

Adaptive behavior in a tritrophic interactions consisting of plants, herbivores and carnivores

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Abstract

We investigated the population dynamics of such tritrophic interactions using a model of Abstract chemistries, Abstract Rewriting system of Multi-Sets (ARMS) which is a new research method in Complex Systems and Artificial Life. In ARMS model, we regarded a tritrophic interaction mediated by herbivore-induced plant volatiles that attract carnivorous natural enemies of herbivores as chemical reactions of four reagents (plants, herbivores, carnivores and volatiles). The intensity of interactions between individuals corresponded to reaction speed in the ARMS model. We compared the case where plants produce herbivore-induced volatiles vs the case where they do not with the model. Further, by changing the reaction speed, we found that there was a case where herbivore-induced volatiles that attract carnivores resulted in the population increase of the herbivores. We will discuss several conditions in tritrophic interactions that differently affect the population density of plants, herbivores and carnivores based on the prediction by the ARMS model.

1. Introduction

A phenomenon that plants respond to herbivore feeding activities by producing volatiles that in turn attract carnivores enemies of the herbivores has been reported recently(2, 4). These volatiles are not the mere result of mechanical damage, but are produced by the plant as a specific response to herbivore damage.

In mathematical ecological studies concerning with the system, one notable study is that of, Sabelis and

de Jong(1996)(6) who reported that, when herbivore-induced volatiles profitable for plants, the kinds of the volatiles become polymorphic within species. They use game theory and show that ESS corresponds to the case when each species of plant produces the volatiles in polymorphic way.

In order to investigate the population dynamics of the tritrophic systems, we introduce an abstract rewriting system on multisets, Abstract Rewriting System on Multisets (ARMS) (7, 8). This system is modeled as an *abstract chemical system* which is new research field in Artificial life and Complex systems.

In ARMS model, we regarded a tritrophic interaction mediated by herbivore-induced plant volatiles that attract carnivorous natural enemies of herbivores as chemical reactions of four reagents (plants, herbivores, carnivores and volatiles). The intensity of interactions between individuals corresponded to reaction speed in the ARMS model. We compared the case where plants produce herbivore-induced volatiles vs. the case where they do not with the model. Further, by changing the reaction speed, we found that there was a case where herbivore-induced volatiles that attract carnivores resulted in the population increase of the herbivores. In ARMS, a reaction rate is realized as the frequency of applying a rule.

2. ARMS

We will introduce the multiset rewriting system, “*Abstract Rewriting system on MultiSets*” in this section. Intuitively, *ARMS* is like a chemical solution in which *molecules* floating on it can interact with each other according to reaction rules. Technically, a chemical solution is a finite multi-set of elements denoted by $A^k = \{a, b, \dots, \}$; these elements correspond to *molecules*. Reaction rules that act on the molecules are specified in

ARMS by rewriting rules. As to the intuitive meaning of *ARMS*, we refer to the study of chemical abstract machines (1). In fact, this system can be thought of as an underlying “*algorithmic chemistry* (3).”

Let A be an *alphabet* (a finite set of abstract symbols). The set of all strings over A is denoted by A^* ; the empty string is denoted by λ . (Thus, A^* is the free monoid generated by A under the operation of concatenation, with identify λ .) The length of a string $w \in A^*$ is denoted by $|w|$.

A *rewriting rule* over A is a pair of strings (u, v) , $u, v \in A^*$. We write such a rule in the form $u \rightarrow v$. Note that u and v can also be empty. A *rewriting system* is a pair (A, R) , where A is an alphabet and R is a finite set of rewriting rules over A .

With respect to a rewriting system $\gamma = (A, R)$ we define over A^* a relation \Longrightarrow as follows: $x \Longrightarrow y$ iff $x = x_1 u x_2$ and $y = x_1 v x_2$, for some $x_1, x_2 \in A^*$ and $u \rightarrow v \in R$. The reflexive and transitive closure of this relation is denoted by \Longrightarrow^* . A string $x \in A^*$ for which there is no string $y \in A^*$ such that $x \Longrightarrow y$ is said to be a *dead* one (in other words, from a dead string no string can be derived by means of the rewriting rules).

From now on, we work with an alphabet A whose elements are called *objects*; the alphabet itself is called a *set of objects*.

