

Note

# Comparison between parallel and serial dynamics of Boolean networks

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## Abstract

In this article we study some aspects about the graph associated with parallel and serial behavior of a Boolean network. We conclude that the structure of the associated graph can give some information about the attractors of the network. We show that the length of the attractors of Boolean networks with a graph by layers is a power of two and under certain conditions the only attractors are fixed points. Also, we show that, under certain conditions, dynamical cycles are not the same for parallel and serial updates of the same Boolean network.

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*Keywords:* Boolean network; Synchronous update; Asynchronous update; Attractor; Dynamical cycle; Fixed point

## 1. Introduction

Boolean networks have applications in many areas including circuit theory, computer science [4,13] and molecular biology [7–9]. These networks are defined by a set of states, a transition function and a schedule of update. We are interested in studying its limit behavior, i.e. its attractors. In biology attractors can represent a memory trace, a pattern of motor nerve activity, a state of an immune network or a cell type. For example, in the modeling of gene regulatory networks, the attractors are associated with distinct cell states defined by patterns of gene activity. In particular, the fixed points are often associated with phenomena such as cell proliferation and apoptosis [6]. Consequently, the knowledge of the number of attractors is essential to understand the function of the studied system.

The transition function of the network defines a directed graph, which we call the graph associated with the network. Some properties of this graph can help us to know some features about the attractors of the network [1,2,5,12], for example, the existence of dynamical cycles and the length of them.

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Boolean Networks can be updated in several different ways, in this case we study two of them: either all the arguments of the transition function are the values of the previous step (parallel update), or some of the arguments are already updated values, as if memory cells are updated one-by-one in some order (serial update). We see that a Boolean network with a parallel update is the same as a synchronous Boolean Network, and serial update is similar to asynchronous Boolean Network. The difference is that in asynchronous Boolean Network only one state is updated in each time-step, and in serial update every state is updated in each time-step. In this article, we study the difference of the limit behavior between a parallel and a serial update schedule.

The first model of Boolean networks proposed by Kauffman [8,9] to model genetic regulatory networks considers a parallel update schedule, but the question about whether this hypothesis is realistic remains open. Hence, it is interesting to study the difference between the set of attractors in both cases, since the set of attractors determines the behavior of the Boolean network. It is known that the fixed points are the same in both cases, but dynamic cycles are sensitive to the update schedule. This topic has been studied from a point of view of infinitesimal deviations from parallel update and test the stability of the attractors in Boolean networks by Klemm and Bornholdt [10]. One of the first structural analysis of comparison between different update schedules was done by Robert by using a discrete version of spectral radius [11]. Further, Tchente established that if the associated graph with the network is a specific kind of graph by layers, then the parallel and serial updates have exactly the same dynamical behavior [12]. Now, if we can find some relationship between the set of dynamical cycles in both cases, we can choose the update schedule in order to know the attractors of the network, taking the schedule that allows, possibly, to find attractors in a simpler way. But, we show that under certain conditions the serial and parallel update produce completely different set of cycles.

The paper is organized as follows. Section 2 introduces the notations and the definitions used in the paper. In Section 3 the results about networks with a graph by layers are presented. The result showing that dynamical cycles are different when we use a parallel and a serial update is given in Section 4. Finally, we draw our conclusions in Section 5.

## 2. Definitions and notations

A Boolean network  $N$  is defined by a finite set of variable states  $\{x_1, \dots, x_n\}$ , where  $x_i \in \{0, 1\}$ , a global transition function  $F : \{0, 1\}^n \rightarrow \{0, 1\}^n$ , where  $F(x) = (f_1(x), \dots, f_n(x))$  and  $x = (x_1, \dots, x_n)$ ,  $x_i \in \{0, 1\}$ , and an update schedule. In this case we study two types of schedule: parallel and serial updates.

The iteration of the Boolean network with parallel update is defined by the equation:

$$x^{r+1} = F(x^r), \quad (1)$$

where  $x^0 \in \{0, 1\}^n$ .

