\psi$ belongs to L then L transforms into* $L \cup \{\varphi\beta\psi\}$. We could proceed in the same way for any other string rewriting system. More interesting examples of metabolic systems are the string rewriting systems studied by Turing in [40], where also quantitative parameters are considered in order to show morphogenetic phenomena. In the next section we introduce a formal notion of a *metabolic model* where only some aspects are formalized, which nevertheless seem to be sufficient to express typical chemical and biochemical situations.

4 A first order formalization of metabolism

Consider the following *syntactic model*:

$$\mathcal{N} = (\mathbf{N}^*, \cdot, |\ |)$$

where $\mathbf{N}$ is the infinite alphabet of natural numbers into we can embed any finite alphabet, $\mathbf{N}^*$ the free monoid generated by this set, $\cdot$ the monoid operation (indicated as usual by juxtaposition), λ the neuter element of the monoid, and $|\ |$ the operation that associates whit each word its length.

It is possible to show (but details are beyond the aims of this paper, see [26]) that any string rewriting system determines a predicative theory on the alphabet $\{\lambda, \cdot, |\ |\}$ constituted by a finite first order theory ϕ of formulas $\varphi(x, y)$ with two free variables in such a way that a derivation relation holds between two strings α and β, if for some formula φ of ϕ, the proposition $\varphi(\alpha, \beta)$ is true in the above syntactic model. For example, the rewriting of α into β according to a production $\gamma \rightarrow \delta$ of a Chomsky grammar is described by the following formula $\exists xy(\alpha = x\gamma y \wedge \beta = x\delta y)$. In a Post system we have a similar logical structure, but there is no bound to the length of the existential prefix. In L-systems we also need universal quantification, and formulae are much more complex [26]. This logical approach introduces not only a uniform way to describe different string rewriting patterns, but also allows us to integrate different mechanisms in a natural way. However, for the aims of the present discussion, we limit ourselves to applying this idea to the following definition of a (symbolic) metabolic system.

Consider the following structure

$$(\mathbf{N}, \mathbf{N}^*, C, C^*, R, \lambda, \cdot, \epsilon)$$

where:

1. $(C^*, \lambda, \cdot)$ is the free monoid of chemical types generated by the finite set C (the alphabet of chemical types); $(\mathbf{N}^*, \lambda, \cdot)$ is the free monoid over the infinite alphabet $\mathbf{N}$ of natural numbers, and concatenation $\cdot$, as usual indicated by juxtaposition, denotes both the operations of C^* and $\mathbf{N}^*$, while λ denotes the neuter element of the two monoids;

2. R is a set of symbols of relations encoding certain localization properties

3. ϵ is the usual membership relation;

A *metabolic state* is a finite language whose elements are strings of the two following types (we use a colon just as an auxiliary symbol):

1. $n{:}\alpha$, where $n \epsilon \mathbf{N}$ and $\alpha \epsilon C^*$;

2. $r{:}\mu$, where r is a relation symbol in R and μ is a string in $\mathbf{N}^+ = \mathbf{N}^* - \{\lambda\}$

For example, a molecule of water is a metabolic state described by the following language:

$$\{n_1{:}H,\ n_2{:}H,\ n_3{:}O,\ m{:}HHO,\ \mathbf{In}{:}n_1m,\ \mathbf{In}{:}n_2m,\ \mathbf{In}{:}n_3m\}$$

where n_1, n_2, n_3, m are natural numbers, and **In** is a symbol of R encoding the membership relation of an atom in a molecule.

Let us take the set $\mathcal{L}$ of all possible metabolic states. We can extend the previous structure and consider the following first order heterogeneous relational structure $\mathcal{M}$:

$$(\mathbf{N}, \mathbf{N}^*, C, C^*, R, \mathcal{L}, \lambda, \cdot, \epsilon)$$

In order to describe the evolution of a metabolic state, let us consider a finite set Φ of first order formulas, with m and m' free variables denoting metabolic states:

$$\Phi = \{\ \varphi_i(m, m')\ \}_{i\in\ 1,\dots,n}$$

We say that a metabolic state M *evolves* in one step to the other metabolic state M' according to φ_i, and we write $M \xrightarrow{\varphi_i} M'$, if and only if $\varphi_i(M, M')$ is satisfied in the model $\mathcal{M}$:

$$M \xrightarrow{\varphi_i} M' \ \textit{ if and only if } \ \mathcal{M} \models \varphi_i(M, M').$$

Let us consider, therefore, the binary relation "$\rightarrow$", obtained from the union of all $\xrightarrow{\varphi_i}$. By means of this relation, language evolution can be conceived like a metabolic states succession $M_0 \rightarrow M_1 \rightarrow \dots \rightarrow M_n \rightarrow \dots$, where each state is obtained from the previous language, by making the transformations described in the theory Φ.