A *multiplicity* over a set of objects A is a mapping $M : A \rightarrow \mathbf{N}$, where \mathbf{N} is the set of natural numbers, $0, 1, 2, \dots$. The number $M(a)$, for $a \in A$, is the *multiplicity* of object a in the multiplicity M . Note that we do not accept here an infinite multiplicity. The set $\{a \in A \mid M(a) > 0\}$ is denoted by $\text{supp}(M)$ and is called the *support* of M . The number $\sum_{a \in A} M(a)$ is denoted by $\text{weight}(M)$ and is called the *weight* of M .

We denote by $A^\#$ the set of all multisets over A , including the empty multiset, \emptyset , defined by $\emptyset(a) = 0$ for all $a \in A$.

A multiset $M : A \rightarrow \mathbf{N}$, for $A = \{a_1, \dots, a_n\}$, can be naturally represented by the string $a_1^{M(a_1)} a_2^{M(a_2)} \dots a_n^{M(a_n)}$ and by any other permutation of this string. Conversely, with any string w over A we can associate a multiset: denote by $|w|_{a_i}$ the number of occurrences of object a_i in w , $1 \leq i \leq n$; then, the multiset associated with w , denoted by M_w , is defined by $M_w(a_i) = |w|_{a_i}$, $1 \leq i \leq n$.

The union of two multisets $M_1, M_2 : A \rightarrow \mathbf{N}$ is the multiset $(M_1 \cup M_2) : A \rightarrow \mathbf{N}$ defined by $(M_1 \cup M_2)(a) = M_1(a) + M_2(a)$, for all $a \in A$. If $M_1(a) \leq M_2(a)$ for all $a \in A$, then we say that multiset M_1 is included in multiset M_2 and we write $M_1 \subseteq M_2$. In such a case, we define the multiset difference $M_1 - M_2$ by $(M_2 - M_1)(a) = M_2(a) - M_1(a)$, for all $a \in A$. (Note that when M_1 is not included in M_2 , the difference is not defined).

A *multiplicity rewriting rule* (we also use to say, *evolution rule*) over a set A of objects is a pair (M_1, M_2) , of ele-

ments in $A^\#$ (which can be represented as a rewriting rule $w_1 \rightarrow w_2$, for two strings $w_1, w_2 \in A^*$ such that $M_{w_1} = M_1$ and $M_{w_2} = M_2$). We use to represent such a rule in the form $M_1 \rightarrow M_2$.

An *abstract rewriting system on multisets* (in short, an *ARMS*) is a pair

$$\Gamma = (A, R)$$

where:

1. A is a set of objects;
2. R is a finite set of multiset evolution rules over A ;

With respect to an *ARMS* Γ , we can define over $A^\#$ a relation: (\Longrightarrow) : for $M, M' \in A^\#$ we write $M \Longrightarrow M'$ iff

$$M' = (M - (M_1 \cup \dots \cup M_k)) \cup (M'_1 \cup \dots \cup M'_k),$$

for some $M_i \rightarrow M'_i \in R$, $1 \leq i \leq k$, $k \geq 1$, and there is no rule $M_s \rightarrow M'_s \in R$ such that $M_s \subseteq (M - (M_1 \cup \dots \cup M_k))$; at most one of the multisets M_i , $1 \leq i \leq k$, may be empty.

With respect to an *ARMS* $\Gamma = (A, R)$ we can define various types of multisets:

- A multiset $M \in A^\#$ is *dead* if there is no $M' \in A^\#$ such that $M \Longrightarrow M'$ (this is equivalent to the fact that there is no rule $M_1 \rightarrow M_2 \in R$ such that $M_1 \subseteq M$).
- A multiset $M \in A^\#$ is *initial* if there is no $M' \in A^\#$ such that $M' \Longrightarrow M$.

2.1 How ARMS works

Example In this example, an *ARMS* is defined as follows;

$$\begin{aligned} \Gamma &= (A, R), \\ A &= \{a, b, c, d, e, f\}, \\ R &= \{a, a, a \rightarrow c : r_1, b \rightarrow d : r_2, c \rightarrow e : r_3, \\ &\quad d \rightarrow f, f : r_4, a \rightarrow a, b, b, a : r_5, f \rightarrow h : r_6, \}. \end{aligned}$$

The set of the rewriting rules, R is $\{r_1, r_2, r_3, r_4, r_5, r_6\}$. We assume the maximal multiset size is 4 and the initial state is given by $\{a, a, b, a\}$. In *ARMS*, rewriting rules are applied in parallel. When there are more than two applicable-rules, then one rule is selected randomly. Figure 1 illustrates an example of rewriting steps of the calculation from the initial state.

