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PATTERNS OF HERBIVORY ALONG A PRODUCTIVITY GRADIENT: AN EMPIRICAL AND THEORETICAL INVESTIGATION¹

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Abstract. According to classical exploitation theory, an increase of primary productivity should result in increased herbivore grazing pressure, thus maintaining a low plant standing crop. However, field data obtained from a salt marsh revealed a maximal grazing pressure by hares, rabbits, and geese at intermediate levels of plant standing crop. Grazing pressure was relatively low in the more productive parts. We argue that this pattern is due to a low foraging efficiency of these herbivores in dense vegetation. In order to investigate this hypothesis, we examine a plant–herbivore model where grazing becomes less efficient in dense vegetation, and analyze the behavior of this model along a gradient of primary productivity. In systems of intermediate productivity, the model predicts that a plant–herbivore system may have two stable states. In one state, the herbivore maintains a low standing crop. The other state is dominated by a dense vegetation unsuitable for herbivore grazing. In systems of high productivity, the herbivore is unable to keep plant growth in check and a dense vegetation develops. Thus, in line with our field data but in contrast to classical exploitation theory, our model does not predict “top-down” control in productive environments.

Key words: *foraging efficiency; functional response; geese; hare; herbivory; multiple stable states; plant–herbivore model; predator–prey theory; primary productivity; rabbit; salt marsh.*

INTRODUCTION

Many models relating community structure to ecosystem functioning predict “top-down” control along a gradient of primary productivity (e.g., Hairston et al. 1960, Fretwell 1977, Oksanen et al. 1981, DeAngelis 1992). At low productivity, the vegetation is too sparse to support herbivores. At intermediate productivity, plant biomass is kept at a low level by herbivores. Any increase of primary productivity results in an increase of grazing intensity without enhancing plant biomass. The vegetation is relieved from herbivore control when productivity is high enough to support a carnivore population.

These predictions are not always compatible with field observations, and at the moment the topic of top-down control is hotly debated (e.g., Leibold 1989,

Ginzburg and Akçakaya 1992, Oksanen et al. 1992, Abrams 1993, 1994). In this paper, we report on a natural productivity gradient where herbivores were unable to control plant standing crop. At high levels of primary productivity we found a dense vegetation but a low herbivore grazing pressure, even though large carnivores were absent.

The paper is organized as follows. First, we give a brief description of our study area: a natural productivity gradient along a salt marsh grazed by rabbits, hares, and geese. Then we document the patterns of plant standing crop and herbivore grazing pressure observed in this area. We argue that a low foraging efficiency in dense vegetation causes the observed decline in herbivore grazing pressure with increased primary productivity. This inspired us to reexamine standard plant–herbivore models where we incorporate a reduction of the foraging efficiency of the herbivores at high plant standing crop.

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FIELD STUDY

Study area

Our study was performed on the salt marsh of the island of Schiermonnikoog, The Netherlands. This island extends gradually to the east, which offers a good opportunity to study relations between vegetation succession and herbivory, since various stages of salt marsh development are situated next to each other (De Leeuw et al. 1993, Olff 1992). At the moment, the salt marsh ranges from 0 to >100 yr of age, over a distance of ≈ 6 kilometers. During the course of succession, nitrogen accumulates in the system. The earliest successional stages are characterized by a sparse vegetation and a very low nitrogen content of the soil. The older stages are covered with a dense vegetation and have a large pool of soil nitrogen (Olff 1992). Hence, this successional sequence constitutes a natural productivity gradient.

Several vertebrate herbivores forage on the salt marsh. Barnacle geese (*Branta leucopsis*) use the salt marsh in winter and early spring, whereas brent geese (*Branta bernicla bernicla*) are mainly present in April and May. Hares (*Lepus europaeus*) and rabbits (*Oryctolagus cuniculus*) graze on the salt marsh during the whole year.

Natural enemies of these herbivores are scarce. Geese do not suffer from predation on this island. There is some predation of hares and rabbits by raptors, and occasional hunting by humans. However, mortality due to predation seems low for these lagomorph species, and does not show a clear pattern along the productivity gradient.

Methods

Six locations along the productivity gradient were selected. The age of these locations was estimated at about 3, 10, 25, 35, 65, and 100 yr, based on aerial photographs and old maps (Olff 1992). At these locations, we described both vegetation characteristics and herbivore grazing pressure.

We sampled aboveground biomass in June 1994. Within each location, we chose two subsites and at each subsite took three vegetation samples of 80×10 cm each. These samples were sorted by hand into dead and living biomass, and weighed to the nearest 0.1 g after being dried at 70°C. Canopy height was determined using a polystyrene disc (120-g mass, 15-cm radius) that slid along a graduated stick and was allowed to come to rest 10 times on the canopy. The distance between the disc and the ground surface was measured to the nearest centimetre. When necessary, these data were log-transformed prior to statistical analysis in order to improve the homogeneity of variances.

