III.3 The model of Gause

$$
(1) \quad \begin{cases} \dfrac{dR}{dt} = f(R) - g(R)X & \text{(resource)} \\[2ex] \dfrac{dX}{dt} = \gamma g(R)X - \delta X & \text{(consumer)} \end{cases}
$$

Assumptions

- f, g continuously differentiable
- $f(0) = 0$, and $\exists K > 0 : f(R) > 0$ for $0 < R < K$ and $f(R) < 0$ for $R > K$.
- $g(0) = 0$, and $g(R), g'(R) > 0$ for $R > 0$.
- $\exists R_0 > 0 : \gamma g(R_0) = \delta$. (since $g' > 0$, R_0 is also unique if it exists.)

Remarks

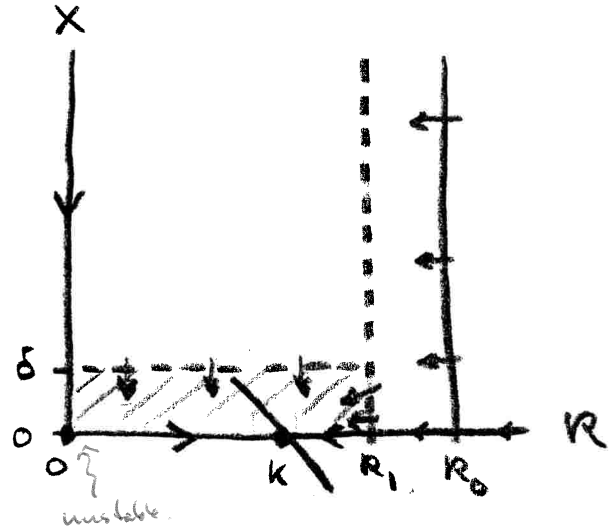
- Resource dynamics without consumer has a globally attracting equil. $R = K$.
- By monotony of g, there exists only one $R_0 > 0$ such that $\gamma g(R_0) = \delta$.
- If there were no such $R_0 > 0$, then $\gamma g(R) < \delta \ \forall R \geq 0$ (since $g(0) = 0$), so that $X \to 0$ as $t \to \infty$, and hence also $R \to K$ as $t \to \infty$.
- $g(R)$ is called the <u>functional response</u> of the consumer.

Phase plane analysis

$$\frac{dR}{dt}=0 \iff R=0 \text{ or } X=\frac{f(R)}{g(R)}$$

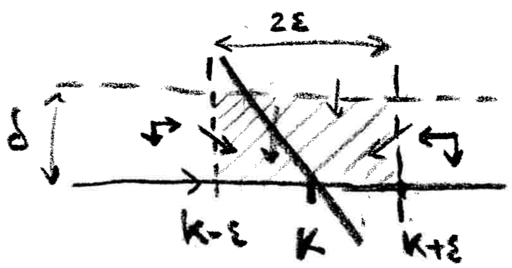
$$\frac{dX}{dt}=0 \iff X=0 \text{ or } R=R_0$$

Case $R_0 \geq K$



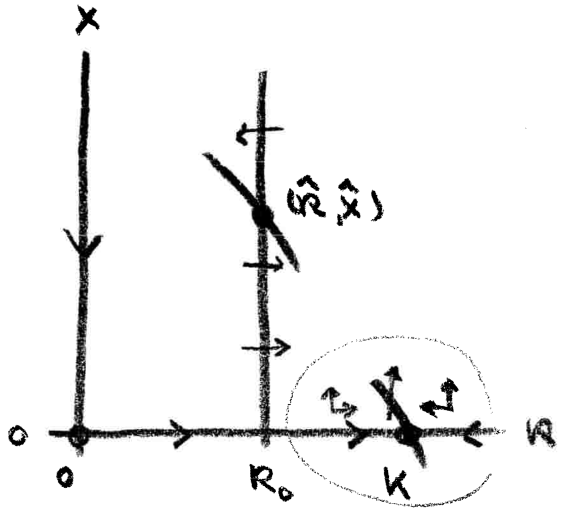
- Since $\frac{f(R)}{g(R)}<0$ for $R=R_0$, there exists no positive equilibrium.
- The point $(K,0)$ is globally stable.

