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NULLCLINES AND NULLCLINE INTERSECTIONS

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One purpose of this paper is to document the fact that, in dynamical systems described by ordinary differential equations, the trajectories can be organized not only around fixed points (steady states), but also around lines. In 2D, these lines are the nullclines themselves, in 3D, the intersections of the nullclines two by two, etc.

We precise the concepts of "partial steady states" (i.e. steady states in a subsystem that consists of sections of phase space by planes normal to one of the axes) and of "partial multistationarity" (multistationarity in such a subsystem).

Steady states, nullclines or their intersections are revisited in terms of circuits, defined from nonzero elements of the Jacobian matrix. It is shown how the mere examination of the Jacobian matrix and the sign patterns of its circuits can help interpreting (and often predicting) aspects of the dynamics of systems.

The results reinforce the idea that chaotic dynamics requires both a positive circuit, to provide (if only partial) multistationarity, and a negative circuit, to provide sustained oscillations. As shown elsewhere, a single circuit may suffice if it is ambiguous (i.e. positive or negative depending on the location in phase space).

The description in terms of circuits is by no means exclusive of the classical description. In many cases, a fruitful approach involves repeated feedback between the two viewpoints.

Keywords: Nullclines; circuits; nuclei; partial steady states; partial multistationarity; chaotic flows.

1. Introduction

In dynamical systems described by ordinary differential equations, the **steady states** are defined as the real, nondegenerate, solutions of the set of steady state equations. Multistationarity is the situation in which there is more than one such solution.

Taken separately, each of the steady state equations defines a **nullcline**. Obviously, in two-variable systems the two nullclines are lines and their intersects, if any, are the steady states themselves. In a three-variable system, the three nullclines are surfaces, their intersects two by two, if any, are lines and the intersects between these lines, if any, are the steady states of the system. More generally, in an *n*-variable system the nullclines are of dimension

n-1, their intersects of dimension n-2 and so on, down to the steady states (dimension 0). In what follows the nullclines $\dot{x}=0, \dot{y}=0, \dot{z}=0,\ldots$ will be called $nu_x, nu_y, nu_z \ldots$, respectively, their intersections two by two, $nu_{xy}, nu_{yz}, nu_{zx}$, etc.

As discussed in earlier publications, **circuits** (defined in terms of sets of nonzero elements of the Jacobian matrix) play an essential role in the determination of the number and stability properties of steady states. Here, we extend this relation from steady states proper to nullclines and their intersections, punctual (steady states) or not, and discuss the relations between circuits and nullclines (or their intersections).

We develop the concepts of "partial steady state" (a point that is steady in a subsystem) and of "partial multistationarity" (multistationarity in a subsystem).

There seems to be a more or less tacit agreement on the idea that trajectories are organized essentially around the steady states. That the shape of trajectories is also influenced by the nullclines or their intersections, is quite obvious, however, as it is there that time derivatives change sign. We wish to emphasize this role, and illustrate the fact that in three-dimensional systems trajectories can be organized not only around steady states, but also around lines at the intersection of two nullcline surfaces. This is especially clear in systems that lack any steady state.

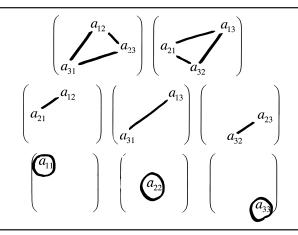
The first two sections below may seem at first view unrelated to each other and with the main object of this paper, namely, the structural role of nullcline intersects in the shape of trajectories. However, these sections are required for a proper understanding of our analysis.

- 2. A Brief Reminder About Circuits (for a more detailed description, see for example [Thomas & Kaufman, 2001, 2005]).
- (i) (Oriented) links, represented by arrows in graphs, are defined from nonzero elements of the Jacobian matrix. Since $a_{ij} = \partial F_i/\partial x_j$, a_{ij} nonzero implies that variable x_j influences the evolution of variable x_i , in other words, that there is an arrow from x_j to x_i in the graph of the system. A link is positive or negative depending on the sign of a_{ij} .
- (ii) Circuits are defined from sets of nonzero terms of the Jacobian matrix such that their line (i) and row (j) indices can form a cyclic permutation. Table 1 shows the circuits in three-dimensional systems.