At the first step, the left hand side of rule of r_1, r_2 and r_5 are included in the initial state. In the next step, r_3 and r_4 are applied in parallel and $\{c, d\}$ is rewritten into $\{e, f, f\}$. In step 3, by using r_6 , $\{e, f, f\}$ is transformed into $\{e, h, h\}$. There are no rules that can transform the multiset any further so, the multiset is in a *dead* state.

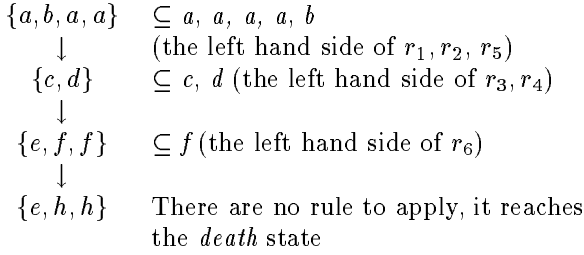
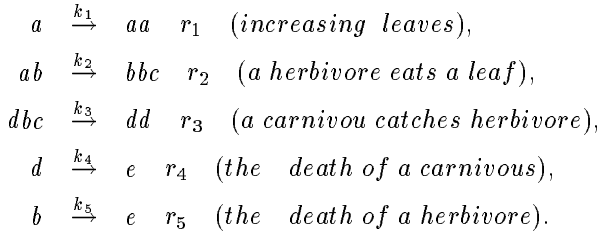


Figure 1: Example of rewriting steps of ARMS

3. Implementing the system by using ARMS

In this section, we model the tritrophic system by using ARMS. We assume the symbol “ a ” as a leaf, “ b ” as a herbivore, “ d ” as a carnivorous and “ c ” as a certain density of herbivore-induced volatiles that attract carnivores, respectively. Furthermore, we add “ e ” as an “empty state” in order to introduce “death state.” A plant is defined implicitly as the certain number of leaves. Evolution rule R_1 is defined as follows;

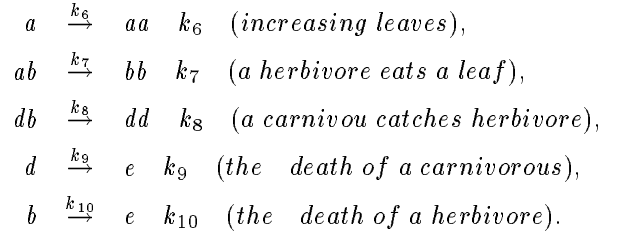


$k_1 \dots k_5$ denotes *reaction rate* that correspond to the frequency of rule application. For example, when $k_4 = 0.1$ and $k_5 = 0.2$ then r_5 will be applied twice as much as r_4 . k_2 is defined according to the state of multiset. It is defined as follows;

$$k_2 = \frac{M(b)}{M(a) + M(b) + M(c) + M(d) + M(e)}.$$

The r_1 corresponds to sprout and growth of a plant, r_2 to the case when a herbivore eats a leaf and the leaf generates volatiles, r_3 to a carnivorous catches herbivore, r_4 to the death of a carnivorous and r_5 to the death of a herbivore, respectively. The r_2 denotes the case when there exists a leaf (a), a herbivore eats the leaf and breeds there (b). Then the leaf produces volatiles compound (c) that will attract carnivorous. r_3 denotes the case when there is a herbivore (b) with the volatiles (c), a carnivorous “ d ” is attracted by it and catches the herbivore and breed there (dd). The breeding rate of carnivorous is expressed as changing the number of right hand side of ds , such as $dbc \xrightarrow{k_3} dddd$.

By using this model, we compared the case when leaves generate volatiles to does not. The evolution rules of the system without volatiles R_2 is defined as follows;



We set reaction rates of k_1, k_4, k_5, k_6, k_9 and k_{10} as 0.5, 0.1, 0.1, 0.5, 0.1 and 0.1, respectively.

4. Simulation and results

In both R_1 and R_2 , the symbiotic relation consisting of plants, herbivore and carnivores (figure 4.) can be found. It is interesting that R_2 (the system without volatiles) is likely to lose the relation under the same conditions (the number of plants, herbivores and carnivores in the initial state, reaction rate of r_3 and r_8).