To see this, first notice that $R(t)$ is monotonically decreasing on the right side of the line $R=R_1$, while on the left side $X(t)$ is monotonically decreasing. Thus, every orbit with a positive starting point eventually enters the set $D_\delta := (0,R_1)\times(0,\delta)$, where $\delta>0$ can be taken arbitrarily small.



Inside D_δ, orbits eventually enter $(K-\varepsilon, K+\varepsilon)\times(0,\delta)$.
We can choose $\varepsilon>0$ arbitrarily small provided we adjust $\delta>0$ accordingly.

$\boxed{\text{Case } 0 < R_0 < K}$



- There exists a unique positive equilibrium $(\hat{R},\hat{x})$ with $\hat{R} = R_0$ and $\hat{x} = \dfrac{f(R_0)}{g(R_0)}$.

- The boundary equilibria $(0,0)$ and $(K,0)$ are obviously unstable.

Local stability of $(\hat{R},\hat{x})$:

Jacobi-matrix of ① (p.71) evaluated at $(\hat{R},\hat{x})$:

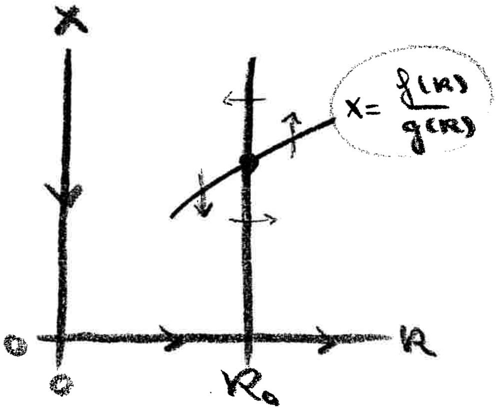
$$J = \begin{pmatrix} f'(\hat{R}) - \hat{x}g'(\hat{R}) & -g(\hat{R}) \\ \gamma \hat{x} g'(\hat{R}) & \gamma g(\hat{R}) - \delta \end{pmatrix} =$$

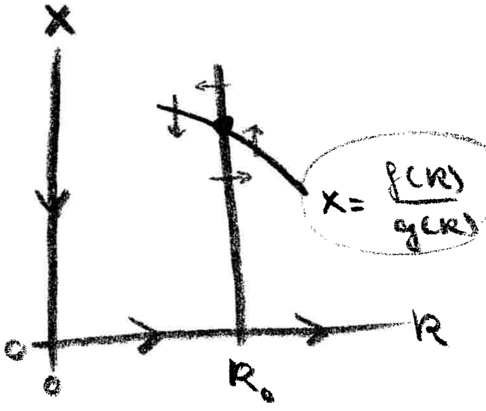
$$= \begin{pmatrix} g(\hat{R}) \cdot \left[\dfrac{f(\hat{R})}{g(\hat{R})} \right]' & -g(\hat{R}) \\ \gamma \hat{X} g'(\hat{R}) & 0 \end{pmatrix}$$

$$\Rightarrow \begin{cases} \det J = \gamma \hat{x} g'(\hat{R}) g(\hat{R}) > 0 \\ \operatorname{trace} J = \underbrace{g(\hat{R})}_{>0} \left[\dfrac{f(\hat{R})}{g(\hat{R})} \right]' \end{cases}$$

slope of the zero-cline of R at $(\hat{R},\hat{x})$

Conclusion (see Appendix A, p. A10)





$$\left[\frac{f(\hat{R})}{g(\hat{R})}\right]' > 0 \qquad\qquad \left[\frac{f(\hat{R})}{g(\hat{R})}\right]' < 0$$