At each location, we measured grazing pressure by collecting dung-droppings along two parallel rows of 10–13 circular sample points of 4 m² each. The droppings were collected from November 1993 until No-

vember 1994 at about weekly intervals, but only every 3 wk after June 1994. Dropping density is commonly regarded as a proper estimate for goose grazing pressure (Owen 1971). Rabbit dropping density is positively correlated with rabbit density (Wood 1988). The droppings were collected separately for geese, hares, rabbits, and unidentified lagomorphs. The last category accounted for 11% of all hare and rabbit droppings, and was excluded from the analysis. Barnacle geese and brent geese used the area at different times of the year: all goose droppings found between 18 April and July were regarded as brent goose droppings, whereas all others were considered barnacle goose droppings. For each sample point, the number of droppings was expressed as the sum of all counted droppings over the whole year. We used regression on the basis of generalized linear modeling, assuming a Poisson error distribution, to analyze these count data (Crawley 1993). The regression was performed stepwise, with forward addition of higher order terms. In order to avoid pseudoreplication, only the mean number of droppings per location was used for the statistical analysis.

Results

Aboveground living biomass (standing crop) increased with salt-marsh age (Fig. 1A: $Y = 216 \log X - 61$; $F_{1,10} = 41.3$, $P < 0.001$, $R^2 = 0.80$). The amount of standing dead material increased with standing crop (Fig. 1B: $Y = 15.5 e^{0.0065X}$; $F_{1,10} = 21.0$, $P < 0.01$, $R^2 = 0.68$), but the ratio between dead and living plant biomass did not change significantly (Spearman rank correlation: $r_s = 0.15$, $n = 12$, NS). Canopy height increased with standing crop (Fig. 1C: $Y = 4.2 e^{0.0045X}$; $F_{1,10} = 7.8$, $P < 0.02$, $R^2 = 0.44$).

Number of droppings of both hares and rabbits increased when standing crop increased to moderate levels, but decreased significantly at higher plant standing crop (Fig. 2A, B; Poisson regressions: hares: $Y = \exp(-0.0000427X^2 + 0.0180X + 0.901)$, $\chi^2_2 = 12.0$, $P < 0.01$, $R^2 = 0.53$; rabbits: $Y = \exp(-0.000398X^2 + 0.165X - 13.6)$, $\chi^2_2 = 56.9$, $P < 0.001$, $R^2 = 0.81$). The total number of goose droppings was also maximal at intermediate levels of standing crop (Fig. 2C: Poisson regression: $Y = \exp(-0.0000223X^2 + 0.00980X + 2.22)$, $\chi^2_2 = 7.9$, $P < 0.02$, $R^2 = 0.61$). When the two goose species were analyzed separately, no significant relation with standing crop could be established, probably due to the low number of droppings per species.

Interpretation of field data

We found a maximal grazing pressure by hares, rabbits, and geese at intermediate levels of standing crop. Although plant biomass in the older and more productive part of the salt marsh is relatively high, the canopy is tall and there is a lot of litter. The grazing pressure in this stage turned out to be low. A somewhat similar pattern was found on arctic salt marshes in Canada (Cargill and Jefferies 1984, Ruess et al. 1989), where

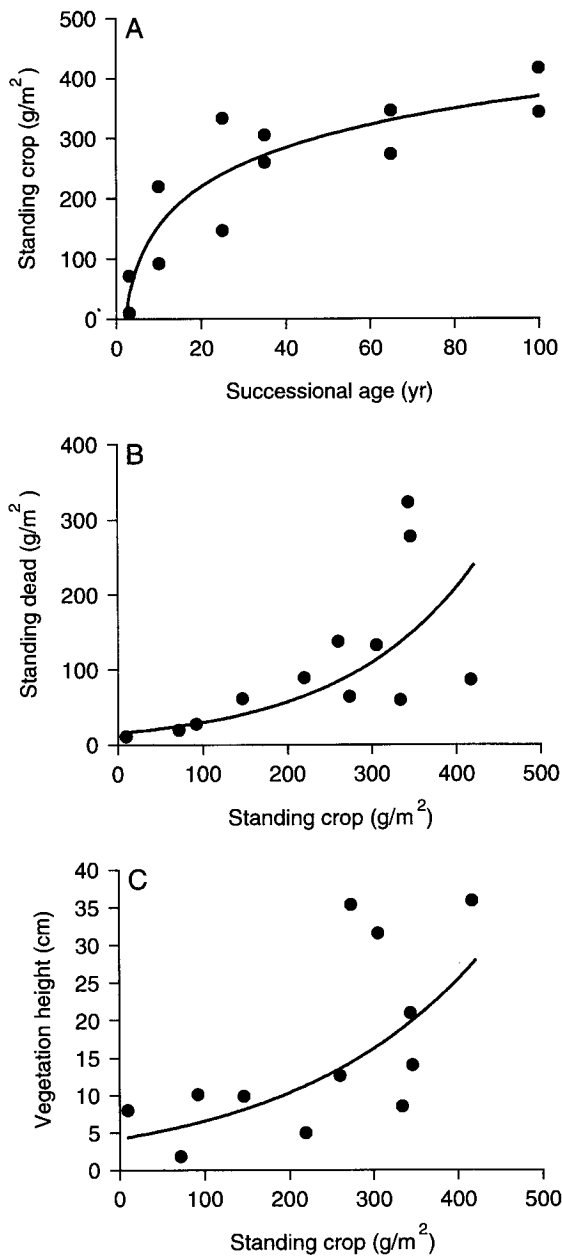


Fig. 1. (A) Aboveground living biomass (standing crop) in relation to successional age. (B) Standing dead plant material in relation to standing crop. (C) Vegetation height in relation to standing crop. The curves are based on linear regression after appropriate data transformation.

goose grazing was more intense in short *Puccinellia-Carex* vegetation than in dense and tall *Calamagrostis* swards.