A serial update is defined by:

$$\begin{aligned} x_1^{r+1} &= f_1(x_1^r, \dots, x_n^r), \\ x_i^{r+1} &= f_i(x_1^{r+1}, \dots, x_{i-1}^{r+1}, x_i^r, \dots, x_n^r), \quad \forall i = 2, \dots, n. \end{aligned} \quad (2)$$

The serial update is equivalent to applying a function  $H : \{0, 1\}^n \rightarrow \{0, 1\}^n$  in a parallel way, where  $H(x) = (h_1(x), \dots, h_n(x))$  is defined by:

$$\begin{aligned} h_1(x) &= f_1(x), \\ h_i(x) &= f_i(h_1(x), \dots, h_{i-1}(x), x_i, \dots, x_n), \quad \forall i = 2, \dots, n. \end{aligned} \quad (3)$$

Since  $\{0, 1\}^n$  is a finite set we have two limit behaviors for the iteration of a network:

- *Fixed Point.* We define a fixed point as  $x \in \{0, 1\}^n$  such that  $F(x) = x$ .
- *Cycle.* We define a cycle of length  $p > 1$  as the sequence  $[x^0, \dots, x^{p-1}, x^0]$  such that  $x^j \in \{0, 1\}^n$ ,  $x^j$  are pairwise distinct and  $F(x^j) = x^{j+1}$ , for all  $j = 0, \dots, p-2$  and  $F(x^{p-1}) = x^0$ .

Fixed points and cycles are called *attractors* of the network.

It is easy to see that for a parallel update the order of the nodes is not important, but for a serial update the order of the node is very important. Then if we have to study a serial and a parallel update of the same network, we will label the states with the order of the serial update.

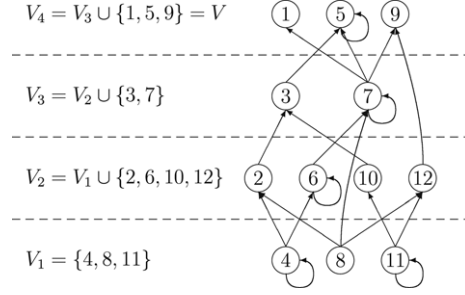


Fig. 1. Example of a graph by layers.

The graph associated with the network  $N$  is the directed graph  $G = (V, E)$ , where  $V = \{1 \dots, n\}$  and  $(i, j) \in E$  if and only if  $f_j$  depends on  $x_i$ , i.e., if there exists  $x \in \{0, 1\}^n$  such that:

$$f_j(x_1, \dots, x_{i-1}, 0, x_{i+1}, \dots, x_n) \neq f_j(x_1, \dots, x_{i-1}, 1, x_{i+1}, \dots, x_n).$$

A circuit of  $G$  is a sequence of distinct nodes (except possibly the extreme ones)  $i_1, i_2, \dots, i_k, i_1$  of  $V$  where  $(i_l, i_{l+1}) \in E$  for  $l = 1, \dots, k-1$  and  $(i_k, i_1) \in E$ .  $k$  is the length of the circuit. A loop is a circuit of length one.

We denote,

$$I(j) = \{i \in \{1, \dots, n\} / (i, j) \in E\}$$

and we can say that  $f_j(x) = f_j(x_i : i \in I(j))$ .

A function  $f : \{0, 1\}^n \rightarrow \{0, 1\}$  is monotonic on input  $i$  if for every  $x \in \{0, 1\}^n$

$$f(x_1, \dots, x_{i-1}, 0, x_{i+1}, \dots, x_n) \leq f(x_1, \dots, x_{i-1}, 1, x_{i+1}, \dots, x_n).$$

A loop in  $i$  is monotonic if  $f_i$  is monotonic on input  $i$ .

### 3. Networks with a graph by layers

In this section we study the particular case of a network where the associated graph does not have circuits of length  $k \geq 2$ , we call this kind of graphs a *graph by layers*. For these networks we obtain some results about the length of the attractors and a relation between the dynamical behavior of serial and parallel update.

**Proposition 1.** *Let  $N$  be a Boolean network such that there are no circuits of length  $k \geq 2$  in its associated graph. Then if  $N$  has any cycle, the cycle has a length  $2^p$ ,  $p \in \mathbb{N}$  for parallel and serial updates. Moreover, in the absence of non-monotonic loop the only attractors are fixed points.*

**Proof.** As shown in Fig. 1, we can define a sequence of set of nodes  $\{V_i\}_{i=1}^M$  such that:

- $i \in V_1 \iff I(i) \subseteq \{i\}$ .
- $i \in V_r \iff I(i) \subseteq \{i\} \cup V_{r-1}$ .
- $V_M = V$ .