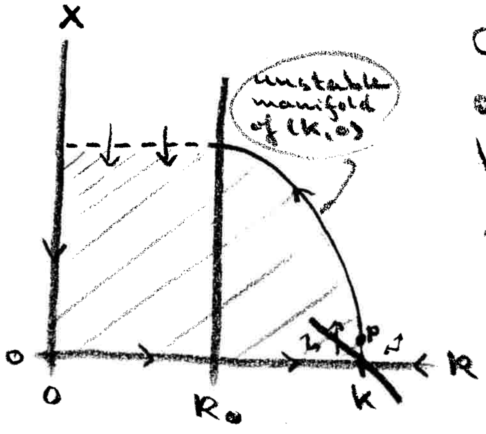
Unstable node or focus

Locally stable node or focus

NOT SADDLE since det J > 0

Appendix B

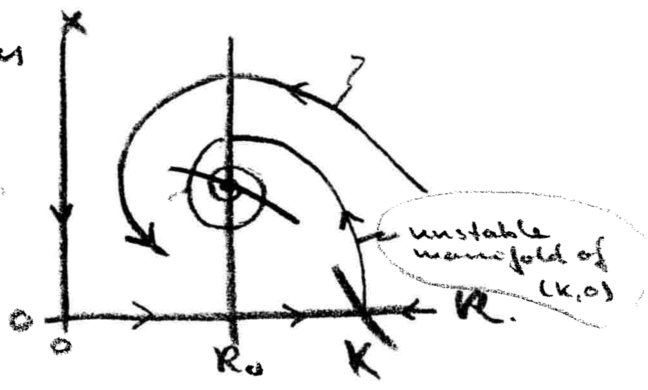
The equilibrium $(K,0)$ is a saddle. Let p be a point in $\mathbb{R}^2_+$ on the unstable manifold of the saddle.



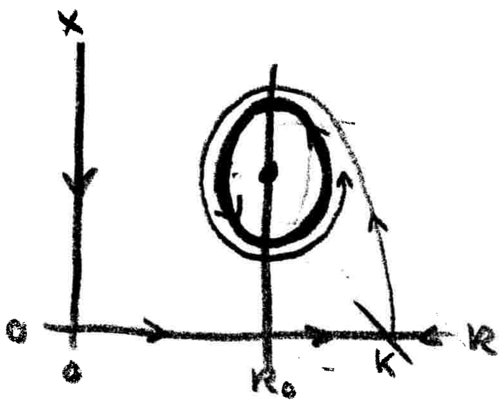
Obviously, the forward orbit through p is bounded.

By the Poincaré-Bendixon theorem (see Appendix B) there are two alternatives

ⓐ The ω-limit contains the point $(\hat{R},\hat{X})$, (which then must be globally stable)

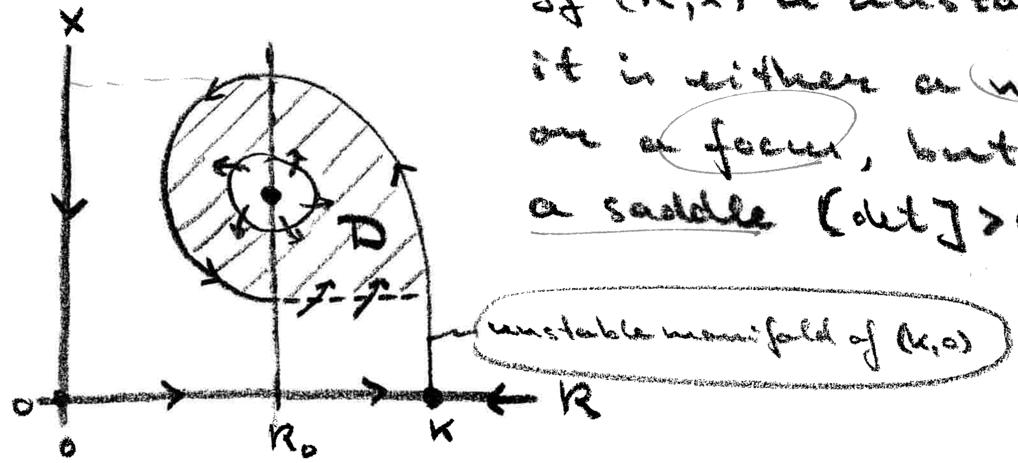


(b) The ω-limit is a closed orbit (limit-cycle)
(which must circle the equil.)



Obviously, in case (a) we must have that $(\hat{K},\hat{x})$ is stable.

From Poincaré-Bendixon it also follows that if $(\hat{R},\hat{x})$ is unstable, then there must exist a limit cycle.



