THE REVERSIBLE LVA MODEL

Peter L. SIMON

Institute of Physics, Technical University of Budapest, Budapest, H-1521 Hungary

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Abstract

We show that the solutions of the reversible LVA model are bounded. We give a sufficient condition for the existence of a globally asymptotically stable stationary point. In the case where only the first reaction is reversible in the LVA model, we use Liapunov functions to investigate the global behaviour of the system. A certain parameter L plays an important role in the phase portrait. The stationary point in the axis x is an attractor for L > 1, with a basin containing the open positive quadrant. For L < 1 there exists a unique positive stationary point, which is stable for L > 1/2 and loses its stability for L < 1/2 via supercritical Hopf bifurcation.

1. Introduction

The Lotka-Volterra model is often used as a base for chemical oscillatory models (e.g. the Explodator [1,2]). It produces conservative oscillations, and this property is not favourable: a more realistic oscillatory model is expected to show limit cycle behaviour. The generalized Lotka-Volterra schemes [2-4] contain the same reactions as the original Lotka-Volterra model does, but use different (higherorder) rate laws. One of these generalized schemes (Lotka-Volterra-Autocatalator, shortly LVA [2,5]) involves the third-order reaction $A + 2X \rightarrow 3X$, which had been used in the oscillatory model "Autocatalator" by Gray and Scott [6].

Consider the LVA model:

$$A + 2X \xrightarrow{k_1} 3X,$$

$$X + Y \xrightarrow{k_2} 2Y,$$

$$Y \xrightarrow{k_3} B.$$
(1)

This was investigated in detail, and it was found that this is explosive for any positive parameter value [2]. Hering [7] used the Dulac criterion to exclude oscillatory solutions in this model.

Including reversed reactions [8,9], the qualitative properties are often essentially changed; for example, the reversible Lotka–Volterra model has a globally asymptotically stable stationary point [7]. We want to know how the behaviour of system (1) changes if the reactions are reversible. In section 2, we consider the case where all the reactions are reversible, and in section 3, only the first reaction will be reversible.

2. Reversible reactions

In this section, we are going to investigate the model (1) where all the reactions are reversible:

$$A + 2X \rightleftharpoons 3X,$$

$$X + Y \rightleftharpoons 2Y,$$

$$Y \rightleftharpoons B.$$

$$(2)$$

This mechanism with mass-action kinetics yields the kinetic equations:

$$\dot{X} = k_1 A X^2 - l_1 X^3 - k_2 X Y + l_2 Y^2,$$

$$\dot{Y} = k_2 X Y - l_2 Y - k_3 Y + l_3 B,$$

where k_i (i = 1, 2, 3) are the rate constants belonging to the forward reactions in (2), l_i (i = 1, 2, 3) are the rate constants of the reverse reactions, X and Y are the concentrations of the intermediates of X and Y. A dot denotes differentiation with respect to time T. The concentration of A and B can be considered constant in time.

Let us introduce the following new variables:

$$x = \frac{k_2 k_3}{l_2 l_3 B} X, \quad y = \frac{k_3}{l_3 B} Y, \quad \tau = \frac{l_2 l_3 B}{k_3} T.$$

With this transformation, the system takes the form:

$$\dot{x} = K_2 (K_1 x^2 + y^2 - L_1 x^3 - xy),$$

$$\dot{y} = xy - y^2 + K_3 - K_3 y,$$
(3)

where the dot denotes differentiation with respect to time τ and the new constants are:

$$K_1 = \frac{kAl_2}{k_2^2}, \quad K_2 = \frac{k_2}{l_2}, \quad K_3 = \frac{k_3^2}{l_2 l_3 B}, \quad L_1 = \frac{l_1 l_2^2 l_3 B}{k_2^3 k_3}.$$

2.1. LOCAL INVESTIGATION

The stationary points of the system are determined by the equations:

$$h(y) = y - \frac{K_3}{y} + K_3 = x \qquad y > 0,$$

$$f(x) = \frac{K_1}{K_3} x^2 \left(1 - \frac{L_1}{K_1} x \right) + 1 = y \qquad x \ge 0.$$