Let  $N_A$  be, a Boolean network defined by the function  $F^A : \{0, 1\}^n \rightarrow \{0, 1\}^n$ , where  $A \subseteq V$  and:

$$f_i^A(x) = \begin{cases} f_i(x) & \text{if } i \in A \\ 0 & \text{otherwise.} \end{cases}$$

Then, it is easy to see that:

- $N_{V_M} \equiv N$ .
- $\forall x \in \{0, 1\}^n$  and  $\forall i \in V_r$ ,  $f_i(x) = f_i^{V_r}(x)$ .

Hence, given  $[x^0, \dots, x^{p-1}, x^0]$ , a cycle for the Boolean network  $N$  with parallel update (serial update, respectively) then  $[x^{r,0}, \dots, x^{r,m(r)-1}, x^{r,0}]$  is a cycle for  $N_{V_r}$  with parallel update (serial update, respectively), where:

$$x_i^{r,l} = \begin{cases} x_i^l & \text{if } i \in V_r \\ 0 & \text{otherwise} \end{cases}$$

and,

$$m(r) = \min \left\{ m \in \{0, \dots, p-1\} / \forall i \in V_r, x_i^{r,m} = x_i^{r,0} \right\}.$$

And then, we have:

- if  $r < r'$  then for all  $i \in V_r$  and  $l < m(r)$ ,  $x_i^{r,l} = x_i^{r',l}$ .
- $m(r+1)$  is a multiple of  $m(r)$ . Indeed, if there exist  $k, d$  such that  $m(r+1) = km(r) + d$ , where  $0 < d < m(r)$ , then  $d = \min \left\{ m \in \{0, \dots, p-1\} / \forall i \in V_r, x_i^{r,m} = x_i^{r,0} \right\}$ , which contradicts the definition of  $m(r)$ .

We say that the cycle  $[x^{r,0}, \dots, x^{r,m(r)-1}, x^{r,0}]$  is a restriction of the cycle  $[x^0, \dots, x^{p-1}, x^0]$  to the set of nodes  $V_r$ .

Now, we will use induction on  $r$  to prove that  $m(r)$  is a power of two for all  $r = 1, \dots, M$ , and then  $l$  is a power of two, and in the absence of non-monotonic loops,  $l = 1$ .

**Base  $r = 1$ .** By the definition of  $V_1$  for all  $i \in V_1$ , we have three possibilities:

- (1)  $f_i^1(x_i) = c_i$  then for all  $q = 0, \dots, l-1$ ,  $x_i^q = c_i$  and  $x_i^{1,l} = c_i$ ,
- (2)  $f_i^1(x_i) = x_i$  then for all  $q = 0, \dots, l-1$ ,  $x_i^q = x_i^1$  and  $x_i^{1,l} = x_i^0$ ,
- (3)  $f_i^1(x_i) = \bar{x}_i$  then for all  $q = 0, \dots, l-1$ ,  $x_i^q = \bar{x}_i^{q+1}$ , and hence  $x_i^{1,0} = x_i^1$  and  $x_i^{1,1} = \bar{x}_i^1$ .

Thus in monotonic case  $m(1) = 1$  and if there exists a non-monotonic loop, we have a function in the third class and  $m(1) = 2 = 2^1$ .

**Hypothesis of induction.** For all  $k \leq r$ ,  $m(k)$  is a power of 2 and in the absence of non-monotonic loops  $m(k) = 1$ .

**Case  $r + 1$ .** Since the cycle  $[x^0, \dots, x^{p-1}, x^0]$  restricted to  $V_r$  has length  $m(r)$ , for every  $i \in V_{r+1} \setminus V_r$ , the cycle  $[x^0, \dots, x^{p-1}, x^0]$  restricted to  $\{i\} \cup V_r$  has length at most  $2m(r)$  and this length has to be a multiple of  $m(r)$ , then this length is either  $m(i, r) = m(r)$  or  $m(i, r) = 2m(r)$ . Now,  $m(r+1)$  is the minimum common multiple of  $m(i, r)$ ,  $i \in V_{r+1} \setminus V_r$  then either  $m(r+1) = m(r)$  or  $m(r+1) = 2m(r)$ .