If $(\hat{R},\hat{x})$ is unstable, it is either a node or a focus, but not a saddle ($\det J > 0$, p. 73)

Then we can construct an annular forward invariant region D that contains no equilibria.

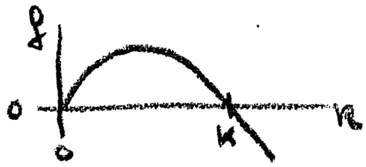
It follows that D contains a limit cycle ($\rightarrow$ appendix B, p. B2)

Example

$$(*)\quad \begin{cases} \dfrac{dR}{dt} = rR\left(1-\dfrac{R}{K}\right) - \dfrac{\beta R}{1+\beta T R}\cdot X \\[2ex] \dfrac{dX}{dt} = \gamma\cdot\dfrac{\beta R}{1+\beta T R}\, X - \delta X \end{cases}$$

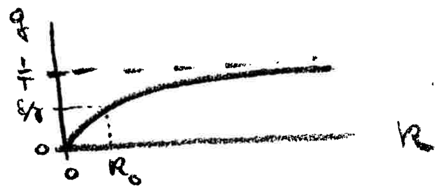
Suppose $\frac{\delta}{\gamma} < \frac{1}{T}$. Then $(*)$ is a special case of the Gause model with

$$\boxed{f(R) = rR\left(1-\frac{R}{K}\right)}$$

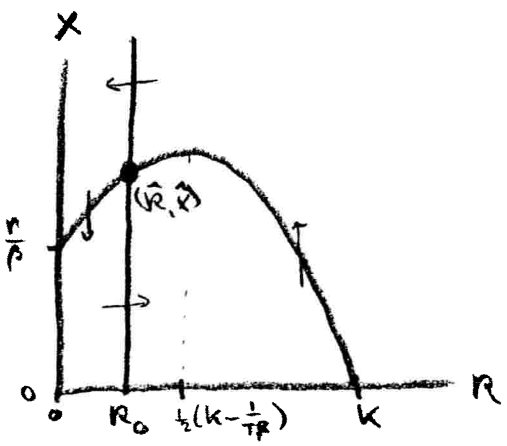


and

$$\boxed{g(R) = \frac{\beta R}{1+\beta T R}}$$

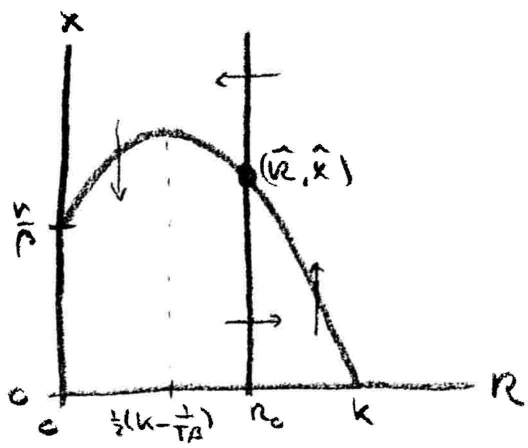


$$\boxed{0 < R_0 < \tfrac{1}{2}\left(K - \tfrac{1}{T\beta}\right)}$$



$\left[\frac{f}{g}\right]' > 0$ at $(\hat R,\hat X)$ $\Rightarrow$
$(\hat R,\hat X)$ is unstable and there exists a limit cycle

$$\boxed{0 < \tfrac{1}{2}\left(K - \tfrac{1}{T\beta}\right) < R_0 < K}$$



$\left[\frac{f}{g}\right]' < 0$ at $(\hat R,\hat X)$ $\Rightarrow$
$(\hat R,\hat X)$ is locally stable

Proposition.

Let $\frac{\delta}{\gamma} < \frac{1}{T}$ and $\alpha\,\frac{1}{2}\left(K - \frac{1}{T\beta}\right) \leq R_0 < K$.

Then $(\hat{R}, \hat{X})$ is globally stable

Proof.

By Poincaré-Bendixson theorem it is sufficient to show that there cannot exist limit cycles.

For this we use the criterion of Dulac (see Appendix B, p B5.)

