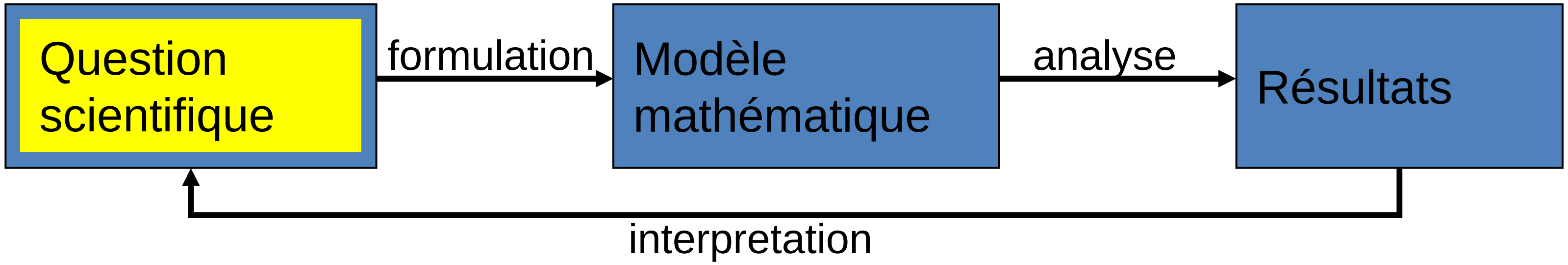
Atelier Méthodes quantitatives en environnement : Modélisation

Retroactions interdisciplinaires

David Claessen, Michael Ghil,
Pietro Peterlongo

Deux objectifs

- Conceptuel: traduction problématique ↔ modèle
- Outil: systèmes dynamiques & analyse de bifurcations


Question scientifique

formulation

Modèle mathématique

analyse

Résultats

interpretation

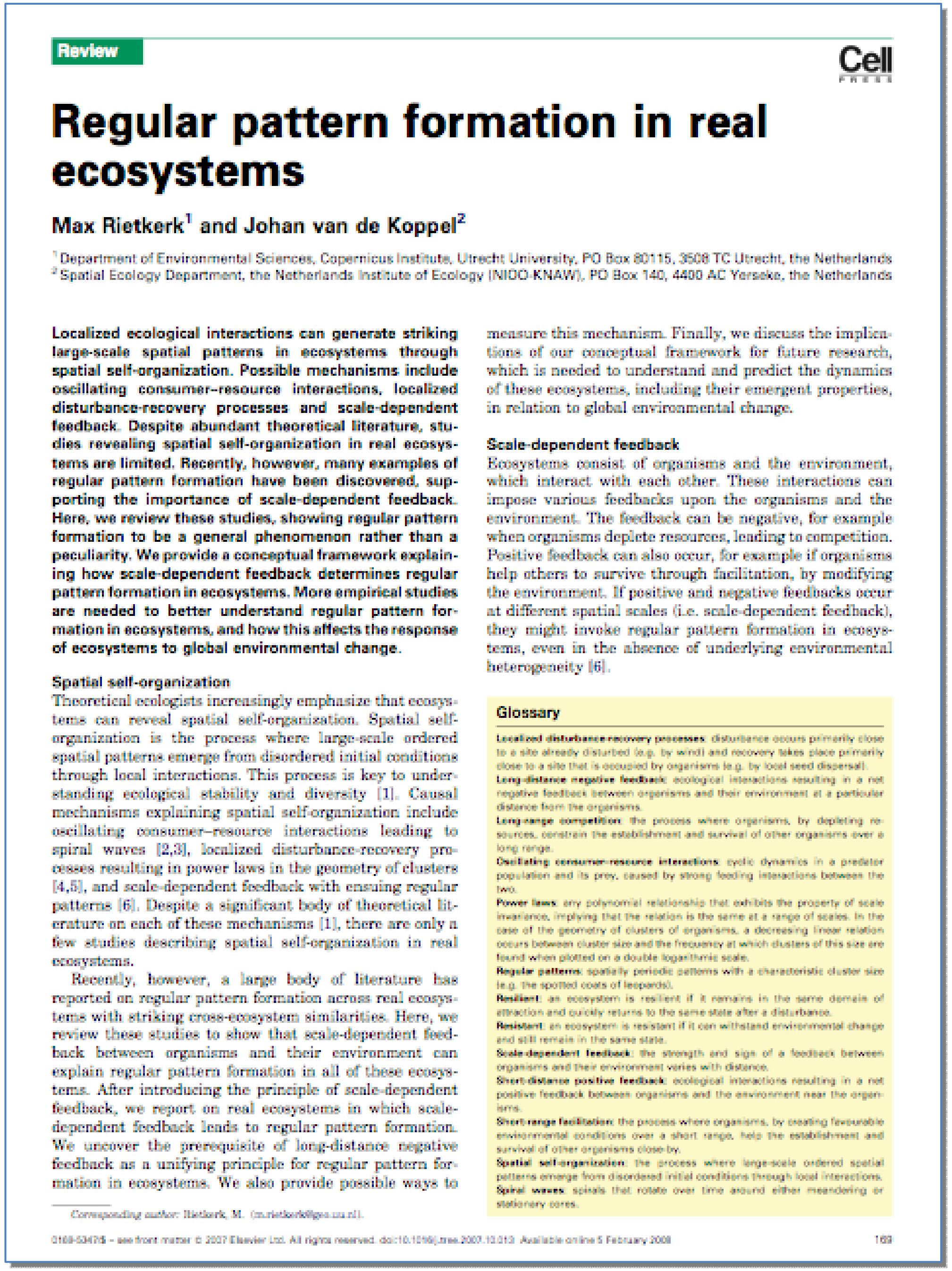
Modélisation

- Objectif: répondre à une question
- Quelles questions nécessite de la modélisation?
- Système
  - Choix de variables (et structure, dimensions)
  - Choix de paramètres
  - Temps discrète / continue

Modélisation écologique

- Dynamique des écosystemes
  - Populations, communautés, ecosystémes
  - Dynamique vs évolution

- Ici: retroactions positive entre « écologie » et « géosciences »
  - Interactions plante-sol
  - Dynamique resultante
  - *Spatial patterns*
  - Implication pour l’exploitation humaine ?
    - *Tragedy of the commons*



Review

Cell PRESS

Regular pattern formation in real ecosystems

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Localized ecological interactions can generate striking large-scale spatial patterns in ecosystems through spatial self-organization. Possible mechanisms include oscillating consumer–resource interactions, localized disturbance-recovery processes and scale-dependent feedback. Despite abundant theoretical literature, studies revealing spatial self-organization in real ecosystems are limited. Recently, however, many examples of regular pattern formation have been discovered, supporting the importance of scale-dependent feedback. Here, we review these studies, showing regular pattern formation to be a general phenomenon rather than a peculiarity. We provide a conceptual framework explaining how scale-dependent feedback determines regular pattern formation in ecosystems. More empirical studies are needed to better understand regular pattern formation in ecosystems, and how this affects the response of ecosystems to global environmental change.

Spatial self-organization

Theoretical ecologists increasingly emphasize that ecosystems can reveal spatial self-organization. Spatial self-organization is the process where large-scale ordered spatial patterns emerge from disordered initial conditions through local interactions. This process is key to understanding ecological stability and diversity [1]. Causal mechanisms explaining spatial self-organization include oscillating consumer–resource interactions leading to spiral waves [2,3], localized disturbance-recovery processes resulting in power laws in the geometry of clusters [4,5], and scale-dependent feedback with ensuing regular patterns [6]. Despite a significant body of theoretical literature on each of these mechanisms [1], there are only a few studies describing spatial self-organization in real ecosystems.

Recently, however, a large body of literature has reported on regular pattern formation across real ecosystems with striking cross-ecosystem similarities. Here, we review these studies to show that scale-dependent feedback between organisms and their environment can explain regular pattern formation in all of these ecosystems. After introducing the principle of scale-dependent feedback, we report on real ecosystems in which scale-dependent feedback leads to regular pattern formation. We uncover the prerequisite of long-distance negative feedback as a unifying principle for regular pattern formation in ecosystems. We also provide possible ways to measure this mechanism. Finally, we discuss the implications of our conceptual framework for future research, which is needed to understand and predict the dynamics of these ecosystems, including their emergent properties, in relation to global environmental change.

Scale-dependent feedback

Ecosystems consist of organisms and the environment, which interact with each other. These interactions can impose various feedbacks upon the organisms and the environment. The feedback can be negative, for example when organisms deplete resources, leading to competition. Positive feedback can also occur, for example if organisms help others to survive through facilitation, by modifying the environment. If positive and negative feedbacks occur at different spatial scales (i.e. scale-dependent feedback), they might invoke regular pattern formation in ecosystems, even in the absence of underlying environmental heterogeneity [6].

Glossary

Localized disturbance-recovery processes: disturbance occurs primarily close to a site already disturbed (e.g. by wind) and recovery takes place primarily close to a site that is occupied by organisms (e.g. by local seed dispersal).

Long-distance negative feedback: ecological interactions resulting in a net negative feedback between organisms and their environment at a particular distance from the organisms.

Long-range competition: the process where organisms, by depleting resources, constrain the establishment and survival of other organisms over a long range.

Oscillating consumer–resource interactions: cyclic dynamics in a predator population and its prey, caused by strong feeding interactions between the two.

Power laws: any polynomial relationship that exhibits the property of scale invariance, implying that the relation is the same at a range of scales. In the case of the geometry of clusters of organisms, a decreasing linear relation occurs between cluster size and the frequency at which clusters of this size are found when plotted on a double logarithmic scale.

Regular patterns: spatially periodic patterns with a characteristic cluster size (e.g. the spotted coats of leopards).

Resilient: an ecosystem is resilient if it remains in the same domain of attraction and quickly returns to the same state after a disturbance.

Resistant: an ecosystem is resistant if it can withstand environmental change and still remain in the same state.

Scale-dependent feedback: the strength and sign of a feedback between organisms and their environment varies with distance.

Short-distance positive feedback: ecological interactions resulting in a net positive feedback between organisms and the environment near the organisms.

Short-range facilitation: the process where organisms, by creating favourable environmental conditions over a short range, help the establishment and survival of other organisms close by.

Spatial self-organization: the process where large-scale ordered spatial patterns emerge from disordered initial conditions through local interactions.

Spiral waves: spirals that rotate over time around either meandering or stationary cores.

