

Full Length Research Paper

Qualitative analysis of livestock-forage system in the stall-feeding smallholder dairy cattle system

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Dynamical systems of forage biomass accumulation under continuous harvesting with and without nutrient cycling are formulated and studied. For one dimensional dynamical system with β being a measure of forage intake relative to forage growth, there is bifurcation at $\beta = 0.70$ whereas at $0.70 < \beta < 0.72$ the system exhibits discontinuous stability, and at $\beta > 0.72$ the system collapses. For a two dimensional dynamical system, there is bifurcation at $\beta = 0.26$, stable equilibrium at $0.26 < \beta < 0.37$ and unstable equilibrium at $\beta > 0.37$. For the three dimensional dynamical system where α is a measure of soil nutrient replenishment, at $1.38 < \alpha < 1.43$ the system exhibits two different stable states (a fixed point and a limit cycle) and one unstable state (limit cycle), and at $\alpha > 1.43$ there is only one stable state (limit cycle), and there is hysteresis. For $y=1$ and $1.38 < \alpha < 1.43$, there is local stability but no global stability. It is shown that the long-term stability of the livestock-forage system primarily depends on the stocking levels and initial forage biomass. Through bifurcation analysis, this study has identified critical points of the system for timely intervention by the farmer. Finally, by using dimensional analysis, it is possible to more readily compare relative effects of biological processes.

Key words: Livestock, forage growth, nutrient, dynamical system, sustainability.

INTRODUCTION

In work done by Tibayungwa et al. (2009) on livestock-forage system the focus was on quantitative analysis. But to answer the question of what type of long-term system dynamics, stability of the system under perturbation, and how the system changes as parameters are varied, the focus should be on bifurcation and stability analysis of the system equilibria (Woodward, 1998). This study focuses on modelling livestock-forage systems for cases where forage biomass is almost always limiting, and therefore necessary to qualitatively analyse the system for dynamical stability over time. Understanding the

dynamical behaviour of the the system over time can be crucial to proper planning for the livestock-forage production system.

METHODS

The models describe forage accumulation under constant harvesting, and livestock-forage interaction with nutrient cycling. The dynamical systems equations were nondimensionalised, using the procedures outlined in Segel (1972), to reduce the number of parameters to dimensionless groupings that determine the dynamics of the system (Murray, 2002), as this reduction always simplifies the analysis Strogatz1994. Moreover, an additional advantage to nondimensionalising the model is increased efficiency over conventional means of sensitivity analysis (Louie et al., 1998). Stability analysis of steady states was done according to Jordan and Smith (2007). All simulations and bifurcation diagrams were

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Table 1. Variables and parameters introduced in the one dimensional model, their description, units and dimension.

Parameter	Description	Units	Dimension
Y	Forage yield	kg/ha	ML^{-2}
r	Dry matter intake per animal	kgDM/(animal.day)	MT^{-1}
n	Stocking density	animals/ha	L^{-2}
K	Maximum forage yield	kg/ha	ML^{-2}
a	Relative forage growth	kg/(kg.day)	T^{-1}
c	Yield at which intake is half-maximum	kg/ha	ML^{-2}

Table 2. Variables and parameters introduced in the liveweight-forage model, their description, units and dimension.

Parameter	Description	Units	Dimension
Y	Forage yield	kg/ha	ML^{-2}
L	Animal biomass (liveweight) per hectare	kg/ha	ML^{-2}
K	Maximum forage yield	kg/ha	ML^{-2}
a	Relative forage growth	kg/(kg.day)	T^{-1}
f	Potential intake per kilogram liveweight	kg/(kg.day)	T^{-1}
c	Yield at which intake is half-maximum	kg/ha	ML^{-2}
v	Feed conversion efficiency	kg/kg	—
m	Feed maintenance requirement	kg/(kg.day)	T^{-1}

done using XPPAUT (Ermentrout, 2002).

Forage growth, intake and stocking density

Forage biomass as a logistic function, with a fixed carrying capacity is given by:

$$\frac{dY}{dt} = aY \left(1 - \frac{Y}{K}\right) \quad (1)$$

Where Y (kg ha⁻¹) is the forage biomass at any point in time, a is the relative forage growth rate, K is the ceiling yield.

Incorporating a Michaelis-Menten saturation function representing the consumption of the animal gives the following equation:

$$\frac{dY}{dt} = aY \left(1 - \frac{Y}{K}\right) - n \frac{rY}{c+Y} \quad (2)$$

Where parameters are defined in Table 1.

