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Competition and facilitation in multispecies plant-herbivore systems of productive environments

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Abstract

We develop a multispecies plant-herbivore model to explore how plant competition for light and the selectivity of herbivores affect abundance patterns of plants and herbivores along productivity gradients. The model considers a small and a tall plant species, a generalist herbivore, and a selective herbivore. The selective herbivore feeds only on the small plant species. In the absence of the generalist herbivore, the tall plant species becomes increasingly dominant with increasing productivity, and the small plant and its selective herbivore disappear. The model shows that generalist herbivores can facilitate selective herbivores by suppressing competition for light. This favours the small plant species, and thereby the selective herbivores. The model predictions are qualitatively consistent with field studies of multispecies plant-herbivore systems.

Keywords

Biodiversity, competition for light, food webs, geese, grazing, plant-herbivore theory, productivity gradient, resource competition, salt marsh.

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INTRODUCTION

Plant-herbivore theory has been dominated by a theoretical framework that considers only one species per trophic level. However, models with multiple species per trophic level often show much more complicated behaviour than their single-species counterparts (e.g. VanderMeer 1980; Abrams 1993; Wootton 1994; Grover 1995). Multispecies interactions are likely to play an important role in many terrestrial plant-herbivore systems. Here we briefly review a field example, and develop a multispecies plant-herbivore model to support our case.

GRAZERS ON THE ISLAND OF SCHIERMONNIKOOG

In collaboration with our colleagues at Groningen University, we studied the dynamics of plants and herbivores on the island of Schiermonnikoog, one of the major National Parks of The Netherlands (van de Koppel *et al.* 1996; Olff *et al.* 1997; Huisman *et al.* 1998). The salt marsh of this island has developed gradually in an easterly direction. As a consequence various stages of salt-marsh development occur adjacent to each other. The youngest stages in the east have a very low amount of

total soil nitrogen, the major factor limiting plant production (van Wijnen & Bakker 1997). Here the vegetation is sparse and consists of small to intermediate-sized grasses and herbs like *Festuca rubra*, *Limonium vulgare*, *Puccinellia maritima*, and *Plantago maritima*. Many of these plants are the preferred forage species of herbivores (Ydenberg & Prins 1981; Prop & Deerenberg 1991; van der Wal *et al.* 1998), and the younger stages of the salt marsh are extensively grazed by rabbits (*Oryctolagus cuniculus*), hares (*Lepus europaeus*), Barnacle geese (*Branta leucopsis*), and Brent geese (*Branta bernicla*). However, total soil nitrogen and plant standing crop increase with successional age. Within ≈ 40 years of salt-marsh development nearly all plant species of low stature are replaced by the tall grass *Elymus athericus*. *Elymus* is not preferred by rabbits, hares, and geese, as it produces a lot of structural tissue in its leaves and stems that reduce its nutritional quality. The density of hares, rabbits, and geese in the older and more productive parts of the salt marsh dominated by *Elymus* is low (van de Koppel *et al.* 1996; Olff *et al.* 1997; Huisman *et al.* 1998). Recently, free-ranging cattle were introduced on the older stages of the salt marsh. Grazing cattle can consume poor quality forage, and they removed most of the *Elymus* stands.

Table 1 Parameter values used in the model simulations. The soil nutrient level, N , was used as the independent variable, thus establishing a productivity gradient (see Fig. 2). The incident light intensity was set at $I_{\text{in}} = 400 \mu\text{mol photons/m}^2/\text{s}$

Parameter	Meaning	Species		Units
<i>Plants</i>		P_1	P_2	
A_L	allocation to leaves	0.4	0.7	–
M	half saturation constant of nutrient limitation	400	200	mg N/kg soil
p_{max}	maximum rate of photosynthesis	0.07	0.04	day^{-1}
h	half saturation constant of photosynthesis	50	10	$\mu\text{mol photons/m}^2/\text{s}$
k	light extinction coefficient of leaves	0.01	0.03	$\text{m}^2/\text{g leaf}$
l	plant mortality rate	0.01	0.005	day^{-1}
<i>Herbivores</i>		H_1	H_2	
a_{j1}	search rate of herbivore j for plant species 1	0.002	–	$\text{m}^2/\text{g herbivore/day}$
a_{j2}	search rate of herbivore j for plant species 2	0.001	0.002	$\text{m}^2/\text{g herbivore/day}$
c	conversion of leaf biomass into herbivore biomass	0.01	0.01	g herbivore/g leaf
m	herbivore mortality rate	0.002	0.002	day^{-1}

Subsequently, many of the plant species of low stature reappeared in the vegetation. This was followed by a marked increase in the abundance of rabbits, hares, and geese (Olff *et al.* 1997).