In the following, letter m (possibly with apices or subscripts) is a variable that ranges on metabolic states, other Latin letters range on $\mathbf{N}$, and Greek letters range on strings. Moreover, in order to keep the standard chemical usage, we abbreviate to X_n the string that consists of n occurrences of X. Further, other natural abbreviations are also allowed.

Example 4.1 Let us take the simple reaction that occurs in the combustion of methane in the presence of oxygen to produce carbon dioxide and water (see Figure 1). If we consider only the aggregative situation of the metabolic states, we can represent them respectively with the two languages:

$$\{\ 1{:}CH_4,\ 2{:}O_2,\ 3{:}O_2,\ \cdots\} \rightarrow \{\ 1{:}CO_2,\ 2{:}H_2O,\ 3{:}H_2O,\ \cdots\}$$

Reaction:

$CH_4 + 2O_2 \longrightarrow CO_2 + 2H_2O$

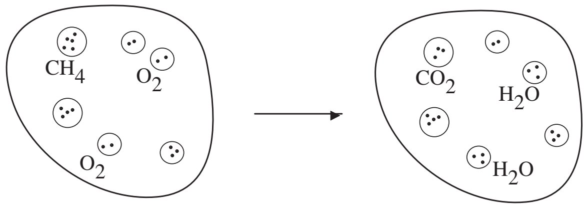


Figure 1 - A molecule of methane (CH_4) combusts reacting with two molecules of oxygen (O_2), and produces carbon dioxide (CO_2) and water (H_2O).

The associated reaction can be described by the following first order formula

$$\varphi(m, m') \equiv \exists\ \alpha,\ \beta,\ \gamma,\ \alpha',\ \beta',\ \gamma'\ x,\ y,\ z\ \Big($$

$$\alpha = x{:}CH_4\ \wedge\ \beta = y{:}O_2\ \wedge\ \gamma = z{:}O_2\ \wedge$$

$$\alpha' = x{:}CO_2\ \wedge\ \beta' = y{:}H_2O\ \wedge\ \gamma' = z{:}H_2O\ \wedge$$

$$\alpha,\ \beta,\ \gamma\ \epsilon\ m\ \wedge\ \alpha,\ \beta,\ \gamma\ \not\epsilon\ m'\ \wedge\ \alpha',\ \beta',\ \gamma'\ \epsilon\ m'\ \wedge$$

$$\forall\ u\ \big(u \neq \alpha,\ \beta,\ \gamma,\ \alpha',\ \beta',\ \gamma'\ \rightarrow\ (u\ \epsilon\ m \leftrightarrow u\ \epsilon\ m')\big)\ \Big)$$

Example 4.2 Let us consider the action of enzyme *ligase* which can join the ends of two DNA chains by catalyzing the synthesis of a bond between two nucleotides. This happens during the replication process of DNA in some procaryotic bacteria, like the well known *Escherichia Coli.*

The reaction mechanism of ligase is illustrated in Figure 2. The enzyme requires that the nucleotides to be joined correspond to a pair of adjacent elements in the unbroken complementary strand. Further, ligase requires as coenzyme a molecule of NAD^+ (nicotinamide diphosphate) as a source of a molecule of AMP (adenosine monophosphate). The DNA ligase reaction takes place in three steps. In the first one, an adenylyl-enzyme compound (AMP–E) is formed on the reaction of the enzyme with NAD^+ and this process produces a molecule of nicotinamide mononucleotide (NMN^+). In the second step, the adenylyl group is transferred from AMP–E to one end of DNA. In the third step, the bond with

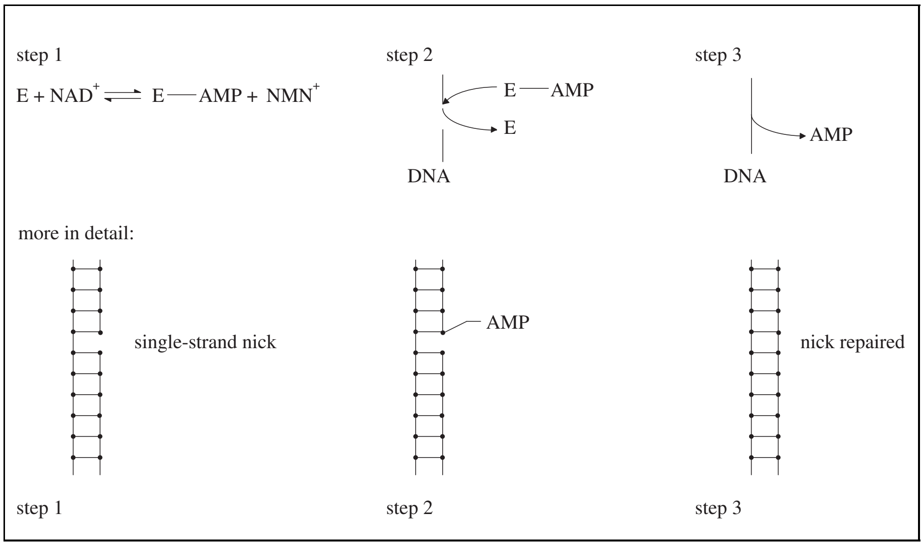
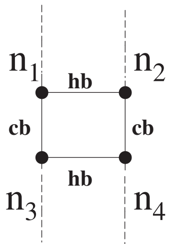