By introducing the following dimensionless variables,

$$\tau = at, \quad y = \frac{Y}{K} \quad (3)$$

substituting and computing the dimensional equation in terms of

rescaled time, $\tau = at$, using the chain rule gives:

$$\frac{dY}{dt} = \frac{d}{dt}(yK) = \frac{d}{d\tau}(yK) \frac{d\tau}{dt} = \frac{d}{d\tau}(yK)a = aK \frac{dy}{d\tau} \quad (4)$$

By substituting these expressions into the dimensional equation, and introducing dimensionless parameters $\delta = c/K$ and $\beta = rn/aK$ we get the following nondimensional equation:

$$\frac{dy}{d\tau} = y(1-y) - \frac{\beta y}{\delta + y} \quad (5)$$

The number of parameters has reduced from five to two, β and δ .

Forage growth, intake and liveweight gain

In Equation 2 intake is in kg of DM d⁻¹, but can also be expressed as kg of DM per liveweight of the animal:

$$I = L \frac{fY}{c+Y} \quad (6)$$

Where I is feed intake and $fY/(c+Y)$ is a Michaelis-Menten response curve to forage availability; other parameters are in Table 2.

Table 3. Parameters and parameter combinations used to produce dimensionless variables in the liveweight-forage model.

Variable	Dimension	Parameters used to non-dimensionalise	Dimension	Dimensionless variable
Y	ML^{-2}	K	ML^{-2}	$y = Y / K$
L	ML^{-2}	K / v	ML^{-2}	$l = Lv / K$
t	T	a	T^{-1}	$\tau = at$

Table 4. Nondimensional parameters and values of the parameters used in the simulations of the liveweight-forage system.

Parameter	Dimension parameters	Parameter values used in the simulations
α	m / av	0.2
β	f / av	0–2
δ	c / K	0–2

Substituting the right hand side of Equation 6 into the intake term of Equation 2 yields:

$$\frac{dY}{dt} = aY\left(1 - \frac{Y}{K}\right) - L \frac{fY}{c+Y} \quad (7)$$

For a growing animal, the forage consumed is used for maintenance and growth and is modelled as:

$$I = v \frac{dL}{dt} + mL \quad (8)$$

Re-arranging and substituting I from equation 6, gives:

$$\frac{dL}{dt} = \frac{1}{v} L \frac{fY}{c+Y} - \frac{m}{v} L \quad (9)$$

Equations 7 and 9 represent a coupled two-dimensional dynamical system for the rates of change of forage yield, Y , and animal liveweight, L . Model parameters are described in Table 2:

$$\frac{dY}{dt} = aY\left(1 - \frac{Y}{K}\right) - L \frac{fY}{c+Y} \quad (10a)$$

$$\frac{dL}{dt} = \frac{1}{v} L \frac{fY}{c+Y} - \frac{m}{v} L \quad (10b)$$

A similar system of equations was proposed by Woodward (1998). However, to ease the difficulty in parameter estimation and analysis, we nondimensionalise the system to reduce the number of parameters and to determine the parameter combinations that control the behaviour of the system (Louie et al., 1998).

From Table 3 we see the following dimensionless variables

$$\tau = at, \quad y = Y / K, \quad l = Lv / K \quad (11)$$

We now solve $y = Y / K$ and $l = Lv / K$ for Y and L to give $Y = yK$ and $L = lK / v$ that we now substitute into the right-hand of the dimensional equations.

Next, we compute the dimensional equations in terms of rescaled time, $\tau = at$, using the chain rule:

$$\frac{dY}{dt} = \frac{d}{dt}(yK) = \frac{d}{d\tau}(yK) \frac{d\tau}{dt} = \frac{d}{d\tau}(yK)a = aK \frac{dy}{d\tau} \quad (12)$$

$$\frac{dL}{dt} = \frac{d}{dt}\left(\frac{lK}{v}\right) = \frac{d}{d\tau}\left(\frac{lK}{v}\right) \frac{d\tau}{dt} = \frac{d}{d\tau}\left(\frac{lK}{v}\right)a = \left(\frac{aK}{v}\right) \frac{dl}{d\tau} \quad (13)$$

By substituting these expressions, and the following dimensionless groups into dimensional equations:

$$\delta = \frac{c}{K}, \quad \beta = \frac{f}{av}, \quad \alpha = \frac{m}{av} \quad (14)$$

We arrive at the following nondimensionalised equations:

$$\frac{dy}{d\tau} = y(1-y) - \frac{\beta ly}{\delta + y} \quad (15a)$$

$$\frac{dl}{d\tau} = \frac{\beta ly}{\delta + y} - l\alpha \quad (15b)$$

By nondimensionalising the system, the number of parameters has reduced from six (a, K, f, c, m, v) to three (α, β, δ). The three nondimensional parameters in terms of the original parameters are listed in Table 4.

Table 5. Variables and parameters used in the livestock-forage-nutrient system.