A circuit has a weight (the absolute value of the product of its elements) and a sign. It is positive if it comprises an even number of negative links, negative if odd. The sign of a circuit can also be defined as the sign of the product of its elements.

Positive and negative circuits play contrasting roles. That positive feedback is involved in epigenetic processes, including differentiation, had been realized already long ago by Rosen [1968]. In fact,

Table 1. The circuits in three-variable systems.



the presence of a positive circuit (of any length) in the Jacobian matrix of a system is a necessary condition for multistationarity, as conjectured by Thomas [1981] and formally demonstrated by others [Plahte et al., 1995; Snoussi, 1998; Gouzé, 1998; Cinquin & Demongeot, 2002; Soulé, 2003]. In contrast, negative circuits behave as thermostats and are involved in homeostasis, as noticed by many long ago. The presence of a negative circuit of at least two elements is a necessary condition of a stable periodicity, as conjectured by Thomas [1981] and formally demonstrated by others [Snoussi, 1998; Gouzé, 1998]. More generally, we conjecture now that the presence of a negative circuit is a **necessary condition** for the existence of an attractor, punctual (a stable steady state), periodic (a limit cycle) or chaotic.

(iii) One should consider not only circuits proper,

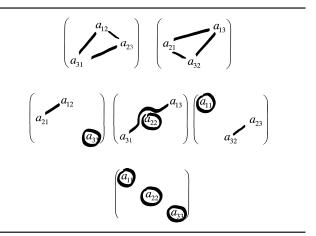
¹I thank Otto Rössler and Olaf Wolkenhauer for having drawn my attention to the importance of Rosen's contribution.

but also unions of two or more disjoint circuits,² that is, of circuits that have no variable in common. In brief, we call them simply **unions**. For example, a_{12} a_{23} a_{31} is a three-circuit and $a_{12}a_{21} \cdot a_{33}$ is the union of the two-circuit $a_{12}a_{21}$ and the one-circuit a_{33}). In practice, the "Eisenfeld sign" (or, for short, the sign) of a union is "+" if it comprises an odd number of positive circuits, "–" otherwise.

(iv) Nuclei are circuits or unions that imply all the variables of the system. Table 2 shows the nuclei in three-dimensional systems. As one can see in this table, a three-variable system can have two three-nuclei, three (2 + 1)-nuclei (the unions of a two-circuit and a disjoint one-circuit) and one (1+1+1)-nucleus (the union of three disjoint onecircuits). The list of the nuclei is nothing else than the list of the terms of the determinant of the Jacobian matrix. For example, in two dimensions the determinant is $a_{11}a_{22} - a_{12}a_{21}$. The nuclei are thus a_{12} a_{21} (a two-circuit) and a_{11} a_{22} (the union of two one-circuits). In the absence of any nucleus, the determinant of the Jacobian matrix is zero everywhere, and hence the system is indeterminate; there is no nondegenerate steady state.

Each nucleus, if taken alone, generates one or more steady states whose nature can be predicted from its sign patterns. How nuclei interact

Table 2. The nuclei (circuits or unions of disjoint circuits that involve all the variables of the system) in three-variable systems.



with each other to yield the actual steady states of a system, is discussed at length in [Thomas & Kaufman, 2001, 2005]. In particular, a conjecture due to M. Kaufman states that multistationarity requires a variable nucleus or two nuclei of opposite Eisenfeld signs.

3. Subsystems, Partial Steady States, Partial Multistationarity

As we will see below, it is often appropriate to consider subsystems. Assigning a fixed value z^* to variable z in a three-dimensional system in xyz, amounts to consider a section of phase space by the plane $z=z^*$. In this subsystem xy, the null-clines, that were surfaces in the whole system, are now lines, and the nullcline intersects, that were lines, are now points. These points are in fact steady states in the subsystem considered and we call them "partial steady states" in the complete system. As we will see, it may happen that multistationarity is not present at the level of the whole system but well at the level of one of its subsystems. In such cases, we speak of "partial multistationarity".