As in any descriptive study, there are several hypotheses that can be invoked to explain the observed pattern. It seems reasonable, however, to assume that these differences in grazing pressure are related to the profits that herbivores can gain from grazing. Several

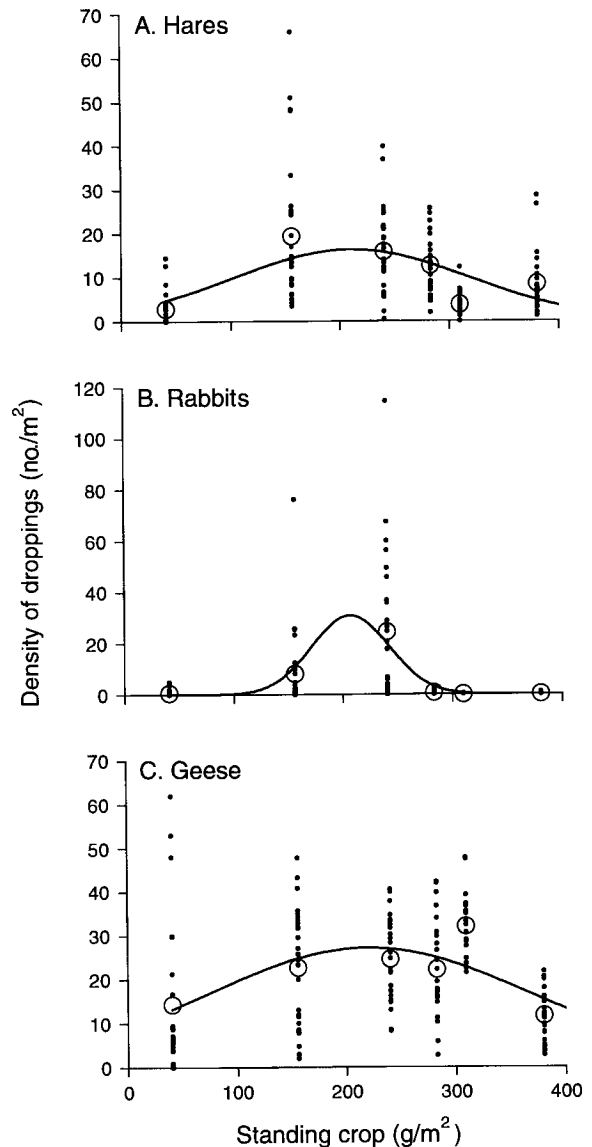


Fig. 2. Number of droppings of (A) hares, (B) rabbits, and (C) geese (barnacle goose and brent goose combined) collected over 1 yr in relation to vegetation standing crop. ● individual observations, ○ mean per site. The curves are based on Poisson regression over the means only.

papers report a decrease of foraging efficiency with increased standing crop (e.g., Arnold 1963, Stobbs 1973b, Chacon et al. 1978, Parsons et al. 1983, McNaughton 1984). A variety of mechanisms may be responsible for this decline. For example, competition for light will favor investment in structural tissues like stems. This may cause a reduction in protein content, palatability, and intake rate (e.g., Stobbs 1973a, Ludlow et al. 1982, Fryxell 1991, Wilmshurst et al. 1995). Aboveground litter accumulation may decrease the quality of the forage (e.g., Bakker et al. 1983, Bazely and Jefferies 1986). Herbivores may be more vigilant

in dense vegetation because of the potential presence of predators, and thus spend less time foraging (e.g., Underwood 1982, Lagory 1986, Loughry 1993). In tall vegetation, many leaves may be difficult for small herbivores to reach. Some herbivores may have difficulties in penetrating dense vegetation, and so on. Note that these mechanisms are related to changes in species composition of the vegetation, but more specifically to changes in vegetation structure.

Surprisingly, the consequences of a reduced foraging efficiency in dense vegetation have hardly been investigated theoretically. In most plant-herbivore models, the foraging efficiency of herbivores is simply assumed to increase with an increase of the standing crop. (There are some exceptions in other predator-prey models. Freedman and Wolkowicz (1986), for example, analyze the case where carnivores are less efficient at high herbivore densities due to group defense.) In the next section, we examine a plant-herbivore model in which herbivores become less efficient in dense vegetation, and analyze the behavior of this model along a gradient of primary productivity.