Variable/ Parameter	Description	Units	Dimension
S	Amount of nutrient available in soil for forage uptake	kg/ha	ML^{-2}
V	Total forage biomass	kg/ha	ML^{-2}
N	Animal biomass	kg/ha	ML^{-2}
t	Time	days	T
g	Relative rate of nutrient uptake per unit biomass of forage	kg/(kg.day)	T^{-1}
F	Supply rate of nutrient input to the system	kg/(ha.day)	$ML^{-2}T^{-1}$
a	Rate of loss of nutrient from soil nutrient pool	kg/(kg.day)	T^{-1}
c	Rate of loss of forage biomass due to senescence	kg/(kg.day)	T^{-1}
k	Fraction of forage biomass that returns to the nutrient pool due to decomposition ($0 < k < 1$)	No Units	—
b	Rate of loss of animal biomass due to excretion	kg/(kg.day)	T^{-1}
f	Relative intake per unit biomass of herbivore	kg/(kg.day)	T^{-1}
K_1	Forage biomass at which animal intake is half -maximum	kg/ha	ML^{-2}
q	Fraction of animal biomass that returns to the nutrient pool due to manure excretion ($0 < q < 1$)	No Units	—
K_s	Soil nutrient level at which half-maximum intake by forage occurs	kg/ha	ML^{-2}

Table 6. Parameters and parameter combinations used to produce dimensionless variables in the livestock-forage-nutrient system.

Variable	Dimension	Parameters used to non-dimensionalise	Dimension	Dimensionless variable
S	ML^{-2}	K_1	ML^{-2}	$x = S / K_1$
V	ML^{-2}	K_1	ML^{-2}	$y = V / K_1$
N	ML^{-2}	K_1	ML^{-2}	$z = N / K_1$
t	T	a	T^{-1}	$\tau = at$

Forage-animal-nutrient system

The model by Ghosh and Sarkar (1998) on interacting species with nutrient cycling is modified by adding a Michaelis-Menten function that is more appropriate for describing forage yield-soil fertility relationships (Wickham et al., 1997).

$$\frac{dS}{dt} = F - aS - \frac{gSV}{K_s + S} + kcV \quad (16a)$$

$$\frac{dV}{dt} = \frac{gSV}{K_s + S} - cV - \frac{fNV}{K_1 + V} \quad (16b)$$

$$\frac{dN}{dt} = \frac{fNV}{K_1 + V} - bN \quad (16c)$$

Where variables and parameters are defined in Table 5.

Introducing dimensionless variables (Table 6) and dimensionless parameters (Table 7) gives the following nondimensional system

$$\frac{dx}{d\tau} = \alpha - x - \frac{xy\beta}{x + \rho} + ky\gamma + qz\eta \quad (17a)$$

$$\frac{dy}{d\tau} = \frac{xy\beta}{x + \rho} - y\gamma - \frac{yz\delta}{1 + y} \quad (17b)$$

$$\frac{dz}{d\tau} = \frac{yz\delta}{1 + y} - z\eta \quad (17c)$$

Table 7. Nondimensional parameters and values of the parameters used in the simulations for the livestock-forage-nutrient system.

Parameter	Dimension parameters	Parameter values used in the simulations
α	F/aK_1	0–2
β	g/a	1.9
δ	f/a	0.2
γ	c/a	0.1
η	b/a	0.1
ρ	K_s/K_1	0.5
q	–	0–1
k	–	0.5

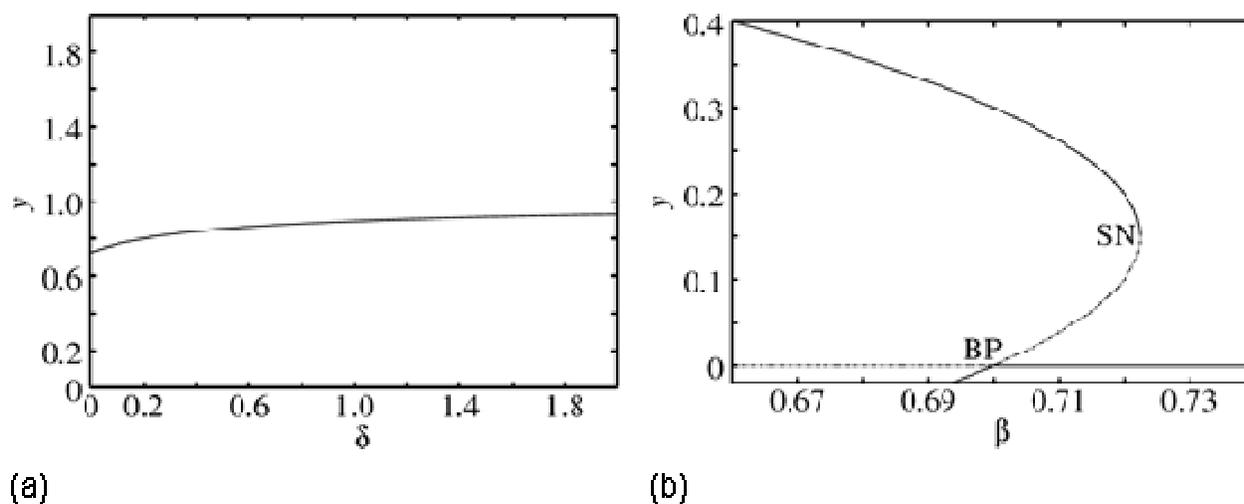


Figure 1. Bifurcation diagrams for Equation 5. a: Bifurcation with δ as the control parameter, $\beta = 0.2$. Notice lack of sensitivity to δ ; b: Stable and nonstable states with $\delta = 0.7$. Solid lines show stable steady states, dashed lines show unstable steady states. SN is the saddle node, BP is the bifurcation point (see text for explanation).