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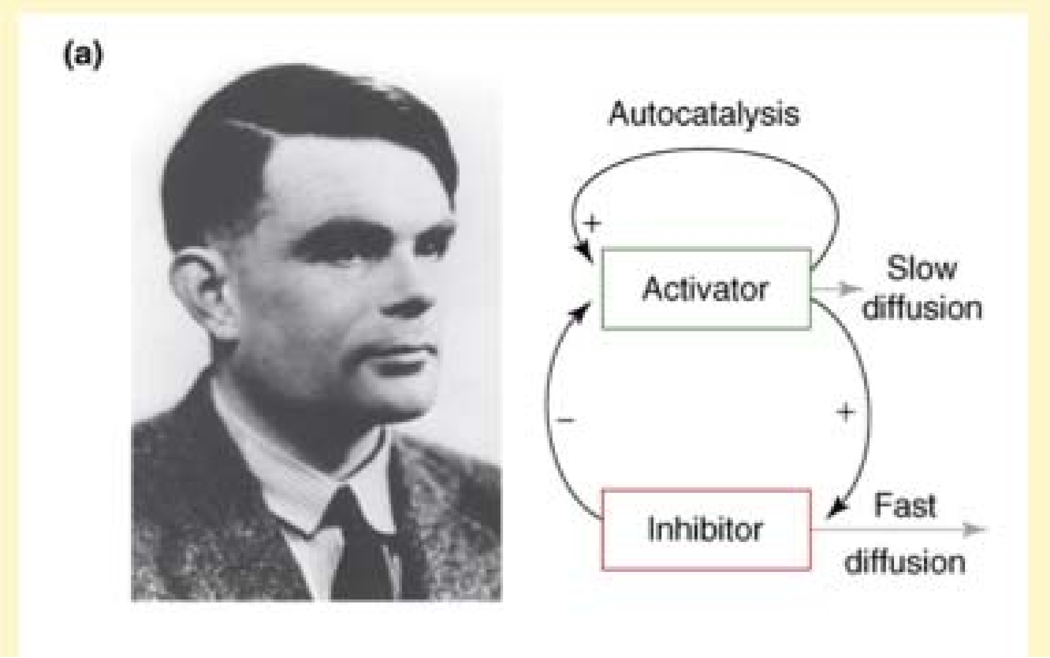
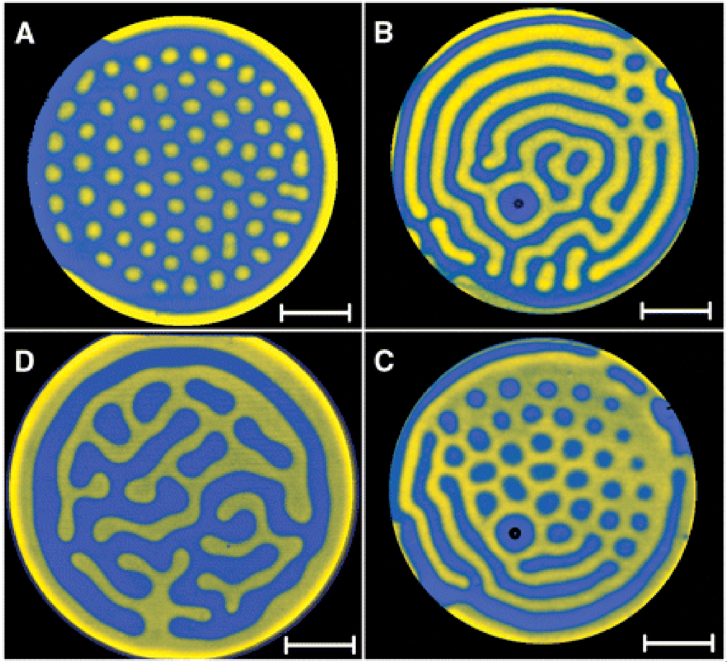
- Rietkerk & Van de Koppel (2008) Trends in Ecology and Evolution Vol.23 No.3

Turing patterns

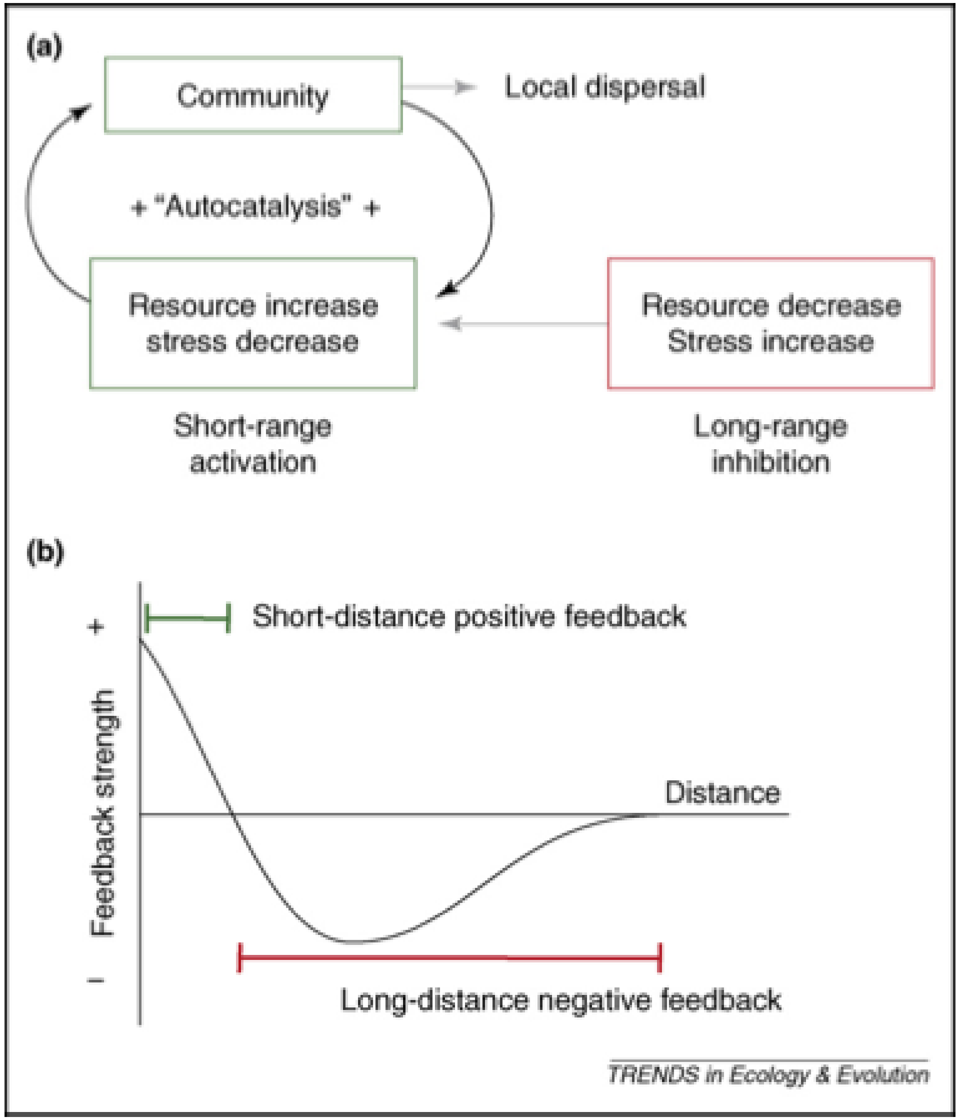


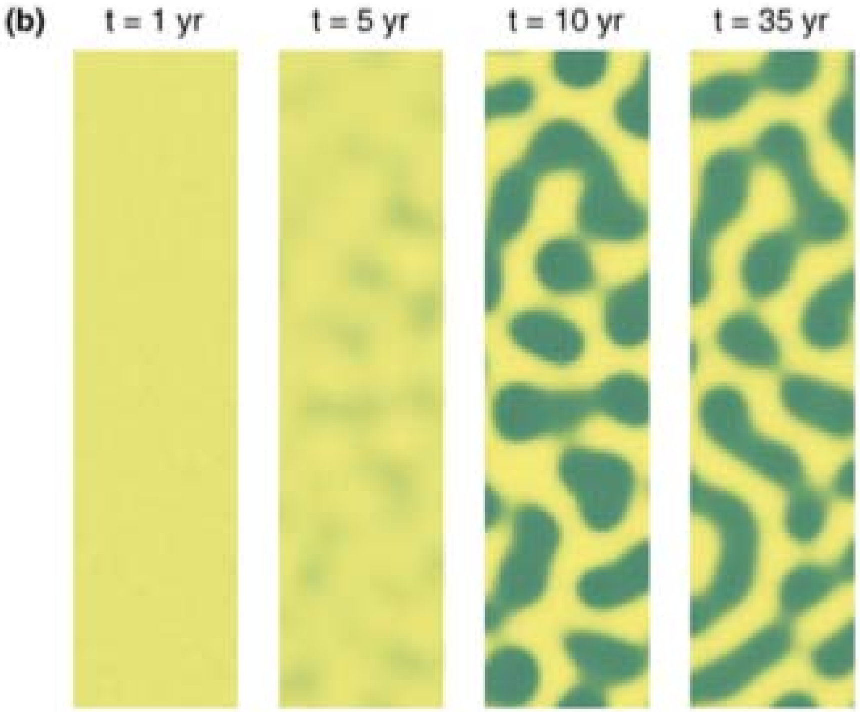


Horváth et al (2009) Science Vol. 324. no. 5928, pp. 772 - 775

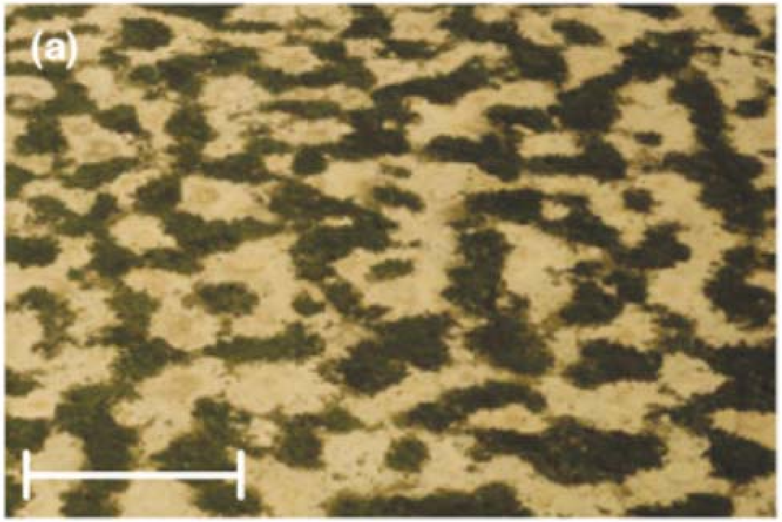
- Alan Turing (1912-1954)
- Autocatalysis in activator-inhibitor system
  - More A → more A produced
  - But also more I, inhibition
- A and I diffuse at different rates
- Turing: if I diffuses faster than A → spatial patterns
- Scale dependent feedback of A and I : positive feedback dominates at short distance, whereas negative feedback dominates at longer distance

Scale dependent feedback in ecology





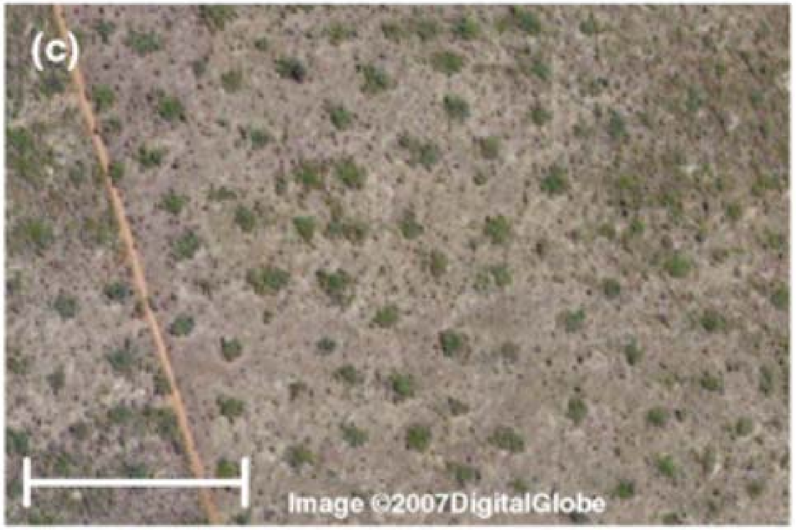
Retroactions positive, catastrophes, transitions, « spatial patterns »



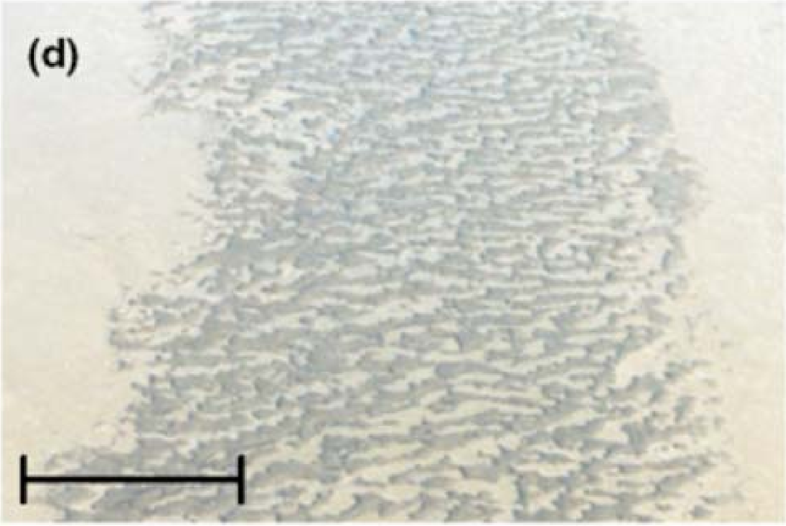
(a) Labyrinth pattern of bushy vegetation in Niger (scale = 100 m).