Let us now consider subsystems in terms of circuits. We will reason for a three-dimensional system in xyz. A two-circuit in, say, xy, becomes a nucleus in subspace xy. What has been told about the relation between nuclei and steady states in the whole system holds as well for subsystems. In particular, a circuit that is not a nucleus in the whole system, but is a nucleus in a subsystem, can generate steady states in this subsystem; these are of course only partial steady states in the whole system.

More generally, the generic statements about systems apply as well to their subsystems. For example, the statement that the presence of a positive circuit is a necessary condition of multistationarity implies that the presence of a positive circuit in a subsystem is a necessary condition for multistationarity in this subsystem, and thus for "partial multistationarity" in the whole system. These concepts of "partial steady state" and "partial multistationarity have been briefly presented already in Thomas [1996, 1999a].

Eisenfeld and De Lisi [1985] introduced the concept of "generalized loop", which covers "circuit" and "union of two or more disjoint circuits". They define the sign of a generalized loop as $(-1)^{p+1}$, in which p is the number of positive circuits in the union. We adopt this definition, but prefer to avoid "loop" because in graph theory it is used only for one-element circuits, and to use distinct words for circuits proper and unions of two or more circuits.

4. Effect of the Suppression of Steady States

Let us begin, without detailed analysis, with a very simple, two-dimensional system:

$$\dot{x} = xy - 0.2
\dot{y} = -(x^2 + x + a)$$
(1)

For a=0.2, there are two steady states, a stable focus and a saddle point. For higher values of a, these steady states disappear. Figure 1 shows trajectories of both systems. In spite of the presence of two steady states in Fig. 1(a) and of no steady state in Fig. 1(b), the trajectories are extremely similar in the two cases.

Consider now the system:

$$\dot{x} = ax - y
\dot{y} = x - z ,
\dot{z} = y^3 - cz$$
(2)

in which a and c are positive parameters. Its Jacobian matrix is:

$$\begin{pmatrix}
a & -1 \\
1 & & -1 \\
& 3y^2 & -c
\end{pmatrix}$$

and one sees that it comprises two nuclei.

Nucleus I:

$$\begin{pmatrix} (+) & -1 \\ 1 & & \\ & & -c \end{pmatrix}^3$$

is the union of the negative two-circuit $a_{12}a_{21}$, which, by itself would generate a focus in xy (unstable in view of the fact that the diagonal term a_{11} is positive) and of the negative one-circuit a_{33} (which renders the system attractive in z). Thus, taken alone, nucleus I would generate a saddle-focus of type (-/++), that is, with a real negative eigenvalue

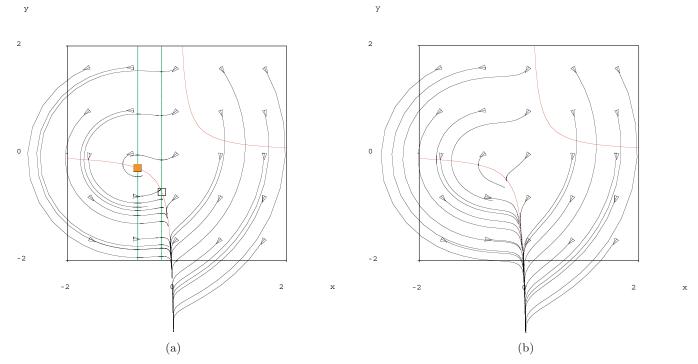


Fig. 1. System $\dot{x} = xy - 0.2$ has two steady states for a = 0.2, but no steady state for a = 0.3. (a) and (b) show the nullclines (red and green lines), the steady states where present (dark square for a stable steady state, empty square for an unstable steady state) and trajectories for the two systems. Trajectories are given as a "grid" from a number (5×5) of different initial states (Program Grind, Rob DeBoer).

³The additional sign (+) between brackets is not part of nucleus I itself. It is there only to recall that the diagonal element considered is positive, and that the partial steady state in xy is thus an unstable focus. In the same way, the additional sign (-) is not part of nucleus II itself. It is there only to remind that the diagonal element considered is negative, and that the partial steady state in yz is thus a stable focus.

and a pair of conjugated complex eigenvalues with a positive real part.