A SIMPLE MODEL

A vast body of literature exists on models describing plant-herbivore or other predator-prey interactions (see, e.g., Yodzis 1989, DeAngelis 1992). These models are often based on the same general structure. Let P and H denote the plant and herbivore density, respectively. The rate of change of both populations is represented by the differential equations:

$$\frac{dP}{dt} = f(P) - c(P)H, \quad (1a)$$

$$\frac{dH}{dt} = g(P)H, \quad (1b)$$

where $f(P)$ describes plant growth as a function of plant density, $c(P)$ is the per-capita consumption rate of the herbivore (also called the functional response), and $g(P)$ is the per-capita growth rate of the herbivore population (the numerical response). It is typically assumed that both the functional and the numerical response are monotonically increasing functions of plant density. This leads to the standard top-down behavior described in the *Introduction*. However, our data suggest that foraging efficiency is reduced at high standing crop, for instance due to the reduced palatability of plant material in tall vegetation. We analyze two versions of the system described in Eq. 1 in which this effect is incorporated. In one version we only consider the effect of a reduced digestion efficiency. Even when the consumption rate is not affected, a reduction of digestive efficiency may result in a reduced growth rate of the herbivore. In the other version, we also consider a reduction of the consumption rate of the herbivore, e.g., when it is more difficult to select high-quality

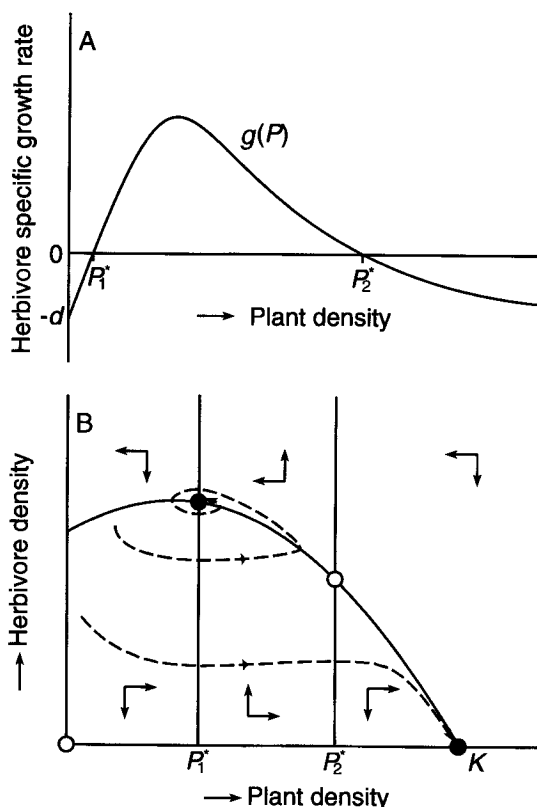


Fig. 3. (A) Per-capita growth rate of the herbivore population as a function of plant density. Herbivore growth equals zero at the plant densities P_1^* and P_2^* . (B) The plant isocline and the two herbivore isoclines in the plant-herbivore plane. Arrows indicate the direction of change. ○ unstable equilibria; ● stable equilibria. Two trajectories, with different initial conditions, are shown by dashed lines.

plant parts or when herbivores are more vigilant in dense vegetation.

Reduced digestion efficiency

Suppose that the per-capita growth rate of the herbivore declines at high plant densities due to for instance a reduced digestion efficiency (Fig. 3A). Then there may be two plant densities, P_1^* and P_2^* , at which the herbivore growth rate equals zero. One might say that below P_1^* the herbivores are limited by the amount of forage, while above P_2^* the quality of the forage limits herbivore growth.

A specific example of such a system is presented in the following model:

$$\frac{dP}{dt} = rP \left(1 - \frac{P}{K} \right) - c_{\max} \frac{P}{a + P} H \quad (2a)$$

$$\frac{dH}{dt} = \left(e_{\max} \frac{P}{a + P} e^{-bP} - d \right) H. \quad (2b)$$

Here plant growth is described by the logistic equation, the per-capita consumption rate of the herbivore is modeled by a saturating functional response (Holling

1959, Type II), consumption is translated into growth by the term $e_{\max}e^{-bP}$, and d is the herbivore mortality rate. In this formulation, we assume that the consumption rate of the herbivore is a monotonically increasing function of plant density. Note, however, that we have incorporated a negative relation between plant density and digestion efficiency by reducing the herbivore growth rate by a factor e^{-bP} .

The dynamics of this simple plant–herbivore model can be analyzed by standard phase-plane methods (e.g., Edelstein-Keshet 1988). In Fig. 3B, we have depicted the plant isocline (given by $dP/dt = 0$) and the herbivore isoclines (given by $dH/dt = 0$) in the plant–herbivore plane. The plant isocline is given by the bent curve. Plant density increases for all combinations of P and H below the plant isocline, while it decreases for all combinations above the plant isocline. There are two vertical herbivore isoclines: one at $P = P_1^*$ and another at $P = P_2^*$. The herbivore population decreases for all plant densities below P_1^* and above P_2^* , and increases for all plant densities between P_1^* and P_2^* .

The plant isocline may intersect the herbivore isoclines in two interior equilibria, called (P_1^*, H_1^*) and (P_2^*, H_2^*) , respectively. In the Appendix, it is shown that the equilibrium (P_1^*, H_1^*) is locally stable if the slope of the plant isocline is negative at the intersection of the plant isocline and the herbivore isocline. If the slope of the plant isocline is positive, this equilibrium is unstable. The equilibrium (P_2^*, H_2^*) is always unstable. There is also a plant equilibrium without herbivores at $(K, 0)$. This equilibrium is stable if K is smaller than P_1^* or larger than P_2^* , but not in between (Appendix). Fig. 3B shows that the system may have two stable states. Depending on the initial conditions, the dynamics either lead to the plant–herbivore equilibrium (P_1^*, H_1^*) or to the plant equilibrium $(K, 0)$.