(b) Regular maze patterns of shrubs and trees in West Siberia (scale = 100 m).

Retroactions positive, catastrophes, transitions, « spatial patterns »

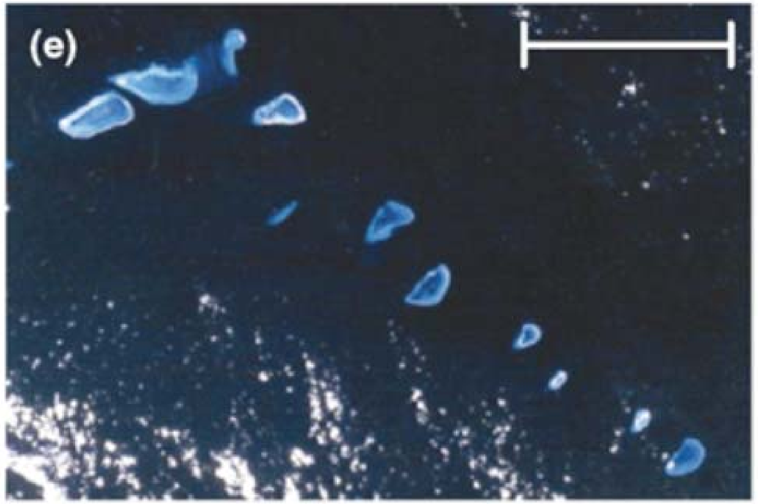


(c) Spotted pattern of isolated tree patches in Niger (scale = 200 m).



(d) Patterned mussel bank in the Wadden Sea, the Netherlands (scale = 50 m).

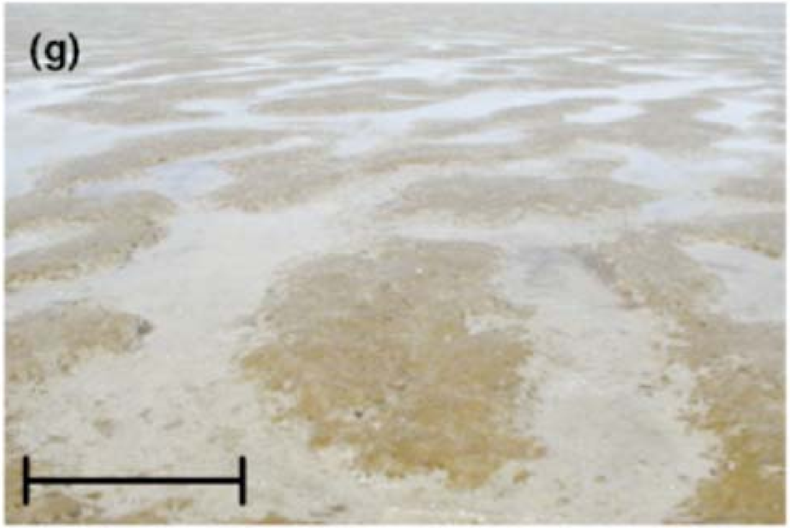
Retroactions positive, catastrophes, transitions, « spatial patterns »



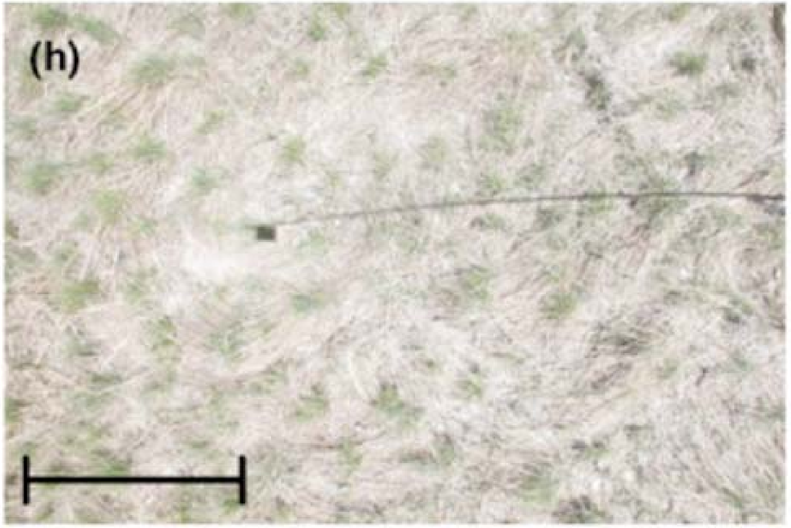
(e) Reef islands oriented in series along the predominating direction of large-scale currents in Australia (scale = 20 km).

(f) Striped pattern of tree lines and snow deposition in ribbon forests in USA

Retroactions positive, catastrophes, transitions, « spatial patterns »

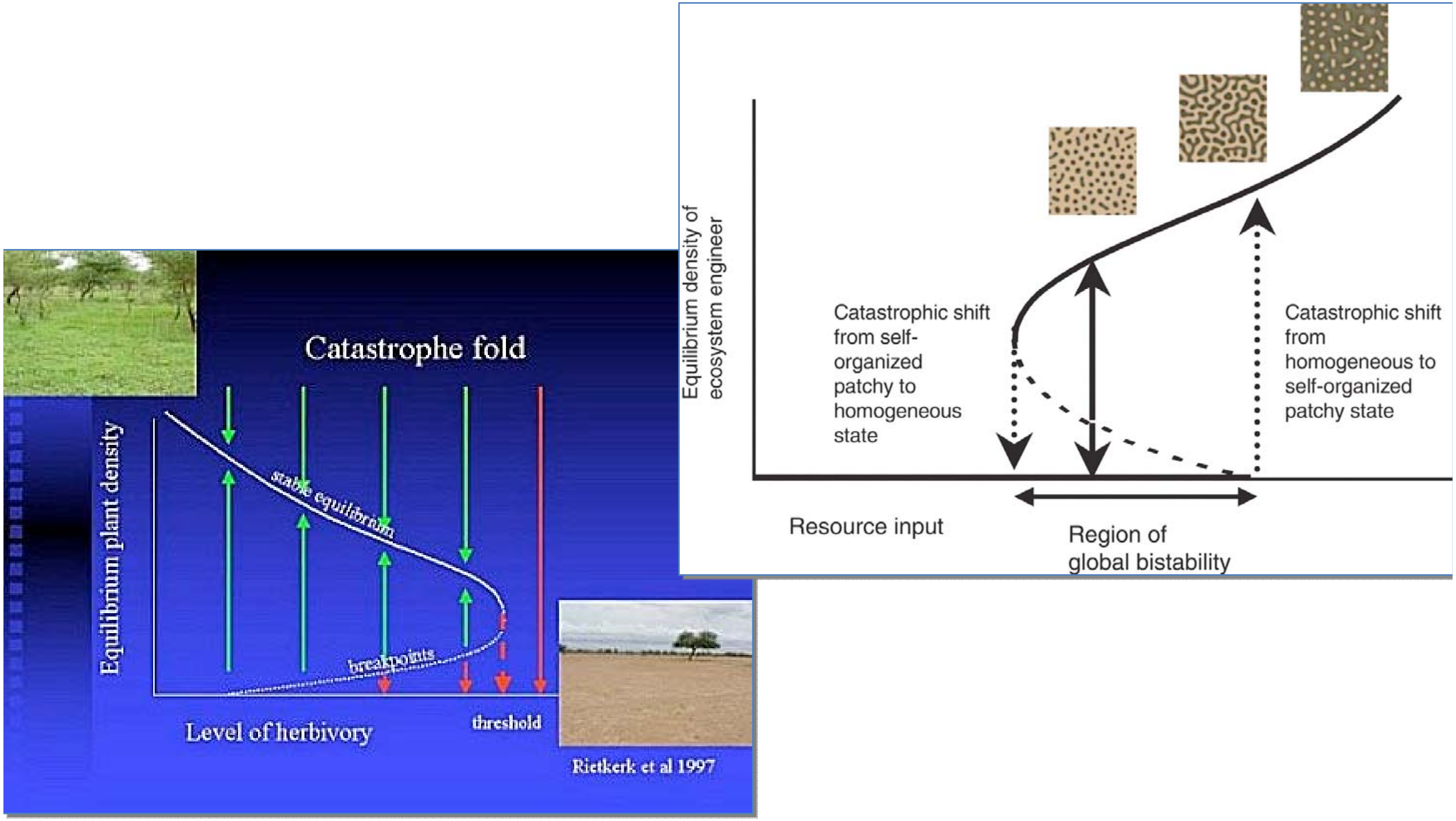


(g) Labyrinth pattern of marine benthic diatoms in the Netherlands (scale = 1 m).



(h) Regular spaced tussocks (touffes d'herbe) of the sedge Carex stricta (scale = 2 m).

A simple model to explain all this?



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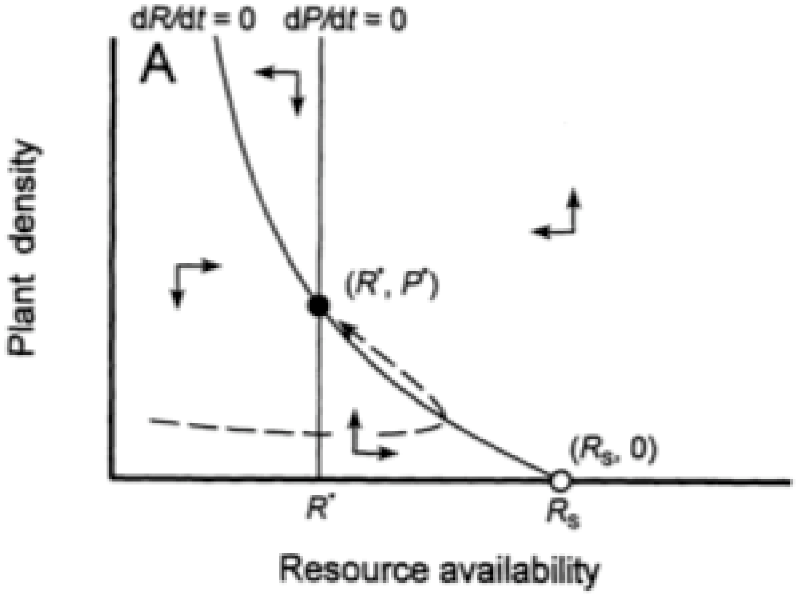
Rietkerk & Van de Koppel
1997 Oikos 79: 69-76