Nucleus II:

$$\begin{pmatrix} a & & & \\ & & -1 \\ & 3y^2 & (-) \end{pmatrix}^3$$

is the union of the negative two-circuit $a_{23}a_{32}$, which, by itself would generate a focus in subsystem yz, (stable in view of the fact that the diagonal term a_{33} is negative) and of the positive one-circuit a_{11} (which renders the system repulsive in x). Thus, taken alone nucleus II would generate saddle-foci (two in fact, one for positive, one for negative values of y) of type (+/--), that is, with a real positive eigenvalue and a pair of conjugated complex eigenvalues with a negative real part. For appropriate values of the parameters, this system has indeed three steady states of the expected nature, and a chaotic attractor. The general shape of this attractor is understandable in terms of the nature of these three steady states, but also of the line

 nu_{xy} at the intersection of nullclines nu_x and nu_y [Fig. 2(a)].

One now asks the question: is it possible to derive from this system a variant that would keep the chaotic dynamics, yet would have kept only one steady state? If one moves the term a_{11} to a_{22} , the system becomes:

$$\begin{split} \dot{x} &= -y \\ \dot{y} &= x + ay - z \,, \\ \dot{z} &= y^3 - cz \end{split}$$

and the Jacobian matrix:

$$\begin{pmatrix} -1 \\ 1 & a & -1 \\ 3y^2 & -c \end{pmatrix}.$$

This system has kept nucleus I:

$$\begin{pmatrix} & -1 & \\ 1 & & \\ & & -c \end{pmatrix}$$

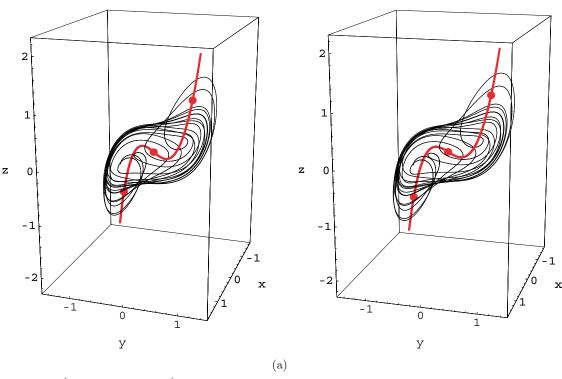
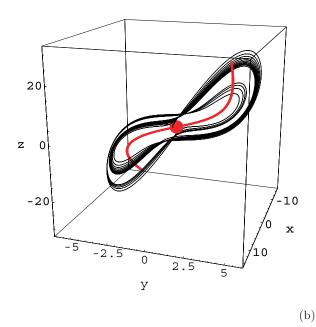


Fig. 2. Systems (a) $\begin{array}{ccc} \dot{x} = ax - y & \dot{x} = -y \\ \dot{y} = x - z & \text{and (b)} & \dot{y} = x + ay - z \end{array}$. These systems differ only by the position of a constant term at posi- $\dot{z} = y^3 - cz$ $\dot{z} = y^3 - cz$

tions a_{11} or a_{22} in the Jacobian matrix. Steady states are represented by red points; system (2a) has three, system (2b), one only. In both cases, the line at the intersection of nullclines nu_x and nu_y has been drawn in red. Parameters are, for (2a), a = 0.8 and c = 1, for (2b), a = 3.3 and c = 4. In both cases, the initial state is $\{0.01, 0.01, 0, 0\}$ and trajectories are recorded between t = 50 and t = 150. The couples of images are seen from slightly different angles (Viewpoints $\{3, 1, 1\}$ and $3.5, 1, 1\}$ in Mathematica) in order to permit stereoscopic view.



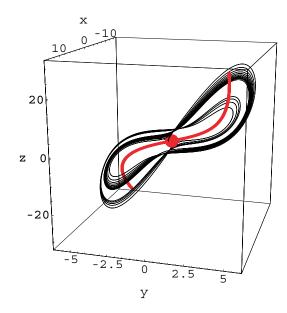


Fig. 2. (Continued)

and

which accounts for the existence of the steady state of type (-/++) at (0,0,0), but nucleus II is replaced by:

$$\left(\begin{array}{cc} a & -1 \\ 3y^2 & -c \end{array}\right).$$

This structure is no nucleus, since variable x is not involved, and it can thus not generate a steady state. In other words, the modified system comprises a single, nonvariable nucleus. In agreement with the Kaufman rule there is no multistationarity. There is a single steady state, of type (-/++), yet for appropriate parameter values (different from those used in the initial system), the chaotic attractor persists [Fig. 2(b)].