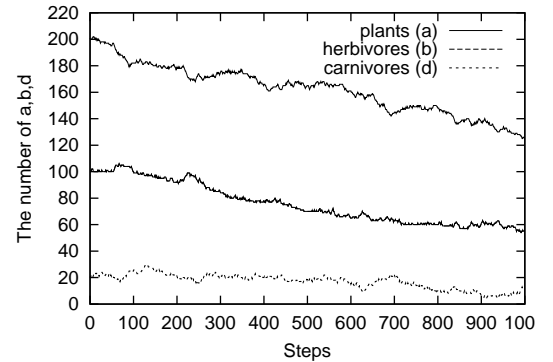


Figure 2: The symbiotic relation consisting of plants, herbivores and carnivores ($R_1, r_3 = 0.55$)

Figure 4. illustrates the symbiotic relation consisting of plants, herbivores and carnivores, R_1 is used and in the initial state, the population size of plants is 200, herbivore is 20, carnivores 10.

On the other hand, figure 4. illustrates that the case when R_2 is used under the same conditions as R_1 used. In this case, at first herbivores extinct thus carnivores can not survive.

The time course of population size of plants, herbivores and carnivores of R_1 (figure 4.) is very different from R_2 (figure 4.). In R_1 there are three attractors around $(a, b, c) = (200, 100, 22)(1), (180, 105, 27)(2), (150, 120, 46)(3)$. At first the time course is attracted by (1) then (2) and finally (3). On the other hand in

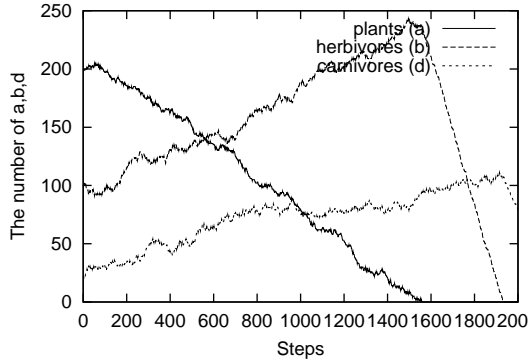


Figure 3: The case when the symbiotic relation is lost ($R_2, r_8 = 0.55$)

R_2 the course is attracted around (120, 200, 82), but departs from there in the long run.

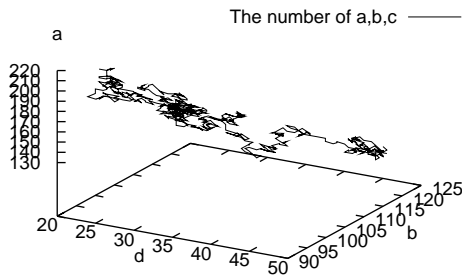


Figure 4: The time course of the population size of plants (a), herbivores (b) and carnivores (c) ($R_1, r_3 = 0.55$)

These results show that the system with volatiles (plants produce volatiles) is more robust than the other. Thus, we are going to investigate the role of volatiles furthermore.

4.1 The role of volatiles

In the simulation, k_3 and k_8 are changed from 0.1 to 0.9 and in the initial state the number of herbivores is set to 100. Then the correlation between population size of herbivores and the value k_3, k_8 are observed. In R_1 , k_3 is regarded as the ability of volatiles attracting carnivorous and in R_2 the ability of carnivore's finding herbivores, respectively. When the value becomes larger each ability is strengthened.

When the k_3 and k_8 are equal to 0.1 the population of herbivores increases. In this case, the number of herbivore in R_1 is larger than R_2 's. When r_3 and r_8 are equal to 0.1, the averages of the number of herbivores

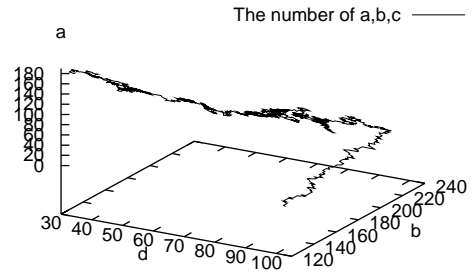


Figure 5: The time course of the population size of plants (a), herbivores (b) and carnivores (c) (until the plants extinct $R_2, r_8 = 0.55$)