We will need the following derivatives:

$$h'(y) = 1 + \frac{K_3}{y^2} > 0, \qquad h''(y) = \frac{-2K_3}{y^3} < 0, \qquad (y > 0)$$

$$f'(x) = \frac{x}{K_3} (2K_1 - 3L_1 x), \qquad f''(x) = \frac{2}{K_3} (K_1 - 3L_1 x).$$

Since *h* is an increasing function, there exists its inverse *g* with the same graph. The intersections of the graphs of *f* and *g* in the first quadrant give the stationary points. It is easy to see that g(0) < 1, g(x) > x if x < 1, g(1) = 1 and g(x) < x if x > 1. Furthermore, with the notation $K = K_1/L_1$, f(K) = f(0) = 1. If $0 \le x \le K$, then $f(x) \ge 1$ and if x > K, then f(x) < 1. Now we can draw the graph of the functions *f* and *g* (see fig. 1).



Fig. 1.

Knowing the above properties of the functions f and g, it is easy to see that there is at least one stationary state. Indeed, for the difference f(x) - g(x) = F(x), we obtain F(0) > 0 and $\lim F = -\infty$; therefore, there exists at least one $x_0 > 0$, for which $F(x_0) = 0$ (F is continuous). Thus, $f(x_0) = g(x_0)$, that is, $(x_0, f(x_0))$ is a stationary point.

It is not difficult to prove the following lemma:

LEMMA 1

If $f(x_0) = g(x_0)$, then

 $1 \le x_0 \le K$ in the case $1 \le K$, and

 $K \le x_0 \le 1$ in the case $1 \ge K$.

That is, the first coordinate of the stationary points is between 1 and K.

Proof

Let us assume that $1 \le K$. If x < 1, then g(x) < 1 and f(x) > 1. If x > K, then g(x) > 1 and f(x) < 1. Thus, if $f(x_0) = g(x_0)$, then $1 \le x_0 \le K$. The proof for the case $K \le 1$ is similar.

COROLLARY

If K = 1, then there is exactly one stationary state and it is the point (1, 1).

Let us introduce the interval: $I = (K/3, +\infty)$.

LEMMA 2

If F(K/3) < 0, then the equation F(x) = 0 has 0, 1 or 2 solutions in the interval *I*. (The case where there is exactly one solution is not generic, because then $F(x_0) = F'(x_0) = 0$.)

If F(K/3) > 0, then the equation F(x) = 0 has exactly one solution in the interval *I*. Thus, we can tell the number of stationary points whose first coordinate is in the interval *I*.

Proof

Let $x \in I$. Then f''(x) < 0 and g''(x) > 0; therefore, F''(x) < 0. By Rolle's theorem, the function F has at most two roots in the interval I. In the case where F(K/3) < 0, the function F can have 0, 1 or 2 roots. In the case where F(K/3) > 0 at the first root in the interval I, the sign of the function F changes from positive to negative; hence, F' is negative. F' is a decreasing function, therefore the function F cannot have another root in the interval I because of the Rolle theorem. \Box

The following theorem is a simple corollary of the previous lemmas:

THEOREM 1

If $K/3 \le 1$, then there exists exactly one stationary state.

2.2. GLOBAL INVESTIGATION

2.2.1. The description of the nullclines

Let Q denote the nonnegative quadrant in \mathbb{R}^2 :

$$Q = \{ (x, y) \in \mathbb{R}^2 : x \ge 0, y \ge 0 \}.$$

Q is a positively invariant set, that is, the trajectories starting in Q do not leave Q. Since x and y are concentrations, they cannot be negative; therefore, we have to consider the system only in Q.

Let us introduce the following notations:

$$\begin{aligned} X_0 &= \{(x, y) \in Q \colon \dot{x} = 0\}, \\ Y_0 &= \{(x, y) \in Q \colon \dot{y} = 0\}. \end{aligned}$$