The system given by Eq. 2 provides us with some explicit predictions about the behavior of plant–herbivore systems in habitats that differ in primary productivity. In the absence of herbivory, an increase in primary productivity is likely to result in an increase in plant density. Following the usual approach (e.g., Rosenzweig 1971), we therefore equate primary productivity with the maximum attainable standing crop K . The behavior of the model at different values of the maximum standing crop K is illustrated in Fig. 4. At values of K below P_1^* only plants can persist. The standing crop is too low to support a herbivore population (Fig. 4A). Hence, for all initial conditions, the system converges to the plant equilibrium. Whenever K is between P_1^* and P_2^* (Fig. 4B), the herbivore is able to invade. For all initial conditions, the system converges to the plant–herbivore equilibrium. At values of K above P_2^* , there are two stable equilibria (Fig. 4C, D). Depending on the initial conditions, the system either converges to the plant–herbivore equilibrium or to a dense vegetation without herbivores. Interestingly, the domain of attraction of the plant–herbivore equi-

librium becomes smaller with increasing K . This implies that at high primary productivity, perturbations may easily bring the system from the plant–herbivore state into the domain of attraction of the dense-vegetation state. This results in a collapse of the plant–herbivore system. An increase of K also shifts the top of the plant isocline farther to the right. As soon as the top appears at the right-hand side of the herbivore isocline at $P = P_1^*$, the plant–herbivore equilibrium (P_1^*, H_1^*) becomes unstable and limit cycles occur (Fig. 4E; see also Appendix). However, limit cycles remain small and only exist in a limited region of the parameter space. At still higher values of K , limit cycles are absent and the system always evolves to a dense vegetation without herbivores (Fig. 4F).

Instead of the factor e^{-bP} in Eq. 2b, we also considered a few other formulations that reduce herbivore growth at high plant densities (e.g., a linear or sigmoid relation). These formulations led to qualitatively similar results. A crucial aspect of the model, however, is that the herbivore population growth rate becomes negative at high plant densities. If herbivore population growth declines with increased standing crop but still remains positive, the point P_2^* does not exist. In this case, multiple stable states do not occur and the system always remains in the plant–herbivore state.

Reduced consumption rate

Suppose that an increase of the standing crop is accompanied by a reduction of the consumption rate. This may be the case when, for instance, herbivores become more vigilant because of potential predators, or when tall and dense stands are more difficult to handle. It seems reasonable to assume that a reduced consumption rate also would lead to a reduced per-capita growth rate of the herbivore, as in the following model:

$$\frac{dP}{dt} = rP \left(1 - \frac{P}{K} \right) - c_{\max} \frac{P}{a + P} e^{-bP} H \quad (3a)$$

$$\frac{dH}{dt} = \left(e_{\max} \frac{P}{a + P} e^{-bP} - d \right) H \quad (3b)$$

This model exhibits a behavior qualitatively similar to that of the previous model (Fig. 5). For values of K above P_2^* , two stable equilibria may occur. Again, the domain of attraction of the plant–herbivore equilibrium becomes smaller with increasing K . At high values of K , the plant–herbivore state no longer exists.

There is, however, a quantitative difference between this model and the model discussed in the previous section. This model shows a stronger decline of the domain of attraction of the plant–herbivore equilibrium with increasing K than the previous one. Furthermore, the plant–herbivore equilibrium becomes unstable at lower values of K . In other words, a reduction of the consumption rate results in an even stronger feedback between enhanced plant growth and reduced herbivory than a reduction of the digestion efficiency.