This example illustrates two features unique to systems with multiple species per trophic level. Firstly, from the bottom up, soil nutrient accumulation led to plant species replacement, which forced a decline in the abundance of small vertebrate herbivores. Secondly, from the top down, a new large herbivore species removed the tall plants, and the small herbivore species returned.

A MULTISPECIES PLANT–HERBIVORE MODEL

The phenomena described above are readily observed in a simple multispecies plant–herbivore model. We develop a model that considers above-ground plant competition and above-ground herbivory, and extends the theory developed in Huisman *et al.* (1998) from one to two herbivore species. The interactions considered by the model are illustrated in Fig. 1. Let P_1 and P_2 denote the biomass of plant species 1 and plant species 2, respectively. Plant species 1 is tall, and shades plant species 2 which is small. And let H_1 and H_2 denote the biomass of herbivore species 1 and herbivore species 2. Herbivore species 1 is a bulk feeder that grazes upon both plant species. Herbivore species 2 is a selective feeder that feeds only on small plant species 2.

The model assumes that the production rates of the plant species depend on the light availability within their respective plant canopies. The light intensity incident upon the canopy of plant species 1 is denoted by I_{in} . The light intensity $I_{\text{out},1}$ is the light intensity that penetrates through the canopy of species 1. This provides the incident light intensity for plant species 2. A light

Figure 1 The interactions considered in this paper. P_1 is a tall plant species, and P_2 is a small plant species. The bulk feeder H_1 feeds on both plant species, and the selective feeder H_2 feeds only on P_2 . (A) The selective feeder alone. (B) The bulk feeder and the selective feeder together. The direction of interaction is shown as an arrow.

intensity $I_{\text{out},2}$, in turn, penetrates through the canopy of species 2. More precisely, according to Lambert–Beer’s law,

$$I_{\text{out},1} = I_{\text{in}} e^{-k_1 A_{L,1} P_1} \quad (1a)$$

$$I_{\text{out},2} = I_{\text{out},1} e^{-k_2 A_{L,2} P_2} \quad (1b)$$

where k_i is the light extinction coefficient of the leaves, and $A_{L,i}$ is the ratio of leaf biomass to total biomass of plant species i .

The net growth rates of the two plant species are described by:

$$\begin{aligned} \frac{dP_1}{dt} = & \frac{N}{M_1 + N} \frac{p_{\text{max},1}}{k_1} \ln \left(\frac{h_1 + I_{\text{in}}}{h_1 + I_{\text{out},1}} \right) \\ & - l_1 P_1 - a_{11} A_{L,1} P_1 H_1 \end{aligned} \quad (1c)$$

$$\frac{dP_2}{dt} = \frac{N}{M_2 + N} \frac{p_{\max,2}}{k_2} \ln \left(\frac{h_2 + I_{\text{out},1}}{h_2 + I_{\text{out},2}} \right) - l_2 P_2 - a_{12} A_{L,2} P_2 H_1 - a_{22} A_{L,2} P_2 H_2 \quad (1d)$$

Here nutrient limitation is formulated by a Michaelis–Menten term, where N is the soil nutrient level and M_i is the half saturation constant. Light limitation is based on integration of photosynthesis over plant canopy depth using Lambert–Beer’s law (as in Monsi & Saeki 1953; Thornley & Johnson 1990; Huisman & Weissing 1994), where $p_{\max,i}$ and h_i are the maximum photosynthetic rate and the half saturation constant of photosynthesis, respectively. The turnover of plant biomass is described by a plant mortality rate, l_i . The remaining terms describe the consumption of plant biomass by the herbivores, where a_{ji} is the search rate of herbivore species j for the leaves of plant species i .

The growth rates of the two herbivore species read:

$$\frac{dH_1}{dt} = c_1 (a_{11} A_{L,1} P_1 + a_{12} A_{L,2} P_2) H_1 - m_1 H_1 \quad (1e)$$

$$\frac{dH_2}{dt} = c_2 a_{22} A_{L,2} P_2 H_2 - m_2 H_2 \quad (1f)$$

where c_j converts leaf biomass into herbivore biomass, and m_j is the mortality rate of the herbivore. Note that the model assumes a linear functional and numerical response of the herbivores. This simplification is introduced for mathematical convenience. It helps to avoid complicated nonequilibrium dynamics like limit cycles and chaos.