There is clearly no hope to figure out the shape of this chaotic attractor only in terms of the unique steady state. However the line nu_{yz} at the intersection of nullclines nu_y and nu_z provides an appropriate skeleton for this attractor.

In this situation, it is instructive to consider the subsystem in yz, in which variable x is frozen at an arbitrary value x^* . Subsystem yz thus writes:

$$\dot{y} = x^* + ay - z$$
$$\dot{z} = y^3 - cz$$

It has two nuclei:

$$\begin{pmatrix} a \\ -c \end{pmatrix}$$
$$\begin{pmatrix} & -1 \\ 3y^2 \end{pmatrix},$$

the first of which codes for a saddle point and the second (provided the trace a-c<0) for a pair of stable foci (one in positive y, one in negative y). It can be checked that contrary to the complete system, sub-system yz has (between two critical values of x^*) three steady states of the nature predicted. These steady states of the sub-system are "partial steady states" of the complete system, and in the domain of values of x^* for which the subsystem has multiple steady states, the complete system displays thus "partial multistationarity".

But what is the relation with the nullclines? The subsystems just mentioned are in fact sections of phase space by the planes $x = x^*$. Thus, as the complete system is 3D, the nullclines, which are surfaces in phase space, become lines in the sections, and the intersects between nullclines, which were lines in phase space, become points in the sections. In particular, the steady states of the subsystem yz ("partial" steady states of the complete system) are the sections of nu_{yz} (the intersects of nullclines

 nu_y and nu_z) by the planes $x=x^*$. Concretely, in the system just described, nu_{yz} , the intersection of nullclines nu_y and nu_z is the solution of the two steady state equations x + ay - cz = 0 and $y^3 - cz = 0$, a line of degree three. Between two critical values of x^* , this line cuts the plane $x = x^*$ at three points. These are the steady states of the subsystem and the "partial steady states" of the full system.

Figures 2(a) and 2(b) show, respectively, trajectories of the initial system with three steady states and the modified system with a single steady state. A look at these figures illustrates the fact that the trajectory is organized around the intersections between the nullclines, and not only around the steady state(s).

5. A Chaotic Flow without Steady State

The observation just above can be made even more striking if one moves to chaotic systems that have **no** steady state at all. Such a system is mentioned in [Sprott, 1995] under the label "A" and described in more detail in [Sprott, 2004] as the Nosé–Hoover oscillator [Nosé, 1991; Hoover, 1995].

$$\dot{x} = y
\dot{y} = -x + yz.
\dot{z} = 1 - y^2$$
(3)

The Jacobian matrix is:

$$\begin{pmatrix} 1 & 1 \\ -1 & z & y \\ & -2y \end{pmatrix}.$$

The absence of any steady state is immediately obvious from the steady state equations, but as well from the fact that the Jacobian matrix has no nucleus.

This conservative system has no attractor. It generates trajectories that are chaotic Fig. 3(b) or not [Figs. 3(a) and 3(b)] depending on the initial state; if not chaotic, they lie on invariant tori.

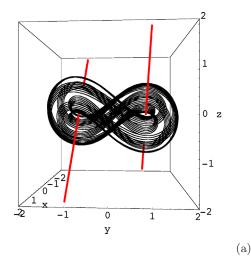
There are two two-circuits (one in xy, one in yz), both negative, and a one-circuit (in z) that is positive for positive values of z.

Subsystem yz (the sections of phase space by planes $x = x^*$) is:

$$\dot{y} = -x^* + yz$$
$$\dot{z} = 1 - y^2$$

Its Jacobian matrix is:

$$\begin{pmatrix} z & y \\ -2y \end{pmatrix}$$
.