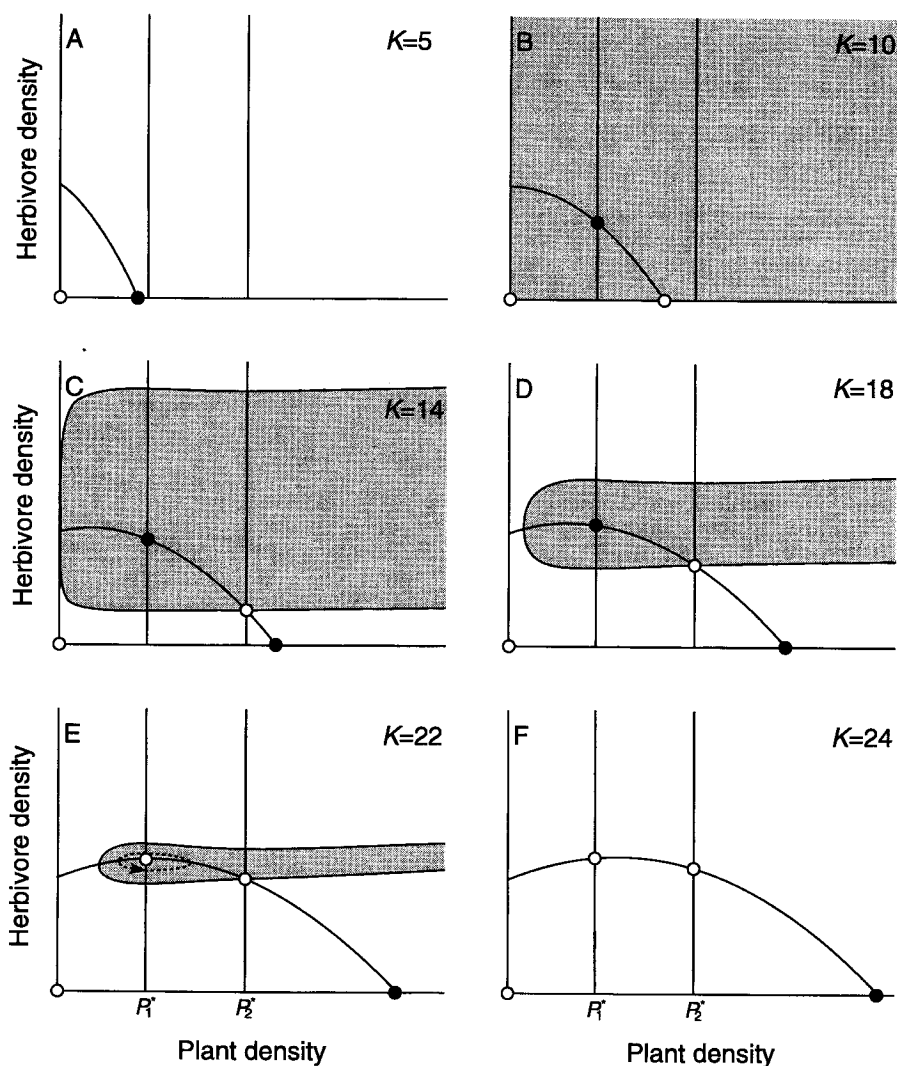


Fig. 4. Phase-plane representations of the plant-herbivore system (Eq. 2a, b) at various values of the maximum standing crop K . ○ unstable equilibria; ● stable equilibria. Shaded areas indicate the domain of attraction of the plant-herbivore equilibrium. Open areas indicate the domain of attraction of the plant equilibrium. Parameter values for graphs A–F (Eq. 2): $r = 1$; $c_{\max} = 1$; $a = 10$; $b = 0.065$; $e_{\max} = 0.4$; $d = 0.1$.

Summary of model results

When the maximum standing crop K is below P_1^* , the vegetation cannot support a herbivore population (Fig. 6B). An increase of K only leads to an increase of the plant density (Fig. 6A). For values of K between P_1^* and P_2^* , plant density is controlled by the herbivores. They maintain the plant density at a constant level. Any increase of K only leads to an increase of the herbivore density without enhancing plant biomass. When K is above P_2^* , two alternative stable states exist. One state contains both plants and herbivores, the other state consists of only the plant population. There is a small region where limit cycles occur. As K is increased further, the vegetation escapes from herbivore control and the herbivores are no longer able to persist. Any

increase of K leads to a further increase of the plant density.

DISCUSSION

Classical exploitation theory (e.g., Hairston et al. 1960, Rosenzweig 1973, Oksanen et al. 1981, DeAngelis 1992) predicts that herbivores are able to maintain plant density at a low level, unless carnivores relieve the vegetation from herbivore control. The data we present, however, reveal a different pattern. In our study area, plant standing crop increased along a natural productivity gradient, and herbivore grazing pressure was maximal at intermediate levels of productivity. The vegetation was relieved from herbivore control in productive environments, even though large carni-