Modelling semi-arid grazing systems



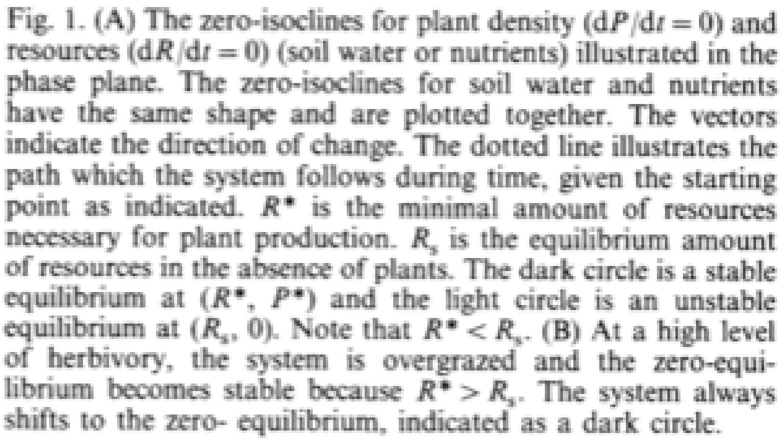
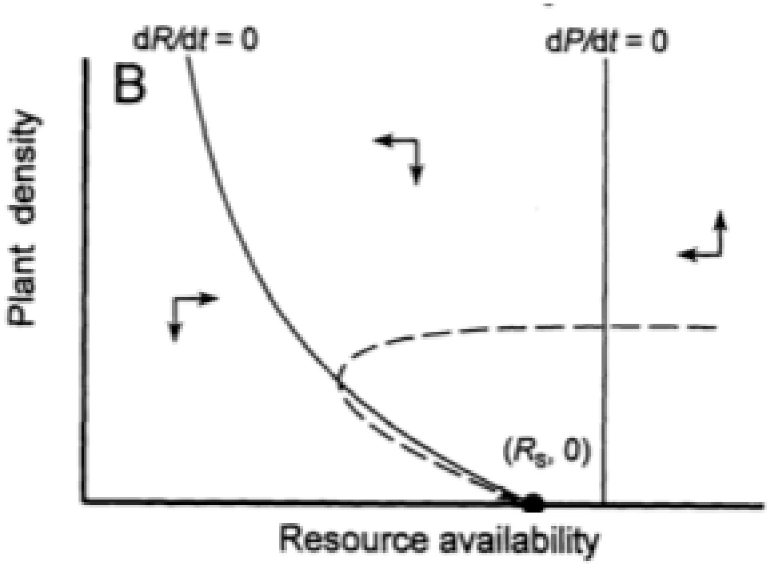


Fig. 1. (A) The zero-isoclines for plant density ($dP/dt = 0$) and resources ($dR/dt = 0$) (soil water or nutrients) illustrated in the phase plane. The zero-isoclines for soil water and nutrients have the same shape and are plotted together. The vectors indicate the direction of change. The dotted line illustrates the path which the system follows during time, given the starting point as indicated. R^* is the minimal amount of resources necessary for plant production. R_s is the equilibrium amount of resources in the absence of plants. The dark circle is a stable equilibrium at (R^*, P^*) and the light circle is an unstable equilibrium at (R_s, 0). Note that $R^* < R_s$. (B) At a high level of herbivory, the system is overgrazed and the zero-equilibrium becomes stable because $R^* > R_s$. The system always shifts to the zero- equilibrium, indicated as a dark circle.

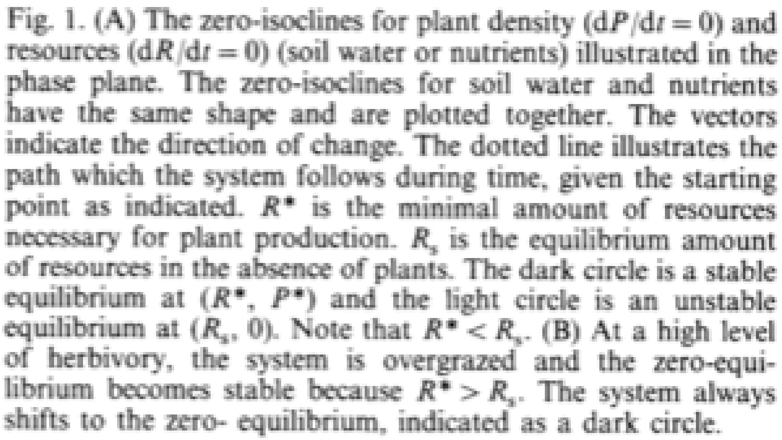
Modelling semi-arid grazing systems

Rietkerk & Van de Koppel
1997 Oikos 79: 69-76



With high herbivory, a higher resource intake rate is required for vegetation growth:
→ Therefore the dP/dt=0 isocline moves to the right

Herbovory too high: overgrazing (*surpâturage*)



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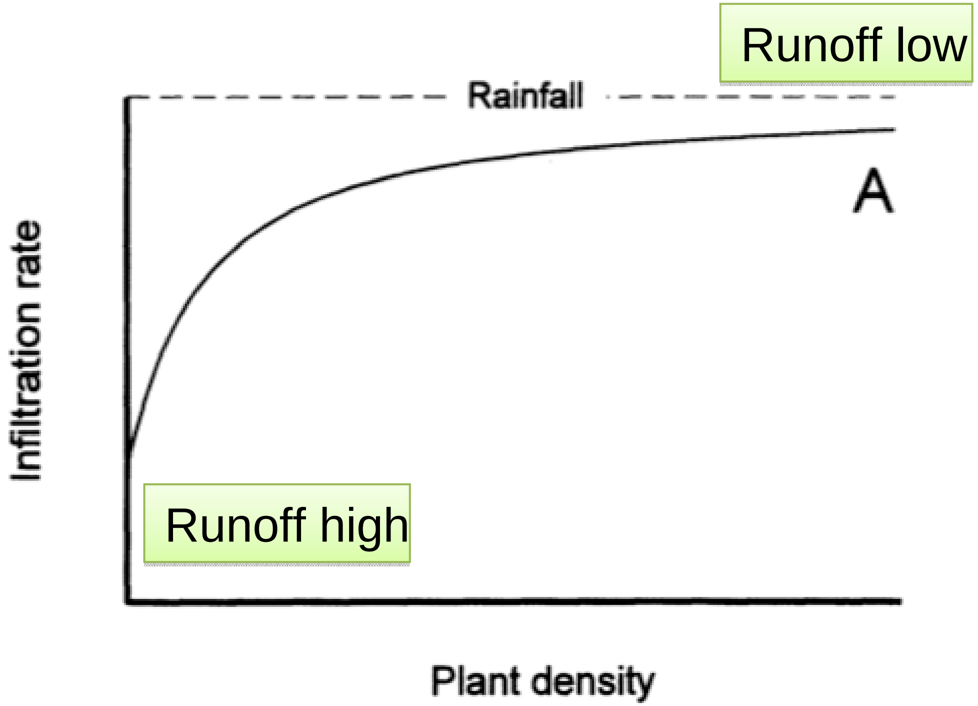
Plant soil relations

Shape of the relationships

The mechanisms underlying the effect of vegetation on the capacity of the soil to absorb water and retain nutrients can be described by two simple relationships. Vegetation improves the structural and water-holding properties of the soil by forming root channels, by preventing crust formation through the interception of raindrops, and by stimulating biological activity in the soil, resulting in higher infiltration rates (Glover et al. 1962, Kelly and Walker 1976, Van Wijngaarden 1985,

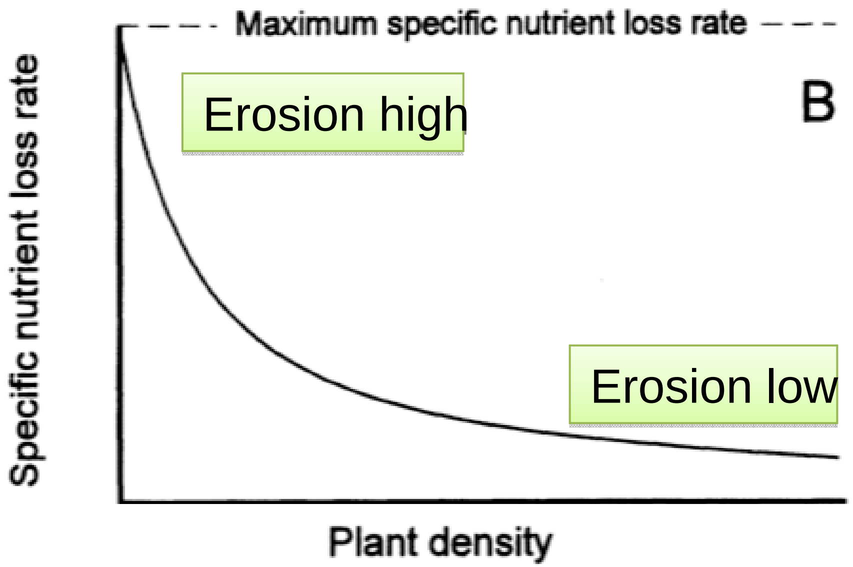


Runoff low

Runoff high

Fig. 2. (A) The shape of the feedback relation between infiltration rate and plant density [after Walker et al. (1981)]. Empirical evidence for the shape of this relationship can be found in Van Wijngaarden (1985). The infiltration rate is defined in relative terms as the amount of water entering the soil expressed as a proportion of the amount which enters when plant density is at its maximum. (B) The shape of the feedback relation between the specific nutrient loss rate and plant density based on the results of experiments by Elwell and Stocking (1974, 1976) and Lang (1979).

Vegetation protects the soil against wind and water erosion by the physical binding of soil by stems and living roots, raindrop interception, and the retention of runoff (Elwell and Stocking 1974, 1976, Lang 1979, Graetz 1991, Stocking 1994). Consequently, a higher plant density leads to a lower nutrient loss.



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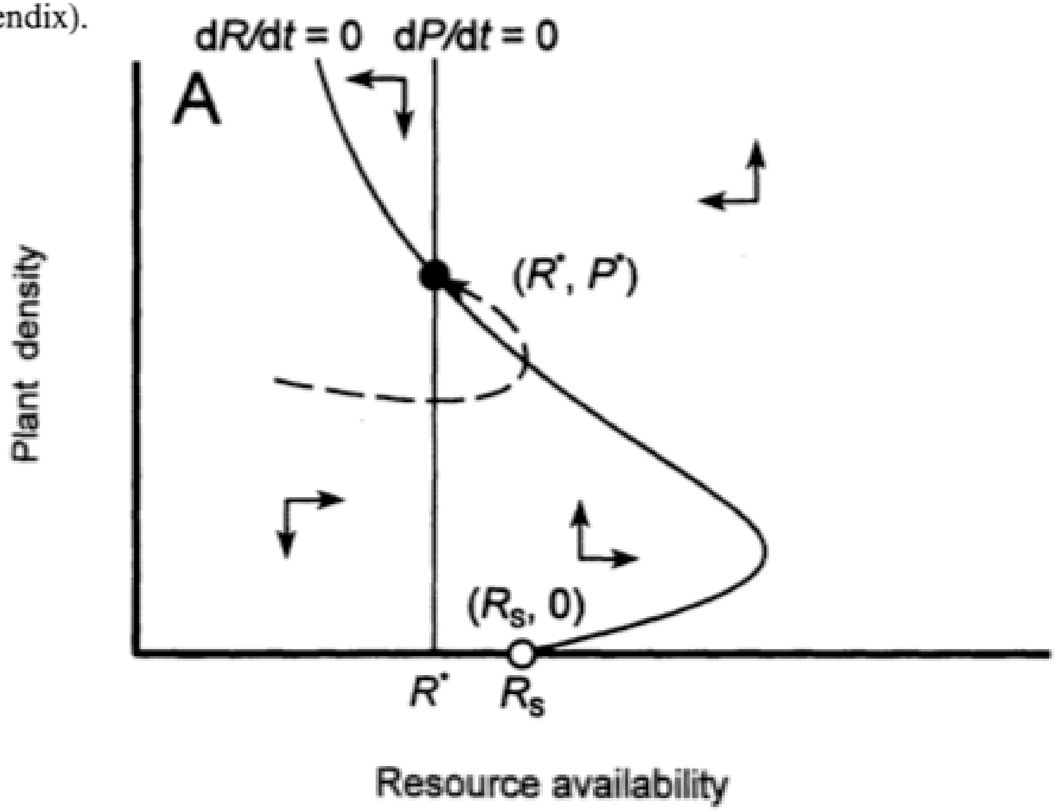
Effect of plant-soil relations

If a feedback relation between the rate of infiltration and plant density is incorporated in the water-limitation model, the shape of the soil water isocline in the phase plane alters. At low plant density, any increase in density results in a relatively large increase in the infiltration rate, possibly even exceeding the increase in the rate of water uptake by plants. In this case, the isocline has a positive slope (Fig. 3). Above a certain plant density, however, the effect of increasing plant density on water infiltration declines, and as a result the increase of water uptake by the plants will exceed the increase of water infiltration. Consequently, a hump appears in the soil water isocline (see Appendix).