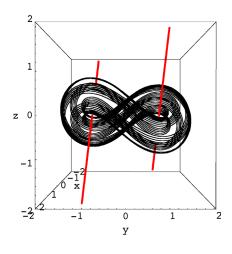


Fig. 3. Systems [(a) and (b), Sprott A] $\dot{y} = -x + yz$ and [(c) and (d)] $\dot{y} = -x + yz$. These systems differ only by the presence $\dot{z} = 1 - y^2$ or absence of a term at position a_{13} in the Jacobian matrix. The first system has no steady state, the second has two. For (a) and (c) the initial state is (1.5, 0, 0) and for (b) and (d), it is (0, 5, 0). In all cases, the lines (two skew straight lines) at the intersection of nullclines nu_x and nu_y have been drawn in red. Steady states, where present, are represented by red points. The value chosen for parameter a is 0.2. Trajectories are recorded between t = 50 and t = 250. Viewpoints are $\{2, 0, 0\}$ and $\{2, 0.1, 0\}$.

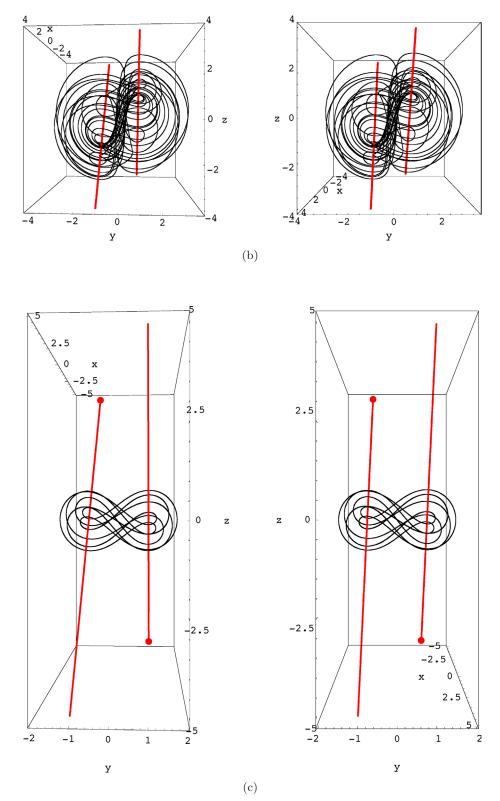


Fig. 3. (Continued)

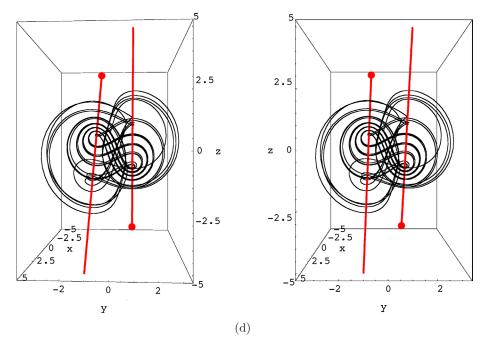


Fig. 3. (Continued)

In this subsystem, there is a nucleus:

$$\begin{pmatrix} & y \\ -2y & \end{pmatrix}$$

(whose elements formed a circuit, but not a nucleus, in the complete system). Taking into account the nature of the nonlinearities, its two distinct sign patterns, namely $\binom{}{+}$ and $\binom{}{-}$ allow for two potential steady states, more precisely, two foci running in opposite directions (and moreover, stable or unstable depending on the sign of z) in plane $x=x^*$. There are indeed two such foci in subsystem yz: see Fig. 4. These are "partial steady states" of the whole system, and since there are two of them, we have thus "partial multistationarity" in the whole system.

We have mentioned elsewhere that a chaotic dynamics apparently requires both a negative circuit of at least two elements to permit sustained oscillations and a positive circuit to permit (if only partial) multistationarity. The fact that Sprott's system displays a chaotic behavior in spite of the absence of any full steady state is consistent with this view. Indeed, there are two negative circuits, the functionality of at least one of which is demonstrated by the existence of foci in subspace yz. The positive one-circuit that is present in the region z > 0 is also functional, as shown by the partial multistationarity of subsystem yz.