RESULTS AND DISCUSSION

Forage growth, intake and stocking density

Figure 1b shows the bifurcation diagram of system 5 for parameter β (there was lack of sensitivity to parameter δ). A bifurcation diagram is a graph from a series of points generated by a control parameter that is set at a given value and allowing the system to evolve to an equilibrium state, then recording the equilibrium values for the variables; by repeating this process at successive parameter levels, and finally plotting the recorded values the bifurcation diagram is generated. For low values of β , with initial value of $y > 0$ and up to about 0.7, the system moves towards the high steady state. This is the

bifurcation point (BP), where the sudden change in behaviour occurs as a parameter passes through a critical value (Jordan and Smith, 2007, beyond which the system exhibits discontinuous stability up to about 0.72. Beyond this limit point, known as saddle node (SN), the system moves towards zero-forage biomass steady state. Farmers practicing zero-grazing tend to maximally utilize their forages, which happens to be the region between BP and SN. The danger of operating in this critical zone (discontinuous stability) is that a small perturbation to the system, for example drought or increased stocking density, can lead to collapse of the system. In addition, if the forage estimates are made without putting into consideration the need to match forage with the growth of the animals, this too leads to collapse of the system unless alternative sources of feed are sought or the

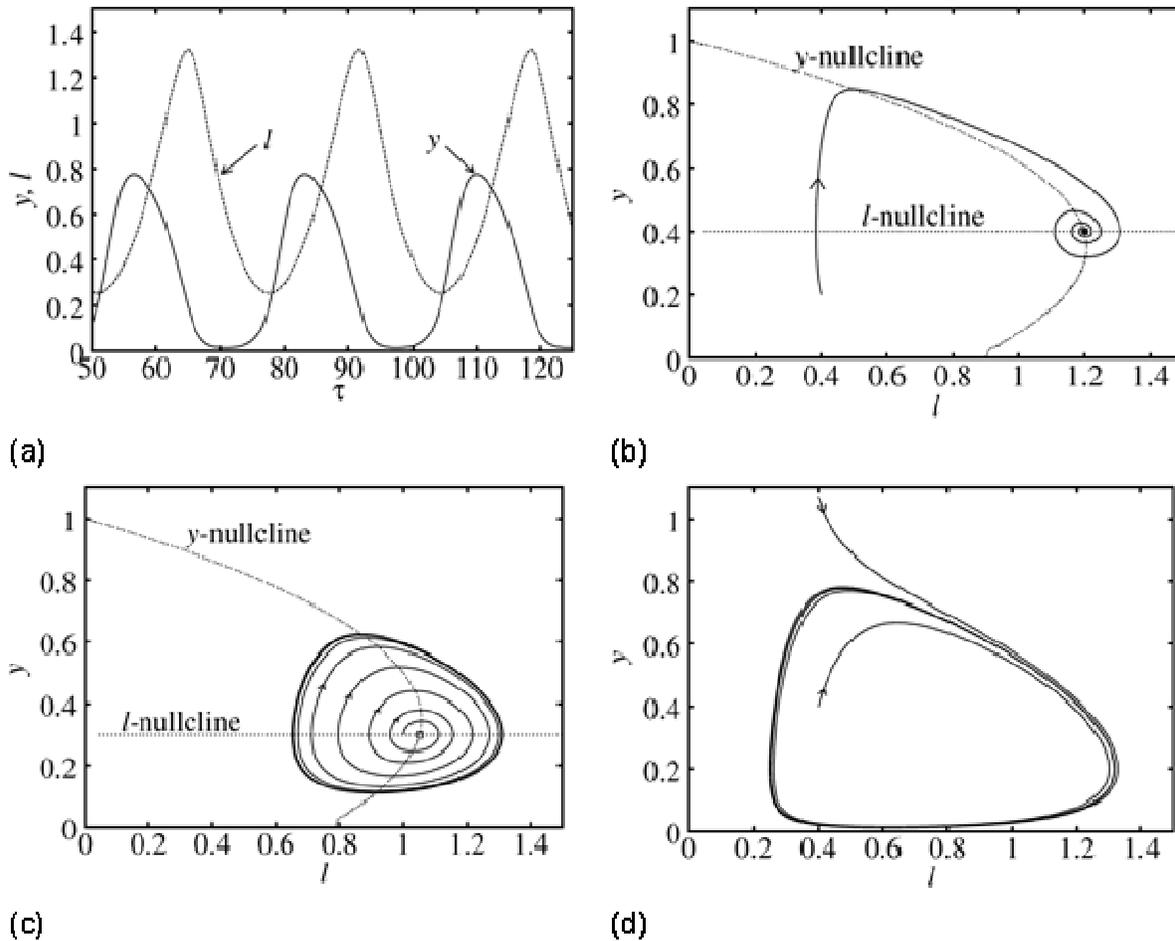


Figure 2. Time plot and phase portrait diagrams for livestock-forage model. a: Time plot showing the oscillatory behaviour of the system when the steady state is a stable limit cycle; b: Stable spiral with a trajectory moving to a stable fixed point, $\beta = 0.35, \delta = 0.3, \alpha = 0.2$; c: Unstable spiral with trajectories moving away from unstable fixed point to a limit cycle, $\beta = 0.40, \delta = 0.3, \alpha = 0.2$; d: Stable limit cycle with trajectories on either side moving towards the limit cycle for $\alpha = 0.2, \delta = 0.3, \beta = 0.4$.

animal numbers are reduced.

Forage growth, intake and liveweight gain

Figure 2 shows the dynamics of Liveweight-forage system (15). The nullclines represent the system state where neither liveweight nor forage biomass is changing. The horizontal nullcline indicates that the forage available is just enough for feeding the animal at maintenance level, and the intersection point for the two nullclines is the equilibrium point for the system. Stability of the equilibrium point is determined by the direction in which the nearby trajectories evolve; stable equilibrium attracts nearby trajectories whereas unstable equilibrium repels nearby trajectories. Thus, the equilibrium in Fig 2b is stable and that in Fig 2c is unstable. However, the stability of the equilibrium or steady state depends on the

parameter values, for example, β at 0.35 and 0.40 gives results shown in Figure 2b and 2c respectively.

Tracking the behaviour of the system as the parameters change is done by a two-parameter bifurcation analysis as shown in Figure 3b, where parameter coordinates for β and δ above the curve lead to a fixed point whereas coordinates below the curve lead to a limit cycle.

In Figure 3a at $\beta \ll 1$ (intake \ll forage growth), y stays at 1.0 up to BP where it drops dramatically to HB. At HB, the equilibrium solutions lose stability and the system evolves to a stable limit cycle surrounding the unstable equilibrium. Explanation for the bifurcation diagrams with reference to δ is as follows: for Figure 3d increasing δ from 1 (likely when carrying capacity has declined or stocking density has increased) means there