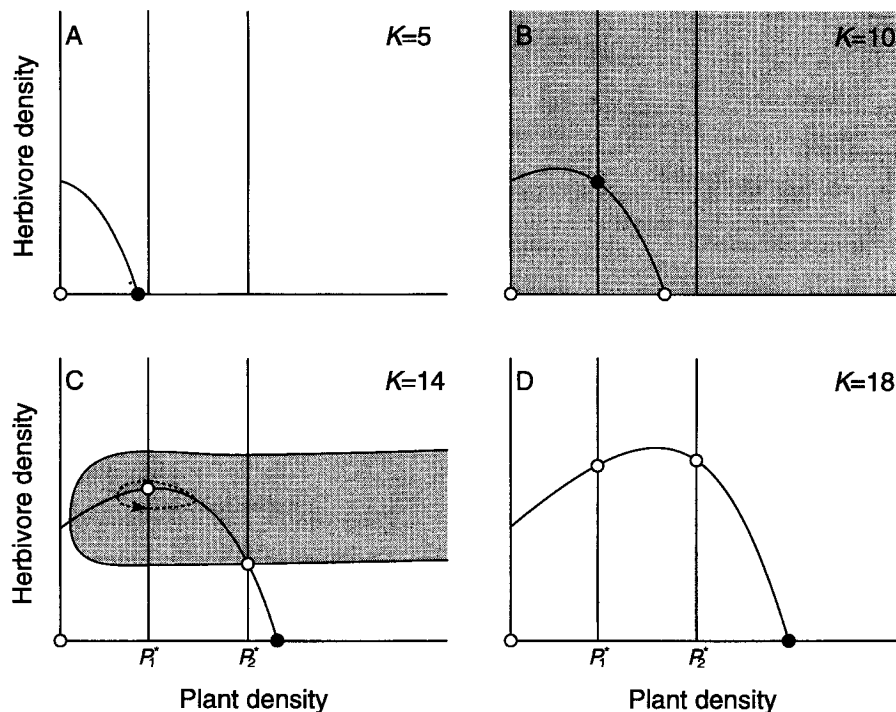


Fig. 5. Phase-plane representations of the plant-herbivore system (Eq. 3a, b) at various values of the maximum standing crop K . Symbols as in Fig. 4. Parameter values for graphs A–D (Eq. 3): $r = 1$; $c_{\max} = 1$; $a = 10$; $b = 0.065$; $e_{\max} = 0.4$; $d = 0.1$.

vores were absent. The model examined in this paper puts forward a hypothesis that explains this pattern. For a number of herbivore species, grazing may become less efficient at high plant standing crop (e.g., Arnold 1963, Underwood 1982, Bakker et al. 1983, Fryxell 1991). Especially in productive environments, this will lead to a strong feedback between reduced herbivory and enhanced plant growth. As a consequence, the herbivores would be unable to keep plant growth in check, and a dense vegetation would develop. In other words, in contrast to classical exploitation models, our model does not predict “top-down” control in productive environments. This corresponds to our field observations.

The model also predicts that a reduction of grazing efficiency at high standing crop favors the existence of two stable states. In one state, the herbivore population maintains a low standing crop. The other state is dominated by a dense vegetation unsuitable for herbivore grazing. The theoretical possibility of multiple stable states has been recognized by many authors (e.g., Noy-Meir 1975, May 1977, Dublin et al. 1990, Law and Morton 1993, Scheffer et al. 1993). Several empirical studies indicate that multiple stable states can also be found in natural plant-herbivore systems.

For example, the echinoid species *Diadema antillarum* was once the most abundant herbivore on many Caribbean coral reefs. Mass mortality of *Diadema*, due to a pathogen, resulted in a spectacular algal bloom

and an apparently persistent shift from palatable algal turfs to a dominance by macroalgae (Carpenter 1990, Knowlton 1992, Hughes 1994). Many of these macroalgal species are not consumed by herbivores.

Dobson and Crawley (1994) discuss the effects of mass mortality of rabbits, due to the *Myxoma* virus, on oak recruitment at Silwood Park (Great Britain). Before the introduction of the virus in 1953, rabbits feeding on acorns and browsing on oak seedlings maintained an open grassland, even without pasturage of sheep or cattle. After the rabbit population had crashed, oak woodland established. Even though the rabbit population had largely recovered by the end of the 1970s, the established woodland is now immune to the depredations by the rabbit population.

An experimental indication of the existence of multiple stable states in a Canadian salt marsh was obtained by Bazely and Jefferies (1986). They found that feeding by geese maintained a short *Carex-Puccinellia* community. Cessation of grazing by means of herbivore exclosures led to an increase of the standing crop, changed the composition of the plant community, and increased the ratio of dead to living biomass. The high standing crop remained only poorly grazed when the fence was removed again.

These three examples show a transition from a community dominated by grazers to a community largely composed of primary producers. We have not found an example of a transition in the opposite direction, where

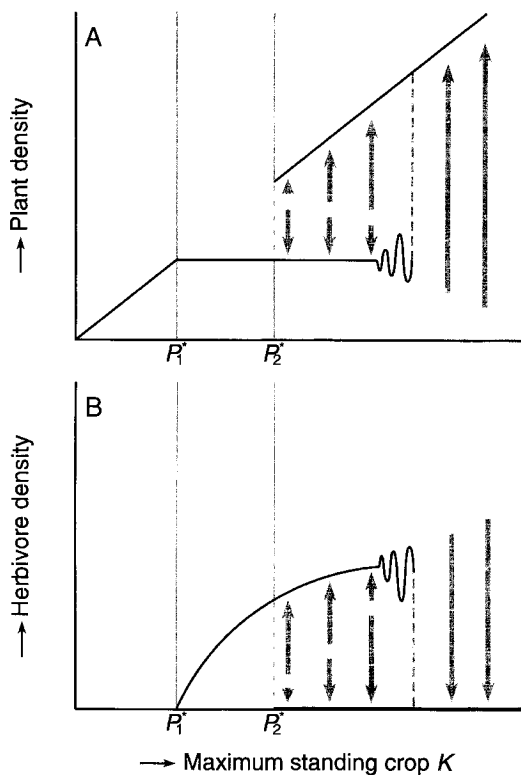


Fig. 6. (A) Plant density and (B) herbivore density as a function of the maximum standing crop K . At intermediate values of K , two stable states are possible (as indicated by the gray arrows).

removal of a dense vegetation enables herbivores to maintain a low standing crop again. Olff (1992), however, reports facilitation of geese by cattle grazing. Cattle were introduced into a >100-yr-old, highly productive part of our salt marsh study area dominated by a dense and tall stand of the grass *Elymus athericus*. The cattle removed the dense vegetation, which in turn led to the reappearance of the geese.