First, we deal with the sets X_0 and Y_0 (nullclines). Y_0 is the graph of the function g defined above. The points of X_0 are determined by the expression

$$K_1 x^2 + y^2 - L_1 x^3 - xy = 0. (4)$$

The set X_0 is a curve the equation of which can be expressed in a parametric form [10]. Substituting the expression y = xt in (4), we obtain the parametric form for X_0 with the parameter t:

$$x = \frac{K_1 + t^2 - t}{L_1}, \quad y = xt = \frac{K_1 + t^2 - t}{L_1} t$$

Let us introduce the curve $\gamma: [0, \infty) \to \mathbb{R}^2$ with the coordinate functions:

$$\gamma_1:[0,\infty) \to \mathbb{R}, \qquad \gamma_1(t) = \frac{K_1 + t^2 - t}{L_1},$$
$$\gamma_2:[0,\infty) \to \mathbb{R}, \qquad \gamma_2(t) = \gamma_1(t)t = \frac{K_1 + t^2 - t}{L_1}t.$$

After a short calculation, we obtain that in the case where $K_1 > 1/4$, the points of γ are in Q and in the case where $K_1 < 1/4$, the curve goes out of Q at the parameter t_1 and comes back at the parameter t_2 , where t_1 and t_2 are the roots of the equation $K_1 + t^2 - t = 0$ (see fig. 2).



Fig. 2.

Let us calculate the derivatives of the functions γ_1 and γ_2 :

$$\gamma_1'(t) = \frac{2t - 1}{L_1}, \qquad \gamma_2'(t) = \frac{3t^2 - 2t + K_1}{L_1} ;$$

$$\gamma_1''(t) = \frac{2}{L_1} , \qquad \gamma_2''(t) = \frac{6t - 2}{L_1} .$$

It is easy to see that $\gamma(t)$ is below the line x = y if t < 1, and it is above the line x = y if t > 1. Figure 2 shows the curve γ .

The intersection points of the curve γ and the graph of the function g are the stationary points. Multistationarity can occur: for example, at the parameter values

$$K_1 = \frac{7}{48} < \frac{1}{4}, \quad L_1 = \frac{1}{864}, \quad K_3 = \frac{275}{4},$$

there are three stationary points.

2.2.2. The behaviour of the trajectories

Let us introduce the notation:

$$X_{+} = \{(x, y) \in Q : \dot{x} > 0\},$$

$$X_{-} = \{(x, y) \in Q : \dot{x} < 0\},$$

$$Y_{+} = \{(x, y) \in Q : \dot{y} > 0\},$$

$$Y_{-} = \{(x, y) \in Q : \dot{y} < 0\},$$

The curve γ divides Q into two parts, X_+ and X_- . Similarly, the graph of g divides Q into two parts, Y_+ and Y_- . In other words, in the case where $K_1 > 1/4$:

$$X_{+} = \{(x, y) \in Q : x < \gamma_{1}(t), y = \gamma_{2}(t), t \ge 0\},\$$

$$X_{-} = \{(x, y) \in Q : x > \gamma_{1}(t), y = \gamma_{2}(t), t \ge 0\},\$$

$$Y_{+} = \{(x, y) \in Q : y < g(x)\},\$$

$$Y_{-} = \{(x, y) \in Q : y > g(x)\},\$$

If $K_1 < 1/4$, then $X_+ = X_{+1} \cup X_{+2}$, where

$$X_{+1} = \{(x, y) \in Q : 0 \le t \le t_1, x = \gamma_1(t), y < \gamma_2(t)\},\$$

$$X_{+2} = \{(x, y) \in Q : t \ge t_2, x < \gamma_1(t), y = \gamma_2(t)\}.$$

These regions can be seen in fig. 3.



THEOREM 2

Each solution of system (3) is bounded.

Proof

To prove this theorem, we construct a globally attracting rectangle: $[0, a] \times [0, b]$. Since $\lim \gamma_1 = +\infty$, there exists s > 1 for which $\gamma_1(s) > 1$. Let $a = \gamma_1(s)$, $b = \gamma_2(s)$. If t > 1, then $\gamma_2(t) > \gamma_1(t)$, and if x > 1, then g(x) < x. Therefore, $g(a) < a = \gamma_1(s) < \gamma_2(s) < b$ (see fig. 4).



Fig. 4.