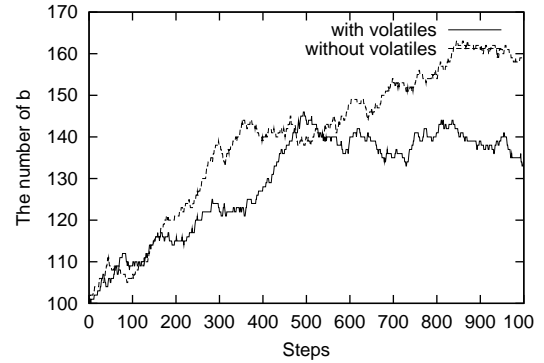


Figure 6: The number of herbivores of R_1 and R_2 ($k_3 = 0.1$)

after 1000 steps are respectively 141.96 and 163.31 (table 1, in 100 trials). Hence, when leaves produce volatiles herbivores are more caught by carnivorous than do not produce it (figure. 4.1).

k_3, k_8	0.1	0.2	0.3	0.4	- 0.9
Ave. (k_3)	141.96	49.79	49.75	49.77	49.00
Ave. (k_8)	163.31	2.43	0.00	0.00	0.00

Table 1: The average of the number of herbivores after 1000 steps.

But, when k_3 and k_8 are more than 0.2, the number of herbivores decrease. It is noticed that population size of herbivore is reversed. It denotes that when leaves do not generate volatiles, the number of herbivores are more increased than generate it (figure 4.1). This tendency are kept during k_3 and k_8 are more than 0.9 (figure 4.1). When k_3 and k_8 exceed 0.2, R_2 's herbivore must extinct, however, R_1 's herbivore never extinct (figure 4.1).

We set the population size of herbivore to 100 in the initial state, and observed the number of herbivore af-

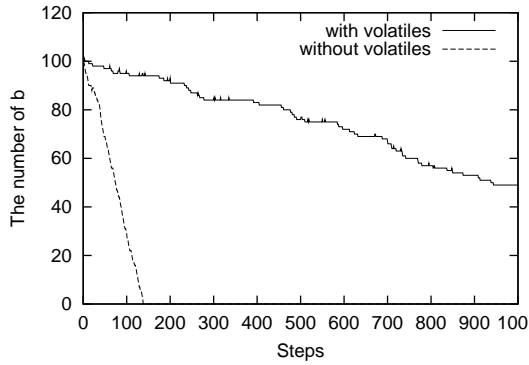


Figure 7: The number of herbivores of R_1 and R_2 ($k_3 = 0.8$)

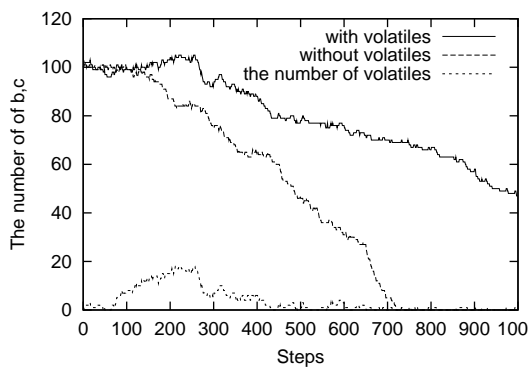


Figure 8: The correlation among the number of volatiles, the number of herbivore of R_1 (with volatiles) and R_2 (without volatiles), (k_3 and k_8 are 0.2)

ter 1000 steps. We repeat the simulation 100 times on each value and observe the average step when herbivore extinct. The average of the number of herbivore's extinction shows that herbivores of R_1 never extinct and R_2 's must extinct when k_3 exceeds 0.1.

5. Discussion

Throughout the simulation, we discovered that herbivores could keep their population for at least 1000 generations in the system where the infested leaves generated the volatiles, whereas the herbivores were exterminated by the carnivores in around 100 generations in the system where leaves did not do so. In our model, the carnivores that use the volatiles to find the herbivores are not able to find their victims in a plant from which the volatiles were emitted under the detectable level for carnivores. This is probably the reason why the herbivores survived in the system where leaves generated the carnivore attractant.