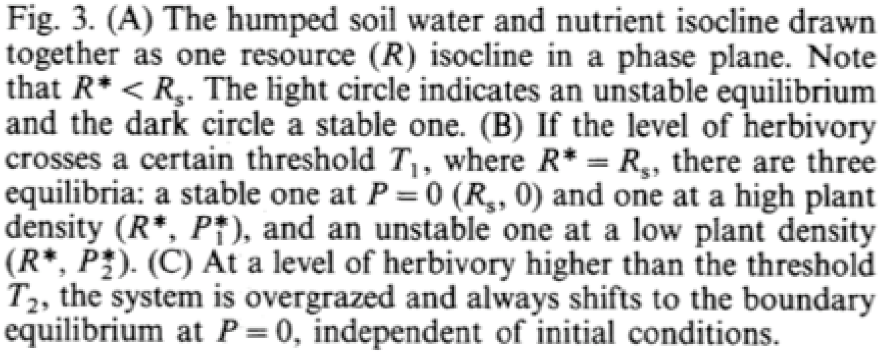
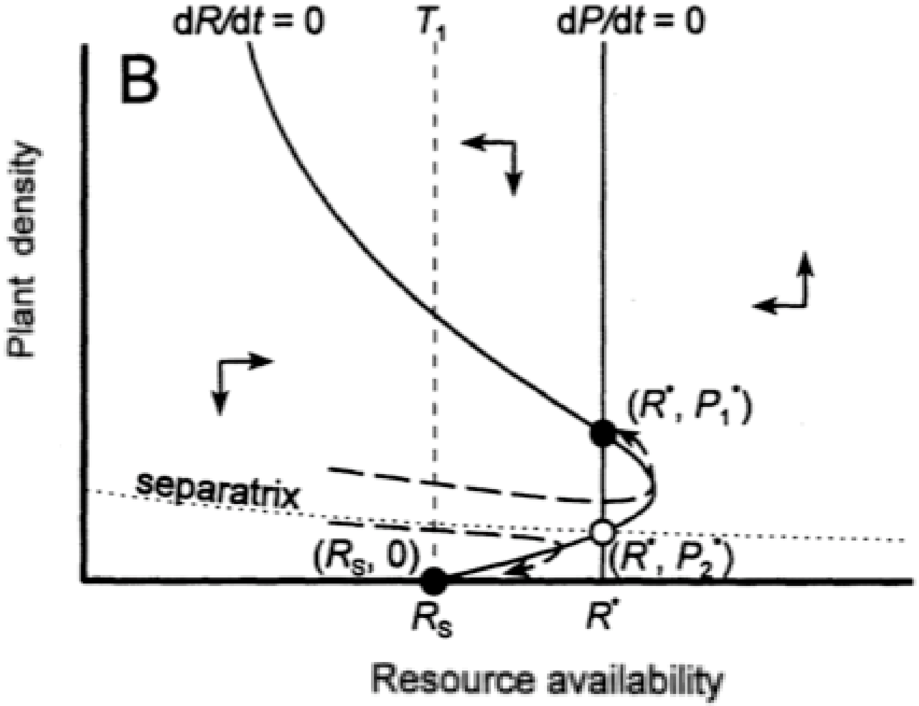


Fig. 3. (A) The humped soil water and nutrient isocline drawn together as one resource (R) isocline in a phase plane. Note that $R^* < R_s$. The light circle indicates an unstable equilibrium and the dark circle a stable one. (B) If the level of herbivory crosses a certain threshold T_1, where $R^* = R_s$, there are three equilibria: a stable one at $P = 0$ (R_s, 0) and one at a high plant density (R^*, P_1^*), and an unstable one at a low plant density (R^*, P_2^*). (C) At a level of herbivory higher than the threshold T_2, the system is overgrazed and always shifts to the boundary equilibrium at $P = 0$, independent of initial conditions.

Three equilibria: bistability



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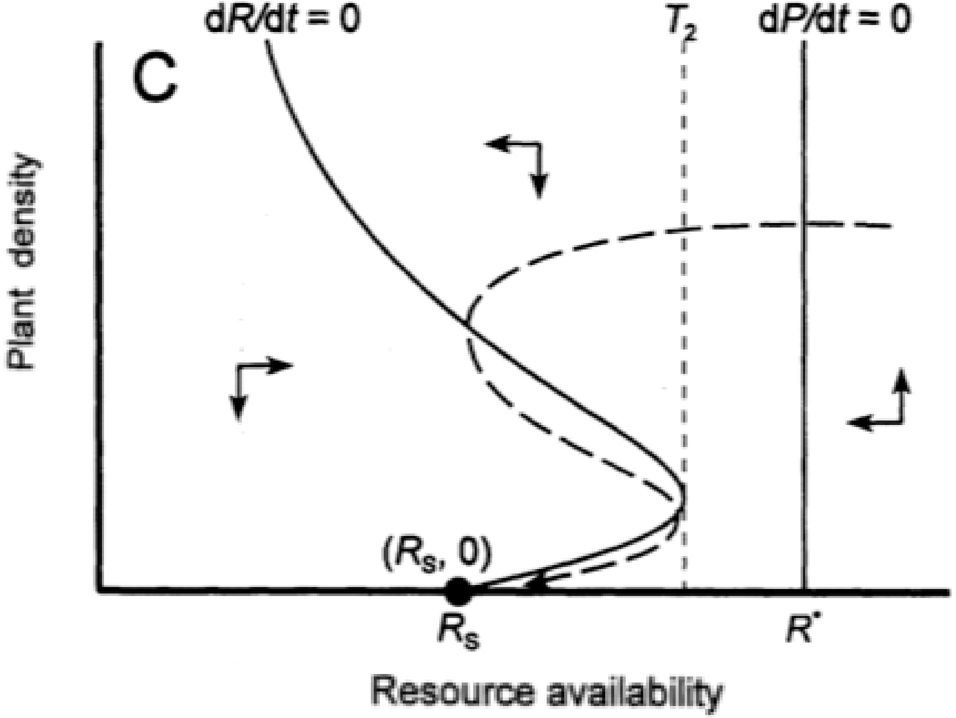
High herbivory: overgrazing



REVIEWS

Catastrophic vegetation shifts and soil degradation in terrestrial grazing systems

Johan van de Koppel, Max Rietkerk and Franz J. Weissing

It has long been recognized that alternative vegetation states may occur in terrestrial grazing systems. This phenomenon may be of great importance as small environmental fluctuations may lead to relatively sudden and irreversible jumps between vegetation states. Early theoretical studies emphasized saturation of herbivore feeding to explain multiple stable states and catastrophic behaviour. Recent studies on semi-arid grasslands and arctic salt marshes, however, relate catastrophic events in these systems to plant–soil interactions.

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Many terrestrial grazing systems have proved to be vulnerable to changes in grazing pressure. Increase in human population size coincided with an increased grazing pressure by livestock in the Sahel region in Africa[1]. Livestock numbers, including cattle, sheep and goats, have increased from 40 million in 1950 to over 125 million in 1993. Resulting vegetation changes have been dramatic. The perennial grasses that were relatively abundant in the Sahel region were replaced by annual vegetation, which is very sensitive to disturbance[2]. In years with relatively low rainfall, this led to a collapse of the herbaceous vegetation[3,4], leaving a vegetation consisting of a sparse cover of unpalatable annual herbs and unpalatable shrubs[5]. Eventually, these processes resulted in desertification and famine in various parts of the Sahel region[2,6].

A collapse of the vegetation following changes in grazing pressure has also been reported for arctic plant communities along the coast of the Hudson Bay in Canada[7,8]. The mid-continent population of lesser snow goose (*Chen caerulescens caerulescens*) has increased from 1.2 million to almost two million birds between 1973 and 1989. This has resulted in a dramatic increase in the numbers of geese that breed on the salt marshes of the Hudson Bay coast. Increase in foraging and grubbing for roots and rhizomes in the soil has led to the destruction of existing plant communities and has created large bare patches lacking organic soil.

A number of ecological indicators point to the existence of multiple stable states in the systems described above[8]. First, increases in herbivore grazing pressure resulted in irreversible shifts between vegetation states in both the Sahel and along the Hudson Bay[7,8]. Attempts in the Sahel to restore the former vegetation in bare areas by reducing herbivore numbers had little effect; the areas have remained in their new barren state for at least 20 years and have not reverted to their original vegetated state[1,3]. Secondly, mosaics consisting of densely vegetated patches alternating with almost bare areas may also reflect multiple stable states[10]. These two-phase mosaics occur on different scales in semi-arid systems[11-13]. Two-phase mosaics are also found along the Hudson Bay, most likely resulting from intensive grazing and grubbing by lesser snow geese[14].

Similar phenomena have been described for other grazing systems around the world. Destruction of vegetation and subsequent desertification have been related to increased herbivore grazing pressure in other semi-arid regions in Africa[15,16], south-western USA[17], the Russian Federation[18], Australia[13,19] and in American salt marshes[20]. Additionally, a number of studies stress that overgrazed systems in Africa, America and Australia cannot easily be restored on a practical time-scale by simply lowering the level of herbivory[9,21,22].

The theoretical possibility of multiple stable states in terrestrial grazing systems has long been recognized[23,24]. Recent empirical studies have produced valuable insights into the causes of these phenomena. They may aid in the development of a general mechanistic framework for explaining catastrophic behaviour in terrestrial grazing systems.

Mechanistic explanations

Models that describe the dynamics of grazing systems are typically based on the same general structure[23,24]. The rate of change of plant standing crop P is represented by the differential equation

$$\frac{dP}{dt} = G(P) - C(P)$$

in which $G(P)$ describes plant growth as a function of plant standing crop and $C(P)$ is the loss rate due to consumption by herbivores. For example, $G(P)$ may be given by the logistic growth equation, $G(P) = rP(1 - P/K)$, whereas losses due to overgrazing are proportional to both plant standing crop and herbivore density: $C(P) = \alpha HP$ (see Boxes 1 and 2). The models often incorporate H as a fixed parameter, that is, herbivore density is assumed to be more or less constant and independent of plant standing crop. This is not unreasonable for many managed grazing systems[21], but not necessarily applicable to more natural systems. In the example above, a single stable state is found independent of herbivore density (Fig. 1a). At low plant standing crop, plant growth exceeds grazer-induced losses. Beyond a certain plant standing crop (denoted by P_1), growth is lower than grazer-induced losses, because plant growth is limited by high vegetation density. Figure 1b shows that equilibrium plant standing crop P_1 is negatively related to herbivore density. At high herbivore density, plants cannot compensate for herbivore induced losses, and consequently plants are unable to persist in the system.

This article reviews a number of mechanisms that produce multiple stable states in terrestrial grazing systems. Two groups of mechanisms are considered: mechanisms affecting the consumption term $C(P)$ and mechanisms affecting the growth term $G(P)$ (Ref. 25).