Figure 2 - Representation of the three steps action of DNA ligase in *Escherichia Coli*. **At the bottom of the figure the molecules of the double strand are represented with bullets and the bonds between molecules are drawn as dashes.**

the other end of DNA segment takes place and the molecule of AMP is then released [41].

From a structural point of view, such a situation is more complex than the previous example. In fact, this time we also need another kind of information that encodes the reciprocal positions of molecules. Without considering the inner structure of DNA nucleotides, the double strand can be modeled with the help of two relation symbols, we say **cb** (covalent bond) and **hb** (hydrogen bond). Thus, a DNA portion such as:



will be represented by the following strings (n_1, n_2, n_3, n_4 are the natural numbers corresponding to each nucleotide):

$$\{\, \mathbf{hb}{:}n_1 n_2,\ \mathbf{hb}{:}n_3 n_4,\ \mathbf{cb}{:}n_1 n_3,\ \mathbf{cb}{:}n_2 n_4,\ \cdots \}$$

Now, for the sake of brevity, we model formally the third step only. In this case, the sealing of the nick is obtained simply by adding the covalent bond $\mathbf{cb}{:}n_2n_4$:

$$\varphi(m, m') \equiv \exists\, a,\ n_1,\ n_2,\ n_3,\ n_4\ \Big($$

$$a{:}\mathrm{AMP},\ \mathbf{cb}{:}an_2\ \ \epsilon\ m\ \wedge$$

$$\mathbf{cb}{:}n_1n_3,\ \mathbf{hb}{:}n_1n_2,\ \mathbf{hb}{:}n_3n_4\ \epsilon\ m\ \wedge$$

$$\mathbf{cb}{:}an_2\ \ \not\epsilon\ m'\ \wedge\ \mathbf{cb}{:}n_2n_4\ \epsilon\ m'\ \wedge$$

$$\forall\ u\ \big(u \neq \mathbf{cb}{:}an_2,\ \mathbf{cb}{:}n_2n_4\ \rightarrow\ (u\ \epsilon\ m \leftrightarrow u\ \epsilon\ m')\big)\ \Big)$$

Example 4.3 If we put the following general definitions

- $L \overset{\varphi_i}{\rightsquigarrow} L'$ if and only if $L' = \bigcap\{M' \mid \mathcal{M} \models \varphi_i(M, M')\}$
- $L \overset{\Phi}{\rightsquigarrow} L'$ if and only if $L \overset{\varphi_i}{\rightsquigarrow} L'$ for some $\varphi_i\ \epsilon\ \Phi$
- $G(L_0, \Phi) = \bigcup\{L_j \mid L_j \overset{\Phi}{\rightsquigarrow} L_{j+1}\}_{j\ \epsilon\ \mathbf{N}}$

then the language

$$\overline{L} = \{a^n b^n c^n \mid n\ \epsilon\ \mathbf{N}\}$$

can be obtained by considering the initial language $L_0 = \{\lambda, abc\}$ (we identify $0:\alpha$ with α) and the theory $\Phi = \{\exists\ \alpha, \beta\ (\alpha b \beta\ \epsilon\ m \rightarrow a\alpha bb\beta c\ \epsilon\ m')\}$. In fact, it is easy to see that $G(L_0, \Phi) = \overline{L}$.

5 Conclusions

If we add more structure to the metabolic model $\mathcal{M}$ we can express other kinds of chemical situations. For example, if we allow formulae such as $q\#\alpha$, where q is a number expressing a quantity and α is a chemical type in C^*, then typical chemical laws correspond to suitable predicative formulae (often very complex), and quantitative aspects of reaction can also be managed.

Furthermore, in order to model adequately some real situations it is appropriate to require that metabolic states have to satisfy some conditions. For example, since a metabolic state m is a *proper* chemical metabolic state it has to verify that

$$\forall\ x,\ \alpha,\ \beta\,(x:\alpha\epsilon m\ \wedge\ \alpha \neq \beta\ \rightarrow x:\beta \not\epsilon m).$$

However, the introductory level of this paper does not allow us to go into technical details. In [28], in a similar perspective, several logical formalizations are considered: the classical Daniell model of voltaic effect ($Cu + Zn + ZnSO_4 + CuSO_4$) and the DNA replication of *Escherichia Coli*.

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