In the case of non-monotonic loops, by the hypothesis of induction  $m(r)$  is a power of two, then  $m(r+1)$  is a power of two.

On the other hand, in the absence of non-monotonic loops  $m(r) = 1$ . Let  $x^* = x^{r,0}$ . Now we have only two possibilities  $m(r+1) = 1$  or  $m(r+1) = 2$ . If  $m(r+1) = 2$  then there exists  $i \in V_{r+1} \setminus V_r$  such that:

$$f_i(x_1^*, \dots, x_{i-1}^*, 0, x_{i+1}^*, \dots, x_n^*) = 1 \quad \text{and} \quad f_i(x_1^*, \dots, x_{i-1}^*, 1, x_{i+1}^*, \dots, x_n^*) = 0$$

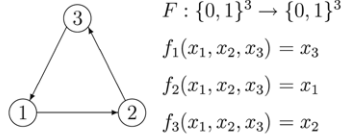
which is a contradiction with the monotonicity of the loops, then  $m(r+1) = 1$ .  $\square$

At this point it is worth remarking that not all Boolean networks have cycles of length a power of 2. Indeed, in Fig. 2 we can see an example of a Boolean network having a cycle of length 3.

**Proposition 2.** *Let  $N$  be a Boolean network such that for all  $i = 1, \dots, n$ ,  $I(i) \subseteq \{i, \dots, n\}$  then serial and parallel dynamics are identical.*

This proposition was proved by Tchunte [12] and we are interested in the converse of this proposition. The graphs of these networks do not have circuits of length  $k \geq 2$ , the only circuits possible are the loops, i.e., they are a particular case of graphs by layers. An example of graph of these networks is depicted in Fig. 3.

We consider networks where the associated graph does not have loops, then these networks satisfy the hypothesis of Proposition 1 without non-monotonic loops, and then all their attractors are fixed points.



Fixed Points:  $(0, 0, 0), (1, 1, 1)$   
 Cycles:  $[(1, 0, 0), (0, 1, 0), (0, 0, 1), (1, 0, 0)]$   
 $[(1, 1, 0), (0, 1, 1), (1, 0, 1), (1, 1, 0)]$

Fig. 2. Network with an attractor of length 3.

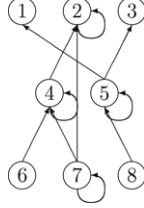
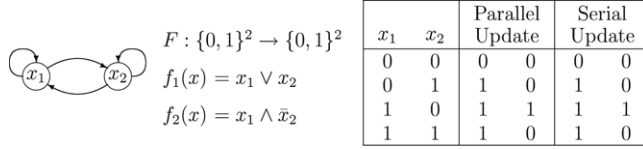


Fig. 3. Graph of a network such that  $I(i) \subseteq \{i, i + 1, \dots, n\}$ .



Attractors: Fixed point:  $(0, 0)$  Cycle:  $[(1, 0), (1, 1), (1, 0)]$

Fig. 4. Example of a Network with the same serial and parallel update where  $I(i) \not\subseteq \{i + 1, \dots, n\}$ .

**Theorem 3.** Let  $N$  be a Boolean network such that  $N$  does not have any loop. If serial and parallel dynamics are identical then, for all  $i = 1, \dots, n$ ,  $I(i) \subseteq \{i + 1, \dots, n\}$ .

**Proof.** By contradiction, let us suppose that there exists  $i$  such that  $f_i$  depends on the value  $x_j$  where  $j < i$ . Let

$$j_* = \min\{j \in \{1, \dots, n\} / \exists i > j, f_i \text{ depends on } x_j\}, \text{ and} \quad (4)$$

$$i_* = \min\{i \in \{j_* + 1, \dots, n\} / f_i \text{ depends on } x_{j_*}\}. \quad (5)$$

Since  $f_{i_*}$  depends on  $x_{j_*}$  then there exists  $x' = (x'_1, \dots, x'_{j_*-1}, 0, x'_{j_*+1}, \dots, x'_n)$  and  $x'' = (x'_1, \dots, x'_{j_*-1}, 1, x'_{j_*+1}, \dots, x'_n)$  such that,  $f_{i_*}(x') \neq f_{i_*}(x'')$ . Next, we apply the function  $H$  (defined in (3)) to  $x'$ , that is equivalent to the use a serial update schedule.