Consider the Dulac function

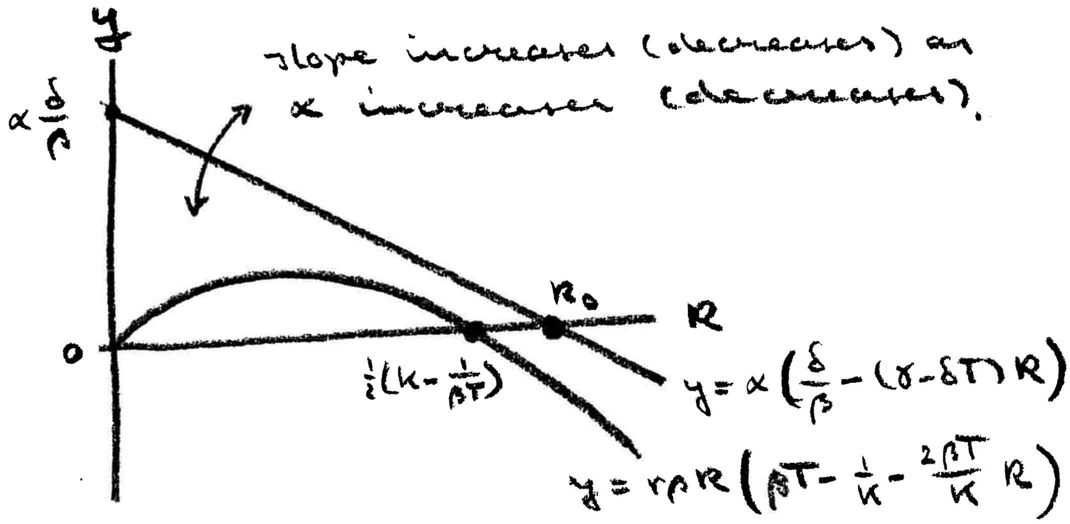
$$\boxed{u(R,X) = \frac{X^{\alpha-1}}{g(R)}}$$

where $\alpha > 0$ will be chosen later.

$$\operatorname{div}\begin{pmatrix} u\,\frac{dR}{dt} \\ u\,\frac{dX}{dt} \end{pmatrix} =$$

$$= X^{\alpha-1}\left(\left[\frac{f(R)}{g(R)}\right]' + \alpha\left(\gamma - \frac{\delta}{g(R)}\right)\right)$$

$$= R^{-1} \cdot X^{\alpha-1}\left(\underbrace{r\beta R\left(\beta T - \frac{1}{K} - \frac{2\beta T}{K}R\right)}_{\text{valley parabola}} - \alpha\underbrace{\left(\frac{\delta}{\beta} - \overbrace{(\gamma-\delta T)R}^{(>0)\ \text{by assumption}}\right)}_{= R\left(\gamma - \frac{\delta}{g(R)}\right)}\right)$$

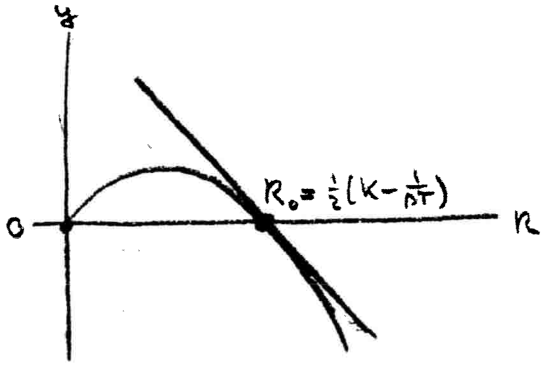


Obviously, $\alpha>0$ can be chosen such that the straight line always lies above the parabola.

(E.g. we can choose α such that the slope of the line is equal to the slope of the parabola at $R=\frac{1}{2}(K-\frac{1}{\beta T})$)

Then $\operatorname{div}\begin{pmatrix} u\frac{dR}{dt} \\ u\frac{dX}{dt}\end{pmatrix} \leq 0$ for all (R,X)

(with equality to zero only if $R=R_0$ and $R_0=\frac{1}{2}(K-\frac{1}{\beta T})$; see figure below.)



Hence, there exist no limit cycles