It is clear that the field situations we have discussed are much more complex than the simple model that we have analyzed. For example, our model neglects the patchiness of the vegetation, seasonal changes in primary productivity, herbivore migration, and social behavior of the herbivores. These additional factors may have a large influence on the quantitative predictions of our model. Nevertheless, we expect that the qualitative behavior of the model will remain intact. That is, when grazing efficiency is low in dense vegetation, we may expect multiple stable states in environments of moderate productivity and communities dominated by primary producers in more productive environments.

Both our theoretical and our empirical investigation strengthen the view of Rosenzweig (1971) that plant-herbivore systems can be very vulnerable to nutrient enrichment. However, the mechanism is different (cf.

Freedman and Wolkowicz 1986). In the systems that we have studied, nutrient enrichment is capable of triggering a positive feedback between increased standing crop and reduced herbivory. This feedback may relieve the vegetation from herbivore control. In contrast to Rosenzweig's model, our model predicts that herbivores will be unable to reinvade once the vegetation has developed a dense canopy. Thus, nutrient enrichment may not only destabilize but also permanently destroy a plant-herbivore system.

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APPENDIX

STABILITY ANALYSIS

In order to establish the local stability of the equilibria, we investigate the Jacobian matrix of the system. Following the notation of Eqs. 1a, b, this matrix, J , reads

$$J = \begin{bmatrix} A_{11} & A_{12} \\ A_{21} & A_{22} \end{bmatrix} = \begin{bmatrix} \frac{df}{dP} - \frac{dc}{dP} H^* & -c(P^*) \\ \frac{dg}{dP} H^* & g(P^*) \end{bmatrix},$$

where the asterisks (*) indicate that the matrix is to be evaluated at equilibrium. We consider three equilibria: the boundary equilibrium $(K, 0)$, and the two plant–herbivore equilibria (P_1^*, H_1^*) and (P_2^*, H_2^*) . These equilibria are locally stable if (e.g., Edelstein-Keshet 1988)

$$\text{trace}(J) = A_{11} + A_{22} < 0, \quad (1)$$

and

$$\det(J) = A_{11}A_{22} - A_{12}A_{21} > 0. \quad (2)$$

The boundary equilibrium

If the herbivore is absent and the vegetation at its maximum standing crop (i.e., $H^* = 0$ and $P^* = K$), the stability criteria simplify to $\text{trace}(J) = (df/dP) + g(K) < 0$ and $\det(J) = (df/dP)g(K) > 0$. It is easily verified that, at the boundary equilibrium, $df/dP < 0$. Hence, the boundary equilibrium is stable if $g(K) < 0$ and unstable if $g(K) > 0$. In other words, whenever $P_1^* < K < P_2^*$ (see Fig. 3A), the vegetation density K is suitable for herbivore grazing and the boundary equilibrium $(K, 0)$ is unstable.

The plant-herbivore equilibria

At the plant-herbivore equilibria (P_1^*, H_1^*) and (P_2^*, H_2^*) , the per-capita growth rate of the herbivore is (by definition) zero, i.e., $g(P) = 0$. Hence, the stability criteria simplify to $\text{trace}(\mathbf{J}) = (df/dP) - (dc/dP)H^* < 0$ and $\det(\mathbf{J}) = c(P^*)(dg/dP)H^* > 0$. Since $dg/dP < 0$ at $P = P_2^*$ (see Fig. 3A), while $c(P^*)$ and H^* are both positive, it follows that the equilibrium (P_2^*, H_2^*) is unstable whenever it exists.

Since $dg/dP > 0$ at $P = P_1^*$ (see Fig. 3A), $\det(\mathbf{J}) > 0$ at the equilibrium (P_1^*, H_1^*) . Hence, the stability of the equilibrium (P_1^*, H_1^*) is determined by the sign of $\text{trace}(\mathbf{J})$. This sign depends on the slope of the plant isocline, as in the classical plant-herbivore models (see, e.g., Rosenzweig and MacArthur 1963). That is, the equilibrium (P_1^*, H_1^*) is locally stable when the slope of the plant isocline is negative (right of the peak), while it is locally unstable when the slope is positive (left of the peak).

Existence of a limit cycle

When K is increased, the top of the plant isocline is shifted farther to the right. This destabilizes the plant-herbivore equilibrium (P_1^*, H_1^*) ("paradox of enrichment"; Rosenzweig 1971, Gilpin 1972). At the transition from stable to unstable behavior (i.e., when (P_1^*, H_1^*) is on top of the plant isocline), the eigenvalues are complex since $\text{trace}(\mathbf{J}) = 0$ and $\det(\mathbf{J}) > 0$. Hence, a Hopf bifurcation occurs. This bifurcation ensures the existence of a limit cycle (e.g., Edelstein-Keshet 1988), at least for values of K just above the transition from stability to instability of (P_1^*, H_1^*) . However, in our model the range of K values at which limit cycles occur is rather restricted. A further increase of K leads to a crash of the limit cycle (by a homoclinic bifurcation) when the limit cycle collides with the unstable equilibrium (P_2^*, H_2^*) . Further details of this bifurcation pattern, albeit in a different context, can be found in Wolkowicz (1988).