$$h_{i_*}(x') = f_{i_*}(h_1(x'), \dots, h_{i_*-1}(x'), x'_i, \dots, x'_n).$$

But,  $f_{i_*}$  depends on states of variables whose indices are greater than or equal to  $j_*$ , and then:

$$h_{i_*}(x') = f_{i_*}(h_{j_*}(x'), \dots, h_{i_*-1}(x'), x'_i, \dots, x'_n). \quad (6)$$

Thanks to (5), for  $j_* \leq k < i_*$ ,  $f_k$  does not depend on  $x_{j_*}$ , thus  $h_k$  does not depend on  $x_{j_*}$ , either. And then (6) becomes,

$$h_{i_*}(x') = f_{i_*}(h_{j_*}(x''), \dots, h_{i_*-1}(x''), x'_i, \dots, x'_n)$$

$$h_{i_*}(x') = h_{i_*}(x'').$$

Therefore, there exist vectors  $x' \neq x''$  such that the values on the input  $i_*$  after a parallel update are different ( $f_{i_*}(x') \neq f_{i_*}(x'')$ ), and equal after a serial update ( $h_{i_*}(x') = h_{i_*}(x'')$ ), which is a contradiction.  $\square$

Last theorem does not hold for networks with loops as in Fig. 4. In fact we see that the associated graph is not by layers and one of the attractors is a cycle, which it is not possible for networks that satisfy the hypothesis of Theorem 3.

#### 4. Cycles in parallel and serial update

It is well-known fact that the fixed points of a Boolean network are the same if the update mode is parallel or serial. In this section, we prove that for a class of Boolean networks the cycles are not the same.

**Theorem 4.** *Let  $N$  be a Boolean network such that the loops are monotonic, if  $[x^0, \dots, x^{p-1}, x^0]$  is a cycle, of  $N$  for parallel update, then  $[x^0, \dots, x^{p-1}, x^0]$  is not a cycle of  $N$  for serial update.*

**Proof.** Let us suppose on the contrary that there exists a cycle  $[x^0, \dots, x^{p-1}, x^0]$  for serial and parallel updates. Since serial and parallel updates are the same for the cycle, we have that for all  $l = 0, \dots, p-1$ , and  $i = 1, \dots, n$ :

$$\begin{aligned} x_i^{l+1} &= f_i(x_1^l, \dots, x_{i-1}^l, x_i^l, \dots, x_n^l) && \text{parallel update} \\ x_i^{l+1} &= f_i(x_1^{l+1}, \dots, x_{i-1}^{l+1}, x_i^l, \dots, x_n^l) && \text{serial update.} \end{aligned}$$

Since  $[x^0, \dots, x^{p-1}, x^0]$  is a cycle, we note that  $x^p \equiv x^0$ .

Let  $i_* = \max\{i \in \{1, \dots, n\} / \exists l, m = 0, \dots, p-1, x_i^l \neq x_i^m\}$ , which is well-defined since the  $x^l$ 's are pairwise distinct. We have that:

$$\begin{aligned} x_{i_*}^l &= f_{i_*}(x_1^l, \dots, x_{i_*-1}^l, x_{i_*}^{l-1}, \dots, x_n^{l-1}) && \text{serial update} \\ x_{i_*}^{l+1} &= f_{i_*}(x_1^l, \dots, x_{i_*-1}^l, x_{i_*}^l, \dots, x_n^l) && \text{parallel update.} \end{aligned}$$

By the definition of  $i_*$ ,  $x_{i_*}^l$  are constant for all  $i = i_* + 1, \dots, n$ , and then,

$$\begin{aligned} x_{i_*}^l &= f_{i_*}(x_1^l, \dots, x_{i_*-1}^l, x_{i_*}^{l-1}, x_{i_*+1}^l, \dots, x_n^l) && \text{serial update} \\ x_{i_*}^{l+1} &= f_{i_*}(x_1^l, \dots, x_{i_*-1}^l, x_{i_*}^l, x_{i_*+1}^l, \dots, x_n^l) && \text{parallel update.} \end{aligned}$$

If  $f_{i_*}$  does not depend on  $x_{i_*}$  then  $x_{i_*}^l = x_{i_*}^{l+1}$ , for all  $l = 0, \dots, p-1$ , which contradicts the definition of  $i_*$ . Then  $f_{i_*}$  depends on  $x_{i_*}$ .