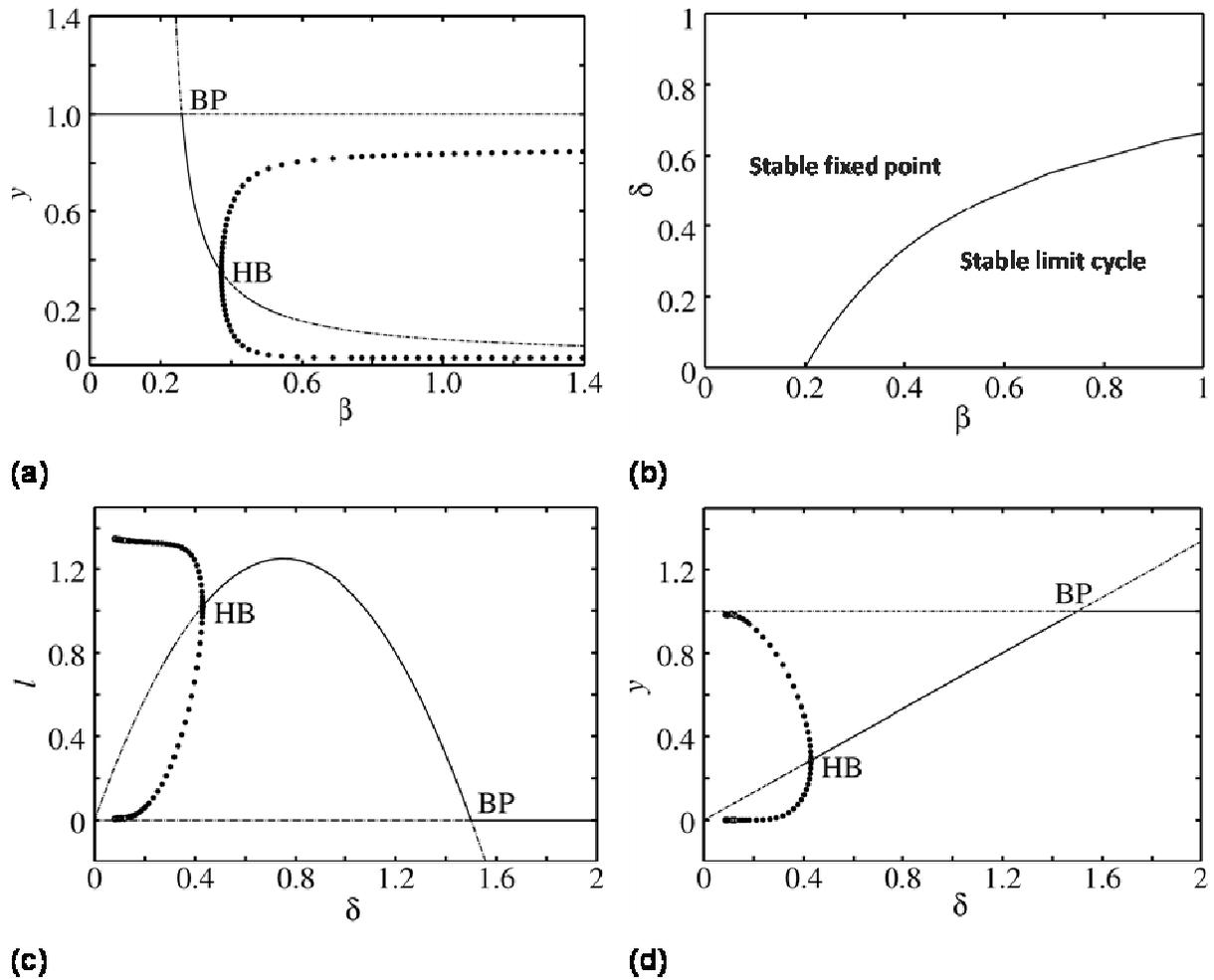


Figure 3. Bifurcation diagrams for the livestock-forage model. Solid lines show stable steady states, dashed lines show unstable steady states, filled circles show stable limit cycle oscillations, open circles show unstable limit cycle oscillations. a: Steady state dimensionless forage biomass with β as the control parameter, for $\alpha = 0.2, \delta = 0.3$; b: Stability diagram showing the two parameter (β and δ), $\alpha = 0.2$; c: Steady state dimensionless liveweight with δ as the bifurcation parameter, for $\alpha = 0.2, \beta = 0.5$; d: Steady state dimensionless forage biomass with δ as the bifurcation parameter, for $\alpha = 0.2, \beta = 0.5$.

is decreasing forage for the animals up to point (BP) when the forage can no longer support any animals. At this point the animals are either sold or alternative sources of feed sought. But farmers do not wait up to this point, they start looking for alternative feed as early enough usually outsourcing from crop residues or roadside forages. Below $\delta=1$ and up to HB (Hopf bifurcation, a point where the equilibrium solutions lose stability) liveweight and forage