This result suggests the possibility that herbivores induce the volatiles for their survival. This may be true

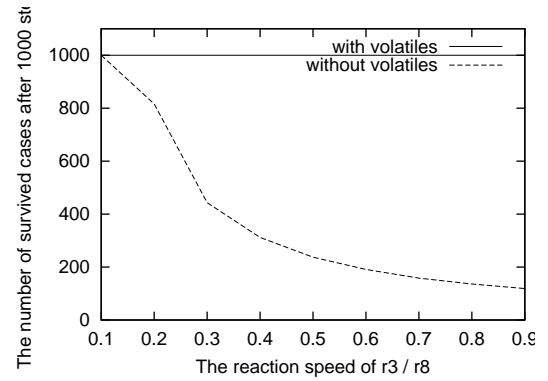


Figure 9: The average value of herbivore extinction of R_1 and R_2 . The horizontal axis illustrates the value of k_3 and k_8 and the vertical axis illustrates the average of the number of survived cases in 1000 trials

in the tritrophic system consisting of plants, two-spotted spider mites (*Tetranychus urticae*) and predatory mites (*Phytoseiulus persimilis*) (Dicke et al. 1998). Two-spotted spider mite is a tiny (ca. 0.6 mm) herbivore. However, due to their rapid population increase on a plant, they tend to overexploit the plant. A kidney bean leaf infested by the spider mites started emitting volatiles that attract predatory mites *P. persimilis* (Maeda et al. 1998). Once in the prey colony, *P. persimilis* overexploit the spider mites. However, the volatiles were induced only after the spider mites increased over certain number per leaf (ca. more than 100-300 females per small plant) (Maeda et al. in prep) and there will be a time lag between the emission of the volatiles and the visitation by the predatory mites. Thus, the spider mites of the next generation that disperse from the current patch before the plant start emitting the volatiles can be free from the predator. Such spider mites will establish a new colony nearby. At the same time, the original colony may be exterminated by the predators. This cycle may be one of the defense strategies of the two-spotted spider mites against the predatory mites that search for them with the volatiles, and may be applicable for the prediction of the model. We will test this in the future experiments.

6. Conclusion

We proposed a new rewriting model, ARMS and applied it in order to investigate an ecological system that plants respond to herbivore feeding activity by producing volatiles that in turn attract carnivorous natural enemies of the herbivores. Throughout a simulation we obtain an interesting result that the possibility that herbivores induce the volatiles for their survival.

Acknowledgements

The authors would like to express many thanks to Dr. Gheorghe Păun for his useful comments, discussion, mathematical refinements on ARMS. This research is supported by Grants-in Aid for Scientific Research No.11837005 from the Ministry of Education, Science and Culture in Japan to Yasuhiro Suzuki and the research for the future program (JSPS-RFTF96L006703), and by the Program for Promotion of Basic Research Activities for Innovative Biosciences (Bio-oriented Technology Research Advancement Institution) to Junji Takabayashi.

References

- Berry, G. and G. Boudol. 1992. The chemical abstract machine. *Theoretical Computer Science* 96: 217–248.
- Dicke, M., Takabayashi, J., Shutte, C., Krips, O. E. Behavioural ecology of plant-carnivore interactions: variation in response of phytoseiid mites to herbivore-induced plant volatiles. *Experimental and Applied Acarology* 22: 595-601, 1997
- Fontana, W. and L.W. Buss, 1994. The arrival of the fittest: Toward a theory of biological organization. *Bulletin of Mathematical Biology* 56: 1–64. 1994.
- Maeda, T., Takabayashi, J., Yano, S. and Takafuji, A. Factors affecting the resident time of the predatory mite *Phytoseiulus persimilis* (Acari: Phytoseiidae) in a prey patch *Applied Entomology and Zoology* 33: 573-576, 1998
- Păun, G. 1998. Computing with Membranes, *J. of Computer and System Sciences* (in press). (also on <http://www.tucs.fi>).
- Sabelis, M. W., and M.,C.M. de Jong, 1988. Should all plants recruit bodyguards? Conditions for a polymorphic ESS synomone production in plants *Oikos*, 53 247-252,
- Suzuki, Y. and H. Tanaka. 1997. Symbolic chemical system based on abstract rewriting system and its behavior pattern. *Journal of Artificial Life and Robotics*:1:211-219, Springer Verlag.
- Suzuki, Y. Tsumoto, S and H. Tanaka. 1996. Analysis of Cycles in Symbolic Chemical System based on Abstract Rewriting System on Multisets, *Artificial Life V*: 522-528. MIT press.