Let

$$A = \{(a, y) \in Q : 0 \le y < b\},\$$
$$B = \{(x, b) \in Q : 0 \le x \le a\}.$$

We shall prove that $B \subset Y_{-}$ and $A \subset X_{-}$, which means that the trajectories move through A and B into the rectangle. If $(x, b) \in B$, then $g(x) \leq g(a) < b$, that is, $(x, b) \in Y_{-}$. Now, assume that $(a, y) \in A$. Let t denote the positive number for which $y = \gamma_2(t)$ (γ_2 is a strictly increasing function, hence t is unique and furthermore t < s). We consider two cases: $t \leq 1/2$ and t > 1/2. If $t \leq 1/2$, then $\gamma_1(t) \leq K < a$, that is, $(a, y) \in X_{-}$. If t > 1/2, then γ_1 is a strictly increasing function, therefore $\gamma_1(t) < \gamma_1(s) = a$, that is $(a, y) \in X_{-}$.

Thus the trajectories move through A and B into the rectangle and every trajectory must enter the rectangle. This completes the proof.

THEOREM 3

Let us assume that there exists a unique stationary state (x_0, y_0) , and let $x_0 = \gamma_1(t_0), y_0 = \gamma_2(t_0)$. If $t_0 > 1/2$, then this stationary state is globally asymptotically stable.

Proof

Let us introduce the regions

$$Q_{11} = X_+ \cap Y_+, \quad Q_{10} = X_+ \cap Y_-, \quad Q_{01} = X_- \cap Y_+, \quad Q_{00} = X_- \cap Y_-.$$
 (5)

We use C to denote the boundary of Q_{00} and Q_{10} and D the boundary of Q_{00} and Q_{01} . We shall prove that in the points of C and D, the trajectories move into Q_{00} , therefore Q_{00} is an attractor. Let us denote the functions on the r.h.s. of (3) by P and Q:

$$P(x, y) = K_2(K_1x^2 + y^2 - L_1x^3 - xy),$$

$$Q(x, y) = xy - y^2 + K_3 - k_3y.$$

Therefore, $X_0 = \{(x, y) \in Q : P(x, y) = 0\}$ and $Y_0 = \{(x, y) \in Q : Q(x, y) = 0\}$. At a point of X_0 , the trajectory moves from X_- into X_+ or in the opposite direction according to the angle of the vector grad P and the tangent vector of the trajectory [11]. If this angle is an acute angle, then the trajectory goes from X_- into X_+ , and if this angle is an obtuse angle, then it moves in the opposite direction. We can similarly determine the direction of the motion of the trajectories at the points of Y_0 .

Since $C = X_0 \cap Y_-$, therefore at a point of C the vector (0; -1) is a tangent vector of the trajectory. The scalar product of this vector with grad P at the point (x, y) is x - 2y (see fig. 5).

Because of the conditions of the theorem, we have $C \subset \{\gamma(t): t > 1/2\}$. Therefore, if $(x, y) \in C$, then $x - 2y = \gamma_1(t) - 2\gamma_2(t) = \gamma_1(t)(1 - 2t) < 0$. Consequently, at a point of C the scalar product is negative; therefore, the trajectories move from Q_{10} to Q_{00} . One can similarly calculate that at the points of D the trajectories move from Q_{01} into Q_{00} , thus Q_{00} is an attractor.

Since Q_{00} is an attractor, then periodic orbits cannot exist because they ought to pass through Q_{00} . By theorem 2, the trajectories enter a rectangle in which there is a unique stationary state (no periodic orbit); thus this stationary state is globally asymptotically stable.

COROLLARY

If K < 1, then there exists a unique globally asymptotically stable stationary state.



Fig. 5.

Proof

We have already seen that if K < 1, then there exists a unique stationary point for which $x_0 > K$. Hence, $t_0 > 1 > 1/2$, and consequently this stationary point is globally asymptotically stable.