0169-5347/97/$17.00 PII: S0169-5347(97)01133-6 *TREE vol. 12, no. 9 September 1997*

- Van de Koppel, Rietkerk & Weissing (1997) TREE 12(9)

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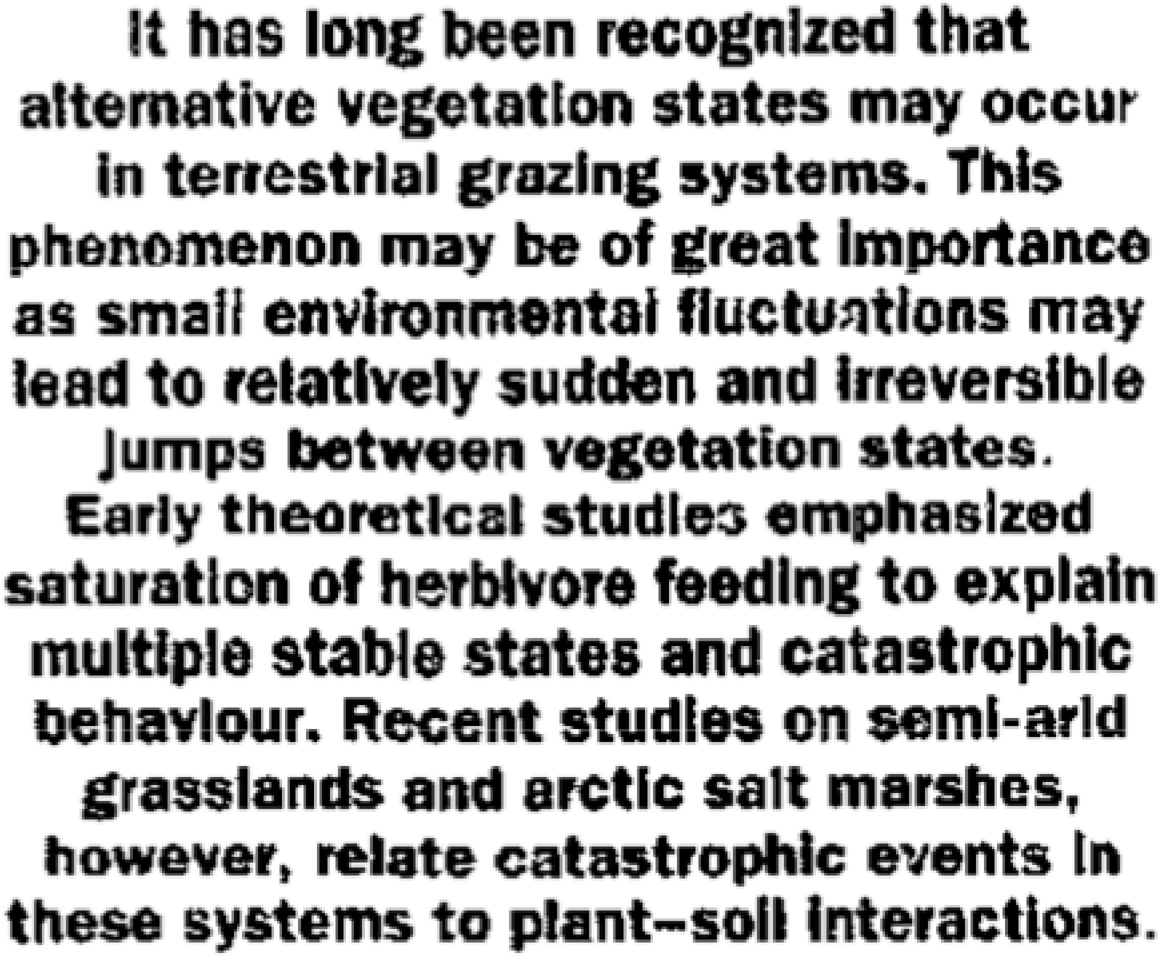


It has long been recognized that alternative vegetation states may occur in terrestrial grazing systems. This phenomenon may be of great importance as small environmental fluctuations may lead to relatively sudden and irreversible jumps between vegetation states. Early theoretical studies emphasized saturation of herbivore feeding to explain multiple stable states and catastrophic behaviour. Recent studies on semi-arid grasslands and arctic salt marshes, however, relate catastrophic events in these systems to plant–soil interactions.

Box 1. Feedback between plant standing crop and water infiltration

Here, we present a simplified version of the water-limitation model analysed by Rietkerk and van de Koppel[33]. In semi-arid systems, plant growth is mainly limited by the availability of water[31]. Therefore, plant growth increases if water availability increases. Assume that the dynamics of the plant population P is characterized by the following differential equation:

$$\frac{dP}{dt} = rP(1 - \frac{P}{K})f(W) - \alpha HP$$

where r is a plant growth coefficient, K is the carrying capacity of the vegetation, $f(W)$ is a function describing the effect of water availability W on plant growth, α is a herbivore consumption coefficient and H is herbivore density. For example, $f(W)$ might be given by $f(W) = W/(W + b)$, where b determines how quickly growth increases with water availability.

The availability of soil water is governed by a number of factors, including water infiltration, losses of water from the soil due to evaporation and percolation, and the uptake of water by plants. The changes in water availability due to these factors may be represented by a differential equation:

$$\frac{dW}{dt} = W_{in}\frac{P + aq}{P + a} - eW - uWP$$

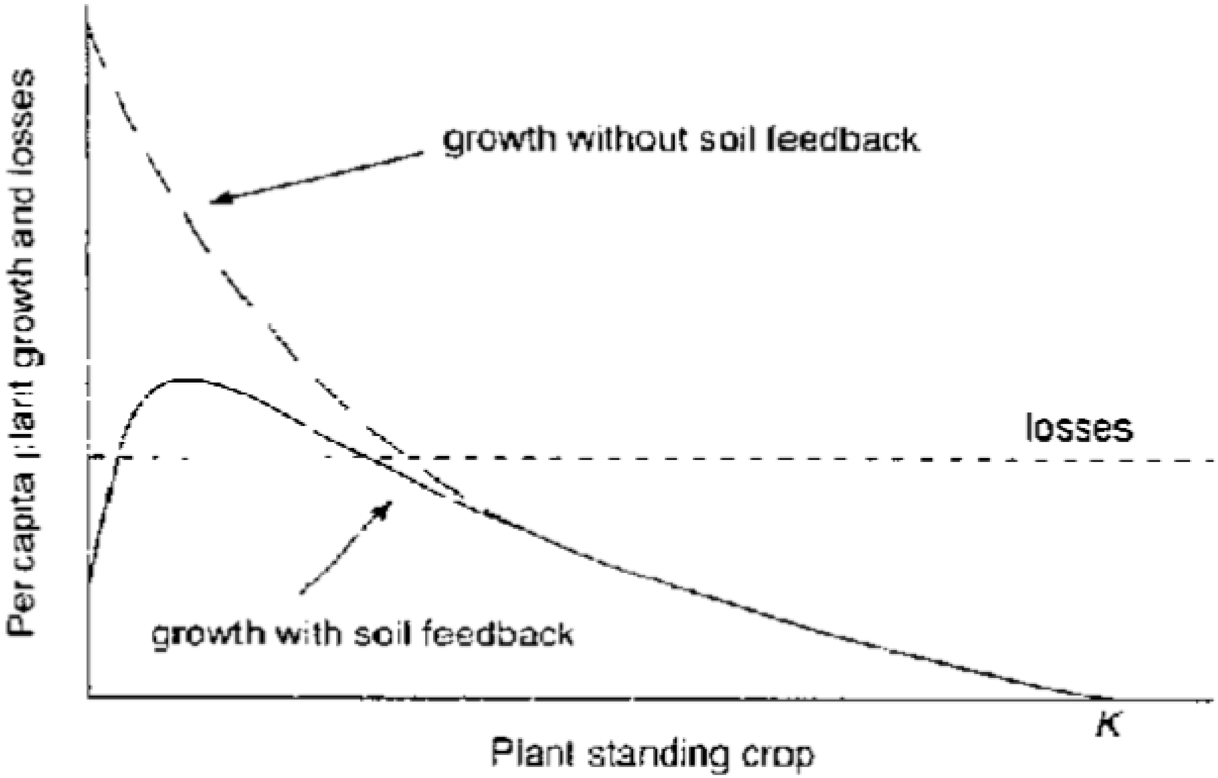
Here, water infiltration is an increasing but saturating function of plant standing crop P. W_{in} stands for rainfall, a determines how quickly infiltration increases with plant standing crop, q is the fraction of rainfall that infiltrates into bare soils, e is the specific loss rate of water from the soil and u is a plant uptake coefficient. Since the dynamics of soil water act on a much faster time-scale than growth of plants, we assume soil water conditions to be in equilibrium with respect to plant growth (a quasi-steady-state approach[42]). The equilibrium condition $dW/dt = 0$ yields water availability $W^*(P)$ as a function of plant standing crop. In our example, $W^*(P)$ is given by

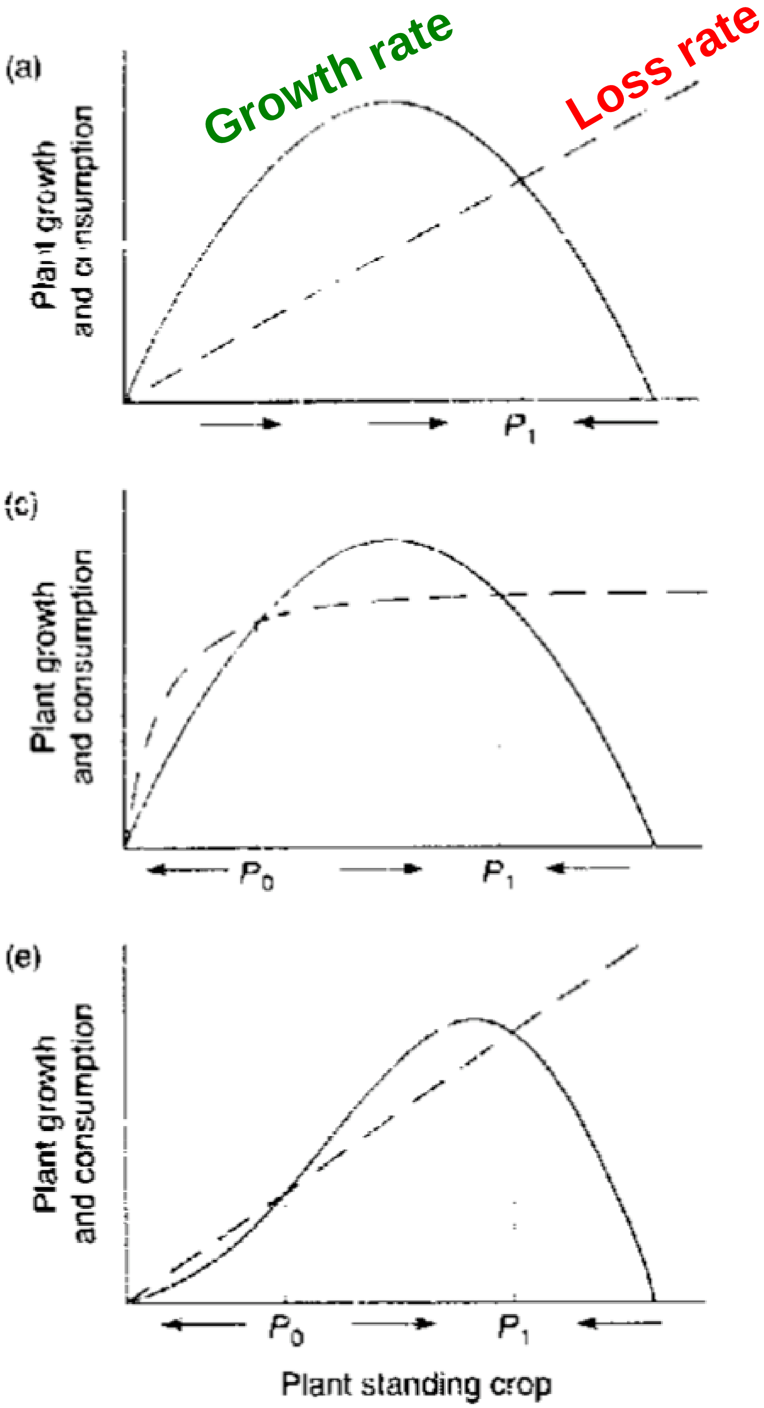
$$W^*(P) = W_{in}\frac{P + aq}{P + a} \cdot \frac{1}{e + uP}$$