Let us suppose that there exists  $l = 0, \dots, p-1$  such that  $x_{i_*}^{l-1} = x_{i_*}^l$ . We obtain:

$$\begin{aligned} x_{i_*}^l &= f_{i_*}(x_1^l, \dots, x_{i_*-1}^l, x_{i_*}^l, x_{i_*+1}^l, \dots, x_n^l) && \text{serial update} \\ x_{i_*}^{l+1} &= f_{i_*}(x_1^l, \dots, x_{i_*-1}^l, x_{i_*}^l, x_{i_*+1}^l, \dots, x_n^l) && \text{parallel update.} \end{aligned}$$

Thus  $x_{i_*}^l = x_{i_*}^{l+1}$ . Using induction we can suppose, without loss of generality that  $x_{i_*}^0 = x_{i_*}^1$  and we obtain that the  $i_*$ th component of the vectors in the cycle is constant, which contradicts the definition of  $i_*$ .

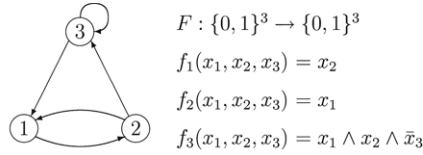
Now, we suppose that  $f_{i_*}$  depends on  $x_{i_*}$  and  $x_{i_*}^l \neq x_{i_*}^{l+1}, \forall l = 0, \dots, p-1$ . Then, there exists  $l = 0, \dots, p-1$ , such that  $x_{i_*}^{l-1} = 1, x_{i_*}^l = 0$  and  $x_{i_*}^{l+1} = 1$ :

$$\begin{aligned} x_{i_*}^l &= 0 = f_{i_*}(x_1^l, \dots, x_{i_*-1}^l, 1, x_{i_*+1}^l, \dots, x_n^l) && \text{serial update} \\ x_{i_*}^{l+1} &= 1 = f_{i_*}(x_1^l, \dots, x_{i_*-1}^l, 0, x_{i_*+1}^l, \dots, x_n^l) && \text{parallel update.} \end{aligned}$$

This is a contradiction with the monotonicity of  $f_{i_*}$  with respect to  $x_{i_*}$ , thus we do not have common cycles for serial and parallel update modes.  $\square$

As seen in Fig. 5, this theorem is not true if we have a non-monotonic loop. In this case we see that the cycle  $[(1, 1, 0), (1, 1, 1), (1, 1, 0)]$  is a cycle for serial and parallel update modes.

We finally remark that Theorem 4 is valid for discrete networks and not only for Boolean networks. The proof is similar. Indeed in the last part we suppose that  $f_{i_*}$  depends on  $x_{i_*}$  and  $x_{i_*}^{(l)} \neq x_{i_*}^{(l+1)}, \forall l = 0, \dots, p-1$ . Then, if  $x_{i_*}^{(0)} > x_{i_*}^{(1)}$  (or  $x_{i_*}^{(0)} < x_{i_*}^{(1)}$  resp.), by monotonicity we obtain  $x_{i_*}^{(0)} > \dots > x_{i_*}^{(p-1)} > x_{i_*}^{(p)} = x_{i_*}^{(0)}$  (or  $x_{i_*}^{(0)} < \dots < x_{i_*}^{(p-1)} < x_{i_*}^{(p)} = x_{i_*}^{(0)}$  resp.) which is a contradiction.



Attractors for Parallel Update	Attractors for Serial Update
<i>Fixed Point:</i> (0, 0, 0)	<i>Fixed Point:</i> (0, 0, 0)
<i>Cycles:</i> [(1, 1, 0), (1, 1, 1), (1, 1, 0)] [(0, 1, 0), (1, 0, 0), (0, 1, 0)]	<i>Cycles:</i> [(1, 1, 0), (1, 1, 1), (1, 1, 0)]

Fig. 5. [(1, 1, 0), (1, 1, 1), (1, 1, 0)] is a cycle for parallel and serial update.

## 5. Conclusions

The main result of this paper is the proof that in a big class of Boolean networks the dynamical cycles are not the same for serial and parallel update in opposition with the fixed points.

In this article we have shown that Boolean networks with an associated graph by layers have only attractors of length a power of two, and in the absence of non-monotonic loops the only attractors are fixed points.

## For further reading

[3]

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