We shall not attempt a formal stability analysis of this dynamical system here. In all our simulations, however, the system approached an equilibrium state that appeared independent of the initial conditions. Figure 2 shows the equilibrium predictions of the model in relation to the soil nutrient level (i.e. along a productivity gradient).

If the selective feeder is present, it maintains the leaf biomass of the small plant species at a constant level. According to eqn 1f, this constant level equals

$$L_2^* = A_{L,2} P_2^* = \frac{m_2}{c_2 a_{22}} \quad (2)$$

This level corresponds to the minimal amount of leaves of plant species 2 that is required for the selective herbivore to persist.

When the selective feeder is alone, the tall plant species is not consumed (Figs 1A, 2A). Because the tall plant is also not affected by the small plant species, the tall plant species increases with increasing soil nutrient level. As a result, the small plant species becomes increasingly shaded by the tall plants, and eventually it is unable to maintain a critical leaf biomass L_2^* . As soon as the leaf biomass of

Figure 2 Equilibrium states of plant and herbivore abundances along a productivity gradient, as predicted by eqn 1(a–f). P_1 is a tall plant species and P_2 is a small plant species. The bulk feeder H_1 feeds on both plant species, and the selective feeder H_2 feeds only on P_2 . Parameter values are given in Table 1. (A) The selective feeder alone. (B) The bulk feeder and the selective feeder together.

plant species 2 is reduced below L_2^* , the selective feeder disappears (Fig. 2A). This is an example of bottom-up control of the herbivore population; plant species 1 has an indirect effect on the selective feeder through outshading its food plant (plant species 2) at high productivity levels.

Next, the bulk feeder is introduced (Figs 1B, 2B). The bulk feeder removes most above-ground biomass of the

tall plant species, thus providing light for smaller plants. This paves the way for the selective feeder to return. Note that the selective feeder may experience some competition from the bulk feeder (Fig. 2B). However, provided that the bulk feeder is not too proficient in its consumption of the small plant species, there is sufficient food for the selective feeder to persist. When the two herbivore species act together, they control the standing crop of both plant species. The selective herbivore maintains small plant species 2 at the leaf biomass level given by eqn 2. Combining eqn 2 with eqn 1e, the bulk feeder then maintains the leaf biomass of plant species 1 at:

$$L_1^* = A_{L,1} P_1^* = \frac{m_1}{c_1 a_{11}} - \frac{a_{12}}{a_{11}} \frac{m_2}{c_2 a_{22}} \quad (3)$$

CONCLUSIONS

The disappearance of the selective herbivore with increasing productivity illustrated in Fig. 2 (A) stems from the asymmetric nature of plant competition for light, which leads to plant species replacement beyond the control of selective herbivores (Huisman *et al.* 1998). The model of this paper shows that the introduction of a generalist herbivore (here called a “bulk feeder”) in a productive system may suppress competition for light, thereby facilitating selective herbivores that feed on small plants. Thus, introduction of a bulk feeder can reverse plant–herbivore interactions from bottom-up control (Fig. 2A) to top-down control (Fig. 2B). Interestingly, the diet of the bulk feeder is composed of an exclusive resource (plant 1) and a resource that is shared with the selective herbivore (plant 2). Hence, one might think that the bulk feeder, with support from its exclusive resource, would have a negative impact on the selective feeder. Instead, the bulk feeder facilitates the selective feeder, an unexpected indirect effect mediated by plant competition for light.

Conversely, our model results also imply that the removal of a bulk feeder may have catastrophic effects for selective herbivores, because taller and coarser plants may re-establish their competitive dominance. A sad example is provided by the Ngorongoro Crater in Tanzania, where local pastoralists and their livestock of cattle and donkeys were removed in 1974 (Runyoro *et al.* 1995). Although no data on changes in plant species composition are available, Runyoro *et al.* argue that the removal of the pastoralists and their livestock changed the vegetation towards a coarser sward with less palatable species. Since 1974 populations of Wildebeest, Thomson’s gazelle, Eland, and Grant’s gazelle all declined in numbers (Runyoro *et al.* 1995).

The patterns of competition and facilitation outlined by the model appear to capture the essence of the plant–herbivore interactions that occur in the salt marshes of Schiermonnikoog. We suspect that similar processes also play a role in other multispecies plant–herbivore systems.

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BIOSKETCH

Jef Huisman's research interests include resource competition; competition for light and/or nutrients in particular; phytoplankton ecology; plant ecology; plant–herbivore interactions, both aquatic and terrestrial; and theoretical ecology.