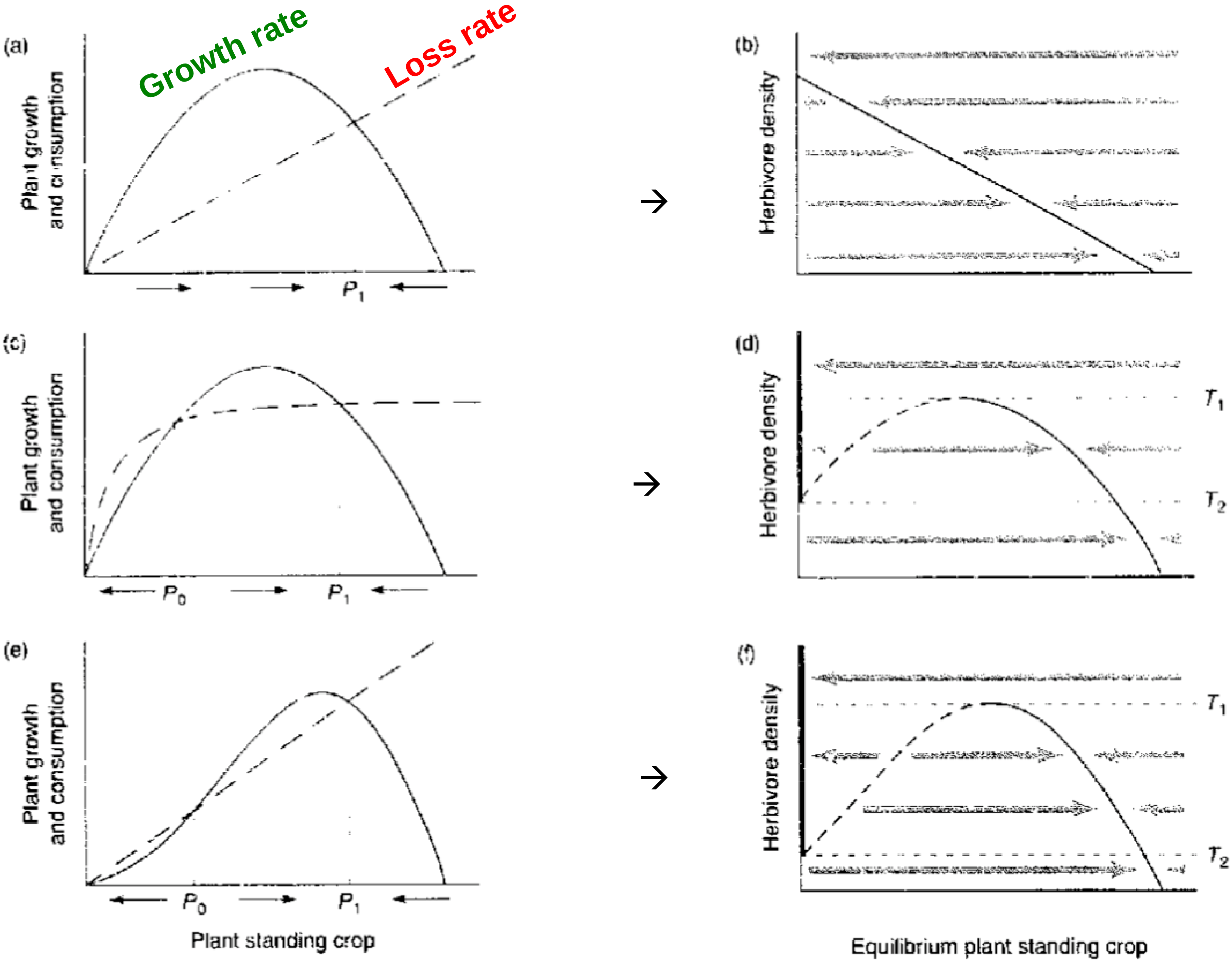
Insertion of $W^*(P)$ into the function f yields the plant growth curve:

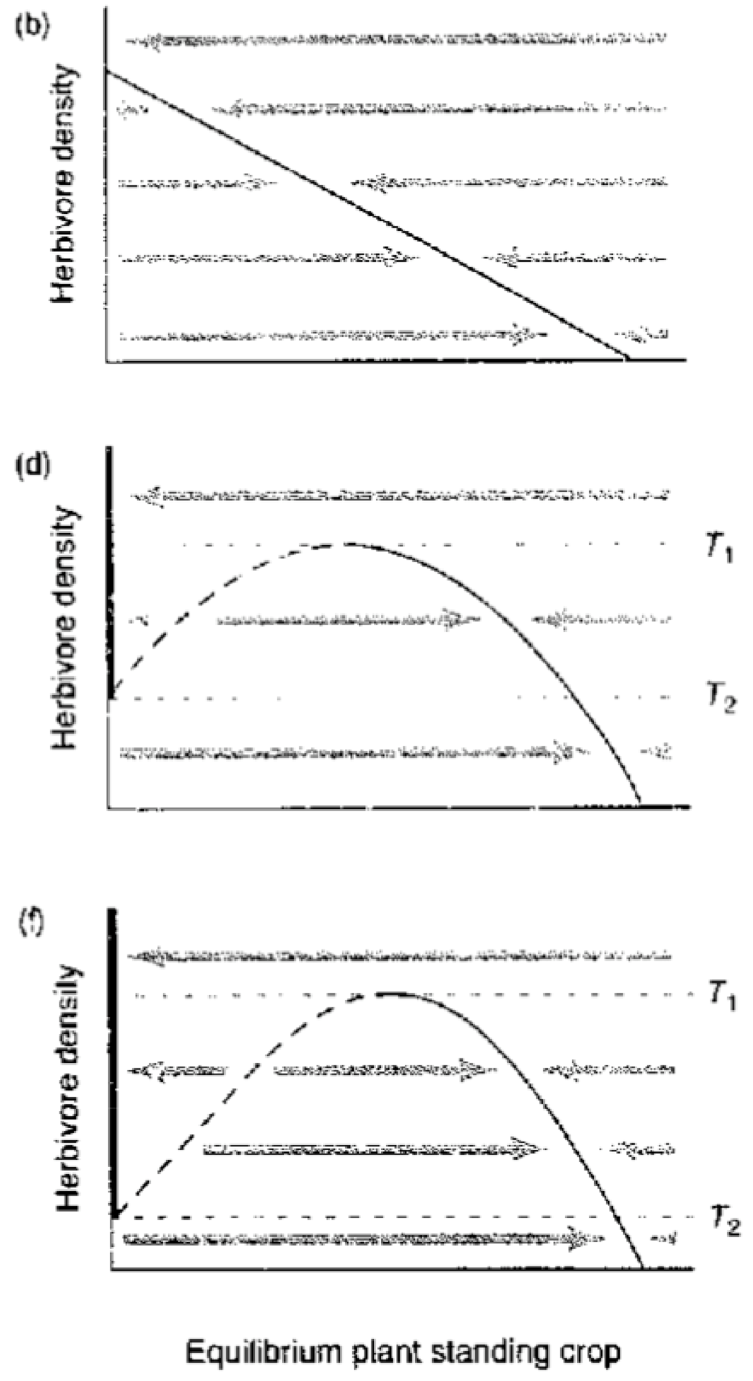
$$G(P) = rP(1 - \frac{P}{K})f[W^*(P)]$$

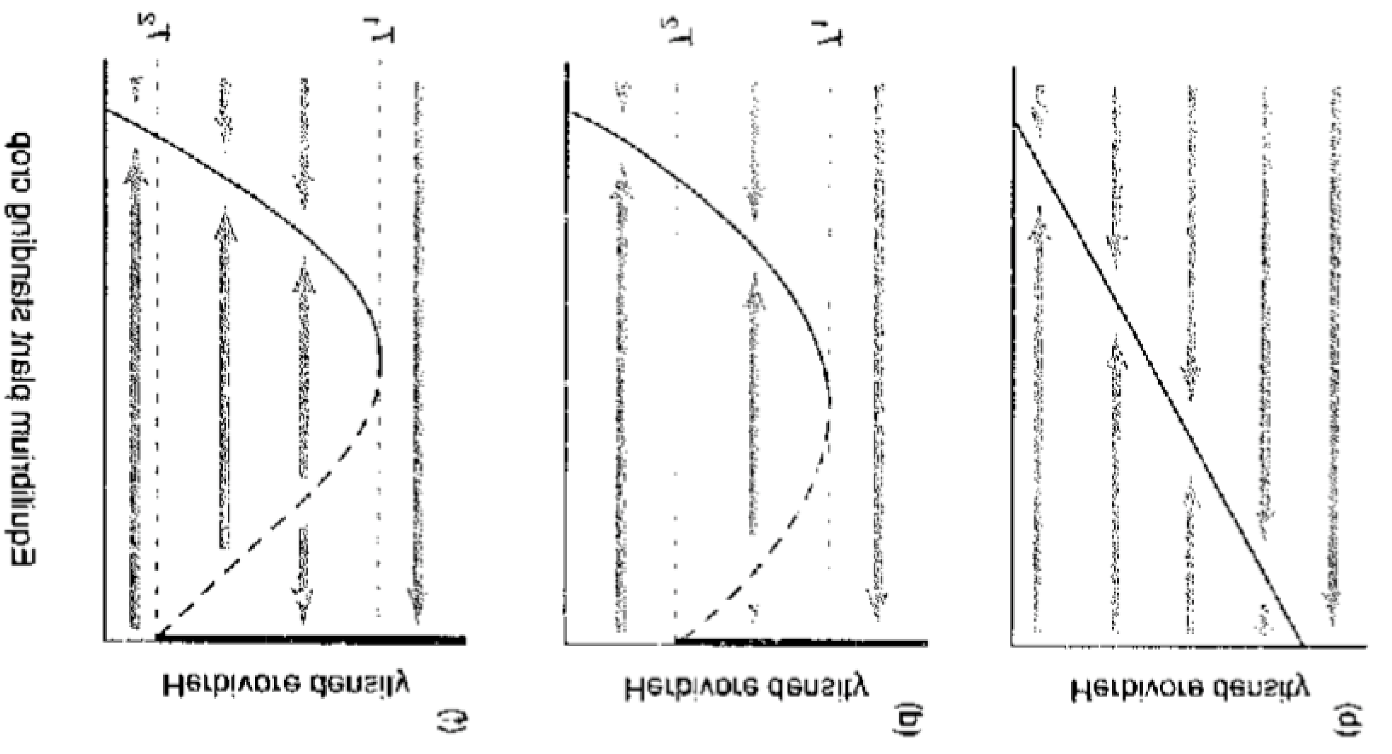
which resembles the growth curve in Fig. 1e. Hence, multiple stable states and catastrophic changes between states are possible if water infiltration is positively related to plant standing crop. An alternative representation is given in the figure below which shows per capita growth $[G(P)/P]$ and losses $[C(P)/P]$ as a function of plant standing crop. The per capita rate of plant growth is reduced due to water limitation, relative to a model without soil feedback (obtained if $a = 0$).