3. Only one reversible reaction

In this section, we shall investigate model (1) when only the first reaction is reversible:

 $A + 2X \rightleftharpoons 3X,$ $X + Y \rightarrow 2Y,$ $Y \rightarrow B,$

This mechanism with mass-action kinetics yields the kinetic equations

$$\dot{X} = k_1 A X^2 - l_1 X^3 - k_2 X Y,$$

$$\dot{Y} = k_2 X Y - k_3 Y,$$

where k_i (i = 1, 2, 3) are the rate constants in (1) and l_1 is the rate constant of the reverse reaction. We can simplify this system with the transformation

$$x = X \frac{l_1}{k_1 A}, \quad y = \frac{l_1 k_2}{k_1^2 A^2} Y, \quad \tau = \frac{k_1^2 A^2}{l_1} T.$$

$$\dot{x} = x(x - x^2 - y),$$

$$\dot{y} = Ky(x - L),$$
(6)

where

$$K = \frac{k_2}{k_1 A}, \quad L = \frac{k_3 l_1}{k_2 k_1 A}.$$

3.1. LOCAL INVESTIGATION

The system has three stationary points in the positive quadrant $Q:(0, 0), (1, 0), (L, L - L^2)$, the last one is in Q only in the case $L \le 1$.

In the point (0, 0), the eigenvalues are: $\lambda_1 = 0$, $\lambda_2 = -KL$; therefore, we cannot decide the stability of the stationary point. If L < 1, then the point (1, 0) is a saddle (the eigenvalues are: $\lambda_1 = -1$, $\lambda_2 = K(1 - L)$), and if L > 1, then it is a stable node. In the point $(L, L - L^2)$, the eigenvalues are

$$\lambda_{1,2}=\frac{L(1-2L)\pm\sqrt{D}}{2},$$

where $D = L^2((1 - 2L)^2 - 4K(1 - L))$. We investigate the behaviour of this stationary state in the (L, K) parameter plane. If D < 0, then it is a focus, and if D > 0, then we have a node. If 1 - 2L < 0, then the stationary state is stable, and if 1 - 2L > 0, then it is unstable. In fig. 6, we can see the bifurcation diagram of the stationary state.



Fig. 6.

3.2. GLOBAL INVESTIGATION (LIAPUNOV FUNCTIONS)

THEOREM 4

If $L \ge 1$, then the stationary point (1, 0) is globally asymptotically stable in the region $(0, \infty) \times [0, \infty)$.

Proof

Let us consider the Liapunov function:

 $V(x, y) = Kx + y - K \ln x.$

The curves V(x, y) = k are determined by the equation $y = K(\ln x - x) + k$ (fig. 7).



The derivative of the function is negative in Q (except in the stationary points):

$$\dot{V} = K \left(1 - \frac{1}{x} \right) \dot{x} + \dot{y} = K \left(1 - \frac{1}{x} \right) x (x - x^2 - y) + Ky(x - L) = -Kx(x - 1)^2 + Ky(1 - L) < 0.$$

Thus, the stationary point (1, 0) is globally asymptotically stable in the region $(0, \infty) \times [0, \infty)$.

PROPOSITION 1

The trajectories starting in the open positive quadrant (the interior of the region Q) cannot enter the stationary point (0, 0).

Proof

We shall prove that the trajectory starting in a point $(x_0, y_0) \in Q$, where $x_0 < L$ cannot tend to the origin. Consider the Liapunov function:

 $V(x, y) = Kx + y - K \ln x.$

The derivative of the function:

 $\dot{V} = K(x - L)(1 - x)$

is negative if x < L; therefore, the trajectory starting in (x_0, y_0) remains in the domain $\{(x, y) \in Q: V(x, y) < V(x_0, y_0)\}$. The origin is not contained in the closure of this domain, because the closure is $\{(x, y) \in Q: y \le V(x_0, y_0) + K(L \ln x - x)\}$. Hence, the trajectory cannot tend to the origin.

PROPOSITION 2

The trajectories cannot go to infinity in Q_{01} .

Proof

Use the Liapunov function

$$V(x, y) = 2Kx + y - 2KL \ln x.$$

The "interior" of the level curves V(x, y) = k (i.e. the domain $\{(x, y) \in Q : V(x, y) < k\}$ are bounded domains. The derivative of the Liapunov function is

$$\dot{V} = K(x-L)(2x-2x^2-y)$$

We shall give an indirect proof. Let us assume that a trajectory (x(t), y(t)) in Q_{01} goes to infinity. Then x(t) > L and y(t) would tend monotonically to infinity. This would involve the existence of a positive number t_0 for which $\dot{V} = K(x(t) - L)(2x(t) - 2x^2(t) - y(t)) < 0$ if $t \ge t_0$. Let $k = V(x(t_0), y(t_0))$. Hence, $(x(t), y(t)) \in \{(x, y) \in Q : V(x, y) < k\}$ if $t > t_0$. This is a contradiction because an unbounded trajectory would stay in a bounded domain.