are in non-zero steady states. At HB the system loses equilibrium stability and evolves to a stable limit cycle surrounding the unstable equilibrium. For values of δ below HB the system oscillates with increasing amplitudes, as indicated in

Figure 3c. This means that at $\delta \ll HB$ there is plenty of forage and the farmer can add more animals to the system or conserve forage; if animals are added to the system this reduces the available forage and the system evolves to decreasing oscillations up to HB (Figure 3c) beyond which the system attains equilibrium.

Forage-animal-nutrient system

For the livestock-forage-nutrient the study focused on the behaviour and stability of the system with or without application of commercial nutrient or excreted nutrient.

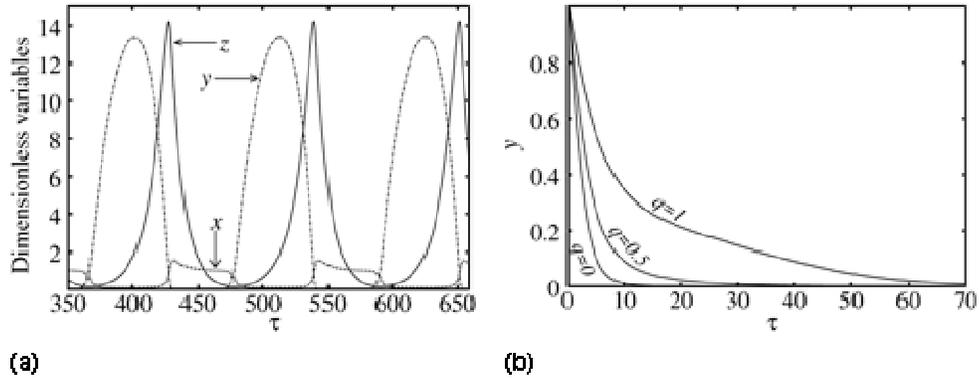


Figure 4. Time plot and excreted manure at different levels for the livestock-forage-nutrient system. **4a:** Time plot, $\alpha = 1, \beta = 1.9, k = 0.5, \gamma = 0.1, \eta = 0.1, \rho = 0.5, \delta = 0.2, q = 0.5$; **4b:** Nutrient at three levels of q , other parameters $\alpha = 0, \beta = 1.9, k = 0.5, \gamma = 0.1, \eta = 0.1, \rho = 0.5, \delta = 0.2$.