growth without soil feedback
losses
growth with soil feedback
Per capita plant growth and losses
Plant standing crop
K

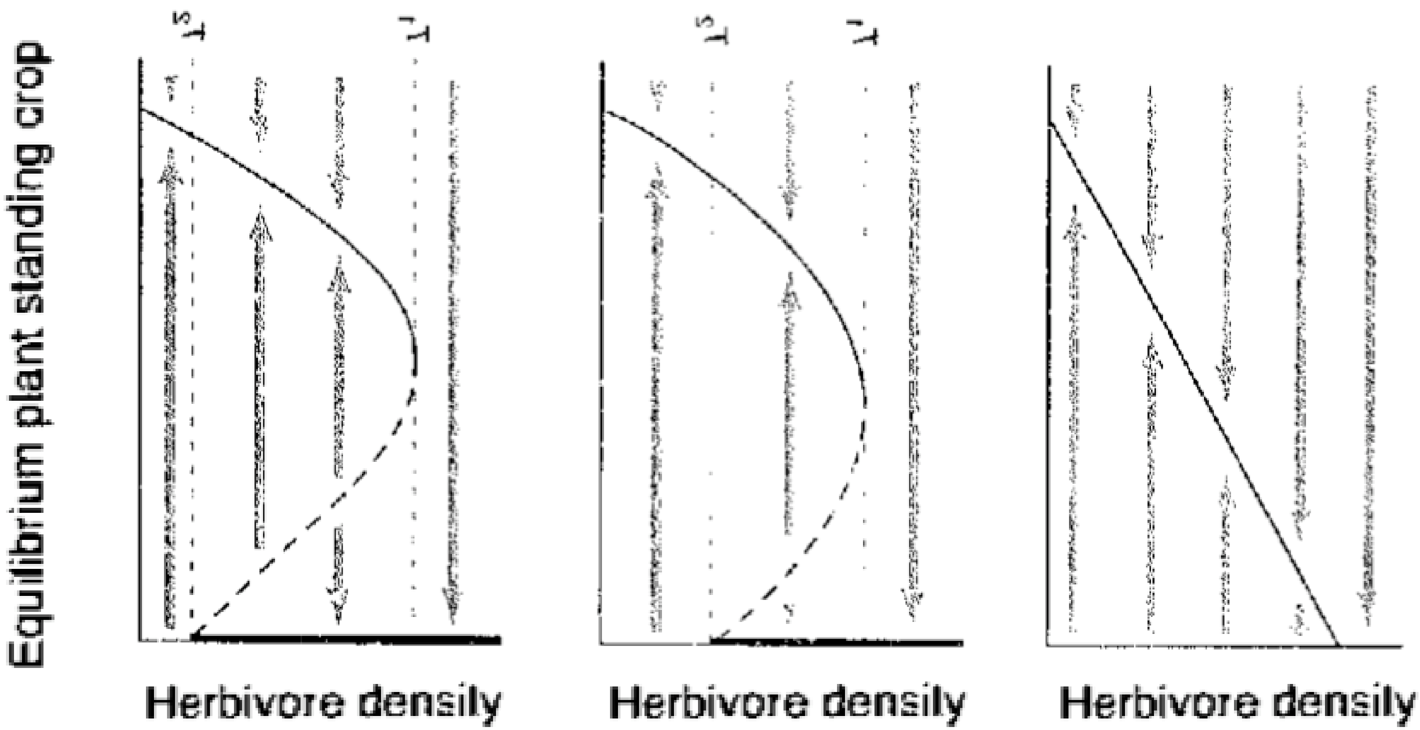

(a)
Growth rate
Loss rate
Plant growth and consumption
P_1
(c)
Plant growth and consumption
P_0
P_1
(e)
Plant growth and consumption
P_0
P_1
Plant standing crop


Growth rate
Loss rate
(a)
Plant growth and consumption
P_1
(b)
Herbivore density
(c)
Plant growth and consumption
P_0
P_1
(d)
Herbivore density
T_1
T_2
(e)
Plant growth and consumption
P_0
P_1
Plant standing crop
(f)
Herbivore density
T_1
T_2
Equilibrium plant standing crop

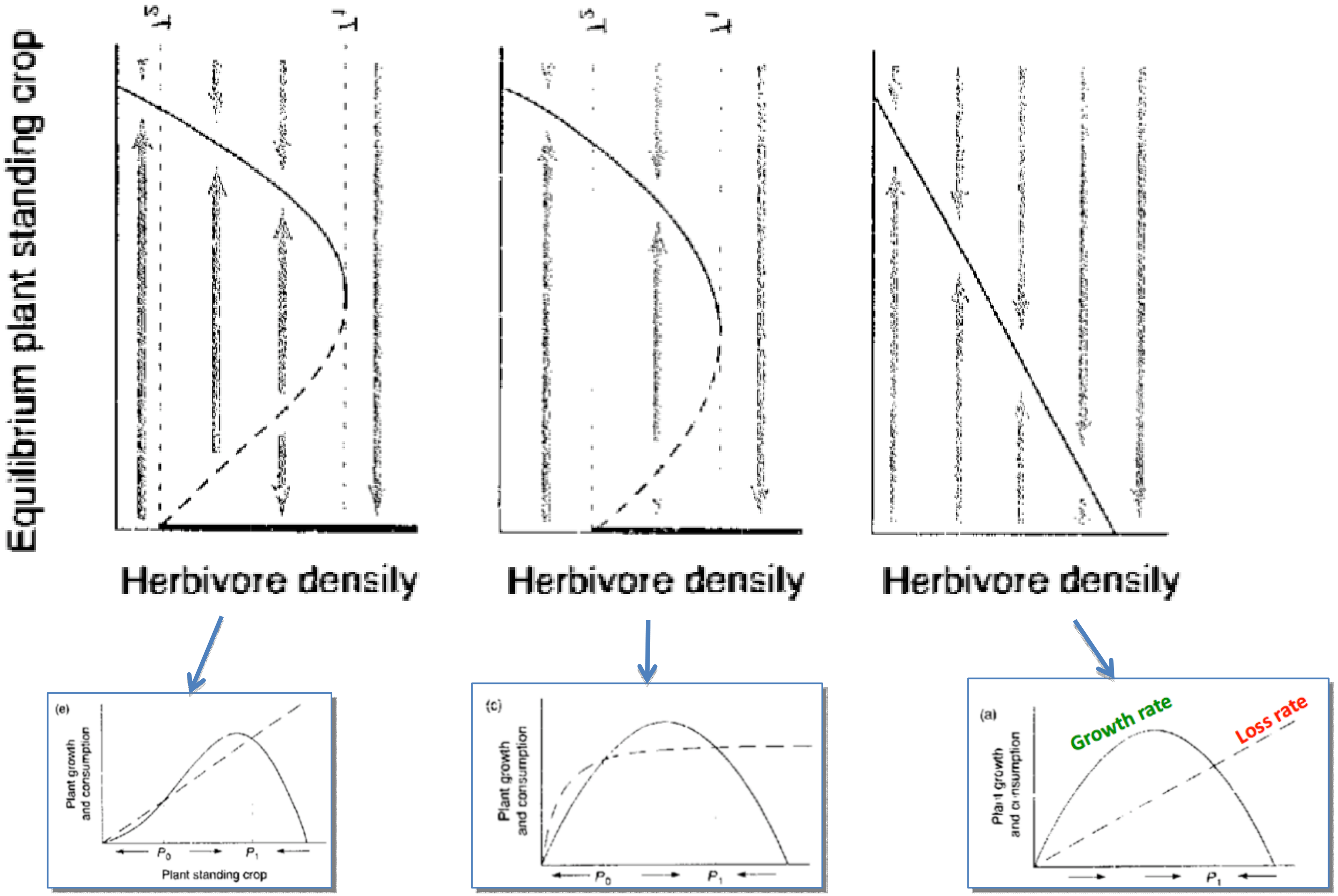

(b)
Herbivore density
(d)
Herbivore density
T_1
T_2
(f)
Herbivore density
T_1
T_2
Equilibrium plant standing crop

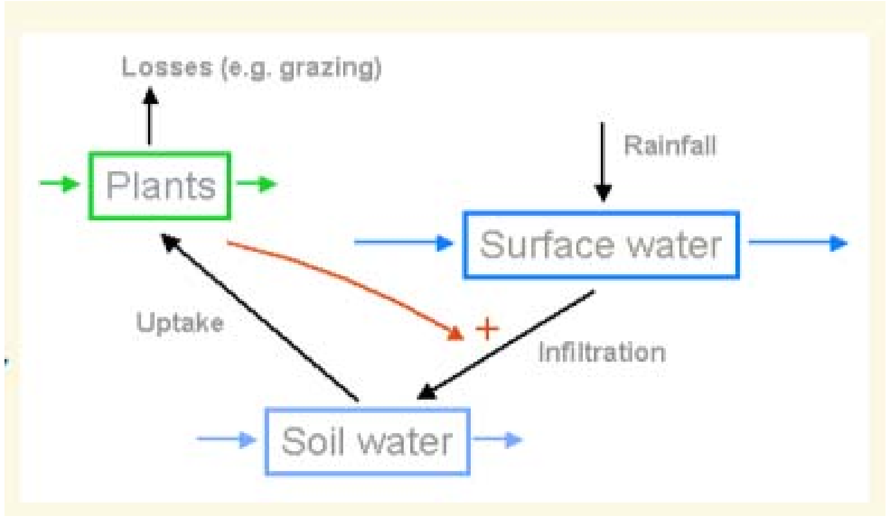

Equilibrium plant standing crop
Herbivore density
T_1
T_2
Herbivore density
T_1
T_2
Herbivore density

« Bifurcation diagram »



« Bifurcation diagram »





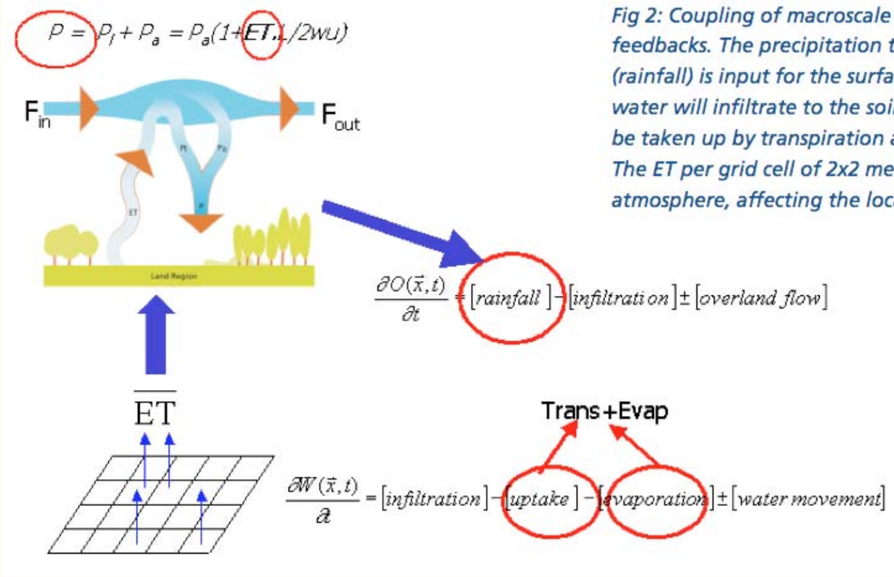


Fig 2: Coupling of macroscale and microscale feedbacks. The precipitation that falls on the land (rainfall) is input for the surface water (O). Surface water will infiltrate to the soil water (W), which can be taken up by transpiration and evaporation (ET). The ET per grid cell of 2x2 meter feedbacks to the atmosphere, affecting the local precipitation (P_l).