Let us now shift back from the viewpoint "circuits" to the viewpoint "nullclines". Nullcline nu_x is

the plane y = 0, nullcline nu_y is the surface x = yzand nullcline nu_z comprises the planes y = -1 and y = 1. It is immediately obvious that nullclines nu_x and nu_z fail to intersect — a sufficient reason to have no steady state — in line with the absence of a nucleus in subsystem xz. The intersection between nullclines nu_x and nu_y is axis z. The intersections between nullclines nu_y and nu_z are two skew straight lines, line x = z in plane y = 1 and line y = -z in plane y = -1. Figures 3(a) and 3(b) show trajectories from two different initial states, one leading to a torus, the other chaotic. A look at these figures shows that in both cases the trajectories are wound around the two skew lines at the intersections of nullclines y'=0 and z'=0. Clearly, the trajectories are organized not only around steady states (absent in the present case) but as well, in three-dimensional systems, around the intersections of nullclines two by two, (and in two-dimensional systems, around the nullclines themselves: see, for example, [Goldbeter & Moran, 1987].

Can one derive from this system a closely related system that **does** have steady state(s)? This is quite easy. As in the present case the lack of a nucleus is the reason for the absence of any steady state, the obvious "recipe" is to add a term that generates a nucleus. In the present case, a_{13} nonzero will fit this requirement as regards the existence of steady states. The nucleus so created is a

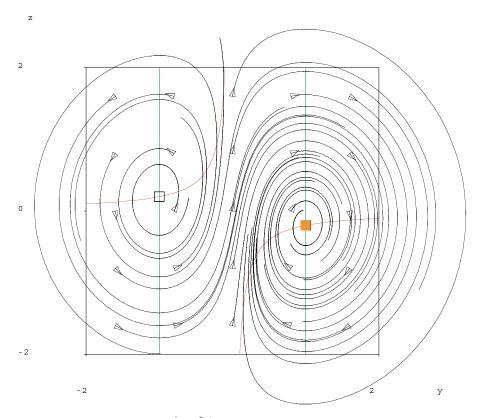


Fig. 4. The subsystem yz of system Sprott A: $\dot{y} = x^* + yz$ Although there is no steady state in the complete system, this subsystem has two foci running in opposite directions, one stable (dark square), one unstable (empty square). The nullclines of this subsystem are drawn in red and green. Trajectories are given as a "grid" from a number (5×5) of different initial states (Program Grind, Rob DeBoer).

three-circuit,

$$\begin{pmatrix} & & a_{13} \\ -1 & & \\ & -2y & \end{pmatrix}$$

that is positive or negative depending on the sign of y (and thus, on the location in phase space). This allows for the presence of two (unstable) steady states, namely two saddle-foci of types +/-- and -/++. The system has indeed two steady states of these types. For reasonably small absolute values of the additional parameter a_{13} , the trajectories (one periodic, one chaotic) remain similar to those of the original Sprott A system. Figures 3(c) and 3(d) show the trajectories, the nullcline intersects nu_{yz} and the two steady states for $a_{13}=0.2$ and the two initial states already used in Figs. 3(a) and 3(b).

6. Concluding Remarks

In this paper, we exploit the predictive possibilities of a proper examination of the sign patterns of the Jacobian matrix of systems. As described in previous papers, it became apparent that such systems as the classical Rössler attractor can be "re-synthesized" by asking which circuits in the Jacobian matrix would be required to obtain the two complementary saddle-foci (-/++ and +/--)that are characteristic of this system. At that time Grégoire Nicolis mentioned his conviction that there should exist closely related systems with a single steady state; however, he had not yet found them. Inspecting the Jacobian matrix in terms of circuits provided immediately an obvious answer. Just moving a term of the Jacobian matrix (in this system, a_{22} to a_{11}) suffices to suppress one of the two nuclei of the system, resulting in the disappearance of one of the two steady states. However, the negative two-circuit that was responsible for the oscillations around this steady state persists and remains functional. As expected, the modified system remains chaotic for appropriate parameter values.

Here, we describe other systems in which the disappearance of steady states does not result in a deep change in the morphology of the trajectories.

The most striking situation is provided by a system described by Sprott. This system displays beautiful chaotic trajectories in spite of the absence of any full steady state. This situation is well understood in terms of circuits and of nullclines and their intersections, and it was quite easy to derive a closely related system with two steady states and yet an extremely similar chaotic trajectory.

Clearly, the trajectories are organized not only around steady states (where present) but also around the nullclines (in 2D) or their intersections (in 3 or more D).

Acknowledgments

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