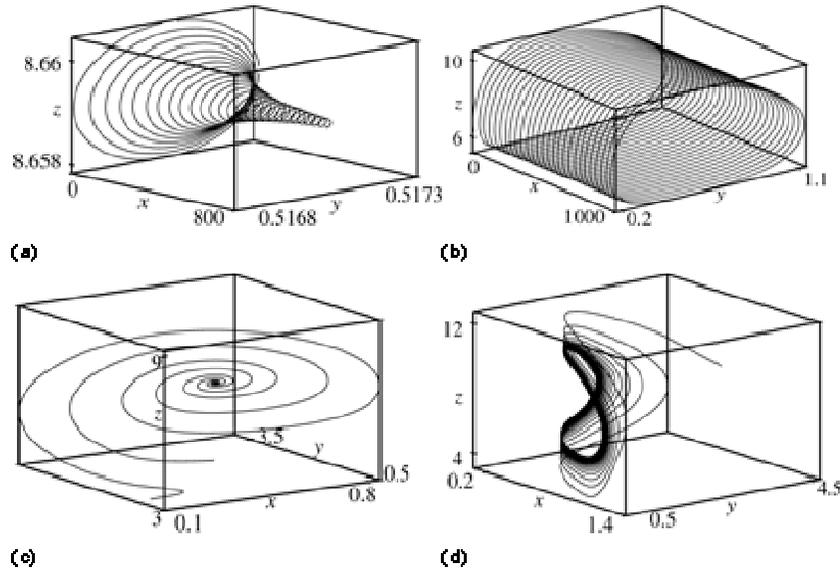


Figure 5. Livestock-forage-nutrient dynamics. a: Funnel spiral behaviour; b: Cylindrical spiral dynamics; c: Spiral dynamics, $\alpha = 1, \beta = 1.9, k = 0.5, \gamma = 0.1, \eta = 0.1, \rho = 0.5, \delta = 0.2, q = 0.2$; d: Limit cycle dynamics, $\alpha = 1, \beta = 1.9, k = 0.5, \gamma = 0.1, \eta = 0.1, \rho = 0.5, \delta = 0.2, q = 0.5$.

Therefore, the control parameters considered are α and q . It is assumed that the nutrient referred to here, is essential to the growth of forage and without it no forage growth can occur. Figure 4b at $q = 0$ (no excreted nutrient added), the system collapses after 10 time-steps ($\tau = 10$), whereas at $q = 50\%$ the system takes 30 time-steps (3 times longer to collapse). This clearly indicates the importance of adding excreted nutrient to the forage

production. Curve $q = 1$ is an ideal situation where all the excreted nutrient is applied to the production of forage (improbable, but just for comparison purposes). Figures 5a and b show the different behaviour of the livestock-forage-nutrient system depending on initial conditions and parameter values. However, at the parameters indicated for Figures 5c and d the system evolves to a stable fixed point and a stable limit cycle respectively. Here the interest was to