Finally, we deal with the stationary point $(L, L - L^2)$ in the case L < 1. Consider the function

$$V(x, y) = Kx + y - KL \ln x - L(1 - L) \ln y.$$

The level curves of this function are closed curves around the stationary point (see fig. 8). The derivative of the function:

$$\dot{V} = \left(K - \frac{KL}{x}\right)\dot{x} + \left(1 - \frac{L(1-L)}{y}\right)\dot{y} = K(x-L)^2(1-L-x).$$



Fig. 8.

Thus, if x < 1 - L, then $\dot{V} \ge 0$, and if x > 1 - L, then $\dot{V} \le 0$. Let k denote the value of the function V on the level curve whose tangent line is x = 1 - L. If L > 1/2, then the stationary state is stable and its attracting domain contains the set $\{(x, y) \in Q : V(x, y) \le k\}$. If there exists a periodic orbit, then it intersects the line x = 1 - L.

We can use the Hopf theorem [12] to prove that Hopf bifurcation occurs at the parameter value L = 1/2. Let us introduce the transformation $\xi = x - L$, $\eta = y - (L - L^2)$ to system (6). We obtain the following equations:

$$\dot{\xi} = \xi(L - 2L^2) - \eta L - \xi \eta + \xi^2 (1 - 3L) - \xi^3,$$

$$\dot{\eta} = K\xi(\eta + L - L^2).$$

Let $\mu = 1/2 - L$. The eigenvalues of the Jacobi matrix in (0, 0) are:

$$\lambda_{1,2}(\mu) = \frac{1-2\mu}{2} \left(\mu \pm \sqrt{\mu^2 - \frac{K}{2}(1+2\mu)} \right).$$

In a suitable neighbourhood of $\mu = 0$, the discriminant is negative; therefore,

$$\operatorname{Re} \lambda(\mu) = \frac{(1-2\mu)\mu}{2}$$

Let $\lambda(\mu) = \alpha(\mu) \pm i \omega(\mu)$, $\alpha(0) = 0$, $\alpha'(0) = 1/2$ and $\omega(0) = \sqrt{K/\sqrt{8}}$. Thus, at the parameter value $\mu = 0$ the system has two purely imaginary eigenvalues and $\alpha'(0) \neq 0$. That is, the conditions of the Hopf theorem are fulfilled. According to the theorem, a periodic orbit occurs. We shall find out that this periodic orbit is a stable limit cycle. At $\mu = 0$, the eigenvalues of the Jacobi matrix are: $\pm i\sqrt{K/8}$ and an eigenvector is:

$$\begin{pmatrix} 1 \\ -i\frac{\sqrt{K}}{\sqrt{2}} \end{pmatrix} = \begin{pmatrix} 1 \\ 0 \end{pmatrix} + i \begin{pmatrix} 0 \\ -\frac{\sqrt{K}}{\sqrt{2}} \end{pmatrix}.$$

Using this eigenvector, we introduce the following transformation:

$$\begin{pmatrix} \xi \\ \eta \end{pmatrix} = \begin{pmatrix} 1 & 0 \\ 0 & -\frac{\sqrt{K}}{\sqrt{2}} \end{pmatrix} \begin{pmatrix} u \\ v \end{pmatrix}.$$

This transformation yields the system:

$$\dot{u} = \frac{\sqrt{K}}{\sqrt{8}} \upsilon + \frac{\sqrt{K}}{\sqrt{2}} u\upsilon - \frac{u^2}{2} - u^3,$$
$$\dot{\upsilon} = -\frac{\sqrt{K}}{\sqrt{8}} u + Ku\upsilon.$$

From this form, we can determine the stability of the limit cycle. Using the expression (3.4.11) in [12], we obtain a = -1/4 < 0. Thus, the bifuraction is supercritical, that is, the limit cycle is stable.

Summarizing, we can establish that in the case $L \ge 1$ system (6) is not explosive, but it is still an open question whether this statement is also valid for L < 1.

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