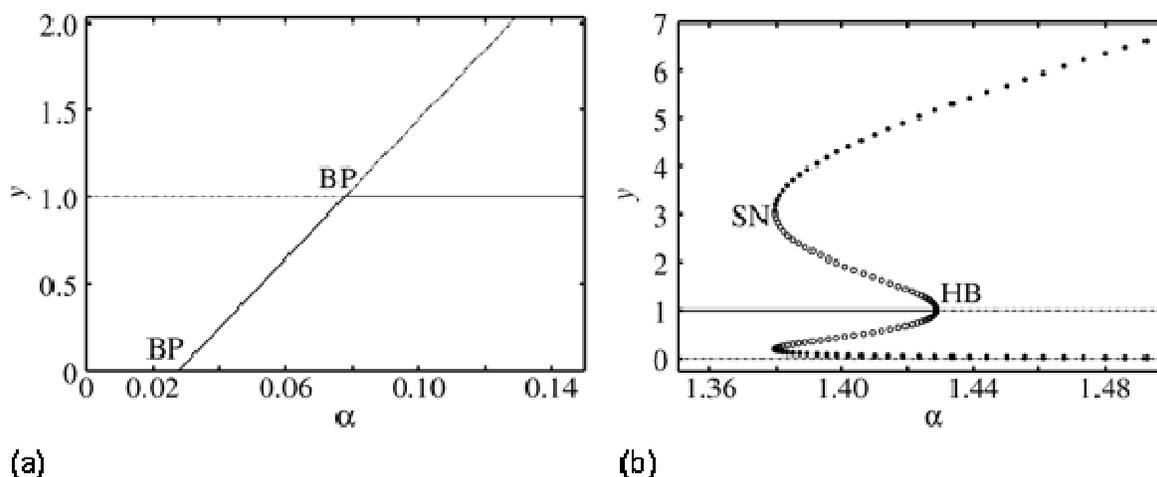


Figure 6. Bifurcation diagrams for the livestock-forage-nutrient system. Solid lines show stable steady states, dashed lines show unstable steady states, filled circles show stable limit cycle oscillations, open circles show unstable limit cycle oscillations. a: Dimensionless forage at $\alpha \ll 1$, $\beta = 1.9, k = 0.5, \gamma = 0.1, \eta = 0.1, \rho = 0.5, \delta = 0.2, q = 0$; b: Dimensionless forage with α as the control parameter, $\beta = 1.9, k = 0.5, \gamma = 0.1, \eta = 0.1, \rho = 0.5, \delta = 0.2, q = 0$.

study the effect of the external nutrient input to the system, and the results are summarised in the bifurcation diagrams (Figures 6a and b).

At very low levels of α ($\alpha \ll 1$) and no application of excreted nutrient, y is at the zero-steady state. As α , which is a measure of nutrient supply to the soil in a relation to nutrient loss from the soil (Tables 5 and 7), increases to the left-most BP, the system moves off the zero-steady state up to BP at $y = 1.0$ (Figure 6a) where it stays for all the values of α up to HB shown in Figure 6b).

The bifurcation diagram in Figure 6b is a continuation of Figure 6a and is explained as follows. For values of α in the range $SN < \alpha < HB$ the system exhibits two different stable states (solid line and the outer limit cycle with filled circles). The system, within this same range of α values exhibits unstable limit cycle (open circles). This means that with α in the range $SN < \alpha < HB$, and y inside the upper and lower bounds of amplitudes of the unstable limit cycle, the system will evolve towards the stable state indicated by the solid line. But with y outside the bounds of the unstable limit cycle, the system evolves to the outer stable limit cycle. Therefore, starting at HB and increasing α switches the system to the outer limit cycle. However, starting from $\alpha > HB$ and decreasing α to HB, does not bring back the system to the steady state of the solid line. Instead the system continues along the amplitudes of the outer limit cycle up to SN. This lack of reversibility as a bifurcation parameter is varied is called hysteresis (Strogatz, 1994) and has great implications for livestock-forage-nutrient system

and is explained as follows. For $SN < \alpha < HB$ and $y = 1$ the system is stable to small perturbations, for example, if dimensionless forage biomass is changed (but not beyond the unstable limit cycle) due to change in dimensionless animal biomass, the system will evolve back to the fixed point $y = 1$. But if the change is past the unstable limit cycle the system jumps to the outer stable limit cycle. But on this limit cycle the lower dimensionless forage biomass tends to zero-state; and from a management point of view the stable state at $y = 1$ may be more desirable. However, even at $y = 1$ steady state, if α increases beyond HB , the only stable state is the outer stable limit cycle. From the definition of α (Table 7), this can happen when there is increased efficiency in retaining external nutrient supply to the system within the forage root domain of nutrient uptake. This increased efficiency can be due to better method of nutrient application, for example, subsurface nutrient application is known to be more efficient than surface application (Kabi and Bareeba, 2007) for the case of Nitrogen. The implication of having the system on the outer limit cycle with $\alpha > HB$ is that the dimensionless animal biomass must change with available dimensionless forage biomass; but this may not be desirable or biologically feasible. For example, it may mean reducing the animal stocking level, outsourcing extra feeds, or allowing the animals to lose weight. If these operations are not the intent of the farmer, then the fixed stable state of $SN < \alpha < HB$ may be an attractive management strategy. However, once the system is in a state where $\alpha > HB$, taking it back to $y = 1$ in the

region $SN < \alpha < HB$ means the system first goes back to where $\alpha = SN$ (along the stable outer limit cycle) before it can settle on the $y = 1$ steady state. Since α is a measure of efficiency for retaining external nutrient supply to the system, the desirable level of α is not SN but HB . In other words, if the aim of the farmer is to maintain the system with $SN < \alpha < HB$ and $y = 1$, then $\alpha = HB$ is the upper limit of efficiency.

This study has shown the importance of evaluating farmers' forage resources before acquisition of animals since initial conditions (forage biomass and stocking level) influence the stability and sustainability of the system. The study has also shown that there are critical points in the system where management intervention is highly effective depending on the goals of the farmer. Furthermore, it is shown that not all parameters show sensitivity to the system, and the parameters that show sensitivity have specific parameter space over which they exhibit different sensitivities; this is important in designing experiments and making management decisions. Finally, by organising parameters into dimensionless groups, it is possible to more readily compare relative effects of biological processes.

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